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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 (Marushka et al., 2019; Quinn, 2018; Wyllie de Echeverria & Thornton, 2019). 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 (Malick & Cox, 2016; Ruggerone & Irvine, 2018). Commercial fisheries for salmon have decreased in response to declining stocks and traditional harvest for many coastal First Nations has also been reduced (Garner & Parfitt, 2006; Healey, 2009). Despite thorough scientific research on salmon, predictions of adults returning to spawn are highly 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 straight towards the estuary and the ocean and are therefore relatively small and must grow quickly (Groot & 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). Mortality for salmon smolts can be high, and research has shown growth in the early marine phase is an important determinant of the cohort strength during the first winter at sea and adult survival (Beamish & Mahnken, 2001).

Prey availability and salmon foraging behaviour are important factors for growing quickly during early marine life (R. D. 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). The salmon species have unique foraging behaviour and preferences (Beamish et al., 2003), for example, pink and chum salmon are both planktivorous during early marine life and therefore have the potential to either compete for food or occupy different trophic niches (Pocheville, 2015).

Niche can be defined as a combination of the conditions allowing a species to satisfy the minimum requirements of survival and the impact of the species on environmental conditions (Chase & Leibold, 2003). Therefore, “trophic niche” can be considered the prey resources consumed to meet energetic demands and the effect of species foraging on the zooplankton 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 or one species will outcompete the other (Hardin, 1960).

Pink salmon are an example of 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 et al., 2018; Ruggerone & Nielsen, 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 (Beamish et al., 2010; Pearson et al., 2012; Ruggerone et al., 2019; Springer et al., 2018). 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 (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).

The zooplankton communities migrating salmon encounter are largely determined by bottom up effects such as 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). 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, 2018). Recent studies have hypothesized these regions to be a “trophic gauntlet” for juvenile salmon, sockeye salmon were indeed food limited in these tidally mixed waters, consuming <0.5% of their body weight (James et al., 2020; Mckinnell et al., 2014). Since pink and chum salmon have similar foraging and migration as sockeye, pink and chum likely also experience this gauntlet, impacting competition, growth and survival. Along this route situated between Vancouver Island and mainland B.C., salmon then migrate through Queen Charlotte Strait, where they may be able to forage successfully and replenish from experienced food shortages (Mcqueen & Ware, 2006).

The conditions salmon encounter in this region of B.C. will likely be representative of environments they will continue to migrate through, along the coast into the Gulf of Alaska (R. D. a 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). 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, and may represent a foraging challenge for pink and chum salmon, that could impact their survival.

This study aimed (a) to quantify juvenile pink and chum salmon diets in the potential trophic gauntlet and foraging refuge area in southern B.C. and (b) describe the trophic niches pink and chum salmon occupy. The diets and niche overlap between salmon species lead to (c) assessment of potential competition and (d) how competition shifts with foraging opportunity.

This research will determine if a trophic gauntlet exists for juvenile pink and chum salmon and how salmon behaviour shifts under high and low foraging (measured by stomach fullness). If foraging is low, species will compete, decreasing survival, or will separate by niche to coexist.

**2.2 Methods**

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 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 is to improve understanding of the early marine phase of Pacific salmon, particularly factors contributing to health and survival (Hunt et al., 2018). This study focussed on 2016, which had the largest spatial coverage of sampling stations in an effort to resolve the primary migration pathways through the region. The previous year 2015 also had similar spatial coverage of sampling but there was expected and observed lower pink abundance, due to their biennial life patterns.

Every field season since 2015, researchers head out on oceanographic surveys, starting in May, to capture outmigrating salmon species, zooplankton samples and oceanographic data. 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). Sites were sampled every 4-7 days throughout the season, depending on weather conditions. For this study, six 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), still acquiring sufficient coverage for each region. The dates were chosen in mid-June (Table 1) to align with the peak out-migration of salmon.

The salmon sampling begins with recording weather and sea state data, followed by a visual survey of salmon surface activity. Afterwards, the purse seine net (bunt: 27 m × 9 m with 13 mm mesh; tow: 46 m × 9 m with 76 mm mesh) on a targeted school of fish, up to 30 sockeye, 10 pink and 10 chum salmon are retained, the remaining salmon counted and released (Hunt et al., 2018). Salmon were euthanized with tricaine methanesulfonate (MS-222) upon removal from the seine net, lengths and weights recorded, and preserved at -196 oC with liquid nitrogen in a dry shipper until the salmon samples were stored in the -80 oC freezer at the lab.

In addition to salmon sampling, zooplankton samples and oceanographic data were also collected during each survey. The YSI measured temperature and salinity at the surface and 1-meter depth, recorded while salmon were held for processing in the net. The zooplankton were collected after salmon and oceanographic sampling with a 50 cm diameter and 250 μm mesh net, towed horizontally at the surface and preserved in 4% formaldehyde for future analysis.

