

**Feeding in troubled waters: a comparative diet analysis of
pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon
during their first months at sea in the Broughton Archipelago,
British Columbia**

by

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Abstract

Closely related species divide shared resources to reduce interspecific competition and to allow for coexistence when resources are limiting. Upon ocean entry, juvenile pink and chum salmon coexist in mixed schools and feed on similar prey. The diet of juvenile pink and chum salmon during their first two months at sea in the coastal waters of the Broughton Archipelago, British Columbia, was described for 2003 and 2006. Full stomach rankings suggested a lack of prey limitation in both years. Stomach content analysis revealed a greater diet separation among pink and chum in 2003 than in 2006. Species specific prey preferences were observed. Electivity comparisons of prey consumed with prey available in the plankton indicated selective feeding in both species. Considering the importance of diet in the survival of juvenile salmon and ultimately in adult recruitment, an understanding of prey conditions provides insight into salmon population trends in the region.

Keywords: juvenile pink salmon; juvenile chum salmon; stomach content analysis; prey electivity; prey preference; diet overlap

To my family.

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Chapter 1.

Introduction

Commercial and recreational salmon fisheries contribute millions of dollars annually to the coastal communities of Canada and the United States of America (Pacific Salmon Commission, 2012). Salmon are of great cultural importance to, and a major component of the traditional subsistence diet of, coastal First Nations in British Columbia, Alaska and Washington. Ecologically, salmon are an integral part of the coastal Pacific Northwest food web. The five species of Pacific salmon (sockeye, *Oncorhynchus nerka*; coho, *O. kisutch*; chinook, *O. tshawytscha*; pink, *O. gorbuscha*; and chum, *O. keta*) present in North America's waters have undergone periods of population fluctuation, affecting in turn the health of ecosystems and the livelihood of people that depend on them.

Factors influencing Pacific salmon population size

In recent decades, Pacific salmon populations have fluctuated in part on dependent on climatic influences. For instance, the climate regime shift of 1977 led to increased production of all species of Pacific salmon with historical high numbers recorded in the mid-1980s (Beamish & Bouillon, 1993). Another shift in climate beginning in the early 1990s, led to record low population numbers in 1998 (Noakes, Beamish, & Kent, 2000). Other studies focus on more regional patterns of salmon abundance, arguing that large scale analysis often overlooks local fluctuations in salmon population trends (Pyper et al, 2001; Pyper et al., 2002). For instance, sea surface temperature recorded within 100km at the time of salmon ocean entry were found to be better predictors of salmon returns than large scale climate measures (Mueter et al., 2002).

In addition to climate stressors, anthropogenic factors such as overfishing, freshwater habitat destruction, and parasite and disease introductions from marine aquaculture operations are believed to be important factors contributing to salmon population decline (Krkosek et al., 2011; Price, Glickman, & Reynolds, 2013; Thomson et al., 2012; Noakes, Beamish, & Kent, 2000). The impact of salmon enhancement activities on natural salmon populations in terms of competition food and habitat resources is an important but often debated issue (Orsi et al., 2005; Noakes et al., 2000).

Pacific salmon are exposed to many abiotic and biotic challenges during their life cycle, and the majority of individuals do not survive to reproduce. Although mortality does occur after the first year at sea (Welch et al., 2011) it is widely acknowledged that survival during the early marine residence is an important predictor of adult returns (Duffy et al., 2010; Parker, 1971; Thomson et al., 2012). For example, it is predicted that 75% of all pink rearing in the nearshore marine environment of Prince William Sound, Alaska, are consumed by predators within the first two months at sea (Cooney et al., 1991). The first year in estuarine and coastal waters is therefore critical to the success of salmon populations. Thus, a thorough understanding of the ecology of salmonids during their early marine residence is crucial to long-term management of salmon fisheries and the conservation of salmon populations across the north Pacific.

Life cycle of Pacific salmon

Pacific salmon hatch as yolk sac alevins in gravel redds in streams and rivers. Here, they absorb the yolk sac before surfacing (an event called swim up). Development quickly continues from the alevin to parr stage, identifiable by vertical parr markings along the flank of the juvenile salmon. Parr marks are present in all salmon species other than pink salmon. Depending on the species, the parr will spend hours to years in fresh water before entering coastal marine waters. Pink and chum salmon have the shortest freshwater residence of all Pacific salmon, often proceeding to the marine environment within hours of swim up. Prior to ocean entry, parr undergo a process of saltwater adaptation called smoltification. The smolt will spend one to five years in the ocean, depending on the species, or the population within a species, before returning to its natal waters to reproduce and begin the cycle anew (Groot and Margolis, 1991).

Pink salmon are the most abundant and widely distributed of the Pacific salmon (Heard, 1991). This species has a two year life cycle that results in genetically isolated populations between even and odd numbered years in rivers and streams in which pink salmon spawn in all years. Some rivers, such as the Fraser River in British Columbia, have only odd year pink salmon returns (Neave, 1952). In the Broughton Archipelago, British Columbia, an area with numerous pink salmon streams, pink salmon return to spawn in both even and odd years (Williams et al., 2003). In contrast to pink salmon, chum salmon have an average three to four year life cycle, a strategy which may have evolved to avoid competition with pink salmon (Ruggerone & Nielsen, 2005). In Puget Sound (USA), for instance, the progeny of even year chum salmon experience less competition with pinks (which show highest abundance in odd years) and, as a result, have greater survival (Ruggerone & Nielsen, 2005).

Feeding during the early marine life of pink and chum salmon

In late March and early April, pink salmon emerge from the gravel and immediately migrate downstream to coastal marine waters. Similar to pink, chum salmon migrate to the ocean soon after emergence but their marine entry is slightly more delayed because of feeding activity in freshwater (Bailey, Wing, & Mattson, 1975; Healey, 1991). Both pink and chum salmon spend weeks to months in nearshore marine waters, often in mixed species schools, before moving offshore. During this period, pink and chum salmon consume similar prey, although with some species-specific diet differences (Kaczynski & Feller, 1973; Murphy, Thedinga, & Koski, 1987). In general, both pink and chum salmon are opportunistic but selective feeders, with diet varying between microhabitats common in the nearshore marine environment (Bollens et al., 2010; Godin, 1981; Healey, 1991; Manzer, 1969).

Upon marine entry, juvenile pink and chum salmon feed incessantly (Parker, 1971) throughout the day (Bailey et al., 1975) and during crepuscular periods (Godin, 1981). When the salmon measure approximately 5.5-6cm in fork length, they migrate from estuarine to outer-coast waters, often in response to decreased food availability or reduced levels of preferred prey larger than 2mm (Kaczynski & Feller, 1973; Willette 2001). As a result of increased gape size and movement into feeding habitat where larger prey are more readily available, diet preference changes from smaller to larger

prey organisms (Bailey et al., 1975; Feller & Kaczynski, 1975). Some studies have found that chum juveniles tend to eat larger prey than their pink counterparts (Bailey et al., 1975; Nagata et al., 2007).

The growth rate of juvenile salmon in nearshore marine waters is highly dependent on both environmental temperature and the abundance and energetic quality of prey encountered (Mortenson et al., 2000). Prey varies in size, handling cost, digestibility and overall caloric content (Nomura & Davis, 2005), with the consumption of more energetically profitable prey resulting in faster growth (Moss & Beauchamp, 2007; Volk et al., 1984). Thus, the timing of marine entry, and whether it is matched or not with peak zooplankton abundance (Chittenden et al., 2010; Cushing, 1990; Mortenson et al., 2000) is of crucial importance to growing pink and chum salmon which are subject to high levels of size selective predation in their first few months at sea (Healey, 1982).

Diet variability in juvenile pink and chum salmon

The diets of juvenile salmon residing in nearshore waters are spatially and temporally variable and are a function of the habitat's physical characteristics (Bollens et al., 2010; Duffy et al., 2010; Healey, 1991). When feeding near sandy beaches, juvenile pink and chum consume primarily epibenthic prey, dominated by harpacticoid copepods (Godin, 1981; Healey, 1991; Kaczynski & Feller, 1973). When feeding along steep rocky shorelines, the majority of prey is planktonic and consists primarily of calanoid copepods (Kaczynski & Feller, 1973; Orsi et al., 2000).

Within a mixed school, chum and pink juveniles show differing preferences for prey. For instance, juvenile pink often favor higher consumption of copepods and nauplii whereas chum often consume larger organisms like insects and gammarid amphipods (Bailey et al., 1975; Bollens et al., 2010; Kaczynski & Feller, 1973; Nagata et al., 2007). Other items commonly reported as prey in both species include harpacticoid copepods, barnacle cyprid larvae and decapod larvae (Bailey et al., 1975; Kaczynski et al., 1971; Nagata et al., 2007). Previous studies have shown no correlation between small dominant zooplankton taxa present in plankton tows and larger zooplankton prey preferably consumed by pink and chum salmon (Bollens et al., 2010; Kaczynski et al., 1971; Mortenson et al., 2010).

As the young salmon disperse from nearshore to offshore marine waters, the diet of both pink and chum salmon becomes increasingly planktonic. New, larger planktonic prey such as euphausiids, hyperiid amphipods, squid and larval fish (Armstrong et al., 2005; Boldt & Haldorson, 2003; Landingham, Sturdevant, & Brodeur, 1998) are now consumed. This trend toward consumption of larger prey with higher caloric value is common among all salmonid species (Price et al., 2013).

Juvenile salmon mortality and adult year-class strength

Survival during the first year at sea is a major determinant of adult return strength. High mortality in the life of salmon occurs during the months following marine entry, especially at the time of dispersal from nearshore to more pelagic waters. This mortality is thought to be driven by size-dependent predation, where vulnerability to predators is a function of both the size of the predator and that of the prey (Parker, 1971). Thus, abundant high-energy food and resultant fast growth to a size at which predation risk is reduced are important factors in the early marine survival of juvenile salmon (Duffy et al., 2010; Moss & Beauchamp, 2007; Willette, 2001) .

A second physiologically-based mortality during the first year at sea was proposed by Beamish and Mahnken (2001) whereby salmon that have not attained a critical size in terms of sufficient lipid stores would not be equipped to survive the stresses of their first winter at sea. The consumption of high energy prey during early marine life permits faster growth and the accumulation of lipids essential for winter survival at sea (Zavolokin & Strezhneva, 2014). Individuals without lipid stores will be vulnerable and weak during periods of low food availability and are more prone to starvation and disease than those with sufficient reserves (Beamish and Mahnken, 2001).

Interspecific competition for prey resources

Under limited prey conditions, pink and chum compete for food resources with other salmon species, including each other. Ruggerone and Nielsen (2005) found evidence that pink salmon are more efficient foragers than chum and sockeye salmon, with similar prey fields. In years of high pink salmon abundance, the diets of other salmon species shifted toward less nutritious prey, including a shift from crustacean to

gelatinous prey in chum salmon (Ruggerone & Nielsen, 2005; Tadokoro et al., 1996). Nagata et al., (2007) found that diet overlapped more in pink and chum salmon greater than 5.5-6cm than at smaller fork length sizes, and that stomach fullness decreased as salmon grew beyond 5.5cm. In contrast, Healey (1991) failed to find evidence of prey limitation or competition for prey resources between pink, chum and sockeye salmon in Hecate Strait, describing the three species as a single ecological feeding unit during the nearshore marine period.

The Broughton Archipelago and sea lice infestations

The Broughton Archipelago is a complex habitat of mainland coast, over 2000 islands and islets, large inlets and small waterways that are home to several populations of pink and chum salmon (Williams et al., 2003). Out-migrating juvenile salmon are exposed to sea lice (*Lepeophtheirus salmonis*) infection believed to originate from Atlantic salmon aquaculture operations in the area (Krkosek et al, 2006). Lice epizootics in the early 2000s were correlated with pink stock collapses, and mathematical modeling predicted the short-term extinction of select pink salmon populations if lice infection level were to remain as high as during these years of observation (Krkosek et al., 2007). This work was controversial, with modelling assumptions argued by some as ecologically problematic (Riddell et al, 2008). Following of active farms along the juvenile salmon migration corridor in 2003 led to a decline in sea lice abundance on juvenile migrants and this correlated with increased pink salmon returns in 2004 (Beamish et al., 2006). Further regulatory action such as monitoring of lice levels on farmed salmon and treatment with a delousing agent at “trigger” infection levels, has led to a decline of sea lice numbers on out-migrating salmon in the region (Krkosek et al., 2011; Patanasatienkul et al., 2013; Peacock et al, 2013).

The extent of impact of sea lice on salmon returns is an area of strong debate. Mathematical model predictions are based on observed correlations between sea lice numbers and adult returns in affected and non-affected populations, but it is possible that some other unidentified factor or synergistic factors could spatially and temporally correlate with the findings attributed to sea lice (Krkosek et al., 2011; Peacock et al., 2013). Diet during early marine life is an important determinant of growth rate of juvenile pink and chum salmon. Jones et al 2008 found that juvenile pink salmon of 0.7g had

lower parasite abundance and decreased mortality rates than pink of 0.3g experimentally exposed to sea lice. As such, diet dependent growth rate would not only lower size-dependent predation risk, but also reduce the risk of mortality due to lethal levels of sea lice infection. Therefore, food available to juvenile pink and chum salmon in the Broughton Archipelago may be a strong predictor of salmon returns.

Thesis Goals

The decline in pink salmon numbers in the Broughton Archipelago during the last decade has led to much research exploring the potential causes of the decline. Because of the well-documented negative impact of salmon aquaculture on wild salmon populations in many regions of the world (Ford & Myers, 2008), most of the research has concentrated on the effects of sea lice on juvenile wild salmon survival (Morton et al., 2011). This thesis characterizes the diet of juvenile pink and chum salmon from the Broughton Archipelago to obtain a better understanding of their feeding ecology during early ocean life and to reveal potential determinants of population strength related to diet.

In particular, the thesis has the following goals:

- 1) to characterize the diets of juvenile pink and chum salmon during early marine residence in the Broughton Archipelago using stomach content analysis, and
- 2) to characterize the prey available to juvenile pink and chum salmon by taxonomic identification of prey organisms present in plankton tows and to identify whether feeding is selective or not.

Chapter two addresses diet composition of pink and chum salmon in 2003 and 2006. It discusses observed interspecific diet differences within each collection year, as well as observed intraspecific diet differences and consistencies in each species among collection years. Variability in diet as a result of collection location is addressed. Fork length as a factor in prey composition is discussed. Chapter three addresses prey availability through the analysis of zooplankton community composition in 2003 and 2006. Evidence for prey selectivity is discussed.

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Chapter 2.

Diet analysis of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon in the Broughton Archipelago, BC, in 2003 and 2006.

2.1. Introduction

The diets of juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon during their first two months at sea in the coastal waters of the Broughton Archipelago (British Columbia, Canada) was described for 2003 and 2006. Although much research has been conducted on the diet of juvenile pink and chum salmon in other coastal areas of the Pacific northwest (Davis et al., 2009), no such analysis previously existed for salmon from the Broughton Archipelago region. Recent diet work focuses on larger juvenile salmon than used in this study that have been in the marine environment for a longer period of time. Research that does exist on prey consumed by pink and chum salmon during their first few months at sea is dated (Bailey et al., 1975; Godin, 1981; Kaczynski & Feller, 1973; Murphy, Thedinga, & Koski, 1987). This descriptive diet analysis allows for insight into prey consumed by pink and chum salmon soon after ocean entry in a previously undescribed region of the British Columbia coast. Considering the importance of diet in the survival of juvenile salmon and ultimately in adult recruitment (Parker, 1971; Beamish & Mahnken, 2001), an understanding of prey conditions may provide insight into recent fluctuations in salmon populations in the study area. Pink salmon entering the marine environment in 2003 experienced exceptional returns as spawners in 2004, whereas pink salmon entering the marine environment in 2006 experienced average returns in 2007. As such, evidence for a difference in feeding conditions during the 2003 and 2006 period of ocean entry would suggest a possible link between early diet and adult return strength.

This chapter will address methodology used in salmon capture, selection of salmon for inclusion in diet analysis, stomach content identification procedure as well as descriptive and statistical methods used to interpret diet results. Stomach content analysis found stronger diet separation among pink and chum in 2003 than in 2006, in which evidence of diet overlap was found. High percent body weight and full stomach rankings in both years suggested a lack of prey limitation in both years. Diet was variable among collection years and between collection locations. Species specific diet preferences were observed. A discussion of results relates these trends to previous studies of salmon diet.

2.2. Methods

2.2.1. Field Sampling

Juvenile pink and chum salmon were collected by Fisheries and Oceans Canada from spring to early summer of 2003 to 2008 as part of a long-term sea lice monitoring program on wild juvenile salmon in the Broughton Archipelago, British Columbia, Canada (Jones & Hargreaves, 2007).

Beach seine sampling was conducted at shallow nearshore marine sites throughout the outward salmon migration habitat of the archipelago (Figure 2.1). A pair of 45.6 meter long by 3.7 meter deep seine nets constructed from three 15.2 meter long panels were used in the collections. Mesh diameter of the outer panels was 1.27cm while the inner panel was constructed from a fine diameter mesh of 0.64cm. A lead rope was attached along the length of the bottom edge of the net. A series of corks were attached along the upper edge of the net to ensure buoyancy of the seine during sampling (Jones & Hargreaves, 2007).

The study area was arbitrarily divided into eleven collection zones labelled A to K (Figure 2.1). Ten beach seine sample collections were taken within each zone during each collection period. Collection period (dates) and location of sampling varied between collection years.

For each successful seine, up to thirty salmon of each species were retained for analysis in the laboratory. Each salmon was bagged individually, labelled with collection set information and assigned an individual identification number. Salmon were immediately frozen at -20° C in an onboard ship freezer. In the laboratory, wet weight and fork length was determined for each defrosted salmon. Attached sea lice were enumerated. A sub-set of 2003 salmon were placed into 4% buffered paraformaldehyde for long term storage.

2.2.2. Selection of salmon for stomach analysis

A subset of juvenile salmon from this extensive sampling program was obtained from Fisheries and Oceans Canada for diet analysis. Well-preserved salmon sets with a minimum of five to ten salmon per species were selected for diet analysis from early April to late May, in 2003 and 2006. In addition to salmon sampling, zooplankton samples were collected by Fisheries and Oceans Canada in 2003 and 2006 in an effort to map the distribution of larval sea lice in the Broughton Archipelago. Salmon collected within ten days of zooplankton collection in matching collection zones were selected for a comparison of diet composition with prey availability in the plankton.

Period and zone of collection varied across years dependent on the availability of samples. Salmon included in diet analysis were collected across various collection zones over four collection periods: period 1-late March to early April, period 2-mid April, period 3-late April to early May and period 4-late May (Figures 2.2-2.3 and Tables 2.1-2.2). Salmon included in the 2003 diet analysis were collected over periods 1-3 in zones G, H and K. The majority of the 2003 sets contained only one species of salmon due to sample loss. The majority of salmon sets from 2006 were intact and contained both pink and chum salmon. Salmon included in the 2006 diet analysis were collected over periods 1, 3 and 4 from zones D, E, F, G, H and I. As in 2003, the majority of the 2006 salmon included in the diet analysis were from period 3, but with greater zone coverage in 2006.

Salmon samples from 2003 were provided for diet analysis by the Institute of Oceans Sciences, (British Columbia, Canada). All salmon of a species retained from each seine were preserved together in a jar of 4% paraformaldehyde (PFA).

Individually frozen 2006 salmon samples were obtained from the Pacific Biological Station (British Columbia, Canada). Salmon identification numbers corresponded to salmon wet weight, fork length and sea lice counts as recorded for each fish in the laboratory by Fisheries and Oceans staff (Jones & Hargreaves, 2007).

Salmon species identification was confirmed based on parr marks and gill raker morphology for both 2003 and 2006 salmon (Pollard et al., 1997). Wet weight and fork length measures were obtained to confirm that the identification number associated with each 2006 salmon matched metadata provided by Fisheries and Oceans Canada. Salmon that did not match the associated metadata were excluded from the analysis. For each 2006 collection set, up to ten salmon were selected at random for diet analysis. Salmon were fixed in individual vials of 4% buffered PFA for a minimum one month prior to stomach removal.

In both collection years, the stomach contents of five to ten salmon per species were identified for each set. In sets with fewer than five salmon per species, all salmon stomachs were analyzed. In sets with greater than five salmon per species, salmon were randomly chosen for inclusion in the diet analysis, with a minimum of one salmon per species randomly selected from each fork-length category present in the collection set, to a maximum of ten salmon (Table 2.3).

Individual fish were removed from the PFA preservative and rinsed with distilled water. Preserved salmon were then patted dry and wet weight and fork length were measured to the nearest 0.01g and 0.1cm, respectively. As paraformaldehyde fixation is known to alter tissue properties such as weight and length (Shields & Carlson, 1996) and pre-fixation values were not available for 2003 salmon, post-fixation wet weight and fork length values are used in all subsequent stomach analysis to allow for a consistent comparison of stomach content versus wet weight and fork length trends in 2003 and 2006 salmon.

2.2.3. Stomach content analysis

For each fish, an incision was made along the abdominal wall from the vent to the opercular plates. The stomach was removed from the intestine at the pyloric sphincter and from the esophagus at the point of attachment to the air bladder. The full stomach was then patted dry and measured to the nearest 0.0001g. The level of prey digestion was graded as either well, medium or fresh. The relative position of the prey in the gut was noted in a j-shaped stomach diagram prior to the removal of the prey items. A visual estimate of stomach fullness was assigned according to the following volumetric index rankings: 0=no prey in the stomach, 1 = 0 to less than 25%, 2 = 25 to less than 50%, 3 = 50 to less than 75% and 4 = greater than 75% of the stomach volume is occupied by prey (Hyslop, 1980). The empty stomach was then re-weighed.

The relative percentage of prey weight to body weight was calculated as:

$$\%BW = (\text{Prey Weight} / (\text{Body Weight} - \text{Prey Weight})) * 100$$

A dissecting microscope was used to count and identify prey to the lowest taxonomic level possible as dependent on the state of digestion. Within each prey category, animals were grouped visually into similar size classes. This was particularly important in prey categories with individuals of a range of sizes as an average width and length of all prey within the category may result in an unrepresentative estimate of total volume. The length and width of a minimum of five individuals per size class were measured to the nearest 0.1mm using an ocular micrometer. A mean length and width was calculated and used in a cylindrical estimate of volume for each size group within each prey category for all prey in each salmon stomach (Hyslop, 1980; Bailey et al., 1975). For prey items with fewer than five individuals, the length and width of each individual was measured and individual cylindrical volumes calculated.

