

Trophic niche and foodweb dynamics within and among juvenile salmon species
in years of contrasting ocean conditions

by

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BSc, Lakehead University, 2004
HBOR, Lakehead University, 2004

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in the Department of Biology

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Abstract

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The ecological niche of a population is dynamic and will be affected by changes in the ecosystem and as a population migrates. An ontogenetic niche shift can also occur as organisms grow and can include changes in morphology, habitat, and feeding behaviour. Although they are the two most abundant salmon species, and are further augmented through hatchery stocking, it is unclear the degree to which the niches of juvenile pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) overlap. Furthermore, juvenile pink salmon and chum salmon undergo a period of rapid growth during their first summer at sea and it is unclear how their ecological niche changes with their ontogeny. Understanding the foodweb dynamics of juvenile salmon in the coastal marine environment is important because a large proportion of the overall mortality of salmon is thought to occur during their first summer at sea. The purpose of this study is to determine the degree to which the niches of juvenile pink salmon and chum salmon overlap, how their trophic position and food source changes as they grow into a new ontogenetic niche, and how these processes are affected by ocean conditions.

I expected that years of poorer feeding conditions and increased competition would result in reduced trophic position and greater overlap of the niches of juvenile pink

salmon and chum salmon. I hypothesized that juvenile salmon would shift their diet to a more offshore-based foodweb as they grew and that their trophic position would increase with size, but that the shift would be stronger when feeding conditions were improved.

Statistical analysis showed evidence that the overlap of the niches of pink salmon and chum salmon increased when the abundance of salmon was high. Contrary to expectations, the trophic position of salmon appeared to decrease under favourable conditions. The trophic position of both pink salmon and chum salmon was higher in the southern portion of the study area, and increased when juvenile abundance was high. I suggest that the higher trophic position among juvenile salmon when there is more competition might result from increased reliance on gelatinous zooplankton, which are carnivorous, but a nutritionally poor food choice compared to other common prey items.

The ontogenetic shift from summer to fall among juvenile salmon included a shift to a more offshore-based diet and a higher trophic position. In the northern portion of the study area, which was comprised of the southern reaches of the Alaska Coastal Current (ACC), the shift to an offshore-based food source was more pronounced than the trophic shift. In the southern portion of the study area, which included the Transition Domain (TD) between the ACC and the California Current System (CCS), the shift to a higher trophic position was more pronounced than the shift in food source.

The results of this study suggest that if climate change leads to poorer feeding conditions, the niches of pink salmon and chum salmon may increasingly overlap when the abundance of these species is high. Hatchery stocking of these species may also contribute to this trend if it leads to a greater abundance of juvenile salmon in the coastal marine environment. There is evidence that the structure of the food web and the nature

of the ontogenetic niche shift are very different in the ACC and the TD, and climate change and hatchery stocking will most likely affect these regions differently.

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Dedication

This thesis is dedicated to my parents, for inspiring me to take an interest in the world around me, for giving me the confidence to take on challenges, and for always being there for me.

Chapter 1: Introduction

The niche of a population can change as that population moves, but it can also change as the individuals within the population move into a new life stage. An ontogenetic niche shift can include changes in the morphology of an organism, its feeding behaviour and habitat, as well as the competitors and predators with which it interacts (Werner & Gilliam 1984). In some cases the shift can be drastic, such as the metamorphosis of a caterpillar into a butterfly, but often it is simply the result of an increase in the size of an organism. Differences in ontogeny are often overlooked in the study of ecological niche (Werner & Gilliam 1984), although the changes that occur in the niche can be substantial. Habitat use, competition, and predation pressure change considerably as an organism grows; in fact, it is common for the adults of a species to prey on the young of the same species (Polis 1981).

The concept of niche has long been central to the study of ecology. Hutchinson (1957) defined 'ecological niche' as a term describing the relational position of a species or population in its ecosystem, and ecologists commonly define niche in terms of the habitat and prey resources used by a population (Whittaker et al. 1973). Niche theory states that two species cannot occupy the same niche indefinitely because one will inevitably outcompete the other (Hardin 1960), but the niche of a population in nature rarely remains static. Available prey can change from season to season and year to year as can other factors such as competition, predation, and suitable habitat availability. A species that is migratory is an example of a species with a dynamic niche; as the species moves into new habitats, the conditions it meets and prey available will change as well.

Pacific salmon (*Oncorhynchus spp.*) are excellent examples of species whose niche is highly dynamic. Not only are Pacific salmon migratory, but also they move from a freshwater to a marine environment when they are juveniles, and some species grow to almost 400 times their initial weight in only the first few months at sea (Quinn 2005). The niche of Pacific salmon is further affected by larger scale climatic changes that can influence the timing and composition of the prey available to them in the marine environment (Brodeur et al. 1996). It is for these reasons that juvenile Pacific salmon in the coastal marine environment offer an excellent opportunity to investigate the dynamic nature of ecological niche.

It would be difficult to find a creature more economically, ecologically, and culturally valuable than Pacific salmon. Commercial catches of Pacific salmon in British Columbia (BC) were worth close to \$54 million in 2010 (Department of Fisheries and Oceans 2011), and salmon also play an important role in generating a further \$288 million through sport fishing in BC (BC Ministry of Environment 2010). The anadromous lifecycle of Pacific salmon creates a vital link between the ocean and freshwater environments, and salmon carcasses contribute nutrients from the ocean to the terrestrial environment, replenishing soils and stimulating growth along the rivers where they spawn (Helfield 2001). Salmon are also an important part of the foodweb of the Pacific coast. Iconic creatures such as grizzly bears and killer whales depend on the yearly return of adult salmon, and salmon in all life stages feed a great variety of animals including fish, birds, wolves, and seals (Quinn 2005). Humans along the Pacific coast have enjoyed salmon for thousands of years, but have also long struggled to sustainably manage this valuable resource (e.g. Hume 1893).

