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**Competition or Coexistence? Pink and chum salmon trophic interactions through a dynamic and challenging section of the early marine migration route in coastal British Columbia**

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**Chapter 2: Juvenile pink and chum salmon divide prey resources in response to low foraging**

**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 (Wyllie de Echeverria and Thornton 2019; Marushka et al. 2019; Quinn 2018) . While pink (*O. gorbuscha*) and chum salmon (*O. keta*) have the highest abundance and biomass (respectively) of all salmon species due to hatchery production, there have been regional declines in British Columbia (Ruggerone and Irvine 2018; Malick and Cox 2016). Commercial fisheries for salmon have decreased in response to declining stocks and traditional harvest for many coastal First Nations has also been reduced (Healey 2009; Garner and Parfitt 2006). Despite thorough scientific research on salmon, predictions of adults returning to spawn are very variable, often lower than expected, and salmon fisheries become difficult to manage (Beamish 2017).

Chum and pink salmon are species that leave freshwater early after emergence and head strait towards the estuary and the ocean and are therefore relatively small and can grow quickly (Groot and Margolis 1991). These young salmon must contend with the physiological challenges of smoltification, multiple predators and successfully capturing prey for energy in their new marine environment (Levings 2016). There is high mortality for salmon smolts, research has shown growth in the early marine phase strongly helps determine the cohort strength during the first winter at sea and adult survival (R. J. Beamish and Mahnken 2001).

Prey availability and salmon foraging behaviour are important factors for growing quickly during early marine life and the salmon species have unique behaviour and preferences (Brodeur 1990). Patchiness of zooplankton in the ocean leads to relatively generalist salmon feeding, however, there are energetic trade-offs and decisions regarding the effort it takes to capture prey items (Gill 2003). Therefore, while pink and chum salmon are both planktivorous during early marine life, these salmon species have the potential to compete for food or occupy different trophic niches (Pocheville 2015).

Pink salmon are dominant competitors for food resources, actively feeding on the crustacean zooplankton of all sizes, and in high abundance years, pink salmon can cause trophic cascades (Batten, Ruggerone, and Ortiz 2018; Ruggerone and Goetz 2004). Emerging studies on competition have shown pink salmon to negatively affect the growth and survival of other salmonids, herring, sea birds and killer whales. Chum salmon, on the other hand, have more adaptable feeding strategies, with the tendency to prey shift towards gelatinous zooplankton in response to competition or limited food resources (Tadokoro et al. 1996; Johnson and Schindler 2009). Competitive pressures for food resources has even led to a specialization of the stomach size of chum salmon being substantially larger than other salmonids to specialize on large gelatinous prey in an evolutionary attempt to capture

The zooplankton communities migrating salmon encounter are largely determined by bottom up effects such as mixing, nutrients, temperature, salinity, and phytoplankton productivity (Mackas, Thomson, and Galbraith 2001). In southern British Columbia, most juvenile salmon migrate northward through the Strait of Georgia, a seasonally stratified and productive region, then salmon reach the Discovery Islands (Osgood et al. 2016). A complex archipelago, the Discovery Islands has tidally mixed waters and high freshwater influence and research has shown most of this area to be food-limiting for sockeye salmon (James et al. 2020). Furthering the difficulty of this migration, the deep and narrow Johnstone Strait is also well-mixed and a “trophic gauntlet” for sockeye salmon, and potentially for pink and chum salmon (Mckinnell et al. 2014). Along this route situated between Vancouver Island and mainland B.C., salmon then migrate through Queen Charlotte Strait, where they may be able to replenish and forage successfully (Mcqueen and Ware 2006).

The conditions salmon encounter in this region of B.C. will likely be comparable to environments they will continue to migrate through, along the coast into the Gulf of Alaska (Brodeur et al. 2007). Coastal ocean conditions can vary from high freshwater inputs to purely oceanic, sheltered inlets to exposed areas, rocky shores to eelgrass habitats and high to low productivity levels (Daly, Moss, Fergusson, and Brodeur 2019). Therefore, not only does the Discovery Islands and Johnstone Strait region represent an important section of the salmon migration route, but is a microcosm of coastal conditions, transitioning from warm, fresh, stratified channels to a cold, saline, well-mixed, deep strait (Khangaonkar, Long, and Xu 2017).

The purpose of this study is to quantify diet similarity between juvenile pink and chum salmon across high and low foraging opportunities to determine potential species competition. Further, is this area of Discovery Islands and Johnstone Strait a trophic gauntlet for juvenile pink and chum salmon and what are the salmon foraging strategies and trophic niches in this area? Analyzing the Discovery Islands and Johnstone Strait as a case study, this research will dive into juvenile pink and chum salmon competition and potential implications for early marine survival.