Unidentifiable material was rare in all stomachs analyzed. Stomachs with greater than 50% of their volumetric content consisting of unidentifiable material were excluded from the analysis (less than 1.5% of all salmon analyzed). The volume of unidentifiable material in each stomach was estimated using a 1mm depressed glass slide with 1mm square divisions, as follows: the unidentifiable material was collected on a fine sieve,

blotted dry and then transferred to the depressed slide where a cover slip restricted the height of the material to 1mm. The number of 1mm³ squares occupied by the material were counted allowing for an estimate of cubic volume (Armstrong et al., 2005; Hellowell & Abel, 1971).

2.2.4. Descriptive measures of diet composition

Different measures of prey data are informative of different aspects of diet composition. The relative volume of prey in the diet informs on the frequency of encounter and subsequent ingestion of prey as well as the relative size of prey items in the diet. Frequency of occurrence of a prey type in the diet of a salmon predator informs on the discreteness and patchiness of the prey as available in the marine environment (Healey, 1991; Hyslop, 1980; Kaeriyama et al., 2000).

Total abundance of prey items was summarized for each salmon species by collection year. Prey composition was summarized for each salmon species by mean relative prey abundance and mean relative prey volume based on taxonomic identification of prey by collection year and collection period.

Presence and absence of prey items was considered across salmon species within and between collection years as a means of describing prey diversity. The frequency of occurrence (FO) of each prey item was determined based on the number of salmon within a species per collection year with the prey item in its stomach. The Index of Relative Importance (IRI) is an informative measure of diet composition that considers three important aspects of prey composition: the relative abundance of prey, the relative volume of prey, and the frequency of occurrence of the prey item in the stomachs of salmon. It is assumed that each of these measures of prey composition provide different information about the diet of salmon. Combining each of these measures provides a more complete description of juvenile salmon diet (Hyslop, 1980; Kaeriyama et al., 2000; Mortenson et al., 2000; Sturdevant et al., 2011; Landingham et al., 1998).

The Index of Relative Importance (Mortenson et al, 2000) was calculated as:

$$IRI = (N + V) F$$

where N = the numerical percentage of each prey item in the diet

V = the volumetric percentage of each prey item in the diet

F = the percent frequency of occurrence of the prey item

The importance of individual prey groups were compared as a percentage of the total IRI for all prey in terms of prey taxonomy, prey size and prey community. For prey size analysis, prey were grouped into the following size categories: <0.7mm, 0.7-2.1mm, 2.2-3.5mm and >3.5mm. For prey community analysis, prey were classified as epibenthic, pelagic or of terrestrial origin (Sturdevant et al., 2011). Relative composition of diet based on percent IRI of prey for each classification were plotted as bar graphs for each salmon species and collection year.

2.2.5. Non-parametric multivariate analysis of diet using PRIMER-E

Statistical analysis of salmon stomach contents was conducted using the non-parametric multivariate statistical package PRIMER-E (Plymouth Routines in Multivariate Ecological Research, v5, Clarke and Warwick 1995, Clarke & Ainsworth, 1993). Stomach content data in the form of prey abundance and prey volume of individual salmon were square-root transformed to reduce the influence of dominant prey and increase the influence of rare prey in the interpretation of comparative diet analysis. Data was then standardized to relative proportional composition of each prey category at the individual salmon level for both count and volume data. Re-classification of prey items from specific taxonomic identity to more general prey size class and prey community type were used to identify size and prey community trends within and between salmon species.

Bray-Curtis similarity matrices based on square-root transformed relative abundance or relative volume data by prey taxonomy were used to construct non-metric multi-dimensional scaling (nMDS) ordination plots of resemblance among individual salmon diets. The nMDS ordination plots were utilized to generate a visual representation of salmon feeding patterns between pink and chum at the species-collection year level. Individual salmon are indicated as a single point in each nMDS plot.

The distance between all points indicates the similarity of the diet among individual salmon of both species, with points in close proximity having a greater diet similarity than those at a greater plot distance. A stress level is associated with each ordination plot. Stress levels of less than or equal to 0.2 are indicative of plots in which the similarity relationship between individual salmon diets is well represented by the position and distance of points in the plot. Plots with a stress level greater than 0.2 should be interpreted with caution as they may not be representative of data relationships.

The Analysis of Similarities (ANOSIM) procedure was used to test the null hypothesis of no difference between rank similarities of compared prey groups across salmon predators. The ANOSIM test statistic R ranges from -1 to +1, with an associated significance level, p . R values greater than 0.25 suggest evidence against the null hypothesis, indicating a detectable difference in the diet of salmon species. A greater degree of diet separation and less diet overlap is indicated as R approaches 1. R values are interpreted as significant when $p < 0.05$. One-way ANOSIM tests between pink and chum salmon diets were used to detect significant prey differences at the collection year-salmon species level. As with nMDS, ANOSIM testing was based on Bray-Curtis similarity matrices on square-root transformed relative abundance or relative volume data, as classified based on prey taxonomy, prey size and prey community type.

A similarity percentage analysis (SIMPER) was used to identify important prey items contributing to the similarity within and dissimilarity between the diets of salmon species as based on comparisons of square-root transformed standardized prey data. In ANOSIM comparisons with a detectable difference in diet ($R > 0.25$, $p < 0.05$), SIMPER analysis revealed diet items accounting for the detected diet difference (SIMPER dissimilarity) among salmon species.

2.2.6. Addressing sampling inconsistencies across collection years

Salmon sampling varied in collection location (zone) within and across collection years at the collection period level. In an attempt to control for the spatial and temporal influences on diet composition introduced with this sampling reality, a comparative analysis of diet variation within and between salmon species for each collection period

by collection zone was conducted for both 2003 and 2006 salmon using ANOSIM and SIMPER methodology as described for salmon species diet analysis at the collection year level.

Collection sets from 2003 and 2006 with both pink and chum salmon were analyzed for interspecific salmon feeding differences at the set level. This analysis allowed for an interspecific comparison of salmon collected at the same time and location in a single beach seine, thus limiting diet variation between species due to spatial and temporal influences. This is especially important because the majority of 2006 sets used for stomach analysis contained both pink and chum salmon whereas in 2003, stomach analysis for most sets was possible only for a single species, due to sample loss. As such, greater spatial and temporal variation exists between pink and chum salmon collected in 2003 than in 2006, and is a larger confounding effect in 2003 than 2006. Within set comparisons of interspecies diet composition allows for a matched-pair analysis of salmon species in space and time, further comparable across collection years. The nMDS plots and one-way ANOSIM analyses by salmon species were conducted for each interspecific collection set as described for previous pink-chum comparisons at the year-species level.

Timing and location of salmon collection across collection years was most similar in collection period three (late April-early May) in zones G and H. As an additional means to confirm trends found at the year-species level, targeted analysis of salmon diet was carried out for 2003 and 2006 salmon collected during period three in zones G and H, using PRIMER methodology as performed at the year-species level.

2.2.7. Diversity index comparison of pink and chum diet

A variety of diversity measures commonly used in juvenile salmon interspecific diet comparisons (Bollens et al., 2010; Healey, 1991; Kaeriyama et al., 2000; Sturdevant et al., 2011) were used to compare pink and chum diet composition. These measures are complementary to PRIMER methodology, informing or expanding on aspects of diet composition not directly addressed with ANOSIM or SIMPER analysis. These measures were used only at the species-year level of analysis.

Species richness was calculated using Margalef's Prey Diversity Index (Clarke & Ainsworth, 1993):

$$d = (S-1) / \text{Log} (N)$$

where S is the total number of species and N is the total number of all prey individuals. This index measures not only the number of prey species present in the diet of salmon predators but also accounts for the number of individuals for each prey species (Sturdevant et al., 2011).

Niche breadth was considered at the year-species level using the Shannon-Weiner Diversity Index:

$$H' = -\text{Sum} (P_i * \text{Ln} (P_i))$$

where P_i is the proportion of the total prey count arising from the i^{th} prey category. The Shannon-Weiner Diversity Index was also calculated based on the proportional Index of Relative Importance of prey as done in Kaeriyama et al., 2000.

Pielou's Measure of Species Evenness was used to compare the distribution of prey abundance among prey categories in the diet of pink and chum salmon from each collection year. Pielou's Evenness Index is calculated based on the Shannon-Weiner Diversity Index:

$$J = H' / \text{Ln} (S)$$

where H' is Shannon-Weiner diversity and S is the total number of species in all samples being considered.

Schoener's Percent Similarity Index was used to identify interspecific diet overlap between pink and chum salmon within a collection year (Bollens et al., 2010):

$$\text{PSI}_{XY} = 100 (1 - 0.5 (\sum | p_{xi} - p_{yi} |))$$

where P is the percent volume of food category i in predator species x or y . Overlap of greater than or equal to 60% is considered evidence for a significant overlap in the diets of predator species.

2.2.8. Fork length dependent diet variation

To test for the influence of salmon fork length on diet composition, salmon were grouped into fork length categories 1 to 9, as follows: 1: 2.4-2.9cm, 2: 3.0-3.5cm, 3: 3.6-4.0cm, 4: 4.1-4.5cm, 5: 4.6-5.0cm, 6: 5.1-5.5cm, 7: 5.6-6.0cm, 8: 6.1-6.5cm and 9: 6.6-7.0cm (Table 2.3). Collection periods and zones varied across collection years. Such variation may complicate the interpretation of trends in diet associated with fork length. As such, ANOSIM testing for differences in diet among fork length categories were carried out using pink and chum salmon prey consumed in period three, zones G and H of both collection years. This period and these zones covered the greatest range of fork length categories and as such were chosen for this analysis. Salmon of fork length categories seven to nine were not sampled in this period. The diet of salmon of this size from other zones were investigated using SIMPER methodology.

The relationship of fork length with indicators of feeding success such as %BW and volumetric fullness ranking were compared using correlation analysis.

2.3. Results

2.3.1. Annual indicators of salmon feeding condition

No correlation was found between the volumetric index of stomach fullness and salmon fork length. Similarly, no correlation was found between %BW and fork length (Figure 2.4 and Table 2.4). These results indicate that differences in the gut fullness of pink and chum was not attributable to differences in fork length present among salmon species. %BW ranged from 2-10% in individual salmon in both collection years. At the year-species level, mean %BW ranged from 2-4%. Mean %BW was significantly higher in 2003 than 2006 salmon. In both years, mean %BW was significantly higher in chum than pink salmon but varied by collection period (Table 2.5). In both species, mean

volumetric estimates of stomach fullness were higher in 2003 than 2006. Within each year, mean stomach fullness was higher in chum than pink salmon. However, this varied by collection period (Table 2.5). In 2003, a vacuity index (the percentage of salmon with empty stomachs) of 5.26% was found for pink salmon versus 0% in chum. In 2006, chum had a vacuity index of 5.16% versus 3.85% in pink.

2.3.2. Annual variation in the size, abundance, and diversity of salmon prey

The total number of prey items consumed by pink and chum salmon in 2003 was significantly higher than that consumed in 2006 (Table 2.6). Nauplii, decapod zoea and calanoid copepods <2.5mm, all consumed in high number in 2003, were largely responsible for the difference in prey abundance among collection years.

The average size of prey consumed was smaller in 2003 than 2006 in both pink and chum salmon diets. This size difference can be attributed primarily to higher nauplii consumption in 2003. In terms of prey size, IRI analysis revealed that prey of 0.7-2.1mm was of greatest relative importance in the diets of pink and chum in both collection years (Figure 2.6). Pink from 2003 fed on a larger proportion of prey smaller than 0.7mm in length than any other year-species salmon group and less on prey of 2.2 to 3.5mm than all other groups. In both years, chum salmon fed on a larger proportion of prey >3.5mm. In contrast to IRI findings, difference in prey size in the diet of pink and chum salmon was not detected using ANOSIM on either relative abundance or relative volume of prey for either 2003 or 2006 (Table 2.7).

All 2003 and 2006 chum salmon fed on a similar diversity of prey items (Table 2.8). Eight of the thirty prey categories were fed on very rarely in terms of total abundance and frequency of occurrence of prey in salmon diets and therefore composed a minor component of the diet in these salmon species in 2003 and 2006. After excluding these rare items, prey diversity was found to be similar among all four salmon species-year groups. 2003 pink fed on twenty one major prey categories, whereas 2003 chum as well as 2006 pink and chum fed on twenty prey categories.

Diversity indices are summarized in Table 2.9. Margalef's Index indicated that species richness in the diets of pink and chum salmon were similar within and between collection years. Species richness was slightly higher in chum than pink salmon in both collection years, in agreement with presence-absence data for prey type in salmon species diets. The Shannon-Weiner Index of dietary niche breadth based on both prey count and Index of Relative Importance indicated a similar niche breadth among pink and chum salmon in 2006 and a wider niche breadth in 2003 chum than 2003 pink salmon. Pielou's Evenness Index based on prey count suggests that prey are more evenly distributed among prey categories in 2006 than 2003 salmon diets. The diet of 2003 pink is less evenly distributed among prey categories than the diet of 2003 chum. Prey evenness is similar in the diets of pink and chum salmon in 2006.

2.3.3. Variation in prey community by collection year

When re-classified as prey community type, IRI analysis reveals a greater dependence on pelagic prey in both pink and chum salmon in 2003 than in 2006 (Figure 2.5). Conversely, a greater reliance on epibenthic prey was observed in 2006 than 2003 salmon. Terrestrial prey was more important in the diet of chum from both collection years than in pink salmon, with the highest percent IRI ranking found in 2006 chum. Using PRIMER methodology, ANOSIM did not detect a difference in prey consumed by pink versus chum salmon when classified by prey community (Table 2.7). This was true for both relative count and relative volume of prey data at the year-species level.

2.3.4. Variation in diet composition by collection year

Prey composition was variable among pink and chum salmon in 2003 (Table 2.6 and Figure 2.6). Calanoid copepods less than 2.5mm were found in 76% of pink stomachs but only 23% of chum stomachs (Table 2.10). Nauplii and harpacticoid copepods were found in more than 50% of all pink salmon stomachs but less than 50% of all chum stomachs. Insects (primarily marine midges) were found in 75% of all chum stomachs but less than 20% of all pink stomachs. Nauplii were the dominant prey numerically for pink salmon at 58% of all prey eaten in 2003. The diet of chum salmon was dominated numerically by decapod zoea (primarily crab zoea) and nauplii, with each

prey accounting for 35% of all prey eaten in 2003. Volumetrically, decapod zoea were the dominant prey in the stomachs of 2003 pink, comprising 42% by volume of all prey eaten in that year. Decapod zoea were also an important prey volumetrically in the diets of 2003 chum, comprising 24% of the overall volume of prey consumed. Similar volumetrically to decapod consumption, calanoid copepods larger than 2.5mm comprised 25% of the overall volume of prey eaten by chum in 2003.

Interspecific variation in the percent IRI ranking of pink and chum salmon prey suggests species-specific differences in prey consumption in 2003 (Table 2.6 and Figure 2.5). Nauplii and calanoid copepods less than 2.5mm account for 35% and 31%, respectively, of the percent IRI of prey consumed by pink salmon in 2003. In contrast, these prey contributed 11% and less than 2%, respectively, to the percent IRI of 2003 chum diets. Decapod zoea were an important prey for both salmon species in 2003, accounting for 45% and 27% of the mean percent IRI in the diets of chum and pink, respectively. Insects and calanoid copepods larger than 2.5mm each contributed to approximately 15% of the mean percent IRI calculated for 2003 chum. These were minor prey items in the diet of 2003 pink, with percent IRI values of less than 0.5% and 3%, respectively.

Differences in the diet composition of pink and chum salmon were also observed in 2006 (Figure 2.6 and Table 2.6). As in 2003, insects were a more frequent prey of chum than pink, present in 84% of chum and 38% of pink stomachs in 2006. They were the second most abundant prey eaten by 2006 chum, accounting for 23% of all prey consumed in this year. In contrast, less than 10% of all prey consumed by pink were insects. Insects had the highest percent IRI value of all 2006 chum prey at 40%, versus only 7% as pink prey. Calanoid copepods larger than 2.5mm were present in 45% of chum and 49% of pink stomachs in 2006. They were the dominant prey volumetrically for both species (28% of the total prey volume in 2006 chum and 49% in 2006 pink). Calanoid copepods larger than 2.5mm had percent IRI rankings of 20% and 36% as prey in the diets of chum and pink salmon, respectively. Harpacticoid copepods were present in more than 50% of stomachs of both salmon species and accounted for 29% of the total volume of all prey consumed by pink and chum in 2006. Harpacticoid

copepods had similar percent IRI values of 21% and 26% in the diets of 2006 chum and pink, respectively.

The relative importance of select prey items varied considerably across collection years (Table 2.6 and Figure 2.5). Decapod zoea were an important prey for both pink and chum salmon in 2003 but a minor prey item in 2006 (Percent IRI: 2003 Chum 45%, 2003 Pink 27%, 2006 Pink and Chum less than 0.5%). This was also true for nauplii (Percent IRI: 2003 Chum 11%, 2003 Pink 35%, 2006 Pink 0.06% and 2006 Chum 0.5%). Calanoid copepods less than 2.5mm were an important prey primarily for 2003 pink salmon (Percent IRI: 2003 Chum 2%, 2003 Pink 31%, 2006 Pink 15% and 2006 Chum 2%). Harpacticoid copepods were of greater importance in the diet of both pink and chum salmon in 2006 than 2003 (Percent IRI: 2006 Chum 21%, 2006 Pink 26%, 2003 Pink 2% and 2003 Chum 7%). Insects were a major prey of 2006 chum (Percent IRI: 2006 Chum 40%, 2006 Pink 7%, 2003 Pink 0.22% and 2003 Chum 13%).

Species specific diet trends as discussed by frequency of occurrence, relative prey abundance and volume and IRI were confirmed with nMDS, ANOSIM and SIMPER methodology. Ordination nMDS plots reveal a visual separation of salmon by collection year (Figure 2.7). Within each collection year, 2003 pink and chum salmon show greater visual separation than 2006 pink and chum. These results suggest an influence of collection year and salmon species in diet composition and more interspecific diet overlap in 2006 than 2003. These trends are more visible in nMDS plots based on mean prey abundance than mean prey volume data. The ANOSIM results based on both relative prey abundance and relative volume suggested greater interspecific diet difference in 2003 (Relative prey abundance: ANOSIM R 0.242, p 0.001, Relative prey volume: ANOSIM R 0.236, p 0.001) than in 2006 (Relative prey abundance: ANOSIM R: 0.143, p 0.001, Relative prey volume: ANOSIM R 0.097, p 0.001). A high within year SIMPER dissimilarity of approximately 80% was found for the diets of pink and chum salmon in 2003 and 2006 for both prey abundance and volume (Table 2.11). The 2003 SIMPER dissimilarities were attributed primarily to species-specific differences in relative abundance and volume of nauplii, calanoid copepod and insects. Species-specific diet differences in the relative abundance and volume of insect, gammarid and calanoid copepod prey explain the majority of the detected SIMPER dissimilarity in 2006.

Schoener's Percent Similarity Index indicated a 54% similarity among the diets of 2003 pink and chum salmon and a 61% similarity in the diets of 2006 pink and chum salmon (Table 2.9). As 60% similarity is the minimum level at which diet overlap is assumed, these results support ANOSIM findings for greater diet overlap in the diets of 2006 pink and chum salmon than in 2003.

Intraspecific diet differences were detected across collection years (ANOSIM R values > 0.25, Table 2.7). Low SIMPER similarities indicate high variability in the diet of individual salmon of each species in each year (Table 2.11). Prey species accounting for the majority of the described SIMPER similarity by relative prey abundance and volume include decapod zoea, calanoid copepods >2.5mm and insects in 2003 chum, calanoid copepods less than 2.5mm, nauplii and decapod zoea in 2003 pink, insects, harpacticoids and calanoid copepods >2.5mm in 2006 chum, and harpacticoid copepods, calanoid copepods (all sizes) and barnacle cyprids in 2006 pink.

2.3.5. Diet comparison of 2003 and 2006 period 3 zone G and H pink and chum salmon

As a means to confirm diet trends found at the year-species level were attributable to salmon species rather than a difference in collection methodology between years, a targeted analysis of salmon diet was carried out on pink and chum salmon collected in zones G and H during late April and early May of 2003 and 2006 using nMDS, ANOSIM and SIMPER methodology, as was done at the year-species level.

The nMDS ordinations for this restricted sample set are similar to those constructed for 2003 and 2006 salmon from all collection periods and zones (Figure 2.8). They demonstrate a similarity in the diets of salmon by both collection year and species, with greater overlap in the diets of 2006 pink and chum than 2003 salmon.

The ANOSIM analysis suggested a difference in diet composition among 2003 pink and chum salmon in terms of both relative abundance and volume of prey (ANOSIM R: 0.565 p 0.001, and R: 0.547 p 0.001, respectively). The SIMPER analysis identified insects, harpacticoid copepods, calanoid copepods smaller than 2.5mm and nauplii as

prey accounting for the dissimilarity between salmon species. The diet of 2003 pink was dominated numerically and volumetrically by calanoid copepods less than 2.5mm, nauplii and decapod zoea (Figure 2.9). In contrast, the diet of 2003 chum was dominated both volumetrically and in terms of relative abundance by calanoid copepods larger than 2.5mm and insect prey. Harpacticoid copepods were important numerically but due to their small size represented a small proportion of the total volume of prey in 2003 chum stomachs. As in 2003 pink, decapod zoea were an important component of the diet in chum, although at lower relative volume than seen in the diet of pink salmon.

In contrast to 2003 results, ANOSIM analysis suggested an overlap in the diet of 2006 pink and chum salmon (Relative count: ANOSIM R 0.06, p 0.019, Relative volume: R 0.017, p 0.205). SIMPER analysis identified insects, harpacticoid copepods and calanoid copepods >2.5cm as important prey in the diet of both pink and chum in 2006 (Figure 2.9).