It is estimated that twenty-nine percent of genetically distinct salmon stocks are now extinct (Gustafson et al. 2007) and, in Canada, four populations are listed as endangered or threatened, while several more populations are listed as high priority candidates and are awaiting assessment (Cosewic 2011). In the US there are 17 threatened or endangered ecologically significant units of Pacific salmon (NOAA 2011). These declines have been attributed to many anthropogenic factors including: habitat loss and degradation, over-fishing, timber harvesting, agriculture, salmon hatcheries, and hydropower production (Raymond 1979, Lichatowich et al. 1999).

The variability in Pacific salmon production does not rest solely on anthropogenic factors; it is also highly influenced by atmospheric and oceanic conditions (Beamish et al. 2004, Farley et al. 2007). This is evidenced by the fact that even under pristine conditions some stocks exhibit declining production (Welch et al. 2000, McKinnell et al. 2001), while other highly impacted stocks occasionally show improvement despite an abundance of human-induced stress (Williams et al. 2005). Although much research in this field has focused on the impacts that humans have on salmon, especially during their freshwater stages, it is difficult to extricate the direct impact of human actions without first understanding the role that ocean conditions play in the growth and survival of Pacific salmon.

Of particular importance during the salmon lifecycle is the early marine phase, when juveniles have recently entered the coastal marine environment and have yet to migrate to the open ocean. This stage is especially important because it is suggested that the majority of marine mortality occurs during this time (Beamish & Mahnken 2001). It has been suggested that salmon must attain a critical size during their first summer at

sea because larger salmon are less likely to be preyed upon and more likely to have stored enough fat to survive the winter (Beamish & Mahnken 2001). Under these circumstances, ocean conditions that lead to greater marine growth and energy accumulation would also be likely to increase the marine survival and production of Pacific salmon.

Pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) are the two most abundant species of salmon in the North Pacific Ocean, and their numbers are further increased every year by hatchery releases of billions of fry (Ruggerone et al. 2010). These two species offer a unique opportunity to study the dynamic nature of ecological niche for several reasons. The early life stages of these two species are very similar. They inhabit freshwater as fry, but are generally close to the ocean and enter the marine environment soon after emerging, unlike other species of salmon such as sockeye salmon (*O. nerka*), Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*), which tend to delay for months or years in lakes and rivers (Groot & Margolis 1991). Pink salmon and chum salmon are morphologically very similar during their juvenile stage, and have even been found in mixed schools (Heard 1991), but chum salmon tend to delay in estuaries for a longer time than juvenile pink salmon (Mason 1974). There is also some evidence that chum salmon rely more heavily on gelatinous zooplankton (Black & Low 1983, Tadokoro et al. 1996, Welch 1997), but it is unclear how consistently and to what degree these behaviours differ between the two species (Johnson & Schindler 2009). Pink salmon and chum salmon offer an opportunity to explore how two species that are very similar in size and morphology, and often occur in the same habitat, can nonetheless occupy different niches.

There is still much to discover concerning the niches of juvenile pink salmon and chum salmon, such as the degree to which the niches of the two species overlap, and how consistent the characteristics of their ecological niches are from year to year and in changing ocean conditions (Johnson & Schindler 2009). Pink salmon and chum salmon offer an opportunity to study how ontogenetic niche changes as a result of increasing size, since both species undergo a period of rapid growth during their first summer at sea (Groot & Margolis 1991). Since they are the most abundant species of salmon, they offer an excellent opportunity to explore the effect of density and competition on the niches of two species occupying the same habitat. Furthermore, the odd-year cycle of pink salmon from the Fraser River, which produces vastly more juvenile pink salmon in even years (Neave 1952), creates a natural experiment ideal for testing the inter- and intraspecific effects of the fluctuating abundance of competitors on the feeding behaviour and trophic niche of species (Ruggerone & Nielsen 2004).

Another interesting and beneficial aspect of studying juvenile pink salmon and chum salmon is that their habitat ranges across 3 of the fisheries production domains of the Northeast Pacific Ocean: the downwelling domain of the Alaska Coastal Current, the upwelling domain of the California Current System, and the transition domain between the two currents (Ware & MacFarlane 1989). These domains offer contrasting conditions in attributes such as the temperature and stratification of the water column, productivity and nutrient transport, as well as the diversity, quality, and quantity of available prey (Lee et al. 2006, Mackas et al. 2010). This variation offers another perspective from which to explore the characteristics of the ecological niches of juvenile pink salmon and chum salmon.

Stable isotope analysis (SIA) is an excellent tool for studying the niche of a population because isotopes offer a time-integrated and practical measurement of such conceptual niche characteristics as trophic level and food source (Peterson & Fry 1987). The variation in stable isotope signatures of organisms within a population has even been used to directly measure the breadth of that populations' niche (Bearhop et al. 2004). The stable isotope signature is essentially the ratio of heavy to light isotopes of an element that have accumulated within the tissues of an organism. The isotope signatures of nitrogen and carbon are widely used in ecological studies because of their unique and consistent behaviour in natural systems. The ratio of heavy (^{15}N) to light (^{14}N) nitrogen atoms (in the tissues of an organism) changes predictably from one trophic level to the next (Peterson & Fry 1987). The lighter isotope is preferentially excreted over the heavier isotope, causing a predictable factor of enrichment in the heavier isotope within the tissues of the consumer; this process is known as 'trophic discrimination' (Vander Zanden & Rasmussen 2001). Because the isotope signatures at the base of the foodweb can vary spatially and temporally, it is important to determine the baseline nitrogen signature for a particular time and location in order to determine the trophic position of a consumer (Cabana & Rasmussen 1996, Matthews & Mazumder 2003).