**2.2 Methods**

In an effort to understand the early marine phase of Pacific salmon, the Hakai Institute, the University of British Columbia, Simon Fraser University and the University of Toronto and Salmon Coast Field Station partnered up and created a field program. Every field season since 2015, researchers head out on oceanographic surveys, starting in May, to capture outmigrating salmon species, zooplankton samples and oceanographic data. First, a visual survey of salmon surface activity is performed, before setting the purse seine net on a targeted school of fish, where up to 10 sockeye, 10 pink and 10 chum salmon are collected (Hunt et al. 2018). In 2015 and 2016, zooplankton were gathered with horizontal surface tows and preserved in 95% ethanol, before oceanographic surveys were performed, collecting YSI and CTD information.

Back at the lab, researchers processed zooplankton samples and dissected juvenile salmon for various samples, the salmon stomachs removed and preserved in 95% ethanol. The zooplankton samples were poured over sieves to be size fractionated and then weighed before they were split into a subsample, to be identified to species, counted and measured. The salmon stomachs required more steps for processing, removing ethanol and soaking for 30 minutes in water to reduce brittleness of sample, before dissecting the stomach open. After the food contents were removed, the entire bolus was weighed, placed on a petri dish with water added, to rearrange the prey items by species, size, life stage and digestive state. For each prey group, minimum and maximum lengths were measured with an ocular micrometer, individuals were counted, and the group was weighed to a tenth of a milligram. Subsamples of ¼ were analyzed if there were > 800 similar individuals within one stomach. Data were recorded in a notebook and entered into an excel sheet for subsequent analyses.

Preparing the data for analysis included combining rare taxonomic prey categories (occurs in less than three stomachs) into higher level groupings and ignoring “digested food.” Fish stomach content weight was multiplied by 1.54 to correct weights after storage in ethanol (James 2019). The dataset was then transformed from long to wide format, relative prey biomass for each stomach was calculated and then arcsine square root transformed for multivariate analysis. A Bray-Curtis dissimilarity matrix was created from transformed data, for non-metric multidimensional scaling (NMDS) and agglomerative hierarchical clustering (AHC).

In addition to the multivariate statistics, various indices were calculated from the raw diet data, including frequency of occurrence of prey for each site and each species, which is the number of stomachs with that certain prey item, divided by the total number of stomachs.

Gut fullness indices were also calculated from the food content weight divided by the weight of the fish, multiplied by 100 to express as percent body weight, a proxy for feeding intensity. The Schoener overlap index was calculated for each site, where relative biomass of prey for each species is compared, and the minimum values for each prey group are then summed (Krebs 2013). The Schoener index is expressed as a percentage and overlap values of 60% are meaningful. Note, the empty stomachs (those with no identifiable prey) in this study were excluded from all the multivariate analyses but were included in the calculation of the above indices.

**2.3 Results**

The environment of Discovery Islands is characterized as warmer and fresher and Johnstone Strait is more oceanic in nature, and different zooplankton occur in each region. D07 has high freshwater influence, with a surface salinity of 25 and temperature of 17oC, at D09 it shifts to 28.5 salinity and 12oC and D11 and J06 are further transition points before the water properties stabilize to become oceanic at J08 and J02, with 32 salinity and 10oC (Figure 1; Figure 2). The zooplankton biomass throughout this area is mostly composed of small zooplankton, in the 250 μm size fraction, mainly calanoid and cyclopoid copepods and the ‘other’ prey types.

Juvenile chum salmon diets shift from *Oikopleura* in Discovery Islands to gelatinous then euphausiids in Johnstone Strait, whereas pink salmon prey on copepods along the way (Figure 3). In addition to active selection for large (>2 mm) calanoid copepods, pink salmon also fed upon decapod larvae, and nearshore animals such as insects and harpacticoid copepods. Discovery Islands can be characterized as *Oikopleura* dominant for chum salmon, with pink salmon also consuming *Oikopleura* but in much lower amounts, mostly eating crustaceans. At the first Johnstone Strait site J06, chum salmon shift to gelatinous prey (possibly Cnidaria jellyfish) and pink salmon have nearshore prey, calanoids and other (gammarids, barnacles). The following Johnstone Strait site J08, chum salmon still consume gelatinous prey but also have higher amounts of large calanoid copepods, and pink salmon dominantly eat calanoids. There is a complete diet shift at the last Johnstone Strait site J02, where both of the salmon species consume calanoids, chaetognaths and euphausiid prey, but in different proportions. Therefore, calanoids are important prey for pink salmon and chum salmon consume larger prey, either gelatinous zooplankton at most sites or euphausiids and chaetognaths at J02.