Evidence was detected for a between year difference in the diet of pink salmon (ANOSIM R: 0.508, p 0.001, and R: 0.536, p 0.001 for prey abundance and volume, respectively) but not chum salmon (ANOSIM R less than 0.25 for both abundance and volume data). The numerical dominance of nauplii and small calanoid copepods less than 2.5mm was unique to the 2003 pink diet, setting this group apart from the diets of 2003 chum and all 2006 salmon.

The average fork length of salmon included in this analysis was calculated for each year-species group and compared using a t-test. Fork length was significantly larger in 2006 pink than 2006 chum and 2003 pink. The majority of salmon analysed here are smaller than the 5.5cm-6cm fork length at which a major shift in diet composition has been observed in juvenile pink and chum salmon in previous work (Kaczynski & Feller, 1973). As such, the statistical difference in fork length found in 2006 pink is likely not of biological significance in terms of differentiation in prey being attributed to fork length rather than salmon species.

2.3.6. Diet comparisons of pink and chum salmon within a collection set

The majority of salmon sets included in the 2003 diet analysis contained only one species of salmon whereas the majority of salmon sets analysed for 2006 contained both pink and chum salmon. To confirm that diet trends observed at the Year-Species level was not attributable to a difference in salmon set composition by year, a one way ANOSIM by salmon species was conducted for each set with pink and chum salmon for both collection years (Table 2.12). Fork length values were similar between salmon species within each set, ruling out fork length as the main factor contributing to observed diet differences between salmon species. As in the year-species comparisons, ANOSIM analyses were based on Bray-Curtis Similarity matrices of square-root transformed relative abundance or relative volume prey data. ANOSIM tests were repeated based on Bray Curtis similarities without data transformation or standardization, revealing additional significant R values in sets with low prey count.

In general, ANOSIM results at the set level were consistent with diet trends observed at the year species level (Figure 2.10). A greater diet difference ($R > 0.25$, $p < 0.05$) between salmon species was detected with higher consistency across 2003 salmon sets than detected in 2006 salmon sets (Table 2.12). The ANOSIM diet comparisons in six out of seven of the 2003 collection sets suggested evidence for a diet difference among pink and chum salmon ($R > 0.25$ $p < 0.25$) as run on relative prey count and/or volume data. In comparison, only five out of thirteen 2006 pink-chum sets met this criteria. As such, the greater diet difference seen in 2003 is robust to between year differences in joint occurrence of pink and chum.

Ordination plots created for all pink-chum salmon sets with a significant ($P < 0.05$) R value greater than 0.25 provide visual confirmation that species-specific feeding differences are detectable at the collection set level (Figures 2.11 and 2.12).

Species specific diet composition trends observed at the year-species level were also reflected in pink-chum salmon sets (Figure 2.10). Pink salmon fed on nauplii at greater abundance than chum salmon in pink-chum sets from both collection years, with nauplii consumed at greater abundance in 2003 pink-chum sets. Decapod zoea were

consumed in greater abundance by chum than pink salmon in 2003 pink-chum sets. Insects were consumed either solely by chum or in greater abundance than as consumed by pink in pink-chum sets from both years.

2.3.7. Interspecific and intraspecific diet comparisons within collection periods among zones

A series of ANOSIM analyses were conducted to test for diet differences within collection periods by collection zone, both within and across salmon species. Variable results were found in ANOSIM analysis between species-zones groups within each collection period for both collection years (Table 2.13 and 2.14). Only select ANOSIM comparisons demonstrated a diet difference ($R > 0.25$, $p < 0.05$). A SIMPER analysis was conducted for each ANOSIM comparison with $R > 0.25$, $p < 0.05$. Prey items were variable between and within period, zone and by salmon species in the relative contribution to mean SIMPER similarity (Table 2.15).

Intraspecific comparisons of pink or chum diets within a period between zones varied more in the relative contribution of prey to SIMPER similarity than in actual composition of prey items. For instance, in 2003, decapod zoea and insects were important prey for period 1 chum salmon in both zones G and H. Insects accounted for more of the mean SIMPER similarity among chum in zone G whereas insects accounted for more of the SIMPER similarity in zone H.

Interspecific comparisons made within collection period and zone showed similarity in prey typical in differentiating pink and chum salmon diets at the year level. Prey items included insects for chum salmon and nauplii and calanoid copepods $< 2.5\text{mm}$ for pink salmon.

In 2003, only three out of seven interspecific within period-zone ANOSIM comparisons provided evidence for a diet difference among salmon species. However, three out of four sets not meeting the $R > 0.25$, $p < 0.05$ criteria for a diet difference closely approached this value. In 2006, only three out of nine interspecific within period-zone ANOSIM comparisons had R values > 0.25 , $p < 0.05$. The six ANOSIM comparisons not meeting this criteria did not approach the minimum $R > 0.25$, $p < 0.05$ standard. These

trends are similar to interspecific comparisons made at the year level, in which a greater diet separation was seen among pink and chum in 2003 than 2006.

Analysis at the collection period-zone level revealed the dependence of pink and chum salmon on fish larvae, a prey item whose importance was lost in comparisons made at the year-level with prey from all weeks and zones combined. Fish larvae were an important prey accounting for SIMPER similarity in the diets of pink and chum salmon in 2006, particularly for salmon collected in period four, zones G and H.

2.3.8. Lack of fork length dependent diet variation

Intraspecific within year comparisons of relative abundance of salmon prey from collection period three, zones G and H were made across fork length categories using ANOSIM methodology. Limited evidence was found for a difference in diet composition across fork length categories (Table 2.16). Salmon of fork length categories seven to nine were not sampled in period three, zone G or H in either collection year. A SIMPER analysis of diet composition on salmon of these large fork length categories revealed diet composition similar to that of smaller salmon. SIMPER analysis revealed that decapod zoea, calanoid copepods larger than 2.5mm and insects were important prey of salmon in all fork length categories in both collection years.

2.4. Discussion

The Broughton Archipelago is a heterogeneous environment with a rugged marine shoreline of mainland and island origin. Its waters are influenced by a combination of marine tides and surface currents, fresh water input from numerous rivers and streams and a strong oceanic influence in the outer zones closer to open ocean (Foreman et al., 2006). These physical factors influence the spatial and temporal dynamics of zooplankton. The SIMPER analysis revealed a low level of diet similarity among individual salmon of a species within a collection year. This result finds a basis in the multi-month collection period and the large geographically diverse area sampled which would be expected to encompass substantial variability in prey.

Diet variability was also detected at a smaller scale within collection periods between collection zones, suggesting variability among zones at the collection set level. Nested ANOSIM analysis of collection set in year-species salmon groupings indicated a greater similarity in the diet of salmon of each species from within a collection set than seen at the year-species level. Such a finding matches observations made during stomach analysis that, although individual salmon diets are quite variable, prey composition is more similar among conspecifics within than across collection sets. Collection locations vary in collection zone, collection date and time, with spatial and temporal differences accounting for local small-scale variation in prey available for juvenile salmon (Healey, 1991). Individual salmon diet preference and competitive interactions for limited prey may also play a role in determining diet composition (Armstrong et al., 2005).

Prey found in the stomachs of pink and chum salmon from the Broughton Archipelago was similar to that observed in other populations during early ocean life (Bailey et al., 1975; Bollens et al., 2010; Godin, 1981; Kaczynski & Feller, 1973; Murphy et al., 1987; Orsi et al., 2000). In general, calanoid and harpacticoid copepods, nauplii, decapod prey and insects of variable relative importance at different feeding locations are common prey for juvenile pink and chum in nearshore marine habitats of the Broughton Archipelago. As observed here, other studies have stressed a greater importance of insects and harpacticoid prey within the diet of chum than pink salmon (Bollens et al., 2009; Kaczynski & Feller, 1973). Northcotte et al., 2007 found that juvenile chum salmon fed closer to shore and closer to the surface than pink salmon when foraging in mixed schools, with pink salmon feeding at greater depths in more pelagic waters. This partitioning of the nearshore marine environment between salmon species may help to explain the greater importance of insects in the diet of chum than pink salmon, as insects would be more available in nearshore surface waters.

Pink salmon, and to a lesser degree chum salmon, fed on nauplii in higher abundance in 2003 than in 2006. Again, this difference may be attributed to the partitioning of the nearshore marine environment between pink and chum salmon, with pink more likely to encounter nauplii when feeding in more pelagic waters than surface oriented shoreward chum. In addition, pink salmon with fine sieve-like gill rakers would

be at a physiological advantage over chum in capturing this prey. In theory, a predator should obtain more energy by feeding on a small number of large prey than a large number of small prey, particularly if the small prey are of lower energetic value (Healey, 1991; Volk et al., 1984). Crustacean nauplii have low mobility and were likely encountered in dense aggregations by salmon. The low foraging effort involved in their capture may make them a preferred prey from an energy expenditure perspective. The presence of nauplii in 58% of 2003 pink salmon stomachs and a dominant IRI prey ranking for pink in this year is consistent with this interpretation. Zooplankton samples collected in 2003 had higher levels of nauplii than those collected in 2006 (see Chapter 3), suggesting greater availability as prey in 2003 and the increased potential for opportunistic foraging on nauplii during that year by pink salmon.

Although variable across collection period, volumetric estimates of stomach fullness were significantly higher in chum than pink salmon for both collection years. This finding is corroborated by the higher average %BW found in chum than pink salmon in both years and a lack of correlation of either measure with fork length. Assuming similar energy content in the diets of pink and chum salmon and similar conversion of prey energy to growth in both salmon species, chum salmon would be at an advantage ecologically to pink salmon. This is because larger, faster growing juvenile salmon have a reduced risk of size-dependent predation and a better chance of surviving the first winter at sea (Beamish & Mahnken, 2001; Healey, 1982; Parker, 1971). The greater prey field of chum salmon, due to their ability to consume larger prey, would explain broader niche breadth results in chum salmon in both years. Chum stomachs may have remained full at a higher degree of maximum capacity because this species is able to feed on a greater range of prey items. The likelihood of encounter with suitable prey would increase when a greater diversity of common organisms is recognized as prey. However, this idea is challenged by the omnipresent nauplii of 2003. Chum as a superior competitor to pink during early ocean life is contrary to diet comparisons made between pink and chum salmon when feeding offshore, where pink salmon are competitively dominant to chum in the preferential consumption of quality prey (Ruggerone & Nielson, 2005; Tadokoro et al, 1996).

The assumption of similar energy content in the diets of pink and chum salmon and similar conversion of prey energy to growth in both salmon species requires further consideration. Different prey items are consumed at different levels in both species of salmon, variable by collection year. A stomach full of insects may not be equivalent energetically to a stomach full of nauplii (Pandian & Helgoland, 1967; Volk et al., 1984). Differences in energetic conversion ratios among different prey items for pink versus chum may complicate comparisons of stomach fullness between salmon species.

Adult pink salmon returns in 2004 were higher than in 2007 (Riddell et al., 2008), the return years corresponding to the 2003 and 2006 years of ocean entry investigated in this diet analysis. Feeding conditions in terms of amount of prey consumed were higher in 2003 than 2006, suggesting a potential link between feeding conditions during early marine life and adult return strength of pink salmon in the Broughton Archipelago. As such, diet analysis of juvenile pink and chum during their first month at sea warrants further consideration as a means to better understand local salmon population trends.

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2.6. Tables and Figures

Table 2.1. 2003 salmon collection information. Map identification number as labelled in Figure 2.2, collection location, zone of collection, date and time of collection and number of chum and pink salmon stomachs included in the diet analysis.

Number on Map	Collection Location	Zone	Date	Time	Chum	Pink
1	Harry Bay	I	02-Apr-03	1310	11	10
3	Deep Harbour	H	03-Apr-03	640	8	0
4	Jumper Island	H	03-Apr-03	810	3	5
5	Arthur Point	H	03-Apr-03	1015	6	0
6	Shoal Harbour	G	03-Apr-03	1340	5	0
2	Denham Island	G	03-Apr-03	1645	5	5
7	Deep Sea Bluff	G	15-Apr-03	1855	10	0
8	Denham Island	G	16-Apr-03	1040	11	0
9	Baker Island	H	16-Apr-03	1240	17	0
10	Deep Harbour	H	16-Apr-03	1420	11	3
11	Jumper Island	H	16-Apr-03	1505	0	10
12	Arthur Point	H	16-Apr-03	1645	0	10
13	Gordon Point	H	16-Apr-03	1800	11	0
15	Lambert Island	K	22-Apr-03	1930	0	5
14	Wolf Point	K	22-Apr-03	1900	0	5
16	Kinnaird Island	K	23-Apr-03	758	10	8
17	Codrington Point	K	23-Apr-03	920	3	0
18	Deep Sea Bluff	G	24-Apr-03	800	0	10
20	Deep Harbour	H	24-Apr-03	945	0	5
21	Jumper Island	H	24-Apr-03	1030	0	15
19	Viner Sound	G	25-Apr-03	1135	5	0
22	Buckingham Island	K	28-Apr-03	1515	5	4
23	Duff Point	H	30-Apr-03	1435	0	8
24	Gordon Point	H	30-Apr-03	1500	5	0
25	Baker Island	H	01-May-03	800	11	11
26	Denham Island	G	01-May-03	1310	10	0

Table 2.2. 2006 salmon collection information. Map identification number as labelled in Figure 2.3, collection location, zone of collection, date and time of collection and number of chum and pink salmon stomachs included in the diet analysis

Number on Map	Collection Location	Zone	Date	Time	Chum	Pink
1	Shelterless Point	D	03-Apr-06	1534	5	3
2	Protection Point	D	03-Apr-06	1610	5	0
3	Echo Bay	G	27-Apr-06	1600	5	5
4	Baker Island	H	27-Apr-06	1800	5	5
5	Viner Sound	G	28-Apr-06	745	11	0
6	Denham Island	G	28-Apr-06	824	11	11
7	Deep Sea Bluff	G	28-Apr-06	1149	10	11
8	Bradley Point	I	28-Apr-06	1430	0	5
9	Thief Island	I	28-Apr-06	1623	5	0
10	Tribune South	F	30-Apr-06	752	10	0
11	Gormely Point	F	30-Apr-06	950	10	11
12	Kwatsi Bay Head	F	30-Apr-06	1315	5	5
13	Brown Point West	F	01-May-06	837	5	3
14	Thompson Sound	F	01-May-06	1109	5	7
15	Doctor Island	D	02-May-06	801	8	2
16	Sargeaunt Passage	D	03-May-06	1641	12	15
17	Sargeaunt Passage	D	03-May-06	1743	10	10
18	Gilford Bay	D	04-May-06	942	0	5
19	Warr Bluff	D	04-May-06	1814	0	6
20	Baker Island	H	24-May-06	1315	5	5
21	Pearse Peninsula	H	24-May-06	1300	4	5
23	Viner Sound	G	24-May-06	1629	5	2
22	Denham Island	G	25-May-06	1104	5	1
24	Lady Island	E	30-May-06	1255	5	4
25	Dinner Point	E	30-May-06	1608	4	4
26	Slope Point	E	30-May-06	1742	5	5

Table 2.3 Number of salmon in each fork length category by year-species group. Fork length average (FL Avg) and standard deviation (StDev), collection period and collection zone are summarized.

Fork Length Category (cm)	2003 Pink	FLAvg (cm)	StDev	Periods	Zones
1: 2.4-2.9	10	2.8	0.17	1-3	HIK
2: 3.0-3.5	47	3.2	0.17	1-3	GHIK
3: 3.6-4.0	31	3.8	0.14	1-3	GHK
4: 4.1-4.5	12	4.3	0.11	3	GHK
5: 4.6-5.0	5	4.8	0.8	3	GHK
6: 5.1-5.5	2	5.2	0.14	3	GK
7: 5.6-6.0	1	5.7	0	3	K
Total 2003 Pink:	108				
Fork Length Category (cm)	2003 Chum	FLAvg (cm)	StDev	Periods	Zones
2: 3.0-3.5	62	3.3	0.14	1-3	GHIK
3: 3.6-4.0	58	3.7	0.14	1-3	GHIK
4: 4.1-4.5	13	4.3	0.12	1-3	GHIK
5: 4.6-5.0	6	4.7	0.15	3	HK
6: 5.1-5.5	6	5.2	0.17	3	HKJ
7: 5.6-6.0	2	5.8	0.7	3	K
Total 2003 Chum:	147				
Fork Length Category (cm)	2006 Chum	FLAvg (cm)	StDev	Periods	Zones
2: 3.0-3.5	29	3.3	0.14	1, 3, 4	DFGH
3: 3.6-4.0	43	3.8	0.14	1, 3, 4	DFGHI
4: 4.1-4.5	31	4.3	0.14	3, 4	DEFGHI
5: 4.6-5.0	19	4.8	0.14	3, 4	DEFG
6: 5.1-5.5	9	5.2	0.17	3, 4	DEFH
7: 5.6-6.0	9	5.9	0.13	3, 4	DEFGH
8: 6.1-6.5	4	6.2	0.19	4	EG
9:6.6-7.0	3	7.1	0.55	3, 4	EFH
Total 2006 Chum:	147				
Fork Length Category (cm)	2006 Pink	FLAvg (cm)	StDev	Periods	Zones
1: 2.4-2.9	7	2.8	0.14	1,3	D
2: 3.0-3.5	17	3.3	0.19	1, 3, 4	DGHI
3: 3.6-4.0	16	3.8	0.15	3, 4	DEFGI
4: 4.1-4.5	37	4.3	0.16	3, 4	DEFGH
5: 4.6-5.0	22	4.7	0.14	3, 4	DEFG
6: 5.1-5.5	15	5.3	0.14	3, 4	DEFGH
7: 5.6-6.0	5	5.8	0.2	4	EGH
8: 6.1-6.5	3	6.2	0.05	4	E
9:6.6-7.0	3	6.9	0.35	3, 4	FH
Total 2006 Pink:	125				

Table 2.4 Correlation co-efficients between fork length (FL) and percent body weight (%BW) and between FL and gut rating (Gut R) for salmon year species-groups, as indicated.

Salmon Group	Correlation	Correlation Co-efficient
03 Chum	FL vs %BW	0.0117
03 Pink	FL vs %BW	-0.2019
06 Chum	FL vs %BW	0.0379
06 Pink	FL vs %BW	0.1256
All 03 Salmon	FL vs %BW	-0.023
All 06 Salmon	FL vs %BW	0.059
All Salmon	FL vs %BW	-0.0371
03 Chum	FL vs GutR	-0.1408
03 Pink	FL vs GutR	-0.1852
06 Chum	FL vs GutR	0.2459
06 Pink	FL vs GutR	0.1975
All 03 Salmon	FL vs GutR	-0.0967
All 06 Salmon	FL vs GutR	0.2169
All Salmon	FL vs GutR	0.0596

Table 2.5 Salmon number (N), mean fork length (FL), mean %BW, mean volumetric stomach rating (GutR) and standard deviation (SD) by year-species and year-species-collection period (Yr-Spp-Per) of salmon included in the diet analysis. P values for t-test comparisons of mean FL, mean %BW and mean GutR between year-species or year-species-period groups are reported.

Yr-Spp-Per	N	Mean FL	SD	Yr-Spp-Per	N	Mean FL	SD	P
03 Chum	146	3.75	0.55	03 Pink	108	3.98	0.62	0.002
06 Chum	148	4.00	0.99	06 Pink	119	4.34	0.88	0.003
03 Chum	146	3.75	0.55	06 Chum	148	4.00	0.99	<0.001
03 Pink	108	3.98	0.62	06 Pink	119	4.34	0.88	<0.001
03C Per1	38	3.65	0.25	03P Per1	16	3.65	0.59	0.987
03C Per2	60	3.50	0.28	03P Per2	23	3.62	0.28	0.071
03C Per3	48	4.14	0.73	03P Per3	69	4.17	0.63	0.813
06C Per1	10	5.17	1.02	06P Per1	3	5.93	0.46	0.104
06C Per3	105	4.04	0.99	06P Per3	97	4.21	0.81	0.202
06C Per4	33	3.50	0.54	06P Per4	19	4.77	0.94	<0.001
Yr-Spp-Per	N	Mean %BW	SD	Yr-Spp-Per	N	Mean %BW	SD	P
03 Chum	146	3.43	2.22	03 Pink	108	2.69	2.22	0.010
06 Chum	148	2.46	1.48	06 Pink	119	1.98	1.41	0.007
03 Chum	146	3.43	2.22	06 Chum	148	2.46	1.48	0.004
03 Pink	108	2.69	2.22	06 Pink	119	1.98	1.41	0.069
03C Per1	38	1.84	1.34	03P Per1	16	3.95	3.03	0.015
03C Per2	60	4.09	1.90	03P Per2	23	2.63	2.88	0.032
03C Per3	48	3.86	2.54	03P Per3	69	2.42	1.61	0.001
06C Per1	10	2.57	0.72	06P Per1	3	2.03	1.30	0.552
06C Per3	105	2.40	1.58	06P Per3	97	1.94	1.33	0.027
06C Per4	33	2.63	1.34	06P Per4	19	2.17	1.85	0.348
Yr-Spp-Per	N	Mean GutR	SD	Yr-Spp-Per	N	Mean GutR	SD	P
03 Chum	146	3.13	0.99	03 Pink	108	2.60	1.18	<0.001
06 Chum	148	2.53	1.07	06 Pink	119	2.46	1.00	0.001
03 Chum	146	3.13	0.99	06 Chum	148	2.53	1.07	0.002
03 Pink	108	2.60	1.18	06 Pink	119	2.46	1.00	0.167
03C Per1	38	3.13	0.96	03P Per1	16	3.19	0.98	0.849
03C Per2	60	3.35	0.84	03P Per2	23	1.78	0.90	<0.001
03C Per3	48	2.85	1.13	03P Per3	69	2.74	1.17	0.595
06C Per1	10	3.30	1.06	06P Per1	3	3.33	0.58	0.946
06C Per3	105	2.60	1.10	06P Per3	97	2.40	1.00	0.181
06C Per4	33	2.06	0.79	06P Per4	19	2.63	1.01	0.042

Table 2.6 Summary of prey composition by year-species groups by total prey abundance, relative mean abundance of prey, relative mean volume of prey and percent IRI ranking for each year-species group.