The ratio of heavy (^{13}C) to light (^{12}C) carbon atoms remains relatively stable as it moves up the food chain and exhibits a smaller degree of trophic discrimination. This characteristic of carbon isotopes makes them ideal for determining the source or mix of sources from which an organism's nutrients originated (Peterson & Fry 1987). In the marine environment, for example, offshore waters tend to be depleted in heavy carbon

isotopes, so an organism's carbon isotope signature becomes increasingly lower as that organism relies more heavily on offshore prey items (Perry et al. 1999).

Understanding the trophic dynamics and feeding behaviour of pink salmon and chum salmon in the coastal marine environment can help to predict the survival of Pacific salmon during this critical life stage. It can also help to determine the effects of shifting ocean conditions and prey resources, as well as the effects of increased salmon abundance (due to natural fluctuations and hatchery stocking), and potentially offer insights that will enable the sustainable management of this iconic complex of species. An exploration into the effects of ontogeny and a dynamic habitat on two co-occurring species will offer insights into the nature of the ecological niche.

The purpose of this thesis is to use stable isotopes to explore the nature of the ecological niche and its spatial and temporal plasticity. Juvenile pink salmon and chum salmon will serve as example subjects in order to compare the niches of two similar species that are affected by similar conditions in the same place and time. I will determine the effect of contrasting ocean conditions in different years and geographic regions on the niches of juvenile pink salmon and chum salmon. I will also explore the changes that occur in the niche of a population as its organisms increase in size and thus enter a new ontogenetic stage.

This thesis has been structured to contain four chapters. The first chapter provides a general introduction to the topics that are studied in chapters 2 and 3. Chapter 2 is entitled '*Resource partitioning between pink salmon and chum salmon in years of contrasting ocean conditions*' and will cover the differences that exist between the niches of pink salmon and chum salmon in different years and regions. Chapter 3 is

entitled '*Ontogenetic niche shift among juvenile salmon in years of contrasting ocean conditions*' and will cover the shift in the niche of pink salmon and chum salmon from summer to fall, again in different years and regions. These two chapters rely on some of the same data, but since they are designed to stand alone (both for publishing purposes and for clarity) some of the sections are similar or identical. Short portions of the *Introduction* sections may appear redundant, and some parts of the *Methods* sections that concern sampling design and sample collection are the same in both papers. The final chapter provides a general conclusion reviewing and synthesizing the results of this thesis project.

Chapter 2:

Resource partitioning between pink salmon and chum salmon in years of contrasting ocean conditions

Abstract

Although they are the two most abundant salmon species, and are further augmented through hatchery releases, it is unclear the degree to which the trophic niches of juvenile pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) overlap. Examining the trophic dynamics of juvenile pink salmon and chum salmon in the coastal marine environment is important because it is during this critical stage that a large proportion of mortality is thought to occur. The purpose of this study was to determine the degree to which the trophic niches of pink salmon and chum salmon overlap in the coastal marine environment, and how this changes in years of contrasting ocean conditions. The study area included the coasts of central and northern British Columbia and Southeast Alaska. It was expected that warmer years would result in poorer feeding conditions in the south, due to a reduction in the abundance of lipid-rich zooplankton prey species, and cause a greater overlap of the niches of juvenile pink salmon and chum salmon as a result of increased competition. It was also expected that increased abundance in even years, due to the greater abundance of pink salmon leaving the Fraser River, would lead to greater niche overlap between the species. The trophic positions of juvenile pink salmon and chum salmon were expected to increase as a result of reduced competition and improved feeding conditions.

Juvenile pink salmon and chum salmon were collected along the coasts of British Columbia and Southeast Alaska in the years 2000 and 2001, which were relatively cool years, and 2004 and 2005, which were relatively warm years. Salmon were measured and weighed and stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was performed. Bulk zooplankton samples were analyzed to determine the isotopic baseline so that the trophic positions of pink salmon and chum salmon could be compared between years and regions.

Statistical analysis showed evidence that the overlap of the niches of pink salmon and chum salmon increased when the abundance of salmon was high. Contrary to expectations, the trophic position of juvenile salmon appeared to decrease under favourable conditions. The trophic position of both juvenile pink salmon and chum salmon was higher in the southern portion of the study area, and increased when juvenile abundance was high. I suggest that the higher trophic position among juvenile salmon when competition is greater might result from increased reliance on gelatinous zooplankton, which are carnivorous, but a nutritionally poor food choice. There is also evidence that improved survival among pink salmon in cooler years might be related to zooplankton subsidies of oceanic origin. Overall, the niches of juvenile pink salmon and chum salmon are similar but dynamic, and the two species most likely compete for the same resources.

2.1. Introduction

2.1.1 Niche and juvenile salmon

Species can coexist in the same habitat by occupying different niches because resource partitioning reduces competition among species (Ross 1986), but the niche occupied and the degree of overlap among species varies depending on the availability of resources (Lawlor 1980). Pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) are the most abundant species of Pacific salmon and share a variety of habitats throughout their lifecycle. After emerging from the freshwater environment in the spring, juvenile pink salmon and chum salmon enter the coastal marine environment of the North Pacific Ocean, where their numbers are further augmented by the release of billions of fry from hatcheries (Ruggerone et al. 2010). Pink salmon and chum salmon are often found together in mixed species schools (Heard 1991), but it is unclear how resources are partitioned between pink salmon and chum salmon at these early stages in their respective lifecycles. It is also unclear how much their niches overlap and how this might change according to the conditions in the marine environment.

The portion of the salmon lifecycle when they have left freshwater, but have not yet migrated to the open ocean, is critically important because most of the ocean mortality within salmon populations is believed to occur during this phase (Parker 1968, Francis & Hare 1994). Salmon must grow quickly during this time in order to avoid predation and also to store enough fat to survive over winter (Beamish et al. 2004). The quality and quantity of food available are important factors that will determine, in part, the growth and survival of juvenile salmon in the coastal marine environment (Mortensen et al. 2000, Mueter et al. 2002). Understanding the trophic dynamics and feeding strategies of juvenile salmon during this stage may elucidate the mechanisms

that lead to changes in growth and, ultimately, in the marine survival of these and other salmon species. Exploring the relationship between pink salmon and chum salmon will also characterize the dynamic nature of competition between species in the natural environment.