In the lab, juvenile salmon were dissected and the stomachs preserved in 95% ethanol. Prior to analysis, salmon stomachs were removed from ethanol and soaked unopened 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, identified to group, and 4) fully digested, and unidentified prey. 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 subsample would be processed, first any rare or large prey were removed, data recorded and then ¼ of remaining prey processed. For example, counting and measuring a couple of decapods and amphipods before subsampling hundreds of *Oikopleura* and cladocerans, multiplying the data by 4 to estimate the sample data.

The zooplankton samples were poured over sieves 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. Each size fraction of zooplankton was identified to species and life stage, enumerated and measured with an ocular micrometer, and subsampled if necessary, using a Motodo splitter.

The spatial variation in prey composition was analyzed using a multivariate approach. Prior to the analysis, rare taxonomic prey categories (occurs in less than three stomachs) into 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).

In addition to the multivariate statistics, various indices were calculated from the raw data. Frequency of occurrence (FO) of prey for each site and each species, was calculated as:

FO = # of stomachs with preyi / total # of stomachs

Gut fullness indices (GFI) were also calculated for each fish, expressed as percent body weight:

GFI = (food bolus weight / fish weight) \* 100

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

PSI = [Σ (minimum preyip, preyic)] \* 100

Where preyip is the proportion by weight of prey *i* in pink salmon stomachs and preyic is the proportion by weight of prey *i* in chum salmon stomachs (Chipps & Garvey, 2006; Krebs, 2013).

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. The prey taxonomic detail was retained in analyses, but for summary tables and figures, “other” is prey grouped together that doesn’t contribute substantially to diets, such as amphipods, barnacle larvae, bivalve larvae, cladocerans, fish larvae/eggs, pteropods, polychaetes, to name a few.

**2.3 Results**

The environment of Discovery Islands is characterized as warmer and fresher and Johnstone Strait is colder and more saline, and different zooplankton occur in each region. D07 had high freshwater influence, with a surface salinity of 25 and temperature of 17oC, at D09 it shifted 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 shifted from *Oikopleura* in Discovery Islands to gelatinous in Johnstone Strait and euphausiids at the northern most site J02, whereas pink salmon prey on copepods throughout (Figure 3). In addition to active selection for large (>2 mm) calanoid copepods, pink salmon also fed upon decapod larvae, and nearshore invertebrates 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 shifted 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 was 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 were important prey for pink salmon and chum salmon consume larger prey, either gelatinous zooplankton at most sites or euphausiids and chaetognaths at J02.

Gut fullness 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 Discovery Islands and J06, the first Johnstone Strait site. The mid-Johnstone Strait site J08, the gut fullness increased to around 1% body weight, which is still relatively low, compared to the around 7% body weight feeding intensity at site J02. Macro- and microplastics were found in juvenile salmon stomachs, with a frequency of % for pink and % for chum, at sites D07/09/11 and J06.

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 as the NMDS, with the two regions 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 outliers.

**2.4 Discussion**

This study examined 120 juvenile pink and chum salmon stomachs to characterize diets during the 2016 peak outmigration through the Discovery Islands and Johnstone Strait routes. This area that was shown to be a trophic gauntlet for juvenile sockeye salmon, is also food limiting for pink and chum salmon, and diet overlap between species was low in response. However, the northern most site of J02 was shown to be a foraging hot spot for juvenile sockeye salmon in June 2015 and this trend continued in 2016 for both pink and chum salmon. Juvenile pink and chum salmon switched trophic niches throughout the region according to prey availability and species interactions, chum occupying a gelatinous niche and pink littoral.

Juvenile pink and chum salmon have similar diets when prey availability is high but utilize different foraging strategies when prey availability is low, indicative of resource portioning. Throughout most of the study sites, chum salmon occupied (or “can be characterized as”) the gelatinous predator niche and pink salmon were found foraging in the littoral niche on nearshore insects, harpacticoids, caprellids and gammarids. 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, pink and chum salmon were observed to both consume higher quality prey such as euphausiids and large calanoids when available but to divide up the resource space when prey was limited. This strategy would be expected 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 patchy feeding conditions, with empty stomachs or decapod larvae prey 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 may be 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 packed with diverse prey including 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 (Chebanova et al., 2018; Godin, 1981; Sibert, 1979). 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 et al., 2019).

Microplastics were not the focus of this study but they were found in % of juvenile salmon stomachs, and one macroplastic was found to be 40% weight of a pink salmon stomach. That 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. Impacts of plastics on salmon and occurrence in empty stomachs with potential for cumulative effects, has incredible potential to start a new area of salmon health research and conservation.

While this research study focused on a snapshot of juvenile salmon feeding in June 2016 in this area, trends cannot 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**

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.

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**Figures**

**A picture containing text, map

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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.

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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 \*).