	<u>Total Abundance of Prey</u>			<u>Mean Abundance of Prey</u>			<u>Mean Volume of Prey</u>			<u>Percent IRI of Prey</u>		
	03C	03P	06C	06P	03C	03P	06C	06P	03C	03P	06C	06P
Nauplii	5132	11625	47	124	34.12	58.12	0.74	2.10	2.48	7.85	0.11	0.36
Calanoid <2.5	617	4331	218	1343	4.10	21.65	3.43	22.78	2.12	23.48	1.56	7.66
Decapod Zoea	5412	3016	71	90	35.99	15.08	1.12	1.53	23.83	41.89	1.41	0.93
Harpacticoid	1221	379	1813	1701	8.12	1.89	28.55	28.85	4.94	2.17	3.78	6.82
Calanoid ≥2.5	592	115	467	655	3.94	0.57	7.35	11.11	25.26	11.74	27.51	49.33
Invertebrate Egg	11	89	46	10	0.07	0.44	0.72	0.17	0.04	1.75	0.06	0.05
Larval Euphausiid	6	86	474	436	0.04	0.43	7.46	7.39	0.03	0.80	5.06	5.36
Insect	1042	58	1487	487	6.93	0.29	23.42	8.26	6.42	1.02	15.05	5.97
Polychaete Larvae	402	45	791	4	2.67	0.22	12.46	0.07	1.08	0.31	1.28	0.00
Cirripide Cypris	7	51	340	660	0.05	0.25	5.35	11.19	0.02	0.36	0.77	2.92
Gammaridae	202	8	393	60	1.34	0.04	6.19	1.02	3.71	0.23	15.81	3.78
Fish Larvae	93	42	100	26	0.62	0.21	1.57	0.44	14.03	5.02	21.37	5.67
Cumacea	22	1	26	188	0.15	0.00	0.41	3.19	0.31	0.02	0.41	6.26
Larvacea	106	20	0	0	0.70	0.10	0.00	0.00	3.16	0.19	0.00	0.00
Fish Egg	38	29	36	46	0.25	0.14	0.57	0.78	3.24	1.96	2.44	4.60
Euphausiid	5	3	3	0	0.03	0.01	0.05	0.00	7.12	0.83	0.74	0.00
Hyperidae	5	0	2	0	0.03	0.00	0.03	0.00	1.45	0.00	2.26	0.00
Other	126	104	36	66	0.84	0.5	0.56	1.12	0.76	0.35	0.36	0.3
	03C	03P	06C	06P	03C	03P	06C	06P	03C	03P	06C	06P
	10.95	34.94	0.06	0.54	10.95	34.94	0.06	0.54	1.92	31.12	1.68	14.63
	44.99	26.82	0.38	0.31	44.99	26.82	0.38	0.31	7.22	2.02	20.88	26.06
	14.55	3.00	19.59	36.02	14.55	3.00	19.59	36.02	0.01	0.30	0.04	0.01
	0.00	0.29	2.31	3.06	0.00	0.29	2.31	3.06	0.00	0.29	2.31	3.06
	13.18	0.23	40.01	6.57	13.18	0.23	40.01	6.57	1.16	0.07	0.92	0.00
	0.00	0.06	2.36	8.82	0.00	0.06	2.36	8.82	1.19	0.01	7.94	0.88
	3.18	0.88	3.46	0.65	3.18	0.88	3.46	0.65	0.03	0.00	0.11	2.00
	0.49	0.02	0.00	0.00	0.49	0.02	0.00	0.00	0.49	0.02	0.00	0.00
	0.44	0.18	0.13	0.26	0.44	0.18	0.13	0.26	0.44	0.18	0.13	0.26
	0.19	0.01	0.02	0.00	0.19	0.01	0.02	0.00	0.19	0.01	0.02	0.00
	0.07	0.00	0.04	0.00	0.07	0.00	0.04	0.00	0.07	0.00	0.04	0.00
	0.44	0.05	0.06	0.18	0.44	0.05	0.06	0.18	0.44	0.05	0.06	0.18

Table 2.7 Summary of ANOSIM R (p values) for diet comparisons between year-species groups as indicated, based on relative abundance and relative volume of prey as classified by prey taxonomy, prey size and prey community. Values in bold indicate evidence for a diet difference among compared salmon groups ($R > 0.25$, $p < 0.05$).

Species-Year Comparison		Prey Taxonomy: Count	Prey Taxonomy: Volume	Prey Size: Count	Prey Size: Volume	Prey Community: Count	Prey Community: Volume
2003 Pink	2003 Chum	0.242 (0.001)	0.236 (0.001)	0.089 (0.001)	0.057 (0.001)	0.069 (0.001)	0.065 (0.001)
2006 Pink	2006 Chum	0.143 (0.001)	0.097 (0.001)	-0.001 (0.468)	-0.005 (0.814)	0.107 (0.001)	0.056 (0.001)
2003 Pink	2006 Pink	0.270 (0.001)	0.218 (0.001)	0.202 (0.001)	0.142 (0.001)	0.177 (0.001)	0.074 (0.001)
2003 Chum	2006 Chum	0.164 (0.001)	0.115 (0.001)	0.025 (0.002)	0.016 (0.01)	0.118 (0.001)	0.044 (0.001)
2003 Pink	2006 Chum	0.472 (0.001)	0.384 (0.001)	0.231 (0.001)	0.142 (0.001)	0.337 (0.001)	0.171 (0.001)
2003 Chum	2006 Pink	0.264 (0.001)	0.220 (0.001)	0.017 (0.031)	0.018 (0.01)	0.134 (0.001)	0.079 (0.001)

Table 2.8 Summary of all prey categories of 2003 and 2006 pink and chum salmon. "P" indicates prey was present in the stomachs of the year-species salmon group. Prey in italics are minor prey categories (less than six total prey per year-species salmon group).

Prey Category	2003 Chum	2003 Pink	2006 Chum	2006 Pink
<i>Chaetognatha</i>	P	Absent	Absent	Absent
<i>Nematode</i>	P	Absent	Absent	Absent
<i>Squat Lobster</i>	P	Absent	Absent	Absent
Larvacean	P	P	Absent	Absent
<i>Mysid</i>	P	P	Absent	Absent
<i>Ostracod</i>	Absent	P	Absent	Absent
<i>Hyperid Amphipod</i>	P	Absent	P	Absent
<i>Epicarid</i>	Absent	Absent	P	Absent
Cladocera	P	P	P	Absent
<i>Euphausid</i>	P	P	P	Absent
Veliger	P	P	Absent	P
Cyphonaut Larvae	Absent	Absent	P	P
Cyclopoida	Absent	P	P	P
Mite	P	P	P	P
Spider	P	P	P	P
Barnacle Cyprid	P	P	P	P
Calanoid <2.5	P	P	P	P
Calanoid >2.5	P	P	P	P
Cumacean	P	P	P	P
Decapod Zoea	P	P	P	P
Euphausid Protozoa	P	P	P	P
Fish Egg	P	P	P	P
Fish Larvae	P	P	P	P
Gammarid Amphipod	P	P	P	P
Harpacticoid	P	P	P	P
Hexapod Collembolla	P	P	P	P
Insects	P	P	P	P
Invertebrate Egg	P	P	P	P
Nauplii	P	P	P	P
Polychaete Larvae	P	P	P	P
Number of Prey Categories	26	24	23	20

Table 2.9 Summary of diversity index calculations as run on prey classified by taxonomic identification: A) Schoener's Percent Similarity Index (prey count), B) Shannon-Weiner Index by count and D) IRI, C) Pielou's Evenness Index (prey count) and E) Margalef's Diversity Index (prey count).

A)	Diversity Measure	Year- Species Comparison	Similarity
	Schoener's PSI : Prey Count	03C vs 03P	54.40%
	≥ 60% Significant diet overlap	06C vs 06P	60.50%

B)	Diversity Measure	Niche Breadth H'	C) Pielou's Evenness- J'
	Shannon-Weiner Index-Count		
	2003 Chum	1.692	0.5323
	2003 Pink	1.202	0.3889
	2006 Chum	2.065	0.6781
	2006 Pink	2.035	0.6911

D)	Shannon-Weiner Index-IRI	Niche Breadth H'
	2003 Chum	1.724
	2003 Pink	1.387
	2006 Chum	1.672
	2006 Pink	1.727

E)	Diversity Measure	Prey Species Richness d'
	Margalef's Index -Count	
	2003 Chum	2.390
	2003 Pink	2.118
	2006 Chum	2.274
	2006 Pink	2.061

Table 2.10 Frequency of occurrence of prey, as expressed as the percent of all salmon from each year-species group that consumed the prey item.

Prey Category	2003 Chum	2003 Pink	2006 Chum	2006 Pink
Barnacle Cyprid	2.8	11.1	31.1	51.6
Calanoid <2.5	23.4	75.9	27.0	39.7
Calanoid >2.5	37.9	26.9	45.3	49.2
Chaetognatha	0.7	0.0	0.0	0.0
Cladocera	1.4	7.4	1.4	0.0
Cumacean	5.5	0.9	10.8	17.5
Cyclopoida	0.0	6.5	2.7	16.7
Decapod Zoea	57.2	51.9	12.2	10.3
Euphausid	2.1	0.9	2.0	0.0
Euphausid Larvae	2.8	25.9	14.9	19.8
Fish Egg	9.7	9.3	3.4	4.0
Fish Larvae	16.6	18.5	12.2	8.7
Gammarid Amphipod	17.9	5.6	29.1	15.1
Harpacticoid	42.1	54.6	52.0	60.3
Hexapod Collembolla	25.5	2.8	7.4	2.4
Hyperid Amphipod	3.4	0.0	1.4	0.0
Insects	75.2	19.4	83.8	38.1
Invertebrate Egg	3.4	14.8	4.1	4.0
Larvacean	9.7	6.5	0.0	0.0
Mite	3.4	3.7	2.7	0.8
Nauplii	22.8	58.3	6.1	18.3
Polychaete Larvae	23.4	14.8	5.4	1.6
Spider	4.1	0.9	1.4	2.4
Veliger	1.4	7.4	0.0	4.0

Table 2.11 SIMPER analysis percent similarity and percent dissimilarity between year-species groups as determined for square-root transformed relative abundance and relative volume of prey as classified by taxonomic identification, prey size category and prey community type.

Species Group(s)	Prey Taxonomic ID		Prey Size		Prey Community		
	SIMPER Measure	Relative Abundance	Relative Volume	Relative Abundance	Relative Volume	Relative Abundance	Relative Volume
2003 Chum	Similarity	27.11	25.51	59.26	55	61.34	59.01
2003 Pink	Similarity	32.82	29.71	58.23	58.26	83.49	82.86
2003 Chum & Pink	Dissimilarity	80.6	81.98	45.49	46.82	34.25	35.82
2006 Chum	Similarity	31.22	27.95	66.49	56.37	55.75	53.58
2006 Pink	Similarity	25.95	24.14	65.35	57.67	55.41	55.02
2006 Chum & Pink	Dissimilarity	76.35	77.14	34	42.82	49.27	48.65
2003 Chum & 2006 Chum	Dissimilarity	77.39	77.83	38.35	45.15	46.97	45.79
2003 Pink & 2006 Pink	Dissimilarity	82.91	82.59	48.19	49.96	42.12	38.22
2003 Pink & 2006 Chum	Dissimilarity	86.88	86.11	47.99	50.4	51.77	45.47
2003 Chum & 2006 Pink	Dissimilarity	83.77	83.09	39	44.89	47.67	46.88

Table 2.12 Within set pink-chum ANOSIM diet comparison of taxonomically identified relative prey count and volume data before and after square-root (Sqrt) transformation. Values in bold suggest evidence for a diet difference ($R>0.25$, $p<0.05$) between pink and chum.

SetID	# Salmon		2006 Prey Count		2006 Prey Volume	
	Chum	Pink	SqrtStd	None	SqrtStd	None
WRBS 137	4	4	0.938 2.9%	0.760 2.9%	0.500 2.9%	0.111 28.6%
WRBS 53	12	15	0.623 0.1%	0.578 0.1%	0.691 0.1%	0.618 0.1%
RRBS 32	5	5	0.342 5.6%	0.318 4%	0.114 2.3%	-0.002 46%
WRBS 26	10	11	0.328 0.3%	0.328 0.3%	0.149 2.2%	0.112 7.0%
WRBS 54	10	10	0.230 1.9%	0.271 0.3%	0.337 0.2%	0.372 0.1%
WRBS 06	10	11	0.158 3.7%	0.176 1.7%	0.054 15.8%	0.058 14.5%
CPBS 67	5	3	0.482 7.1%	0.328 10.7%	0.405 10.7%	0.395 10.7%
WRBS 01	5	5	0.212 6.3%	0.124 15%	0.004 52.4%	-0.048 61.9%
WRBS 134	5	5	0.344 9.5%	0.319 8.7%	0.072 28.6%	-0.068 65.1%
WRBS 02	5	5	-0.02 46.8%	-0.092 82.5%	-0.112 88.11%	-0.108 87.3%
WRBS 04	11	9	0.042 19.9%	0.034 25.8%	0.039 21.2%	0.043 21.6%
WRBS 28	5	5	-0.104 70.6%	-0.026 53.2%	-0.128 77%	-0.148 81.7%
WRBS 33	5	3	0.087 25%	0.149 14.3%	0.015 42.9%	0.118 21.4%
WRBS 35	5	5	0.048 29.4%	0.184 9.5%	-0.032 55.6%	0.124 19%
WRBS 42	1	2	-0.25 80%	-0.208 80%	-0.292 80%	-0.125 70%
WRBS 139	5	5	-0.02 45.2%	-0.024 44.4%	0.056 30.2%	-0.06 61.9%
RRBS 33	5	4	-0.122 73.8%	-0.194 93.7%	0.072 25.4%	-0.016 52.4%
RRBS 36	5	2	-0.182 81%	-0.345 90.5%	-0.2 85.7%	-0.582 100%

SetID	# Salmon		2003 Prey Count		2003 Prey Volume	
	Chum	Pink	Sqrt	None	Sqrt	None
WRPS 185	5	4	0.256 6.5%	0.063 28.6%	0.100 2.3%	0.138 19%
WRBS 186	7	5	- 0.039 60%	0.204 3.5%	0.047 72%	0.084 19%
WRBS 192	5	3	0.754 1.8%	0.754 1.8%	0.641 18%	0.723 1.8%
WRBS 243	11	3	0.133 22%	0.140 17.9%	0.423 0.8%	0.463 0.8%
WRBS 253	10	8	0.416 0.1%	0.386 0.1%	0.284 0.5%	0.211 1.4%
WRBS 301	10	10	0.754 0.1%	0.710 0.1%	0.646 0.1%	0.654 0.1%
WRBS 182	11	8	0.190 2.9%	0.291 0.5%	0.177 4.4%	0.251 1.8%

Table 2.13 Diet comparisons as made within each 2003 collection period between salmon species-zone groups. Each ANOSIM analysis was run on square-root transformed taxonomically identified relative prey count and prey volume. Bold text highlights R values >0.25 (p <0.05) suggesting evidence for a diet difference between groups.

2003-Collection Period 1 Zones G H I	PreyID-Cnt	Prey ID-Vol
Chum and Pink in Zone G:	0.608 (0.010)	0.684 (0.030)
Chum and Pink in Zone I:	0.190 (0.041)	0.177 (0.0540)
Chum and Pink in Zone H:	-0.057 (0.600)	-0.078 (0.625)
Chum in Zones H and I:	0.759 (0.001)	0.737 (0.010)
Chum in Zones H and G:	0.538 (0.001)	0.578 (0.010)
Chum in Zones I and G:	0.183 (0.0170)	0.075 (0.109)
Pink in Zones H and I:	0.307 (0.0140)	0.377 (0.060)
Pink in Zones H and G:	0.744 (0.0180)	0.826 (0.018)
Pink in Zones I and G:	-0.052 (0.661)	-0.044 (0.583)
2003-Collection Period 2 Zones G H	PreyID-Cnt	Prey ID-Vol
Chum and Pink in Zone H:	0.107 (0.020)	0.148 (0.001)
Chum in Zones G and H:	0.165 (0.002)	0.202 (0.001)
2003-Collection Period 3 Zones G H K	PreyID-Cnt	Prey ID-Vol
Chum and Pink in Zone G:	0.764 (0.001)	0.763 (0.001)
Chum and Pink in Zone H:	0.508 (0.001)	0.457 (0.001)
Chum and Pink in Zone K:	0.216 (0.002)	0.180 (0.002)
Chum in Zones H and G:	0.025 (0.230)	0.051 (0.125)
Chum in Zones H and K:	0.123 (0.014)	0.063 (0.097)
Chum in Zones K and G:	0.394 (0.001)	0.325 (0.001)
Pink in Zones H and G:	0.124 (0.063)	0.126 (0.079)
Pink in Zones H and K:	0.168 (0.001)	0.184 (0.001)
Pink in Zones K and G:	-0.016 (0.513)	0.083 (0.150)

Table 2.14 Diet comparisons made within each 2006 collection period between salmon species-zone groups. Each ANOSIM analysis was run on square-root transformed taxonomically identified relative count and volume prey data. Values in bold suggest evidence for a diet difference ($R>0.25$, $p<0.05$) between groups.

	PreyID-Count	Prey ID-Volume
Period 1 Zone D	0.745 (0.007)	0.622 (0.0140)
Period 3 Zones D F G H I		
D: Pink vs Chum	0.306 (0.001)	0.335 (0.001)
F: Pink vs Chum	0.080 (0.015)	0.047 (0.069)
G: Pink vs Chum	0.075 (0.020)	0.028 (0.144)
H: Pink vs Chum	-0.02 (0.468)	-0.112 (0.881)
I: Pink vs Chum	0.630 (0.008)	0.386 (0.040)
Chum H and I	0.180 (0.040)	0.152 (0.135)
Chum I and D	0.163 (0.112)	0.062 (0.251)
Chum G and D	0.110 (0.004)	0.114 (0.005)
Chum H and D	0.067 (0.278)	0.162 (0.098)
Chum F and D	0.044 (0.088)	0.040 (0.112)
Chum F and G	0.041 (0.030)	0.031 (0.063)
Chum G and H	-0.095 (0.726)	-0.009 (0.479)
Chum G and I	-0.134 (0.833)	-0.036 (0.564)
Chum I and F	-0.044 (0.571)	-0.097 (0.786)
Chum H and F	-0.09 (0.802)	-0.077 (0.726)
Pink H and D	0.439 (0.001)	0.420 (0.001)
Pink I and D	0.323 (0.008)	0.315 (0.009)
Pink G and D	0.309 (0.001)	0.336 (0.001)
Pink F and D	0.266 (0.001)	0.277 (0.001)
Pink H and I	0.202 (0.095)	0.082 (0.190)
Pink H and F	0.085 (0.199)	-0.039 (0.573)
Pink G and F	0.033 (0.130)	0.016 (0.221)
Pink G and H	-0.055 (0.704)	-0.052 (0.587)
Pink G and I	-0.231 (0.992)	-0.175 (0.899)
Pink I and F	-0.161 (0.966)	-0.184 (0.966)
Period 4 Zones E G H		
E: Chum vs Pink	0.124 (0.015)	0.019 (0.264)
G: Chum vs Pink	0.123 (0.214)	-0.051 (0.612)
H: Chum vs Pink	0.038 (0.250)	-0.016 (0.523)
Chum E and H	0.346 (0.001)	0.414 (0.002)
Chum E and G	0.154 (0.023)	0.176 (0.015)
Chum G and H	0.020 (0.331)	-0.022 (0.525)
Pink E and H	0.674 (0.001)	0.726 (0.001)
Pink E and G	0.903 (0.002)	0.888 (0.002)
Pink G and H	-0.004 (0.444)	-0.063 (0.556)

Table 2.15 Prey items contributing to SIMPER similarity based on relative abundance of taxonomically identified prey for all year-species-period-zone comparisons with ANOSIM values $R > 0.25$ ($p < 0.05$). SIMPER mean percent dissimilarity is reported.

Year	Yr-Spp-Zone comparison		ANOSIM R (p)	SIMPER mean dissimilarity	Prey contributing to diet similarity within groups based on relative abundance
2003	Per1-Chum-G	Per1-Pink-G	0.608 (0.010)	91.33%	Per1-Chum-G: Insects, Decapod Zoea, Harpacticoids Per1-Pink-G: Nauplii
2003	Per1-Chum-H	Per1-Chum-I	0.759 (0.001)	95.21%	Per1-Chum-H: Decapod Zoea Per1-Chum-I: Insects
2003	Per1-Chum-H	Per1-Chum-G	0.538 (0.001)	61.36%	Per1-Chum-G: Insects, Decapod Zoea Per1-Chum-H: Decapod Zoea
2003	Per1-Pink-H	Per1-Pink-I	0.307 (0.014)	98.97%	Per1-Pink-H: Decapod Zoea Per1-Pink-I: Insects, Harpacticoids, Calanoid >2.5
2003	Per1-Pink-H	Per1-Pink-G	0.744 (0.018)	94.59%	Per1-Pink-H: Decapod Zoea Per1-Pink-G: Nauplii
2003	Per3-Chum-G	Per3-Pink-G	0.764 (0.001)	93.49%	Per3-Chum-G: Insects, Harpacticoids, Gammarid amphipods Per3-Pink-G: Nauplii, Calanoid <2.5
2003	Per3-Chum-H	Per3-Pink-H	0.508 (0.001)	83.45%	Per3-Chum-H: Insects, Decapod Zoea, Harpacticoids, Per3-Pink-H Calanoid <2.5, Decapod Zoea, Nauplii
2003	Per3-Chum-K	Per3-Chum-G	0.394 (0.001)	86.80%	Per3-Chum-K: Decapod Zoea, Polychaete Larvae, Calanoid All Per3-Chum-G: Insects, Harpacticoids, Gammarid Amphipods
2006	Per1-Pink-D	Per1-Chum-D	0.745 (0.007)	85.39%	Per1-Pink-D Calanoid <2.5 Per1-Chum-D: Insects
2006	Per3-Pink-D	Per3-Chum-D	0.306 (0.001)	75.31%	Per3-Pink-D Calanoid <2.5, Cyprids, Harpacticoids Per3-Chum-D: Insects, Gammarids, Harpacticoids, Cyprids

2006	Per3-Pink-I	Per3-Chum-I	0.630 (0.008)	64.89%	Per3-Pink-I: Harpacticoids, Calanoid >2.5, Insects Per3-Chum-I: Insects, Calanoid >2.5, Fish Larvae
2006	Per3-Pink-H	Per3-Pink-D	0.439 (0.001)	81.09%	Per3-Pink-H Insects, Euphausid Larvae, Calanoid >2.5 Per3-Pink-D Calanoid <2.5, Cyprids, Harpacticoids
2006	Per3-Pink-I	Per3-Pink-D	0.323 (0.008)	76.41%	Per3-Pink-I: Harpacticoids, Calanoid >2.5, Insects Per3-Pink-D Calanoid <2.5, Cyprids, Harpacticoids
2006	Per3-Pink-G	Per3-Pink-D	0.309 (0.001)	78.22%	Per3-Pink-G: Calanoid All Sizes, Harpacticoids, Insects Per3-Pink-D Calanoid <2.5, Cyprids, Harpacticoids
2006	Per3-Pink-F	Per3-Pink-D	0.266 (0.001)	77.06%	Per3-Pink-F Calanoid <2.5, Cyprids, Harpacticoids Per3-Pink-D Calanoid <2.5, Cyprids, Harpacticoids
2006	Per4-Chum-E	Per4-Chum-H	0.346 (0.001)	75.15%	Per4-Chum-E: Insects, Harpacticoids Per4-Chum-H: Insects, Calanoid >2.5, Fish Larvae
2006	Per4-Pink-E	Per4-Pink-H	0.674 (0.001)	82.42%	Per4-Pink-E: Harpacticoids, Insects, Cyprids, Nauplii Per4-Pink-H: Calanoid >2.5, Cyprids, Decadpod Zoea, Fish Larvae
2006	Per4-Pink-E	Per4-Pink-G	0.903 (0.002)	80.39%	Per4-Pink-E: Harpacticoids, Insects, Cyprids, Nauplii Per4-Pink-G: Calanoid >2.5, Fish Larvae, Insects

Table 2.16 Period3-GH prey abundance ANOSIM comparisons between salmon fork length categories 1-6. Results in bold suggest a diet difference.