2.1.2 Abundance and competition among salmon species

During both the early freshwater stage and the later open-ocean stage of the salmon lifecycle, high densities have been found to reduce the overall growth and survival of salmon (Mazumder & Edmundson 2002, Ruggerone & Nielsen 2004, Helle et al. 2007). Regarding juvenile salmon in the coastal marine environment, some studies have suggested that there would be no lack of prey resources to limit their growth and survival as a result of large plankton blooms in the late spring and early summer (Walters et al. 1978, Healey 1982, Orsi et al. 2004). Conversely, other studies suggest that competition does indeed play a role in juvenile salmon feeding habits in the coastal marine environment. Healey (1980), for example, suggested that the distribution of juvenile salmon in the Strait of Georgia might be a reflection of prey resources and that the segregation of pink salmon and chum salmon might indicate resource partitioning between the two species.

The degree of competition for prey resources between species may change based on the timing of plankton blooms and the migration of juvenile salmon (LeBrasseur 1969), or in years of reduced productivity, such as an El Niño year (Brodeur 1992). Beamish et al. (2010) found that in even years, when juvenile pink salmon from the Fraser River were abundant in the Strait of Georgia, coho salmon (*O. kisutch*) exhibited higher early marine mortality and juvenile sockeye salmon (*O. nerka*) were smaller and

had less food in their stomachs; this suggests that competition with juvenile pink salmon does, in fact, affect other salmon species in the coastal marine environment

2.1.3 Niche overlap in juvenile pink salmon and chum salmon

Among adult salmon, chum salmon appear to occupy a different niche than pink salmon, though it is not clear how consistently this occurs. Welch and Parsons (1993) reported that adult chum salmon appear to eat from a different branch of the food web than adult pink salmon. Several studies indicate that adult chum salmon feed more heavily on less nutritious, soft-bodied organisms such as ctenophores, jellyfish, and salps (Black & Low 1983, Tadokoro et al. 1996). In fact, the chum salmon's digestive tract appears to be adapted to this type of prey (Azuma 1992, Welch 1997). In contrast, Johnson & Schindler (2009) performed a meta-analysis of existing isotope studies and did not find evidence of consistent food partitioning between adult pink salmon and chum salmon. Niche overlap between adult pink salmon and chum salmon may change depending on the conditions, such as the density of salmon and the abundance of prey resources. For example, it has been reported that adult chum salmon will switch their prey depending on the abundance of pink salmon. In the open waters of the North Pacific, chum salmon consumed a greater proportion of crustaceans in years when pink salmon were less abundant (Tadokoro et al. 1996), which have a higher caloric value than gelatinous zooplankton (Davis 1993). There is evidence that *intraspecific* competition affects feeding behaviour as well; Tadokoro et al. (1996) observed that when abundance was low, pink salmon would eat a greater proportion of larger micronekton, which have similar caloric value to their typical prey, but are larger and therefore a more efficient prey choice (MacArthur & Pianka 1966, Pazzia et al. 2002).

Although there is some evidence of food partitioning and prey switching among *adult* salmon during their oceanic phase, it is unclear at what point in the salmon ontogeny this feeding behaviour begins or how it may change from year to year depending on ocean conditions. In the Strait of Georgia, King & Beamish (2000) suggested that juvenile chum salmon switched to gelatinous zooplankton by late summer, but until that point may have competed heavily for prey with other salmon species. Juvenile salmon are limited to smaller prey items than adults but those salmon that grow quickly will have access to a wider variety of prey resources (Boldt & Haldorson 2003). As juvenile salmon grow into a new ontogenetic niche, it is likely that the trophic dynamics within and among salmon species will also change.

2.1.4 Implications of prey quality and quantity

The abundance and quality of the prey available to juvenile salmon fluctuates as a result of climatic and oceanic conditions (Mackas et al. 2007). It has been suggested that productivity, and thus prey quantity, may increase in warmer years in the Alaska Coastal Current system (ACC) due to increased downwelling and cyclonic winds that lead to an increase in advection of oceanic plankton into nearshore areas. Conversely, productivity further south in the California Current System (CCS), is suggested to decrease in warm years due to decreased upwelling (Gargett 1997, Mueter et al. 2002). Warmer temperatures lead to increased stratification of the water column; in the ACC, which is light-limited, this allows phytoplankton to remain in the euphotic zone longer, resulting in increased primary production. In the CCS, which is not light-limited, increased stratification and reduced mixing of the water column results in lower nutrient availability, which reduces primary productivity (Gargett 1997).

The quality of the prey available varies not only as a function of prey size (Pazzia et al. 2002), but also as a function of lipid content (Trudel et al. 2002). Zooplankton in the north tend to be more lipid-rich because they must store enough lipids to survive the long, dark winters, when they lie dormant (Lee et al. 2006). Along the southern British Columbia coast, warmer years will sometimes bring an influx of lipid-poor southern zooplankton species (Mackas et al. 2004, Hooff & Peterson 2006). Such an influx has been suggested to create conditions of poor quality food, especially along the west coast of Vancouver Island, which could potentially lead to reduced growth and increased competition for resources among juvenile salmon. Conversely, in cooler years, the growth and survival of juvenile salmon along the south and central coasts of BC may improve as a result of a greater abundance of lipid-rich zooplankton species (Trudel et al. 2007). There is also evidence that an abundance of prey that is consistently available to juvenile salmon may improve survival, even if the prey is not lipid-rich. Juvenile pink salmon exhibited higher growth and survival in the Gulf of Alaska when the predominant summer diet items were pteropods, despite the low energy density of this type of prey (Beauchamp et al. 2007).