Feeding intensity was consistently low throughout this area of the salmon migration route, with the exception of incredibly full stomachs at the last site, Queen Charlotte Strait (Figure 4). Gut fullness indices were consistently below 1% body weight throughout the first four sites, and at mid-Johnstone Strait site J08, the gut fullness increases to around 1% body weight, which is still relatively low, compared to the around 7% body weight feeding intensity at site J02. Empty stomachs were found throughout the Discovery Islands and the first Johnstone Strait site. At D07, 20% of pink salmon stomachs were empty, whereas D09 chum salmon were 30% empty. Further, 30% of chum salmon stomachs were found empty at D11 and finally, 40% of pink salmon stomachs from J06 were empty, and no sites had empty stomachs of both species. By region, 7% pink salmon stomachs were empty and 20% of chum salmon in the Discovery Islands and in the Johnstone Strait, 0% of chum salmon were empty, compared to 13% of pink salmon. In total, 10% of all 120 salmon stomachs were empty, equal between pink and chum salmon.

Dietary overlap between pink and chum salmon was relatively low and consistent in the Discovery Islands and shifted in Johnstone Strait from low to high species diet similarity (Figure 4). The first site of the migration route D07 had 25% dietary overlap, D09 saw a slight increase to 33%, then D11 decreased to 22%, and the lowest value was J06, with a mere 5% overlap. Mid-Johnstone Strait J08 had 14% dietary overlap and the final site near the entrance to Queen Charlotte Strait J02, had the highest diet overlap of 60% for pink and chum salmon. Therefore, the Schoener overlap index shows consistently low diet overlap between salmon species throughout this section of the migration route and one site of substantial similarity.

Overall diet composition of salmon species also had no observable trends within the Discovery Islands, whereas Johnstone Strait has a clear gradient of overlap and divergence. The NMDS plot reflects the variability in Discovery Islands, and Johnstone Strait locations show the highest differentiation between species at J06, the eastern most site, then J08 next shows semi-different pink and chum salmon diets and finally, J02 has complete diet overlap (Figure 5). A cluster analysis also displayed this same trend, where the two regions were separated into main clusters and Johnstone Strait was subdivided by both site and species (Figure 6).  The only site to distinctly cluster together was J02, near Queen Charlotte Strait, which was similar to the pink salmon diets from J08, mid-Johnstone Strait. The pink salmon diets were somewhat comparable to the chum salmon diets at J08, but the J06 chum salmon from East Johnstone Strait had a completely separate cluster and J06 pink salmon were outlier values.

**2.4 Discussion**

Juvenile pink and chum salmon have similar diets when feeding intensity is high but utilize different foraging strategies when feeding is low, dividing resources by trophic niche. Throughout most of the study sites, chum salmon filled the gelatinous prey niche and pink salmon were found foraging on nearshore insects, harpacticoids, caprellids and gammarids. The reliance on these niche strategies shifted with the foraging intensity, since at the Queen Charlotte Strait site with ~7% body weight stomach fullness, both species fed very similarly. Therefore, salmon will consume higher quality prey such as euphausiids and large calanoids when available and will otherwise divide up the resource space to limit potential competition.

Juvenile salmon appear to experience a trophic gauntlet during their migration, with areas of ‘winners and losers’, where prey availability dictates which feeding strategy prevails.

The first two sites of Discovery Islands seem to have semi-decent feeding conditions, with decapod larvae prey present at D07 and around 0.5% body weight stomach fullness at D09. The next two sites in the migration is the mid-way point, the transition between the regions, and D11 had more empty chum salmon stomachs and lower amounts of *Oikopleura* prey, whereas pink salmon still fed on nearshore prey and had no empty stomachs at this location. The next site of J06, found the opposite, with no empty chum salmon stomachs feeding on gelatinous prey and empty pink salmon stomachs and unusual prey when food was present. Thus, salmon species feeding strategies will either be beneficial or detrimental depending on prey availability, and how these relationships could shift over time requires further research.

While Discovery Islands has more of an environmental gradient, Johnstone Strait is a foraging gradient, as salmon move west it shifts from low to high feeding and diet similarities. Although Johnstone Strait has a very consistent temperature and salinity, the amount of zooplankton advection from coastal upwelling increases closer to Queen Charlotte Strait. The Johnstone Strait migration begins with little to no calanoid copepods, chum salmon feeding on jellyfish and pink salmon scouring the nearshore for insects and harpacticoids. Mid-way through Johnstone Strait, there is a shift, chum salmon still consume gelatinous but also large calanoids, and pink salmon prey on hundreds of calanoids of all shapes and sizes. Finally, at the last study site at the end of Johnstone Strait, pink and chum are found to have stomachs that are literally bursting full of diverse calanoids, euphausiids and chaetognaths. This region therefore shows the relationship between diet similarity and foraging intensity, and how as conditions improve, species can begin to safely occupy the same trophic niche.