Period 3-G,H	Fork length categories	ANOSIM R (p)
2003 Pink	1,5	-0.417 (0.900)
2003 Pink	2,1	0.054 (0.270)
2003 Pink	2,3	-0.008 (0.482)
2006 Pink	2,3	-0.138 (0.750)
2006 Pink	2,4	-0.057 (0.615)
2006 Chum	2,4	0.055 (0.282)
2003 Chum	2,5	0.455 (0.250)
2003 Pink	2,5	-0.159 (0.906)
2006 Pink	2,5	0.534 (0.005)
2003 Chum	2,6	0.471 (0.250)
2006 Pink	2,6	0.220 (0.111)
2003 Pink	3,1	0.043 (0.350)
2003 Chum	3,2	0.062 (0.116)
2006 Chum	3,2	0.116 (0.049)
2006 Pink	3,4	-0.053 (0.594)
2006 Chum	3,4	-0.169 (0.850)
2003 Chum	3,5	0.557 (0.083)
2003 Pink	3,5	-0.211 (0.800)
2006 Pink	3,5	0.438 (0.025)
2006 Chum	3,5	-0.094 (0.607)
2003 Chum	3,6	0.650 (0.083)
2006 Pink	3,6	0.113 (0.286)
2003 Pink	4,1	0.080 (0.298)
2003 Chum	4,2	0.312 (0.020)
2003 Pink	4,2	-0.06 (0.714)
2003 Chum	4,3	0.211 (0.033)
2003 Pink	4,3	-0.119 (0.843)
2003 Chum	4,5	-0.211 (0.857)
2003 Pink	4,5	-0.177 (0.750)
2003 Chum	4,6	-0.211 (1.00)
2003 Pink	4,6	0.333 (0.143)
2006 Chum	5,2	0.093 (0.255)
2006 Pink	5,4	0.100 (0.142)
2006 Chum	5,4	0.128 (0.268)
2006 Pink	5,6	0.117 (0.203)
2003 Pink	6,1	0.00 (0.500)
2003 Pink	6,2	0.331 (0.087)
2003 Pink	6,3	0.108 (0.286)
2006 Pink	6,4	-0.036 (0.550)
2003 Pink	6,5	1.00 (0.333)

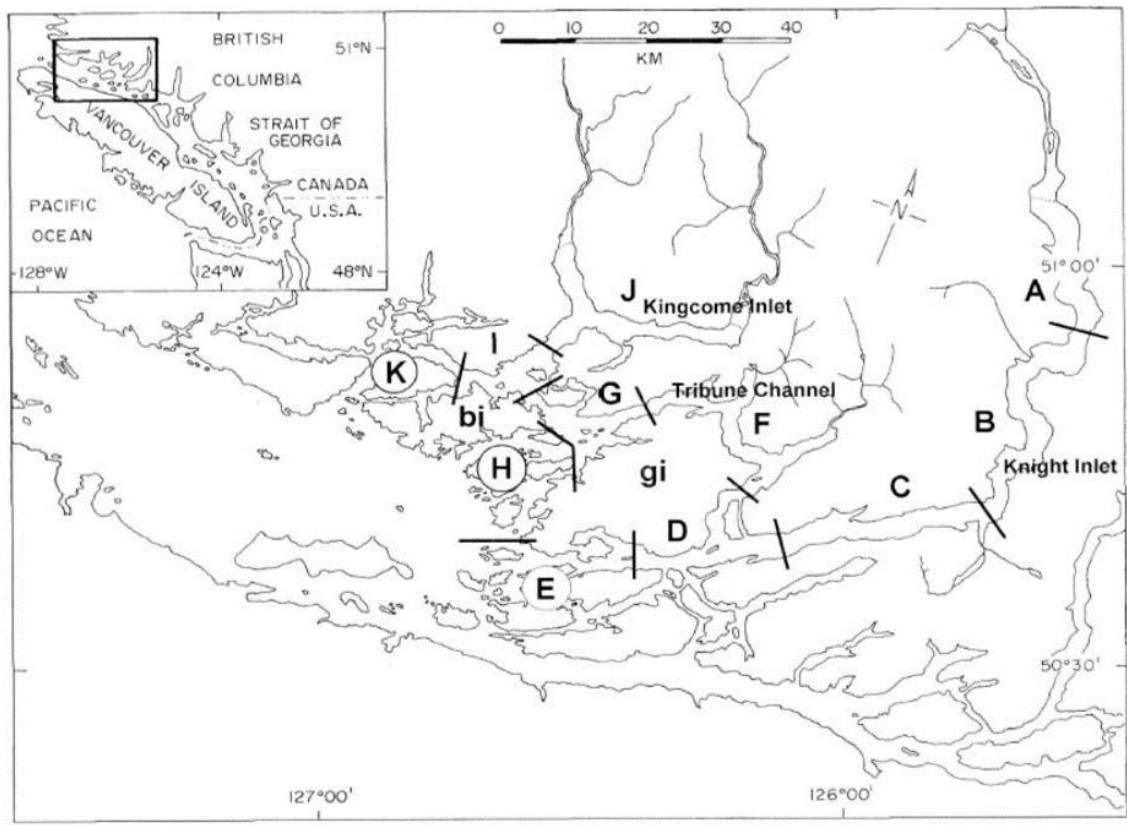


Figure 2.1 Beach seine sample zones (letters A to K) of Fisheries and Oceans Canada juvenile salmon sea-lice infection monitoring program in the Broughton Archipelago. With permission from Jones and Hargreaves, 2007.



Figure 2.2 2003 salmon stomach analysis collection locations. Beach seine collection information associated with labelled collection site numbers 1-26 is provided in Table 2.1.

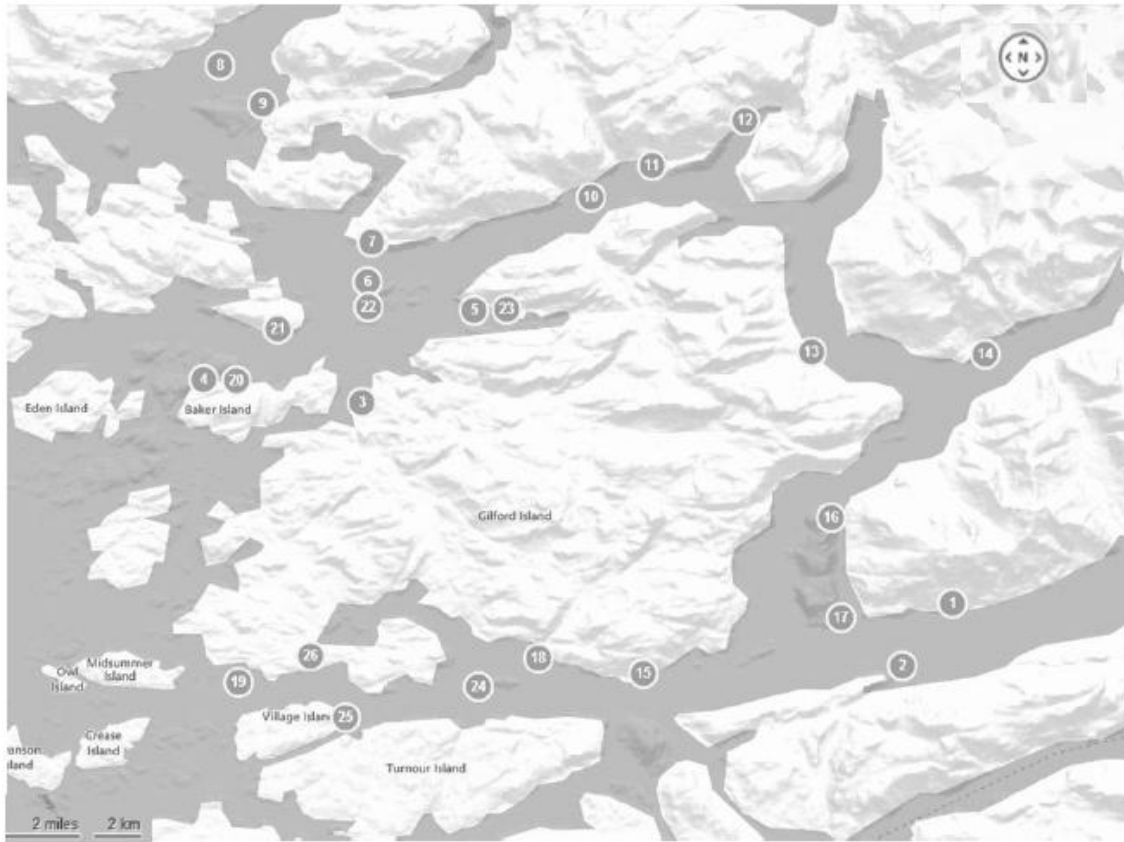


Figure 2.3 2006 salmon stomach analysis collection locations. Beach seine collection information associated with labelled collection site numbers 1-26 is provided in Table 2.2.

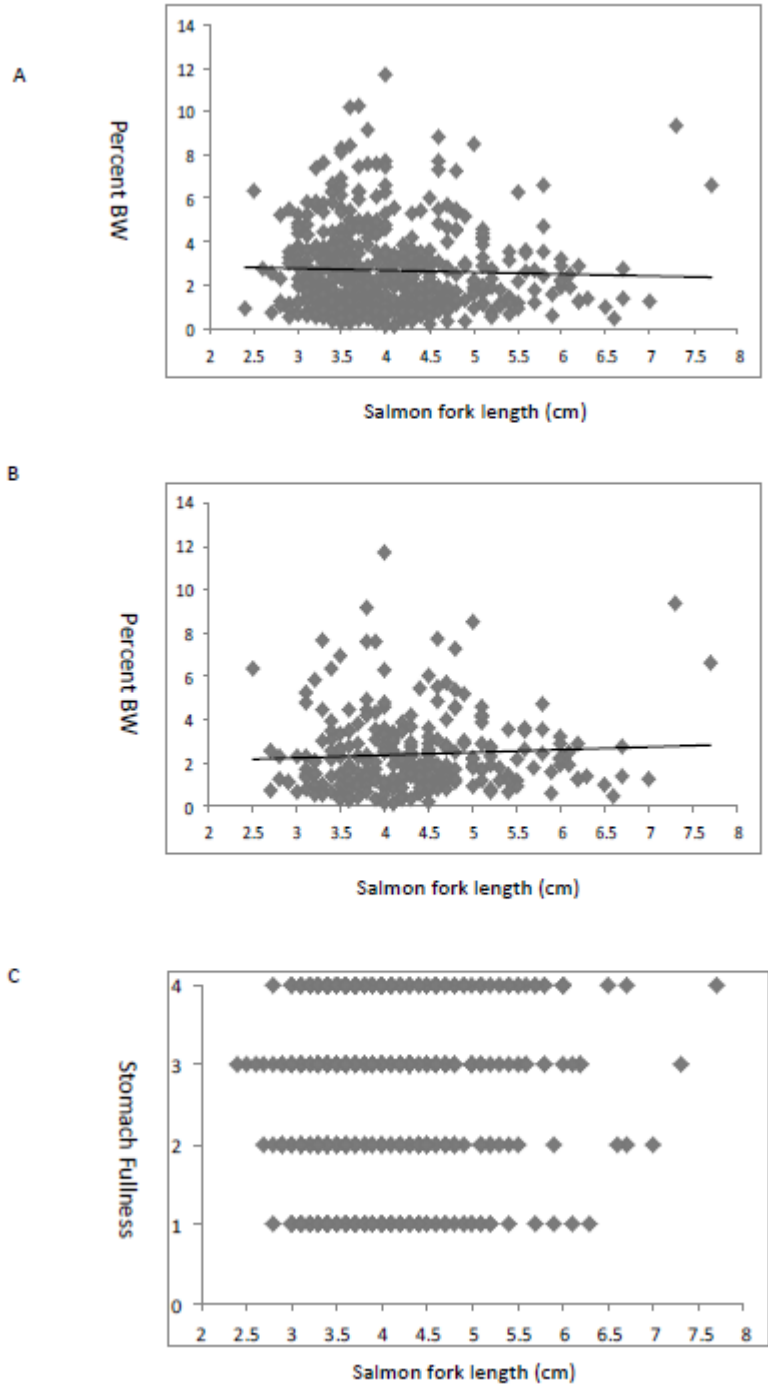


Figure 2.4 Scatterplots demonstrating a lack of relationship between salmon fork length and amount of prey eaten. A) %BW versus fork length in all 2003 salmon, B) %BW versus fork length in all 2006 salmon, and C) Volumetric stomach fullness ranking (1-4) versus salmon fork length for all 2003 and 2006 salmon with prey in their stomachs.

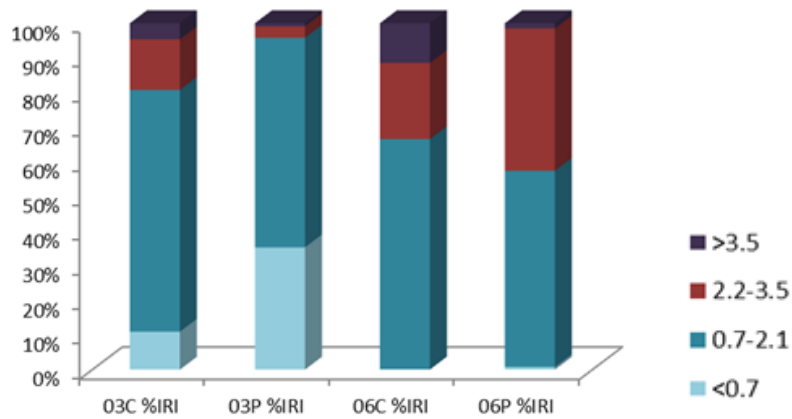
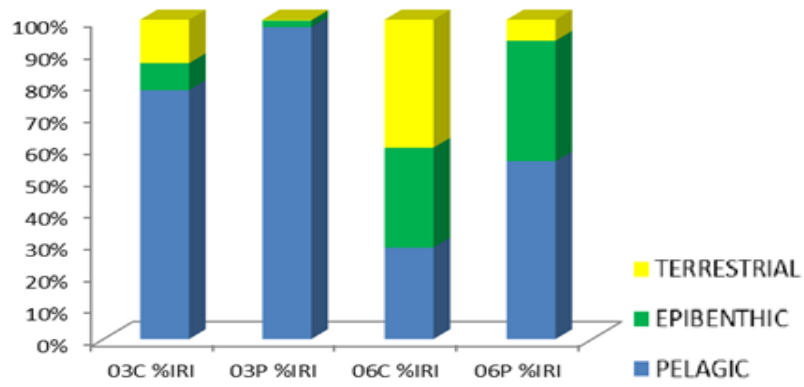
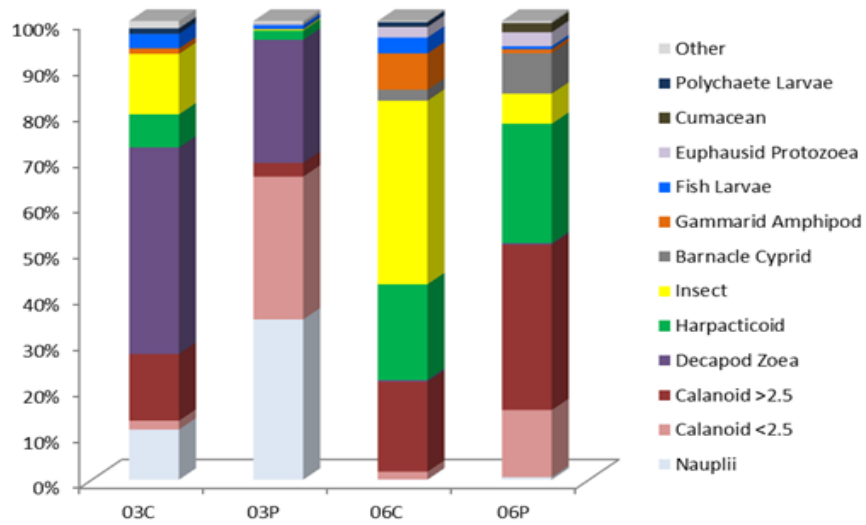


Figure 2.5 Mean relative percent IRI for year-species salmon groups based on taxonomic identification of prey (top), prey community (middle) and size category of prey (bottom). 03: 2003, 06: 2006, P: Pink, C: Chum.

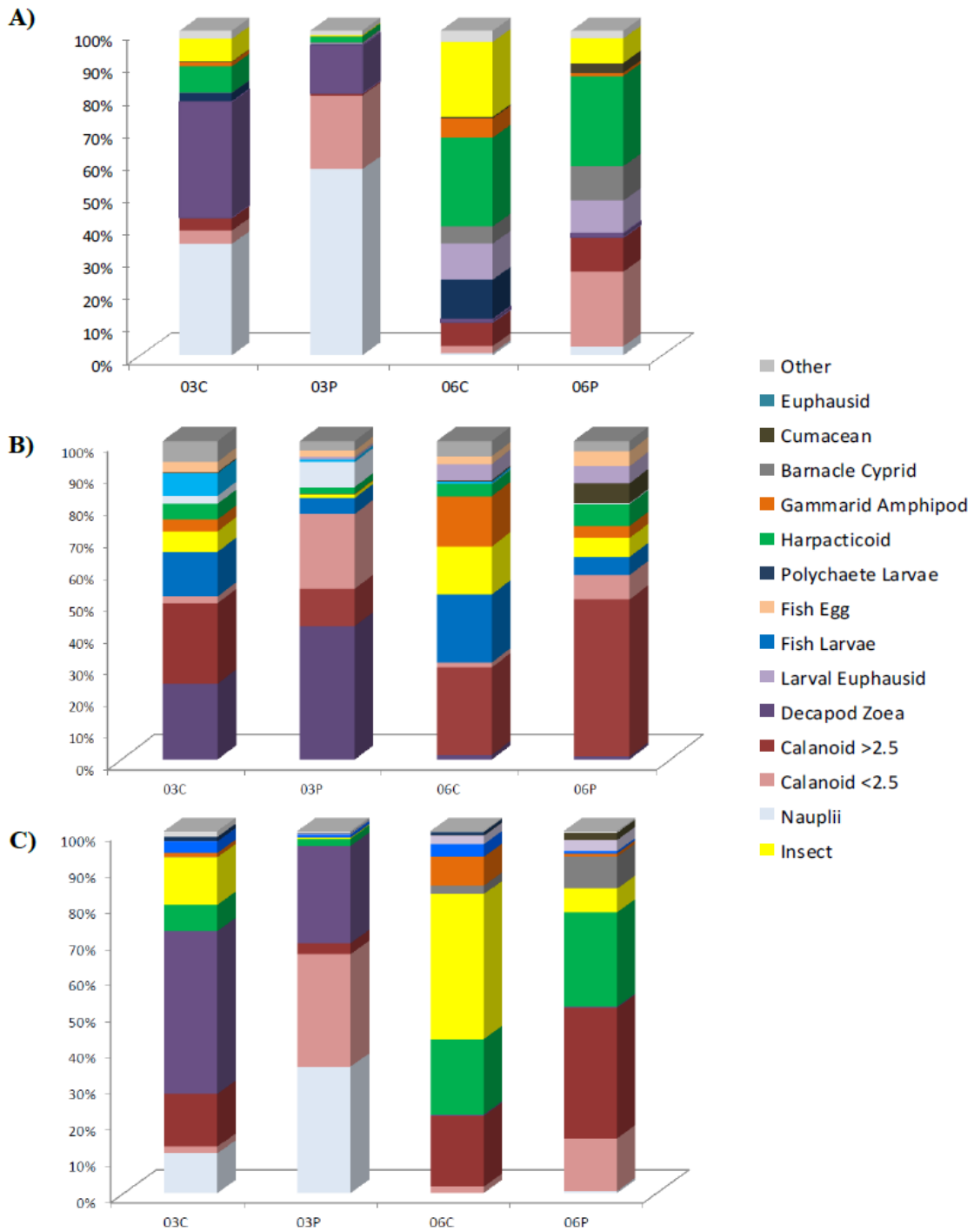


Figure 2.6 Diet composition of year-species salmon groups by A) relative mean abundance, B) relative mean volume, and C) percent IRI. 03: 2003, 06: 2006, P: Pink, C: Chum.