In general, when temperature anomalies occur in the coastal marine environment of the North Pacific Ocean, it causes a shift in the timing of plankton blooms, which may in turn create a temporal mismatch between predators and their prey (Mackas et al. 2007). Such a temporal mismatch could lead to poor feeding conditions for juvenile salmon in years when sea surface temperatures are abnormal (Crawford and Irvine 2010). Conditions resulting in a greater abundance of high quality prey available to

juvenile salmon should reduce the intensity of competition between pink salmon and chum salmon.

2.1.5 Modeling inter- and intra-specific variability using stable isotope signatures

Stable isotope analysis (SIA) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ has emerged as a powerful tool used to study the trophic interactions and feeding behaviour of aquatic organisms, such as Pacific salmon (eg. Welch & Parsons 1993, Kaeriyama 2004, Johnson & Schindler 2009). Stable isotopes represent a time-integrated signature of assimilated diet, and can eliminate some of the bias inherent in gut-content analysis (such as variability in the time of sampling, short-term or anomalous changes in feeding patterns, or varying rates of digestion for different prey items). The rate of digestion can be especially troublesome in the case of chum salmon, which are thought to rely more heavily on gelatinous zooplankton prey; this type of prey is digested quickly and is difficult to identify in gut content analysis (Arai et al. 2003).

Stable isotopes of carbon (^{13}C) can be used to determine the food sources of consumers (Post 2002). For example, $\delta^{13}\text{C}$ tends to increase with greater primary production, so offshore oceanic systems tend to be depleted in heavy isotopes of carbon (more negative $\delta^{13}\text{C}$), while nearshore systems tend to be relatively enriched in heavier ^{13}C (less negative $\delta^{13}\text{C}$) (Perry et al. 1999, Miller et al. 2008). Kline et al. (2008) found that the diet of pink salmon in Prince William Sound, Alaska, was supplemented in some years by a carbon source with depleted carbon isotope signatures, and that $\delta^{13}\text{C}$ was inversely correlated with the marine survival of these cohorts. This suggests that zooplankton of oceanic origin supplemented the diet of juvenile pink salmon in some years and lead to an increased survival rate in the coastal marine environment.

The trophic position of a consumer can be inferred from the stable isotope signature of nitrogen ($\delta^{15}\text{N}$), because heavy isotope enrichment occurs in a predictable manner from one trophic level to the next in marine foodwebs (Peterson & Fry 1987, Post 2002) by a process known as ‘trophic discrimination’. Many studies have used this phenomenon to determine the relative trophic position of consumers to each other (ie. Welch & Parsons 1993, Kaeriyama 2004), but have done so without first determining the baseline signatures of primary consumers. The lack of an isotopic baseline limits the degree to which trophic positions can be reliably compared among seasons, regions, and years, because the baseline can vary depending on biogeochemical processes, such as nitrogen fixation and recycling, that affect $\delta^{15}\text{N}$ at the base of the foodweb (Matthews & Mazumder 2003).

2.1.6 Purpose of this study

The purpose of this study was to examine the feeding habits and trophic interactions of juvenile pink salmon and chum salmon in the coastal marine environment, and to compare these patterns between years of contrasting ocean conditions and salmon abundance. I used stable isotopes to evaluate the patterns of resource partitioning between pink salmon and chum salmon during their early marine life stage.

It is expected that cooler years would produce better feeding conditions for juvenile salmon, especially in the southern portion of the study area, and therefore less competition for food among pink salmon and chum salmon. Due to less competition, I hypothesize that the stable isotope signatures of carbon and nitrogen would reflect a lesser degree of overlap between pink salmon and chum salmon in cooler years. In

warmer years, a greater overlap in stable isotope signatures could indicate that pink salmon and chum salmon must increase their reliance on available prey species even if they are not their preferred diet. I also hypothesize that this difference would be more pronounced in the south than in the north, as the shift from northern to southern zooplankton species tends occur to a greater degree in the southern end of the transition zone (Mackas et al. 2010).

My objective was to test whether cooler temperatures and better feeding conditions would allow both species to eat a greater proportion of high quality prey by reducing the level of competition for food resources. Since higher trophic level prey is often a more efficient prey choice (MacArthur & Pianka 1966), I anticipate that conditions leading to less competition would also lead to higher trophic positions among juvenile salmon. I also wanted to evaluate whether or not the trophic position, determined using the nitrogen stable isotope signatures of salmon and zooplankton, would be higher for both pink salmon and chum salmon in cooler years in the south, and whether or not the trophic position of salmon would be higher in the north due to a greater abundance of lipid-rich prey. Furthermore, I anticipate that increased niche overlap and reduced trophic position would be further amplified in the south in even years, when a large number of pink salmon leave the Fraser River, thus increasing the abundance of juvenile salmon and the level of competition between pink salmon and chum salmon.

2.2. Methods

2.2.1 Study area

The study area extends northward from the northern tip of Vancouver Island to the southern end of Southeast Alaska (Figure 2.2.1). This area represents the southern

portion of the downwelling domain of the Alaska Coastal Current (ACC) and also a transition zone that occurs between the ACC and the upwelling domain of the California Current System (CCS) (Ware & MacFarlane 1989).

2.2.2 Sampling design

Juvenile salmon were collected in the study area in the fall of 2000, 2001, 2004, and 2005. Based on BC lighthouse data available from Fisheries and Ocean Canada (<http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm>) the average sea surface temperatures (SST) in the study area in the months leading up to the sampling time were relatively cool in 2000 and 2001, and relatively warm in 2004 and 2005 (Figure 2.2.2). The zooplankton community shifted from a dominance of northern copepods in the cool years to southern copepods in the warm years (Mackas et al. 2007).