In other areas with similar coastal conditions, pink salmon have been found to utilize nearshore foraging on small crustaceans and chum salmon often prey switch to gelatinous (Godin 1981; Tadokoro et al. 1996). Previous studies have found harpacticoid copepods as a prey for both species, and calanoid copepods were another important component in pink and chum salmon diets (Godin 1981; Sibert 1979; Chebanova, Frenkel, and Zelenikhina 2018). Recently, a study on sockeye salmon diets in this same area found *Oikopleura* to be very important prey in the Discovery Islands, similar to chum salmon, and larger calanoids to be dominant in Johnstone Strait, which is similar to the observed pink salmon diet composition (James et al. 2020). Other research that investigates dietary overlap of multiple species of salmon have found pink salmon to be most similar to either sockeye or chum salmon in their choices of prey (Daly, Moss, Fergusson, and Debenham 2019).

While this research study focused on a snapshot of juvenile salmon feeding in June 2016 in this area, trends can’t be extrapolated without a seasonal or interannual component. The dynamics of each of these regions may shift over time, especially the Discovery Islands which naturally has more variability due to the freshwater influence on the ocean conditions. This study characterized salmon species interactions in high and low foraging scenarios, but other unknown factors could be contributing, and more research is needed to confirm trends. More accurate descriptions of these regions require a longer time series on salmon feeding during the outmigration period and across years, which is the focus of the next data chapter.

**2.5 Conclusion**

In conclusion, juvenile pink and chum diets appear to be influenced by availability of prey and the overlap between salmon species shows a clear relationship to feeding intensity. It is intuitive that prey determines diet composition but counterintuitive that competition may decrease with increased diet similarity between salmon species utilizing the same resources. When 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 gelatinous prey. These salmon species could potentially be used as ecosystem indicators, pink salmon can track calanoid availability and chum salmon diet composition can indicate overall feeding conditions.

The diversity of conditions encountered by salmon migrating through this area shows how species can coexist by utilizing different trophic niches to partition their prey resources. Since pink salmon have the potential to outcompete other species for high quality prey such as large calanoid copepods, chum salmon require a different strategy in order to survive. Salmon species occupy distinct trophic niches from one another, and this relationship shifts across the migration route relative to the foraging intensity, prey types and the environmental conditions.

Juvenile pink and chum salmon interactions are an important component of seasonal coastal ecosystem dynamics, which can impact salmon early marine growth and survival. Outmigrating salmon have to adapt to shifting prey fields and other competitors for those resources, and in some areas, a given feeding strategy will benefit one species over the other. This study highlighted the Discovery Islands and Johnstone Strait region as a trophic gauntlet for juvenile pink and chum salmon, and highly active feeding grounds in Queen Charlotte Strait.

The extended period of starvation during early marine migration will most likely affect the growth of juvenile salmon and potential survival to adult recruitment in the subsequent years. Further research should be conducted on whether the extremes of high and low stomach fullness of outmigrating salmon persists over time and how their foraging strategies change.

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**Figures**

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**Figure 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 by the red box.

A close up of a map

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**Figure 2:** Temperature (left y-axis, black) and salinity (right y-axis, red) values paired with the salmon surveys, the sites are listed in the same order on the x-axis as they appear on the map.

A screenshot of a cell phone

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**Figure 3:** Average relative biomass of the main prey groups for juvenile pink (top) and chum salmon (bottom), the sites are listed in the same order on the x-axis as they appear on the map. ‘Other’ prey group includes amphipods, barnacles, bivalves, cladocerans, pteropods, and more.

A close up of a map

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Figure 4: Gut fullness index (food weight / fish body weight \* 100) values of juvenile pink and chum salmon (left y-axis), the black bar indicates the mean, boxes show the inter-quartile range (IQR), whiskers are data within 1.5\*IQR and shown as points are outliers beyond the 1.5\*IQR. The dark red line (right y-axis) is the percent similarity or diet overlap index between pink and chum salmon, the sites are listed in the same order on the x-axis as they appear on the map.

A screenshot of a cell phone

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**Figure 5:** Non-metric multidimensional scaling (NMDS) plot of juvenile pink and chum salmon diet composition (see text for data transformations). Each data point is a salmon stomach and distance between points express dissimilarity, axes have no units. Shapes show salmon species, color displays sample site and ellipses indicate standard deviation of each region (see legends). “Stress” is how well distances between points are retained when displayed in two-dimensions, stress values under 0.2 are good representations of data. For this NMDS plot, the stress = 0.17.

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**Figure 6:** Cluster analysis of juvenile pink and chum diet composition using average linkage clustering. Dendrogram label colors represent sites (same colors as NMDS, this graph is still in progress to visually differentiate species and make it more readable, I’m still updating it all \*).