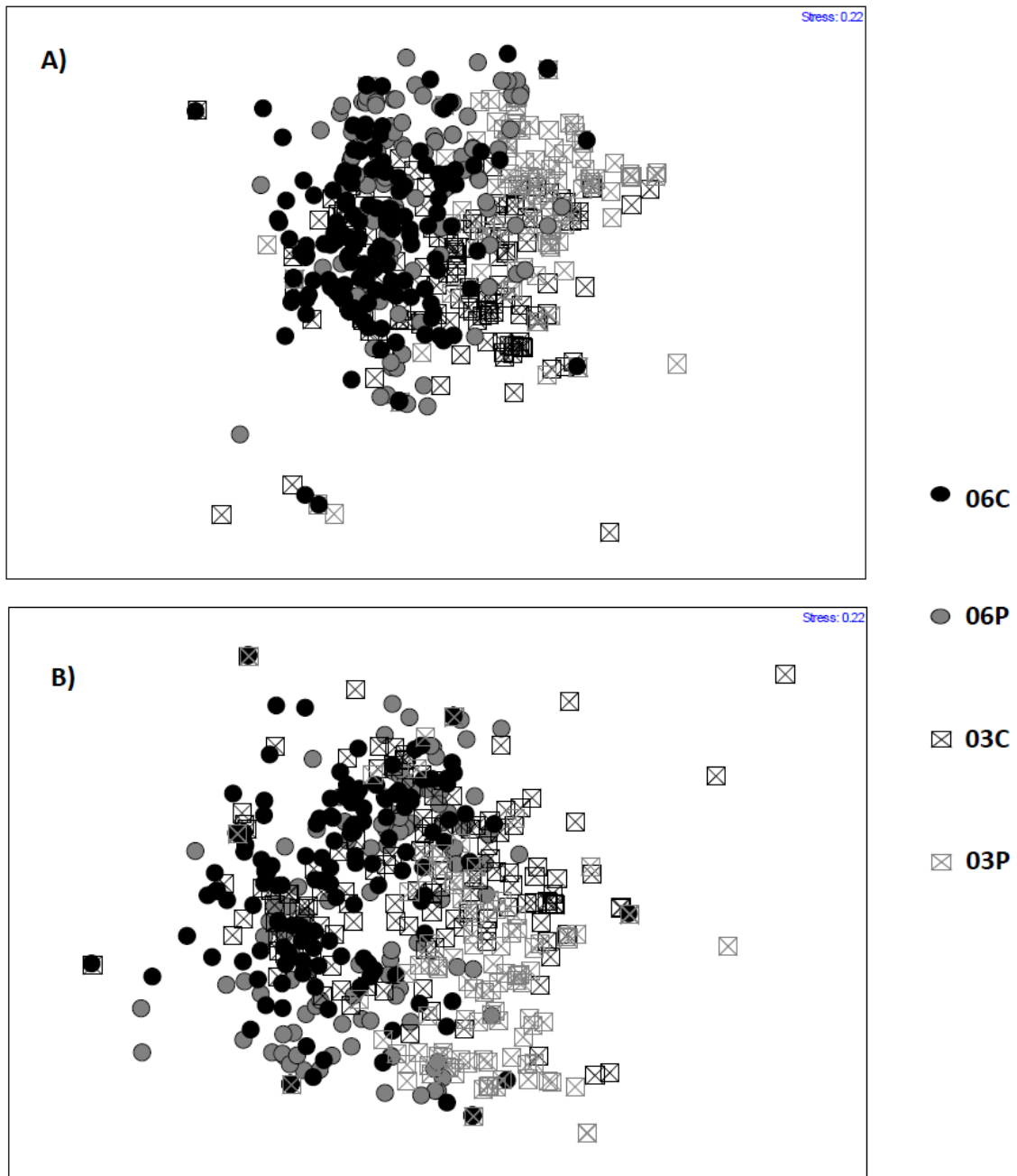


Figure 2.7 The nMDS plots for all 2003 and 2006 pink salmon with prey classified by taxonomic category for A) relative prey abundance and B) relative prey volume. Stress value: 0.22. Plot icon labels: 06C-2006 chum, 06P-2006 pink, 03C-2003 chum and 03P-2003 pink.

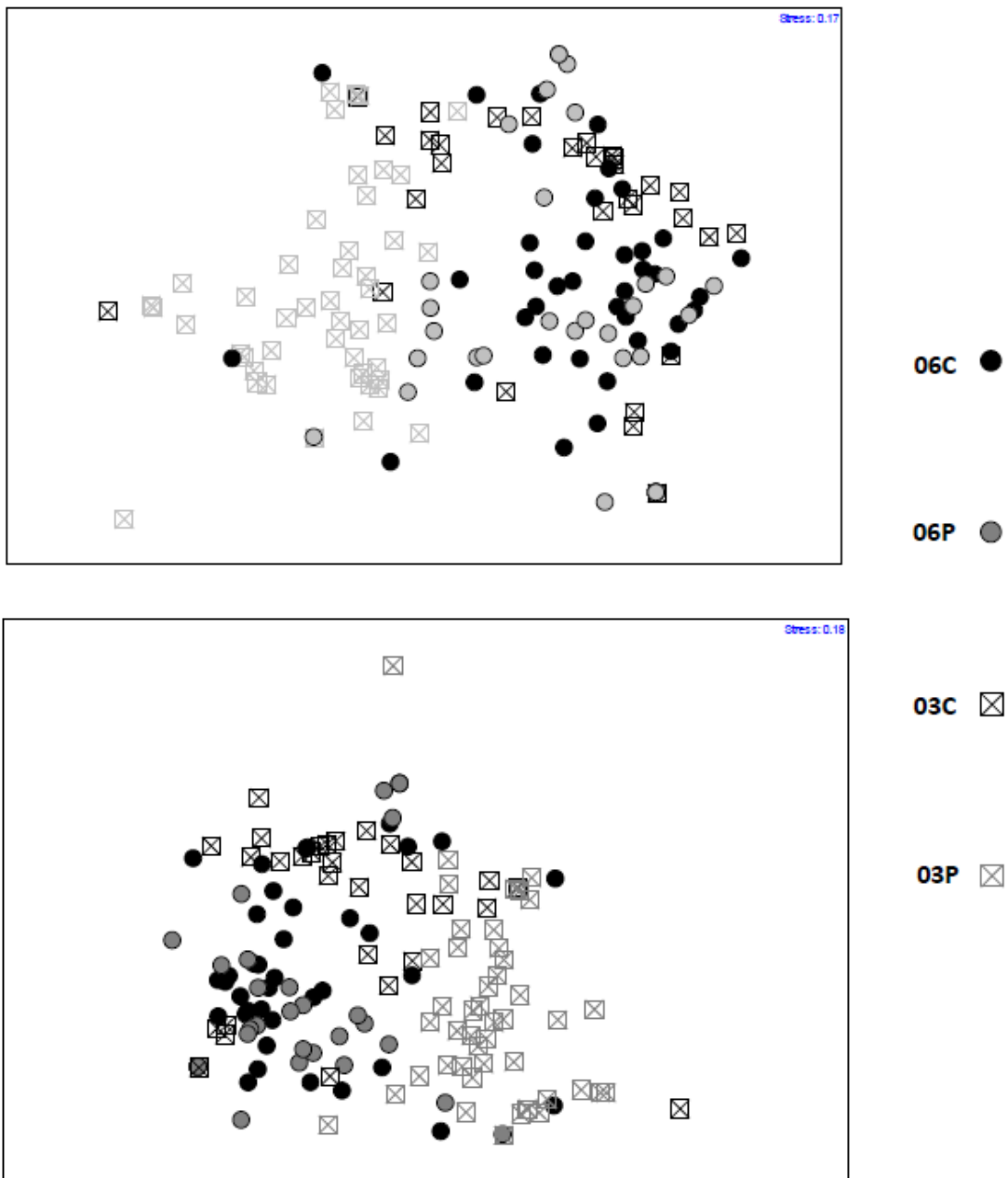


Figure 2.8 The nMDS plots for taxonomic prey comparison of period three zone G and H pink and chum salmon by relative abundance (top: stress 0.17) and relative volume (bottom: stress 0.18). Plot icon labels: 06C-2006 Chum, 06P-2006 Pink, 03C-2003 Chum, 03P-2003 Pink.

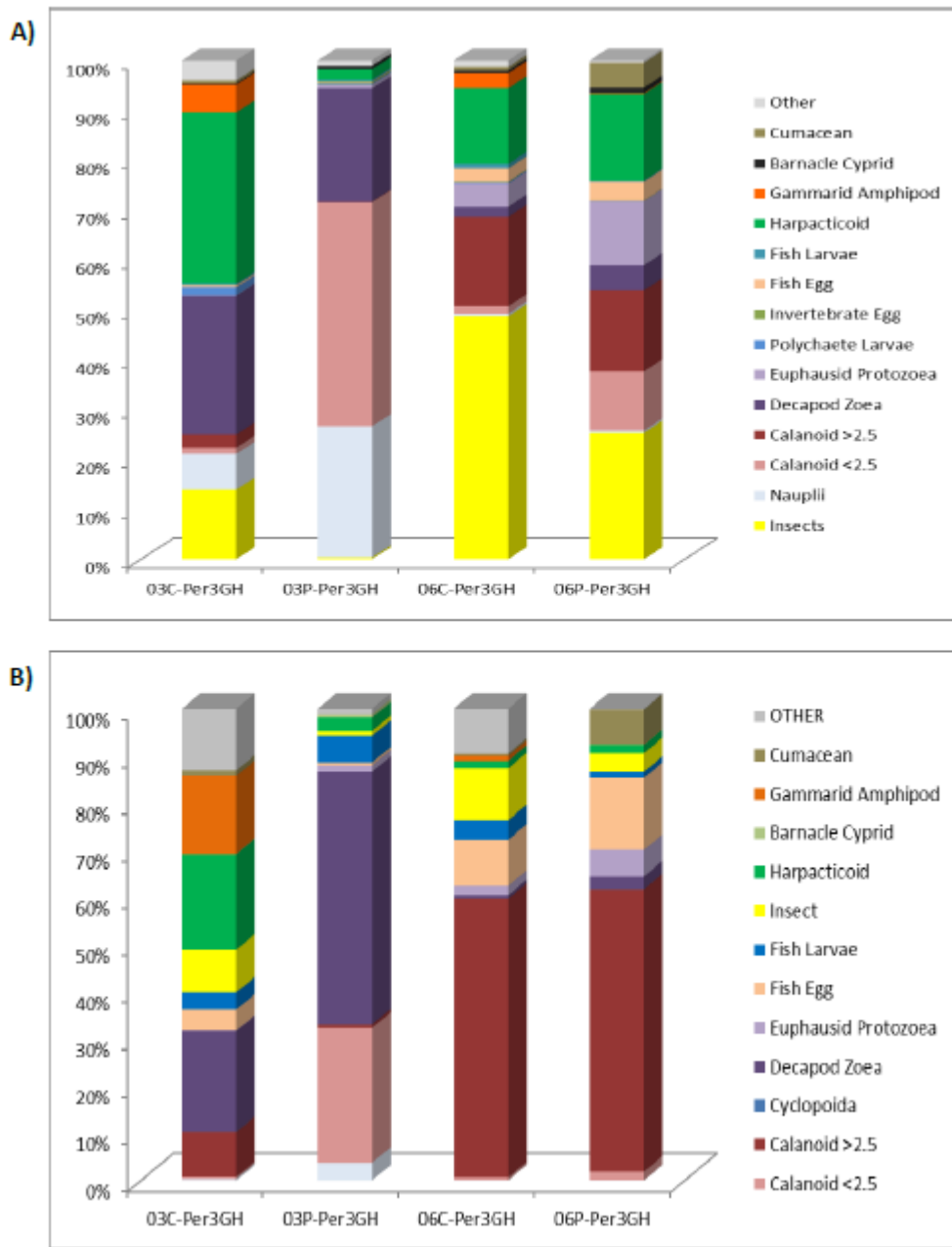


Figure 2.9 Relative composition of taxonomic prey by A) mean abundance and B) mean volume for all pink and chum salmon in collection period three, zone G and H.

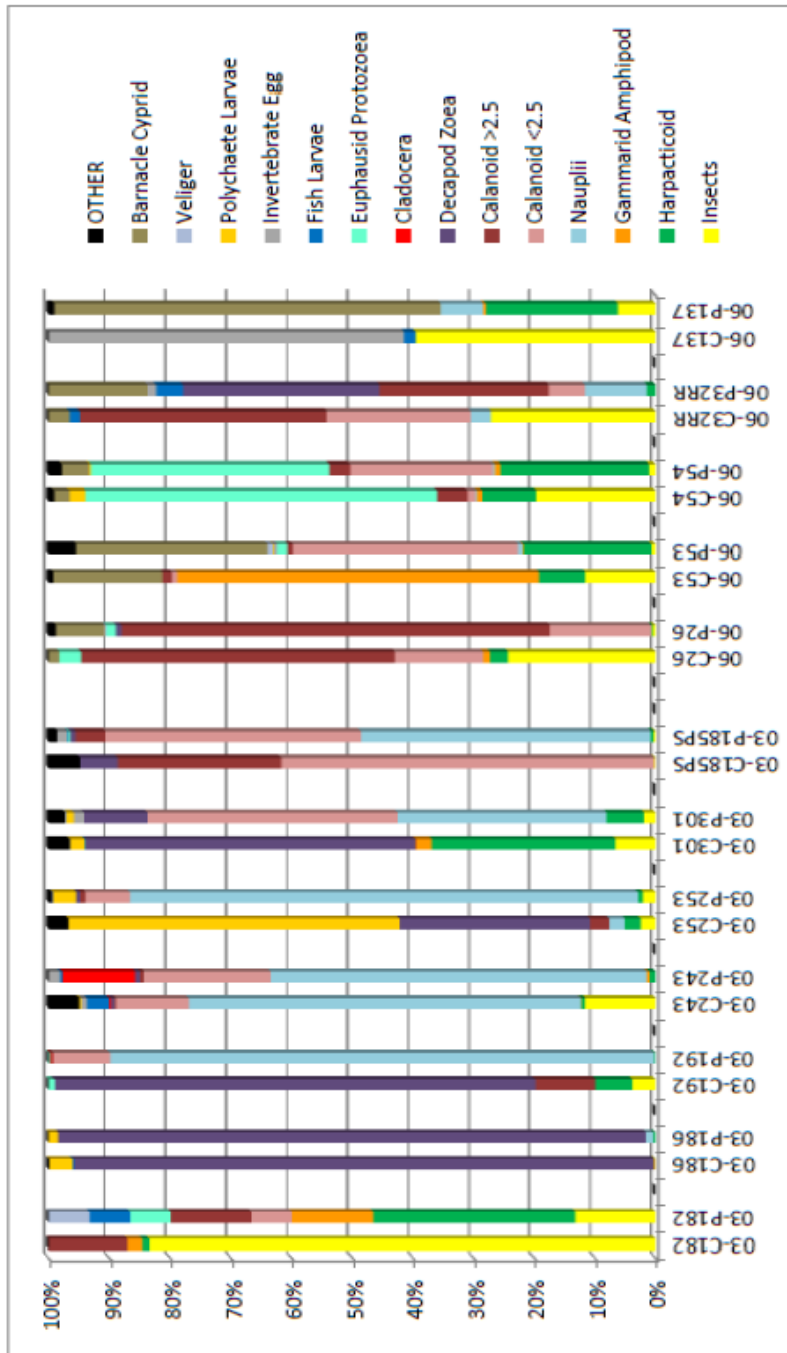


Figure 2.10 Mean relative abundance of taxonomic prey for collection sets containing pink and chum salmon in which ANOSIM suggested a difference ($R > 0.25$ $p < 0.05$) in diet composition.

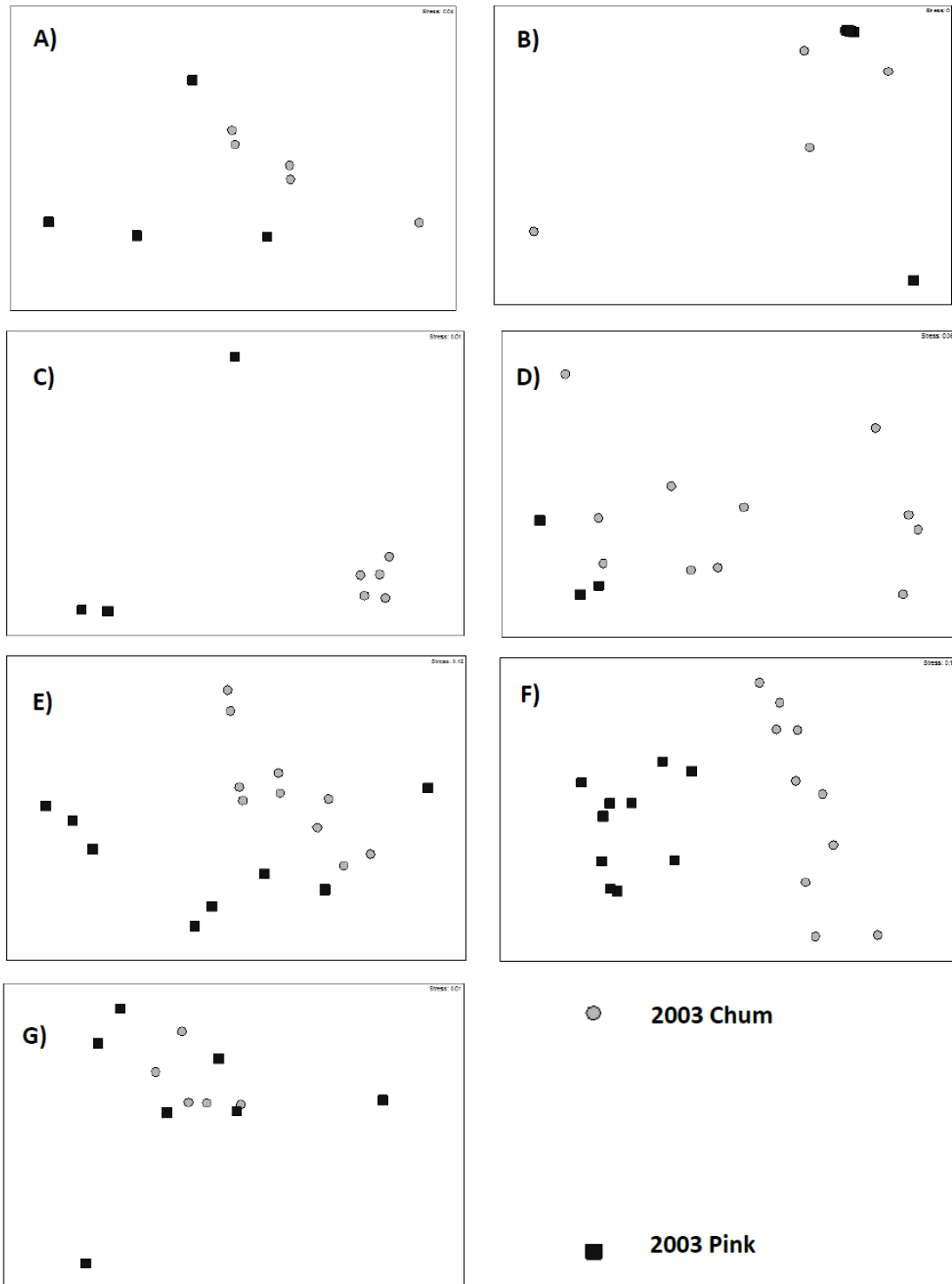


Figure 2.11 The nMDS plots of 2003 pink-chum sets with ANOSIM $R > 0.25$ $p < 0.05$ for relative abundance of taxonomic prey. Set identification for plots A to G: A) WRPS-185 B) WRBS-186 C) WRBS-192 D) WRBS-243 E) WRBS-253 F) WRBS-301 G) WRBS-182. Stress ≤ 0.15 .

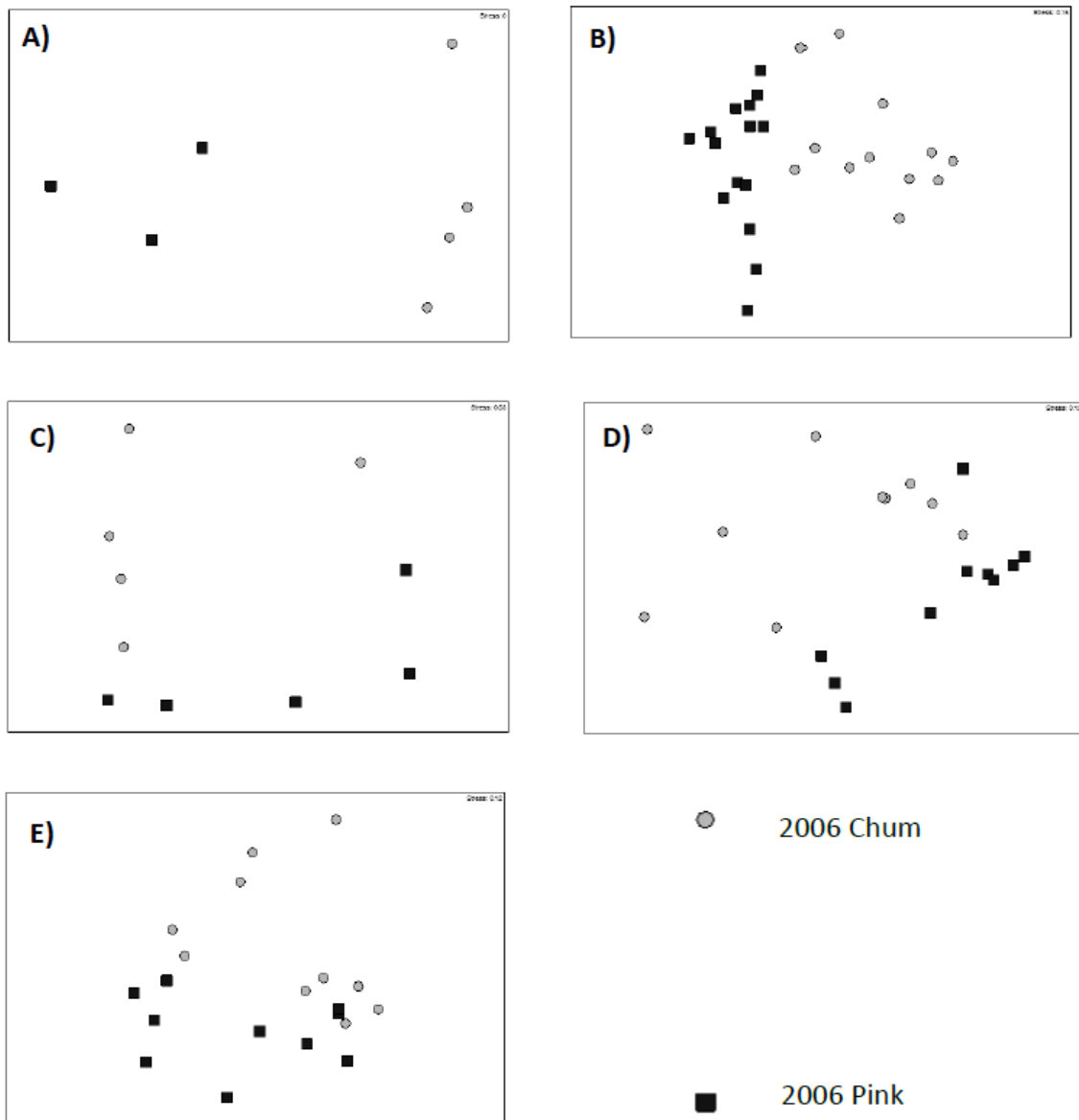


Figure 2.12 The nMDS plots of 2006 pink-chum sets with ANOSIM $R > 0.25$ $p < 0.05$ for relative abundance of taxonomic prey. Set identification for plots A-E: A) WRBS-137 B) WRBS-53 C) RRBS-32 D) WRBS-26 E) WRBS-54. Stress ≤ 0.15 .