The years 2000, 2001, 2004, and 2005 were chosen not only for the contrast in ocean conditions, but also in order to sample from an odd and even year in both warm and cool conditions. Due to the dominance of odd-year spawners that arrive in the fall, the majority of juvenile pink salmon leave the Fraser River in even years rather than odd years (Neave 1952), so there would have been a greater abundance of juvenile pink salmon entering the Strait of Georgia and migrating northward in 2000 and 2004.

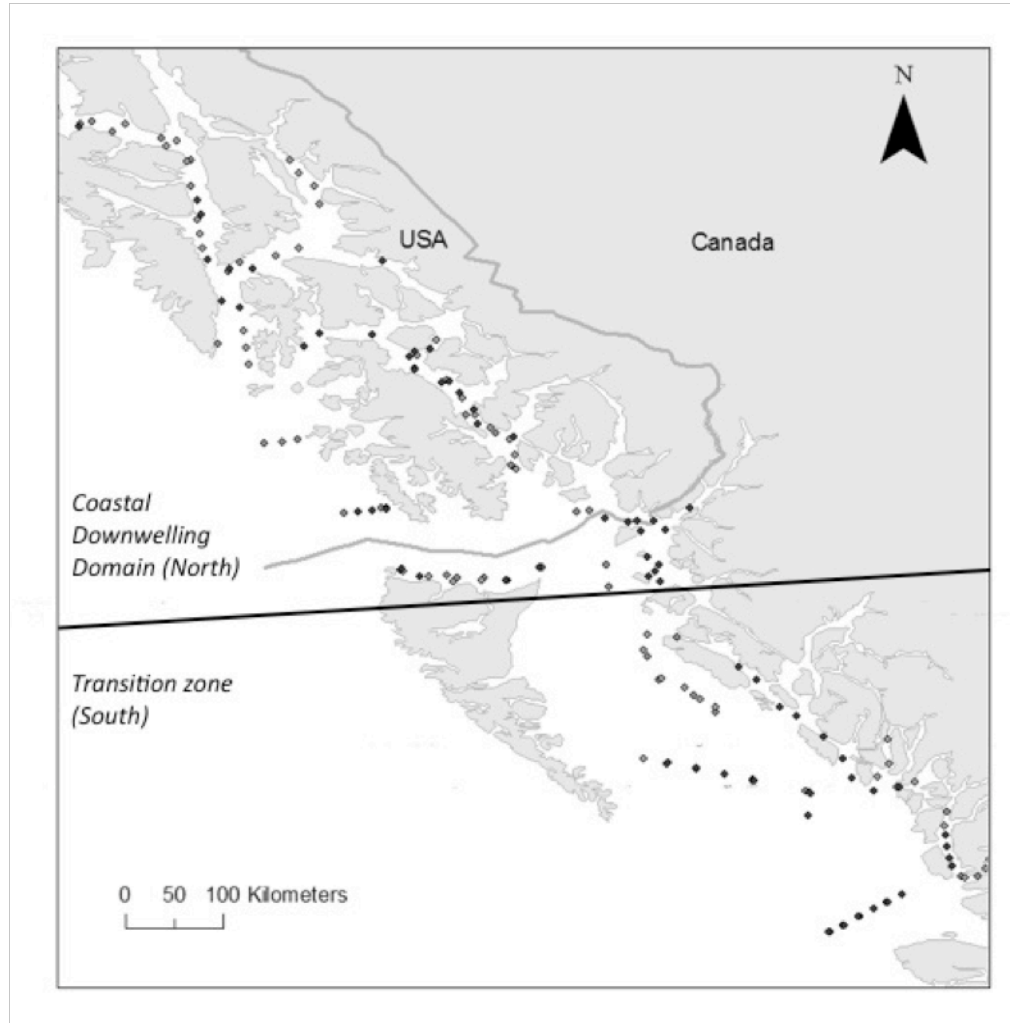


Figure 2.2.1. The study area, which extends from the northern tip of Vancouver Island north to southeast Alaska. Points represent sample sites, although some did not have any fish. For the purposes of this study, the ‘northern’ region includes the sites along the northern edge of Haida Gwaii, and all of the sites further north. The regions are based on the fisheries production domains of the Northeast Pacific Ocean (Ware & MacFarlane 1989); the northern region corresponds to the coastal downwelling domain of the Alaska Coastal Current, and the southern region corresponds to the transition zone between the Coastal Downwelling and Coastal Upwelling Domains.