Chapter 3.

Selective feeding by pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon in the Broughton Archipelago, BC.

3.1. Introduction

Energy from plankton prey consumed during early ocean life allows for rapid growth, decreased size-dependent predation risk, enhanced marine survival and ultimately, high adult returns in Pacific salmon (Beamish & Mahnken, 2001; Chittenden et al., 2010; Parker, 1971; Zavolokin & Strezhneva, 2014). Competition for planktonic prey resources fluctuates with marine productivity levels and with salmon population size (Bailey, Wing, & Mattson, 1975; Mortenson et al., 2000; Orsi et al., 2005). When hungry predators overlap in space and time with an abundance of prey resources, competition for food is expected to be low and predator stomachs are expected to be full. Loss of synchronization in the appearance of juvenile predators and vital seasonal prey is discussed formally in Cushing's "Match/Mismatch" Hypothesis (Cushing, 1990). Trophic mismatch in combination with competition for limited prey resources during a critical period of resource need results in a decline in predator survival and recruitment (Chittenden et al., 2010; Pyper et al., 2001; Saito et al., 2009; Taylor et al., 2002). Neither juvenile salmon feeding nor the availability of plankton prey have been characterized for the Broughton Archipelago region of British Columbia. An understanding of prey availability for juvenile salmon is vital in determining if prey limitations exist during the critical period of early marine life and, if present, if such limitations vary annually.

The goals of this chapter are:

- 1) to characterize juvenile salmon prey availability via taxonomic identification of zooplankton collected in nearshore plankton tows of the Broughton Archipelago in 2003 and 2006,
- 2) to investigate species-specific salmon feeding habits in terms of prey selectivity between collection years.

3.2. Methods

3.2.1. Field sampling: zooplankton collection

Zooplankton samples were collected by Fisheries and Oceans Canada in 2003 and 2006 in an effort to capture and map the distribution of infective planktonic stages of parasitic sea lice in the Broughton Archipelago. In both years, zooplankton samples collected within the same zone and within ten days of salmon collection were selected for an analysis of zooplankton community structure in the Broughton Archipelago. Zooplankton collection zones varied between years (Table 3.1, Figures 3.1 and 3.2). Sampling methodology also varied between years. In 2003, horizontal plankton tows were conducted using a 100µm mesh net. During each horizontal tow, the net was allowed to fluctuate up and down within a 0-5m depth range. A flow meter was attached to the mouth of the net to allow for calculation of volume of water filtered during each tow. In 2006, a flow metered net with 202µm mesh was used in the collection of all zooplankton samples. Horizontal tows were allowed to fluctuate up and down within either a 0 to 5m or 5 to 15m depth range. In both years, samples were preserved in 4% paraformaldehyde (PFA) by volume in seawater.

3.2.2. Taxonomic identification of zooplankton samples

Working in a fumehood, each zooplankton sample was poured over a series of sieves (1mm diameter mesh sieve stacked on top of an 85µm mesh sieve) to separate large mesozooplankton (retained by the 1mm mesh sieve) from highly abundant small

mesozooplankton (retained by the 85um mesh sieve). After rinsing all organisms with distilled water to remove PFA, all mesozooplankton captured on the 1mm sieve were counted and identified using a dissecting microscope. A Folsom Plankton Splitter was used to split the remaining sample captured on the 85um sieve into a sub-sample containing 400 to 500 individuals. Within this split, organisms were identified to the same taxonomic levels used for salmon prey identification (Chapter 2). An estimate of the total abundance within the split sub-sample was then converted to an estimate of abundance within the entire sample based on the split ratio. To allow for comparison of tows of different filtered volumes, tows were standardized to number of zooplankters per liter of filtered seawater by dividing the estimated total abundance of animals in the entire sample by the volume of water filtered during the tow (in liters).

3.2.3. Statistical analysis

Relative densities (number of plankters per liter) of zooplankton prey from each plankton tow were combined and mean proportional density of zooplankton prey for each collection year was calculated. Frequency of occurrence of zooplankton prey among individual plankton samples was determined for each collection year.

Multi-variate PRIMER-E methodology (Clarke & Ainsworth, 1993) was used for a limited analysis of zooplankton community composition based on square-root transformed relative density of zooplankters at the plankton tow level. Zooplankton tows were compared within and between years using nMDS ordination. Within each year, ANOSIM was used to detect differences among sets collected on different dates and in different zones ($R > 0.25$, $p < 0.05$). A SIMPER analysis was used to describe zooplankton groups accounting for mean similarity and dissimilarity between plankton tows, within collection years. Cluster analysis was used to visualize relative similarities among individual plankton sets within and between collection years.

Ivlev's Electivity Index was used to test for evidence that juvenile salmon were feeding selectively on available prey. The index is calculated as:

$$E_i = (r_i - p_i) / (r_i + p_i)$$

where r_i is the numerical proportion of the i th prey category in all salmon stomachs and p_i is the proportion of the same prey in the environment, as sampled in the plankton (Ivlev, 1961). Values for E_i range from -1 to $+1$, where $+1$ indicates high selectivity (prey present in the diet of the salmon but not detected in the plankton), 0 indicates non-selective feeding and -1 indicates low selectivity (prey item is never found in salmon stomachs but is commonly present in the plankton).

Salmon sets collected within ten days of zooplankton tows in the same collection zone were selected for feeding electivity analysis. For each salmon species, prey counts from individual salmon stomachs of all dates and zones were combined and relative proportional abundance of prey types were calculated for both 2003 and 2006. These values were used as r in the electivity analysis.

Salmon were not available for diet analysis from all zones in which plankton was collected. Only plankton sets with matching salmon predators were included in the electivity analysis. Relative prey density of individual salmon-matched plankton tows were used to calculate the average proportional density of zooplankton prey for each collection year. These values were used as p in the electivity analysis.

3.3. Results

3.3.1. Interannual comparisons of zooplankton community composition

2003 zooplankton sets, collected in zones E, G, H, I, and K were more similar (SIMPER mean similarity of 70%) than 2006 zooplankton sets collected from zones D, F, G and I (SIMPER mean similarity of 64%). In both years, plankton samples were dominated numerically by crustacean zooplankters (Table 3.2). Nauplii and calanoid copepods less than 2.5mm in length were ubiquitously present as a dominant component of plankton sets from both collection years. Despite this similarity in dominant zooplankton groups, ANOSIM revealed a difference in community composition among 2003 and 2006 samples ($R = 0.69$, $p = 0.001$). Nauplii accounted for a greater percentage of the mean SIMPER similarity detected among 2003 plankton sets with

small calanoid copepods making the greatest contribution to similarity among sets in 2006. Additional plankters accounting for mean SIMPER similarity among 2003 sets included invertebrate eggs, veliger larvae and decapod zoea. As in 2003, invertebrate eggs and decapod zoea contributed to mean SIMPER similarity among 2006 plankton sets. Barnacle cyprids and larval euphausiids were more common among 2006 plankton samples than 2003 sets, with a greater contribution to the mean SIMPER similarity in this year than in 2003.

Results of ANOSIM analysis suggest a difference in zooplankton composition between tows of select collection zones and dates in 2003 only. As both date of collection and collection zone vary when cross-comparing plankton samples, it cannot be determined which factor is responsible for the detected difference in prey composition among plankton sets (Table 3.3). The nMDS ordination plot and cluster dendograms further suggest the influence of zone and date in similarity groupings of 2003 and 2006 zooplankton collection sets, suggesting both factors may be of influence (Figures 3.3-3.6).

3.3.2. Evidence for selective feeding and avoidance of prey in pink and chum salmon

Positive selection of prey was found for large planktonic organisms relatively rare in plankton samples but common in salmon stomachs. Evidence for prey selection was found for both salmon species in both collection years (Figure 3.7). Prey for which selective feeding occurred included larval fish and fish eggs, larval euphausiids and calanoid copepods larger than 2.5mm in length.

However, not all large organisms were selected as prey. In both years cnidarian medusae and chaetognaths were present at low numerical density levels in the plankton. These large prey were not found in the stomachs of any pink and chum salmon in either collection year, suggesting avoidance of these large prey items.

For both salmon species across collection years, electivity calculations indicated positive selection for epibenthic prey such as amphipods and harpacticoid copepods.

This was also true for insects. Barnacle cyprids were positively selected in all year-species salmon groups other than 2006 chum.

In both collection years, avoidance of highly abundant small mesozooplankton prey, common in the marine environment, was detected for veliger larvae, invertebrate eggs and crustacean nauplii all of which had a negative electivity index. 2003 pink were the only year-species group to positively select for small calanoid copepods less than 2.5mm in length.

Feeding selection in 2006 pink was opposite to that of all other year-species groups for polychaete larvae, mites and cyclopoid copepods. Polychaete larvae and mites were selected against and cyclopoid copepods were selected for as prey by 2006 pink.

3.4. Discussion

Differences in zooplankton composition detected between collection years may represent interannual variability in zooplankton community composition. Alternatively, the difference may be attributed to inconsistent sampling methodology across collection years. Plankton sets collected in both years were dominated numerically by crustaceans. In 2003, plankton sets were dominated by crustacean nauplii whereas calanoid copepods less than 2.5mm in length were the dominant plankter in 2006. Barnacle cyprid larvae were present at greater numerical density levels in 2006 than 2003. These differences are potentially attributable to regional differences in plankton composition with detection a result of inconsistent zone sampling across collection years. Finer mesh used in more restrictive surface tow sampling in 2003 may account for greater collection of nauplii in this year. However, higher abundance and frequency of occurrence of nauplii in the stomachs of 2003 versus 2006 salmon is consistent with the greater numerical density of nauplii observed in 2003 plankton samples. Assuming opportunistic feeding, this finding may suggest that nauplii were more available as prey in 2003. As such, these observations may reflect between-year differences in plankton phenology, with the population of copepodids and cyprid larvae further along in larval stage development in 2006 than predecessor naupliar stages more abundant in 2003.

Representativeness of plankton tows of prey available in the marine environment to salmon should be considered when interpreting electivity scores. Ideally, zooplankton collection would occur on the same date within the same zone as salmon collection. In our analysis, salmon gut content and plankton samples collected within ten days of each other in matching collection zones were combined for electivity analysis at the year level. Number of salmon per species and number of plankton sets were variable by zone as were comparative collection dates of salmon and plankton. Such an analysis complicates the interpretation of trends in prey choice versus prey availability. It may be argued that plankton samples are not representative of prey available to salmon when the prey in their stomachs was consumed. However, ANOSIM analysis revealed that community composition was similar among all collection zones used in the electivity analysis for both collection years. The SIMPER analysis further revealed a high degree of similarity among plankton sets of different zones within a collection year. Thus, it is arguable that despite shortcomings in sampling design, zooplankton samples are representative of plankton prey present in surface waters during daylight hours of late April of 2003 and 2006 due to the homogeneity of major plankton prey groups across collection zones.

Unrepresentative sampling of epibenthic prey communities is likely with plankton tow sampling as conducted. Limited sampling of epibenthic communities results in an under estimate of epibenthic prey availability for juvenile salmon. The use of epibenthic pumps would allow for improved sampling of this prey habitat (Feller & Kaczynski, 1975). Neuston sampling would improve abundance estimates of drift organisms such as insects and other prey of terrestrial origin (Bollens et al., 2010; Landingham, Sturdevant, & Brodeur, 1998) This prey community was likely also under sampled in plankton tows as collected. Under sampling of prey availability would result in an inflated estimate of prey selection. As such, interpretation of positive selection for epibenthic and insect prey as calculated using Ivlev's electivity index should be made with caution. However, juvenile salmon preference for epibenthic prey has been reported in previous studies, including those with epibenthic sampling methodologies allowing for more reliable electivity estimates (Bollens et al., 2010; Kaczynski & Feller, 1973; Mortenson et al., 2000). Common prey items originating from epibenthic habitats included harpacticoid copepods, gammarid amphipods and barnacle cyprid larvae, as was the case in this

analysis, particularly for chum salmon (Bollens et al., 2010; Feller & Kaczynski, 1975; Godin, 1981; Kaczynski & Feller, 1973; Mortenson et al., 2000; Murphy, Thedinga, & Koski, 1987). Insects were found to be preferential prey of juvenile salmon in transitional marine environments such as estuaries (Bailey et al., 1975; Bollens et al., 2010; Duffy et al., 2010; Murphy et al., 1987). Chum salmon were found to feed with high frequency of occurrence on insects in our study in both collection years.

Electivity calculations identified preferential consumption of large, relatively rare prey such as fish larvae and larval euphausiids by both pink and chum salmon. Such prey may be under sampled in plankton tows as a result of diurnal vertical migrations from surface to deeper waters during daylight hours. Such prey may also be under-sampled because capture avoidance responses by these organisms. Juvenile salmon are likely more efficient in capturing such prey items than slow moving plankton nets. As such, the availability of active prey may be underestimated in plankton tows resulting in inflated electivity estimates. However, selection for prey with conspicuous dark eye pigmentation present in both larval euphausiids and larval fish may assist in the visual detection of such prey by foraging salmon (Bollens et al., 2010). In addition, one would expect juvenile salmon to select for large lipid rich prey when available as this would be of great energetic benefit to rapidly growing juvenile salmon (Brodeur, 1991; Kaeriyama et al., 2000; Moss & Beauchamp, 2007; Price, Glickman & Reynolds, 2013). This rationale supports the selection of such prey by foraging juvenile salmon.

In contrast, the lack of predation on cnidarian medusa and chaetognatha, two of the largest members of the zooplankton community sampled in our nearshore plankton tows, may be explained by the low energetic value of these organisms as prey. Alternatively, juvenile salmon in our study may have been gape limited in their consumption of these relatively large plankters or may have found prey distasteful due to defenses such as spines or stings. Also of consideration should be the rate of encounter. Feeding primarily in shallow, neritic waters, during their few months at sea, juvenile pink and chum salmon may not encounter these more pelagic prey at the same frequency at which more typical prey items are available. Predation on gelatinous animals such as cnidarian medusae and chaetagnatha has been reported in larger juvenile chum salmon, feeding in more pelagic waters, with the gelatinous component of chum diets increasing

during their first summer at sea (King & Beamish, 2000; Healey, 1991; Kaeriyama et al., 2000; Manzer, 1969). The more rapid digestion of gelatinous to crustacean prey may also limit the detection of jelly meals in juvenile salmon stomachs (Arai & Welch, 2003). However, this seems unlikely as not a single gelatinous prey or even remnants of this type were found in any of the over 500 salmon stomachs analyzed.

Evidence for selective feeding in juvenile salmon is not uncommon during early marine life (Beacham, 1993; Bollens et al., 2010; Brodeur, 1991; Price et al., 2013) . Improved sampling of epibenthic and neustonic environments would allow for improved prey availability estimates and an improved understanding of the degree to which selective feeding occurs in pink and chum salmon in the Broughton Archipelago. Future work on prey energetics will shed insight into prey choice from an energy perspective.

3.5. References

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3.6. Tables and Figures

Table 3.1 Zooplankton collection information: set identification (Set ID), collection location and zone, collection date and tow depth. Sets in bold were included in the electivity analysis.

Collection Location	Zone	Date	Set ID	Tow Depth (m)
Midsummer Island	E	29/04/2003	2003-3	6.0-4
			2003-4	3.3-0
Maple Bay	E		2003-9	4.5-2
			2003-10	15.3-13.3
South of Gilford	E	30/04/2003	2003-15	4.0-2
			2003-16	8.9-6.9
South of Midsummer Island	E		2003-17	6.0-4
			2003-18	9.6-7.6
Bonwick Island	H		2003-24	6.4-2.4
			2003-25	8.9-4.9
Baker Island	H		2003-27	10.7-6.7
			2003-28	7.1-3.1
Wehlls	K	01/05/2003	2003-31	6.1-2.1
			2003-32	9.9-5.9
Greenway Sound	I		2003-34	9.5-5.5
Wishart Peninsula	G		2003-37	6.9-2.9
			2003-38	10.2-6.2
Gormerly Point	F	25/04/2006	GPN1-06	0-3
			GPN3-06	0-3
			GPN4-06	0-3
Burdwood Islands	G	26/04/2006	BWG2-06	0-2
Viscount Island	D		VIN2-06	0-3
Burwood Islands-Farm Site	G		BWF1-06	0-3
			BWF2-06	0-3
			BWF3-06	0-1
		27/04/2006	BWN1-06	0-3
			BWN2-06	0-1
			VSN1-06	0-3
Viner Sound	G		VSN2-06	0-3
			VSN3-06	0-3
			HPN1-06	0-3
Hayes Point	G-I	27/04/2006	HPN2-06	0-3
			HPN3-06	0-3

Table 3.2 Percent mean abundance of combined zooplankton samples and salmon stomach contents, by collection year. The number of plankton tows or salmon stomachs analyzed (n) and zone of collection are provided.

	n=17 E,G,H,I,K	n=15 D,F,G,I	n=49 G,H,K	n=71 G,H,K	n=107 D,F,G,I	n=96 D,F,G,I
	2003 Plankton	2006 Plankton	2003 Chum	2003 Pink	2006 Chum	2006 Pink
Nauplii	50.5	22.9	11	36.2	0.2	1.4
Calanoida <2.5	38.3	52.6	8.4	40	2.3	30.2
Decapod Zoea	0.9	0.8	23.8	16.4	0.7	1.3
Harpacticoida	0	0.2	27	2.3	35.3	25
Invertebrate Eggs	6.1	1.8	0	0.8	0.1	0.2
Calanoida >2.5	0	1.1	5.4	0.8	9.4	10.4
Euphausid Larvae	0	1.7	0.1	0.6	17.4	12.2
Insects	0	0.2	11.2	0.5	21.9	4.5
Barnacle Cyprid	0	6.2	0.2	0.5	3.1	10.4
Amphipoda	0	0	4.5	0	7.6	0.5
Polychaete Larvae	0.5	0.3	3.5	0.4	0.8	0.1
Fish Larvae	0	0.1	0.4	0.3	0.2	0.1
Veliger Larvae	0.9	7.2	0.1	0.3	0	0.2
Fish Eggs	0	0	0.8	0.3	0.1	0.4
Larvacea	0.2	1.4	2.4	0.2	0	0
Cyclopoida	1.9	0.4	0.1	0.1	0.1	0.9
Collembolla	0	0	0.3	0	0.2	0
Mite	0	0	0.2	0	0	0
Cumacea	0	0	0.5	0	0.4	2
Other	0.7	2.9	0.2	0.2	0.1	0

Table 3.3 Results of within year ANOSIM comparisons of relative taxonomic density (number of plankters/liter) of plankton tows by collection zone and collection date. R >0.25 p<0.05 are highlighted in bold.

2003 ANOSIM Comparisons					
Zone 1	Zone 2	ANOSIM R (p)	Date 1	Date 2	ANOSIM R (p)
E	H	0.465 (0.006)	Apr-29	Apr-30	0.222 (0.083)
E	K	0.672 (0.044)	Apr-29	May-01	0.594 (0.008)
H	K	1 (0.067)	Apr-30	May-01	0.318 (0.025)
H	G	1 (0.067)			
E	I	0.652 (0.222)			
E	G	0.211 (0.244)			
H	I	1 (0.200)			
K	I	-1 (1.00)			
K	G	1 (0.333)			
I	G	1 (0.333)			

2006 ANOSIM Comparisons					
Zone 1	Zone 2	ANOSIM R (p)	Date 1	Date 2	ANOSIM R (p)
F	G	0.086 (0.305)	Apr-25	Apr-26	0.149 (0.250)
F	D	1.000 (0.250)	Apr-25	Apr-27	0.156 (0.206)
F	GI	0.889 (0.100)	Apr-26	Apr-27	0.241 (0.0320)
G	D	0.914 (0.100)			
G	GI	0.193 (0.159)			
D	GI	1.000 (0.250)			



Figure 3.1 2003 zooplankton collection locations. Zone E: 1) Midsummer Island 2) Maple Bay 3) South of Gilford Island 4) South of Midsummer. Zone H: 5) Bonwick Island 6) Baker Island. Zone K: 7) Wehli. Zone I: 8) Greenway Sound. Zone G-I: 9) Wishart Peninsula. Plankton tows from collection locations 5-7 and 9 are used in the prey electivity analysis.



Figure 3.2 2006 zooplankton collection locations. 1) Gormerly Point, Zone F. 2) Viscount Island, Zone D. 3) Burdwood Islands Group, Zone G. 4) Viner Sound, Zone G, and 5) Hayes Point, Zone I. Plankton tows from all locations are included in the prey electivity analysis.