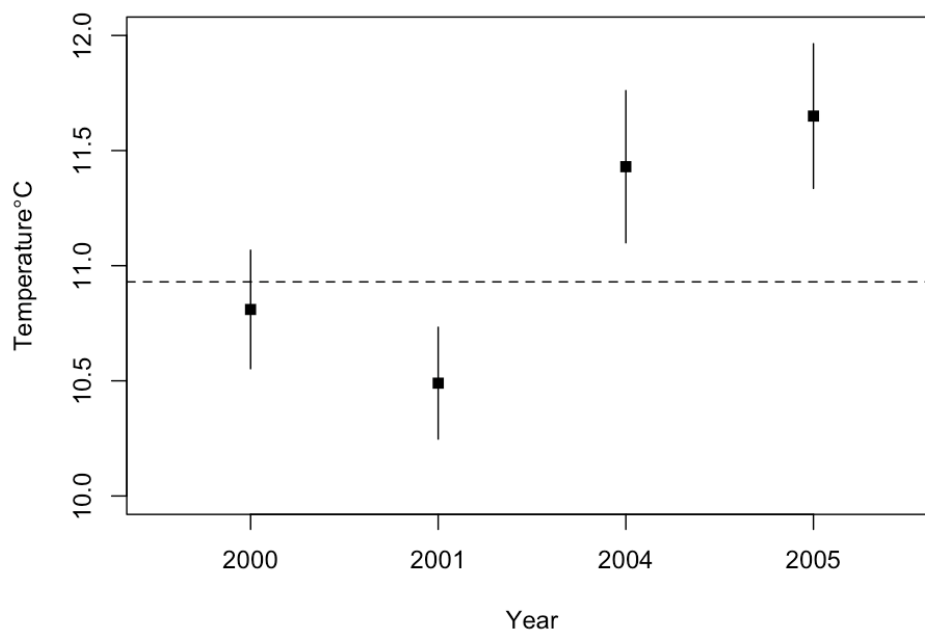


Figure 2.2.2. The mean sea surface temperature for each year studied. The filled squares represent the means, which are based on data from BC lighthouses and include the mean monthly temperature from June to November of the given year. Bars represent the standard error of the mean, and the dashed horizontal line represents the mean temperature from June to November for the years 1999 to 2009. The sea surface temperature data are collected daily at five lighthouse stations within the study area. The lighthouse stations included were Langara Island, Bonilla Island, McInnes Island, Pine Island, and Egg Island.

2.2.3 Sample collection

Juvenile salmon were collected in the fall (October/November) using a rope trawl with an opening 28 m wide and 16 m deep, towed at the surface at approximately 5 knots for 30 minutes. Fish fork length (mm) and wet weight (g) were determined at sea and fish were then frozen individually at -20°C in marked plastic bags for later analysis. Zooplankton were collected during the day from vertical bongo tows using two 58 cm diameter Nitex nets, to a depth within 10 m of the ocean floor or a to a maximum of 150 m deep. Of the 346 sites sampled, 40% were less than 150 m deep,

with the shallowest being 40 m deep. Zooplankton were separated into 4 size classes, weighed, dried, weighed again, and stored for further analysis. Zooplankton density was calculated based on the dry weight of the zooplankton per 1000 cubic meters of water sieved at each sampling site (a flow meter was used to determine the volume of water sieved by the bongo net). The density of zooplankton was then averaged for each year and domain (ACC or TD).

The two smaller size classes (0.25-1.0 mm and 1.0-1.7 mm) were retained for stable isotope analysis, but only the smallest size class was used as the isotope baseline to determine fish trophic level. The larger size was excluded in the baseline calculation in order to be consistent across sites as isotope signatures for the larger size class were very limited or absent at a large proportion of sample sites. The reason for excluding the larger size class was also that it may have included particular species of zooplankton which could have biased the baseline isotope signature at the sites where they were present. Because juvenile pink salmon and chum salmon prey on larger, more visible prey items (Landingham et al. 1998, Armstrong et al. 2005), the larger size class of zooplankton was selected to represent the density of prey available to juvenile salmon.

2.2.4 Stable isotope analyses

The total number of fish retained for isotope analysis was 644. A sample of skinless, boneless, dorsal muscle tissue was removed from each fish posterior of the dorsal fin. Muscle samples and zooplankton samples were freeze dried using a Labconco FreeZone Freeze Dry System, except for muscle samples from the year 2000 which had been previously air dried at 65°C for 72 hours. All samples were then ground to a fine powder using a Heavy Duty Wig-L-Bug grinding mill, and the powder was

precisely weighed to a thousandth of a milligram and packed for analysis with a Thermo Delta IV Isotope Ratio Mass Spectrometer.

Stable isotope ratios are reported using the delta notation, which expresses isotope ratios relative to an international standard, air N₂ for nitrogen and Vienna Peedee Belemnite for carbon, and is defined as follows:

$$(1) \quad \delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000\text{‰}$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. Laboratory protocols included running one standard for every 11 samples, as well as repeating one out of every 11 samples. The standard deviation of the measurements of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was $\pm 0.2\text{‰}$ based on repeated measurements of laboratory standards and $\pm 0.3\text{‰}$ based repeated measurement of samples of muscle tissue from the same fish.

In order to determine the isotopic effect of oven-drying the samples as opposed to freeze-drying them, the muscle samples of 60 fish were divided and one half was oven-dried while the other half was freeze-dried. There was a small but consistent difference between the isotope signatures of freeze-dried and oven-dried samples (approximately 0.25 ‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), so a linear model derived from the subset was used to correct the isotope signatures of all of the oven-dried samples within the study. The best model (adj $R^2 = 0.95$, $F = 541.1$, $df = 2, 56$, $p\text{-value} < 0.0001$) for correcting the carbon stable isotope signature was as follows:

$$(2) \quad \text{Corrected } \delta^{13}\text{C} = -4.20 + 1.01 * \delta^{13}\text{C of oven dried sample} + 1.35 * \text{C:N}$$

where C:N is ratio of carbon to nitrogen molecules in the sample.

The best model (adj $R^2 = 0.90$, $F = 504.9$, $df = 1, 56$, $p\text{-value} < 0.0001$) to correct the nitrogen stable isotope signature was the following:

(3) Corrected $\delta^{15}\text{N} = 0.57 + 0.95 * \delta^{15}\text{N}$ of oven dried sample

Lipids are depleted in ^{13}C compared to muscle tissue, so it is important to correct the $\delta^{13}\text{C}$ based on the lipid content of the tissue sample (McConnaughey & McRoy 1979). Because juvenile salmon tend to have relatively low lipid content ($\approx 3\%$ in my data, based on carbon to nitrogen ratios as per Post 2007) and their lipid content is not highly variable, lipid correction makes little difference to the $\delta^{13}\text{C}$ signature (Post 2007). Zooplankton tend to have slightly higher lipid content ($\approx 12\%$ in my data), so, in order to be consistent, the $\delta^{13}\text{C}$ of all samples (both zooplankton and fish) were corrected mathematically based on the C:N ratio, which was determined during mass spectrometer analysis. The formula for lipid correction based on C:N ratio for aquatic organisms is as follows (Post et al. 2007):

(4) $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$

Correcting $\delta^{13}\text{C}$ in this manner also allows for consistency between this paper and other recent studies of the isotopic characteristics of Pacific foodwebs such as Johnson and Schindler (2009) and Kline (2010).