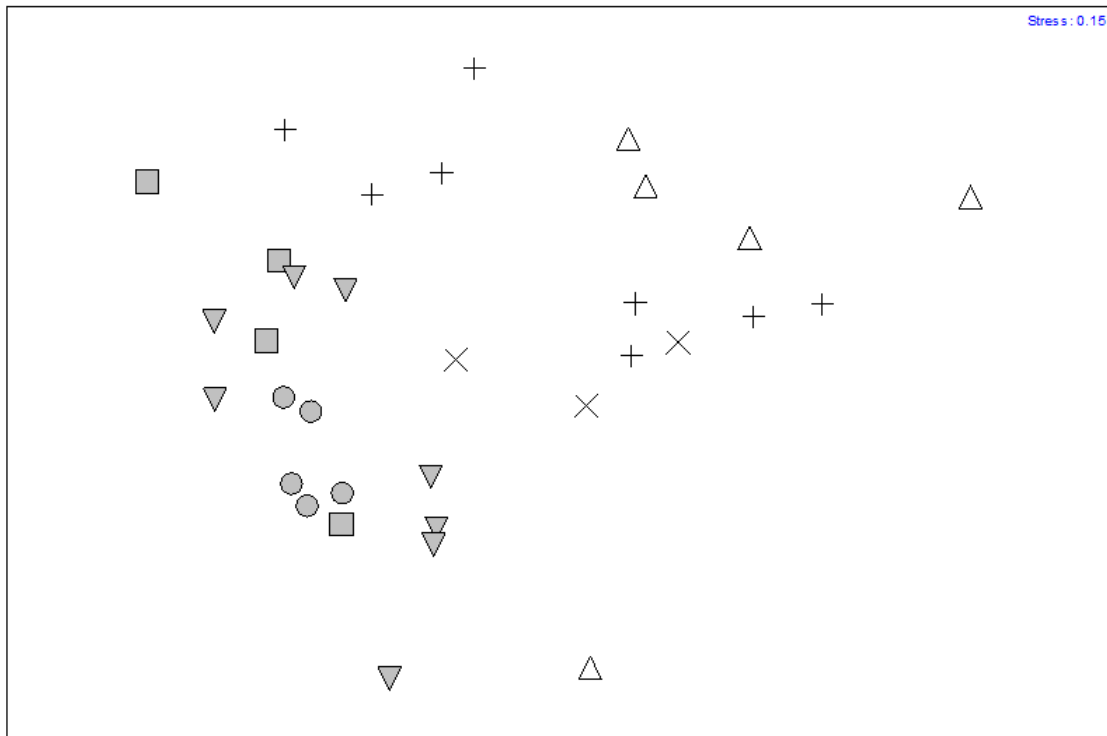


Figure 3.3 The nMDS ordination plot as based on Bray-Curtis similarity of square root transformed relative zooplankton density in 2003 and 2006 plankton tows, plotted by collection date. Stress is low at 0.15.

Markers indicate collection date. X: April 25, 2006. Open triangle: April 26, 2006. + Plus Sign: April 27, 2006. Square: April 29, 2003. Solid triangle: April 30, 2003. Circle: May 1, 2003.

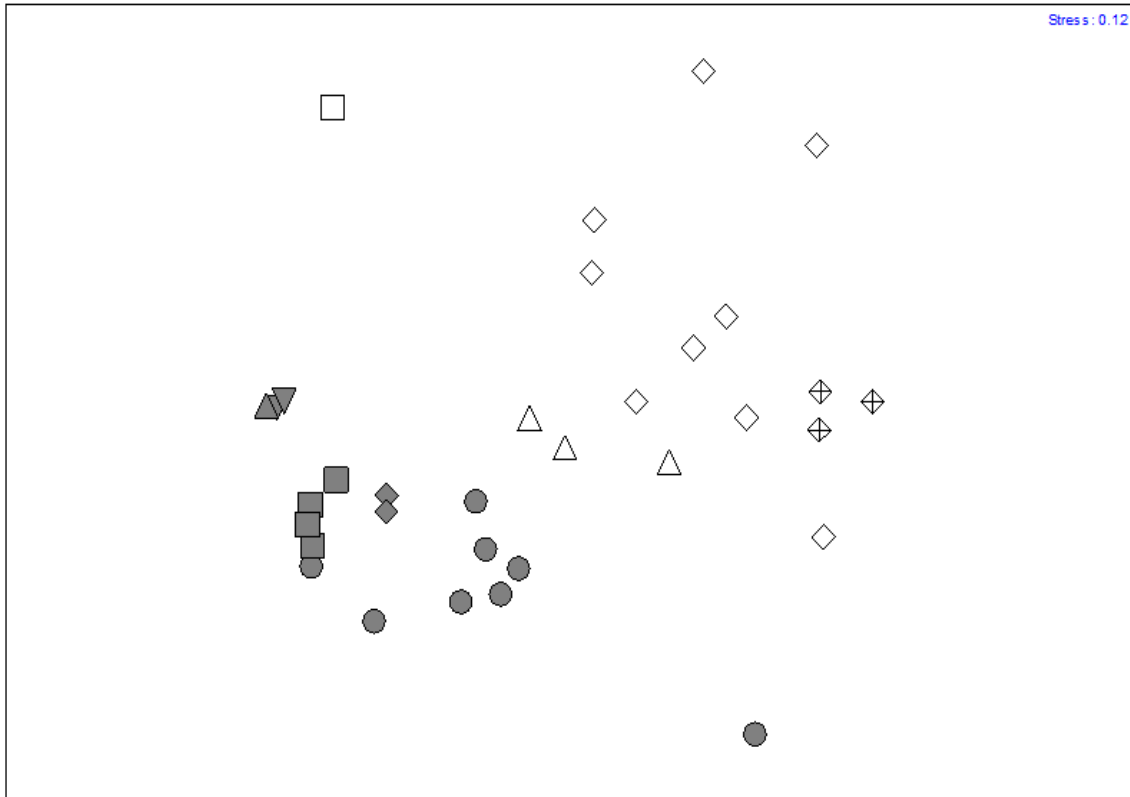


Figure 3.4 The nMDS ordination plot as based on Bray-Curtis similarity of square root transformed proportional density of taxa in 2003 and 2006 zooplankton tows, plotted by collection year and zone. Stress is low at 0.12.

Markers indicate collection year and collection zone. Shaded icons: 2003 tows. Circle: Zone E. Diamond: Zone G. Square: Zone H. Triangle: Zone I. Upside-down triangle: Zone K. Hollow icons: 2006 tows. Square: Zone D. Triangle: Zone F. Diamond: Zone G. Hatched diamond: On the border of zones G and I.

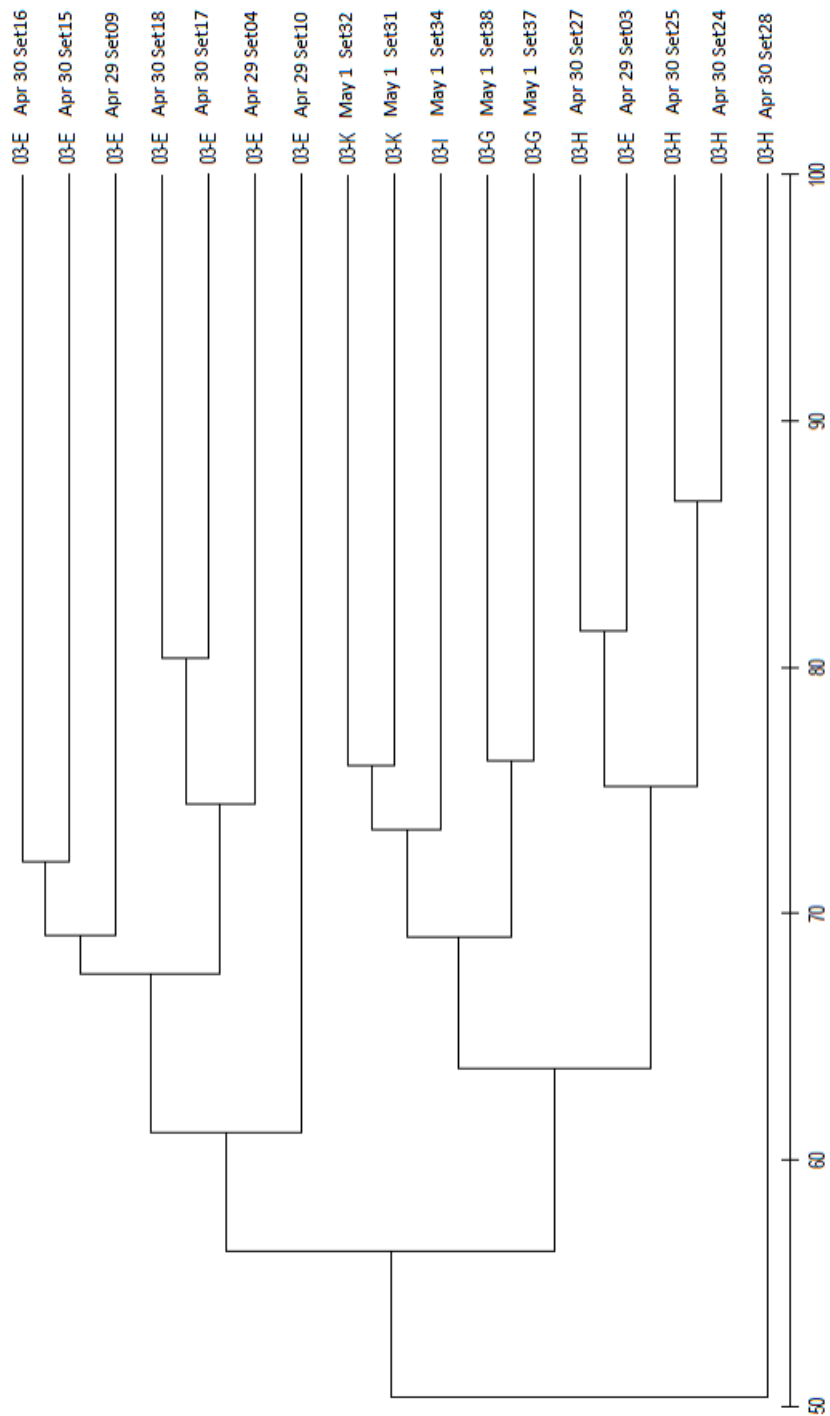


Figure 3.5 Clustering of 2003 zooplankton samples based on similarity in the proportional relative density of taxa in zooplankton tows. Collection date and collection zone appear to be important factors contributing to the similarity among zooplankton sets.

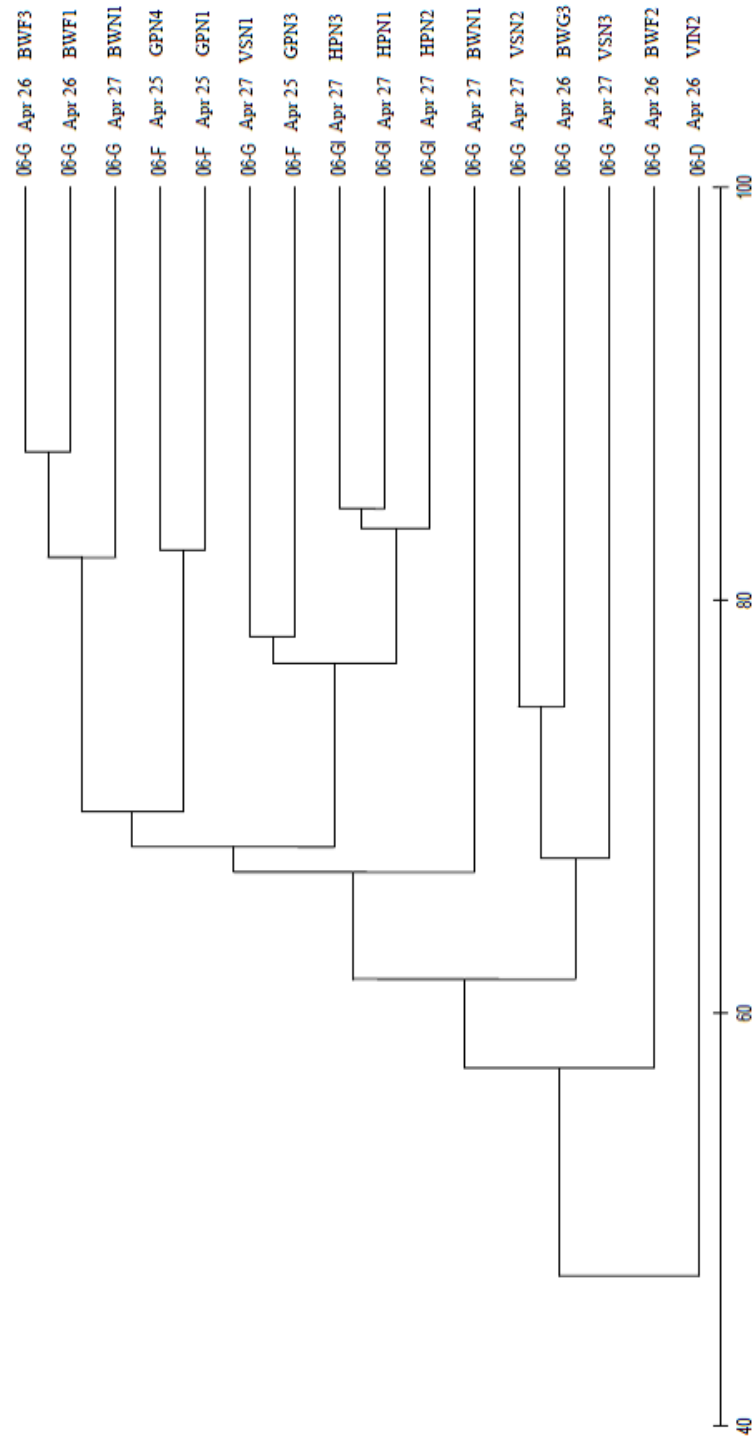


Figure 3.6 Clustering of 2006 zooplankton samples based on percent similarity in the relative density of plankton taxa in zooplankton tows. Collection date and collection zone appear to be important factors contributing to the similarity among zooplankton sets.

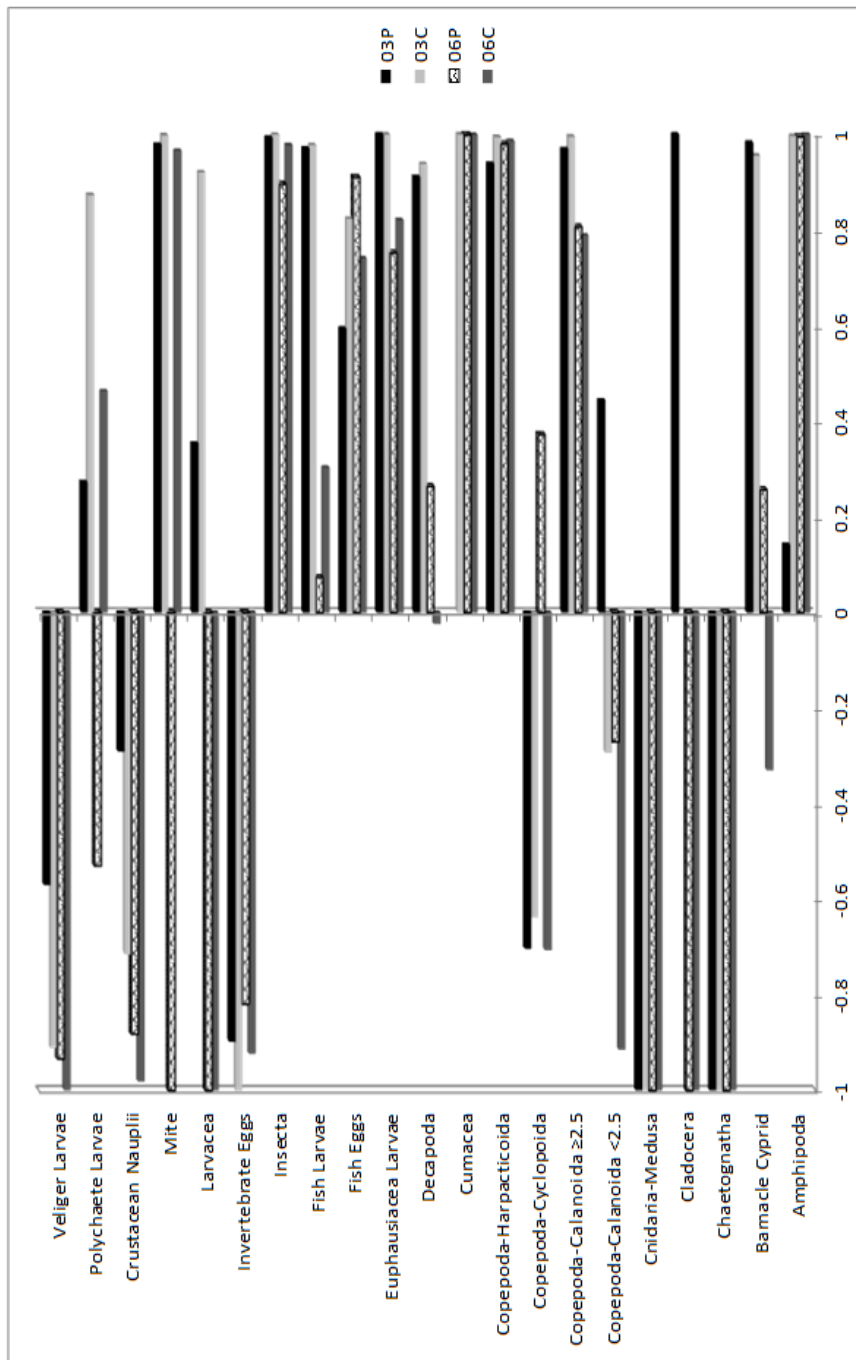


Figure 3.7 Electivity scores for primary prey species of 2003 pink, 2003 chum, 2006 pink and 2006 chum as identified in salmon stomachs collected in the same zone and within ten days of zooplankton collection.

Chapter 4.

General Discussion

The salmon and zooplankton used in this study were collected for purposes other than diet analysis (Jones & Hargreaves, 2007). Despite sampling deficiencies, the results of this analysis were biologically informative. This work provided a descriptive diet analysis of juvenile pink and chum salmon in a previously undescribed habitat region of the British Columbia coast. It allowed for an understanding of feeding trends in juvenile pink and chum in this area and how such trends compared to that of other areas of the Pacific North West. It provided insight into how feeding during early marine life of juvenile salmon may be correlated to adult return strength in the area, a relationship potentially informative on salmon population trends in the area.

Food availability during early ocean life is known to be an important determinant of juvenile salmon survival during their first year at sea, with survival during this critical period an important determinant of adult return strength (Beamish & Mahnken, 2001). Feeding conditions during early marine life and subsequent rapid marine growth may be of particular importance to pink salmon in the Broughton Archipelago, as pink salmon weighing more than 0.7g are more physiologically equipped to resist infection with sea lice than smaller salmon (Jones & Bennett, 2008). In addition to zooplankton sampling, the analysis of salmon diet during early marine life is informative of local ocean conditions during the spring of 2003 and 2006 in the Broughton Archipelago. Future work may correlate measures of feeding condition such as %BW or volumetric stomach fullness ranking recorded here with strength of adult salmon returns. This is of particular interest as pink salmon returns in the Broughton Archipelago were stronger in 2004 than 2007, adult return years corresponding to the better-fed 2003 than 2006 year of ocean pink salmon sampled in this analysis. Stomach analysis of juvenile pink and chum salmon entering the marine environment in 2007 is underway. Pink salmon returned at

below average levels to spawn in 2008, lower than the average return strength seen in 2007 and the above average levels seen in 2004 (Riddell et al., 2008). Analysis to date suggests that the amount of prey consumed was lower in 2007 than in either 2006 or 2003, a preliminary finding warranting further investigation and suggestive of a correlative link between the amount of food consumed during early ocean life and adult return strength in pink salmon populations of the Broughton Archipelago.

In both years, chum salmon had fuller stomachs than pink salmon, suggesting that they are at an advantage to pink salmon in terms of energy available for growth during their first months at sea, a finding contrary to comparative diet analyses of pink and chum salmon later life when feeding in pelagic waters (Ruggerone & Nielson, 2005; Tadokoro et al., 1996). However, prey differences were observed between pink and chum salmon in both years, suggesting a full chum stomach may not be equivalent energetically to a full pink stomach (Kaeriyama et al., 2000; Price, Glickman, & Reynolds, 2013; Volk et al., 1984). Insects were an important component of chum salmon diets, with a lesser dependence of pink salmon on this prey. In 2003, pink salmon fed on nauplii to a greater degree than seen in chum salmon. A consideration of prey energetics is of particular interest here because of differences in diet observed between closely related salmon species. Such an analysis may reveal that a stomach full of insects is superior energetically to naupliar prey, or vice versa. If so, it would be important to consider not only the extent of stomach fullness but the identity of prey when comparing diet condition between salmon species. This would assist in determining if one species is at an advantage energetically to the other during the high growth (and high energy need) early marine period of juvenile Pacific salmon (Beamish & Mahnken, 2001; Parker, 1971). Further consideration of observed selective feeding by pink and chum salmon in terms of prey energetics is recommended.

Improved sampling of prey availability in future work through the use of epibenthic bumps and neustonic sampling in addition to plankton tows would confirm the degree to which selective feeding occurs during the early ocean life of juvenile salmon in the region (Kaczynski & Feller, 1973). A better match in space and time of the collection of such samples with salmon samples would allow for an improved understanding of food availability versus and prey selectivity.

High prey variability was observed within the diets of both pink and chum salmon, suggesting a diversity of prey was available for both salmon species. Local differences in taxonomic prey composition were found via analysis at the collection zone and at the collection set level. A consideration of prey composition by community type at the collection set or zone level rather than as combined prey of salmon from all locales in a collection year may reveal local differences in prey habitat types within the archipelago (Sturdevant et al., 2011). This would be informative in identifying and protecting sites known to be profitable feeding nurseries for young salmon. However, the transient nature of seasonal planktonic prey and fluidity of drift organisms such as insects may make the pin-pointing of profitable habitats difficult in a complex environment like the Broughton Archipelago.

The Broughton Archipelago is a place of breathtaking natural beauty. The ecology and culture of the region, like many other coastal communities, is tightly linked to wild Pacific salmon survival. As salmon population strength is dependent in part on mortality during the first months at sea, and juvenile survival through this period is dependent on stomachs full of high energy prey, stomach analysis is a worthy and informative means to better understand fluctuations in salmon populations, despite its messy and somewhat tediousness nature.

4.1. References

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