Because juvenile salmon are migratory, the baseline isotope signatures were averaged over the sub-region where salmon were caught. Sub-regions were determined based on geographic proximity of sampling locations (Figure 2.2.3); the similarity of sampling sites, based on oceanographic indicators, was also taken into consideration. These oceanographic indicators included sea surface temperature, sea surface salinity, proximity to shore, and depth. These indicators were reviewed and, in some rare cases, sites that were both highly anomalous as well as devoid of pink salmon or chum salmon, were dropped from the average baseline calculation. For example, if a site was the last

in a line of sites at which the depth increased drastically, no fish were caught, and the isotope signatures of zooplankton appeared anomalous compared to the rest in the region, the isotope signatures of that site were not included in the baseline isotope calculation. The trophic position of fish was determined using the following formula (Cabana & Rasmussen 1996, Vander Zanden & Rasmussen 1999):

$$(5) \quad \text{Trophic position} = [(\delta^{15}\text{N}_{\text{salmon}} - \delta^{15}\text{N}_{\text{zooplankton}}) / 3.4\text{‰}] + 2$$

The baseline-corrected $\delta^{15}\text{N}$ value is divided by 3.4‰ because this is the average trophic discrimination factor from one trophic level to the next among marine organisms (Vander Zanden & Rasmussen 2001), and 2 was added because zooplankton are assumed to represent the second trophic level. Although it is an oversimplification to assume that all zooplankton of the small size class are primary consumers (Kling et al. 1992), it is necessary for my purposes because of the massive time and expertise that would be required to separate, identify, and analyze each zooplankton sample. Furthermore, I used bulk zooplankton because assemblages of species are not consistent, and baseline species may vary among regions and between years.

In order to ensure that $\delta^{13}\text{C}$ signatures reflect the food source and not the trophic position of the fish, the $\delta^{13}\text{C}$ of fish was corrected based on a trophic enrichment ($\Delta\delta^{13}\text{C}$) of 1‰ per trophic level (Vander Zanden & Rasmussen 2001). The formula is as follows:

$$(6) \quad \delta^{13}\text{C}_{\text{trophic corrected}} = \delta^{13}\text{C}_{\text{lipid corrected}} - (\text{Trophic position} - 2) * \Delta\delta^{13}\text{C}$$

2.2.5 Statistical Analysis

All statistical analyses were performed with the statistical package R (R Development Core Team 2009). Based on the previously described sampling design,

the salmon caught were grouped based on the species, the year they were collected, and whether they were collected in the northern portion or the southern portion of the study area. When salmon of the same species were caught in the same tow, their stable isotope signatures were averaged in order to avoid pseudoreplication; this reduced the total sample size for the stable isotope data from 644 to 249. The length and weight of fish caught in the same tow are initially reported without being averaged in order to capture the variety of sizes, but when the regression is performed comparing mean length and CPUE (see section 2.5.1), lengths of fish from the same tow are averaged. For a summary of the numbers by year, species, and region, see appendix 1.

2.2.5.1 Estimating juvenile salmon abundance and zooplankton density

The catch-per-unit-effort (CPUE) was calculated for each tow using the following formula (Fisher et al. 2007):

$$(7) \quad \text{CPUE} = [\text{number of fish caught} / \text{tow distance (nautical miles)}] \times 1.5 \text{ nautical miles}$$

Multiplying by 1.5 nautical miles standardizes the CPUE so that it is consistent with recent studies that report abundances of juvenile Pacific salmon, such as Fisher et al. (2007) and Tucker et al. (2009).

The CPUE for each year and region (north or south) of the study area was determined by finding the mean CPUE for that year, region and species. Because the data were not normally distributed and because many sampling sites yielded no fish and thus a value of zero, bootstrapping was used to estimate confidence limits for the mean CPUE (Efron 1981). The abundance of pink salmon and chum salmon will initially be reported separately, but for the majority of the discussion will be considered together in order to better represent the overall density of these species of salmon. The combined

pink salmon and chum salmon mean CPUE and confidence limits were calculated in the same manner as the separated CPUE values. The combined values for CPUE were compared between years and regions using an ANOVA-like permutation test (Manly 2007). This is an alternative to a parametric Analysis of Variance (ANOVA) or non-parametric Kruskal-Wallis test; it has fewer assumptions about the data and the distribution of the test statistic. In addition, there are no degrees of freedom in permutation-based tests (Good 1993). Data was permuted 10,000 times in order to create an empirical distribution of the F-statistics, and to determine an adjusted p-value of the original data set.

Zooplankton density was calculated for both the large and small size classes based on the dry weight (g) of zooplankton per 1000 m³ of volume sieved. The mean density was calculated for each year and domain (ACC and TD) for both of the size classes, and these means were compared using a multi-factor ANOVA with the factors 'warm/cold year', 'region', and 'odd/even year'. The two size classes were tested separately to simplify the interpretation of results.

2.2.5.2 Estimating juvenile salmon size and weight in different years and regions

A Linear mixed-effects model (lme) was used to determine the effect of independent fixed variables on the length of fish. Linear mixed effects models allow for the inclusion of random effects in the model, which can help to avoid pseudoreplication (Zuur et al. 2009). The independent fixed variables included in the model were the factors 'warm/cold year', 'odd/even year', 'season' (summer/fall), 'species' (pink salmon/chum salmon), and 'region' (north/south). The nested random effects included were 'tow' and 'sub-region' (tow being nested within sub-region). In this case 'sub-

region' refers to a group of tows within relatively close proximity, and are the same sub-regions on which the average isotopic baseline was calculated (Figure 2.2.3).

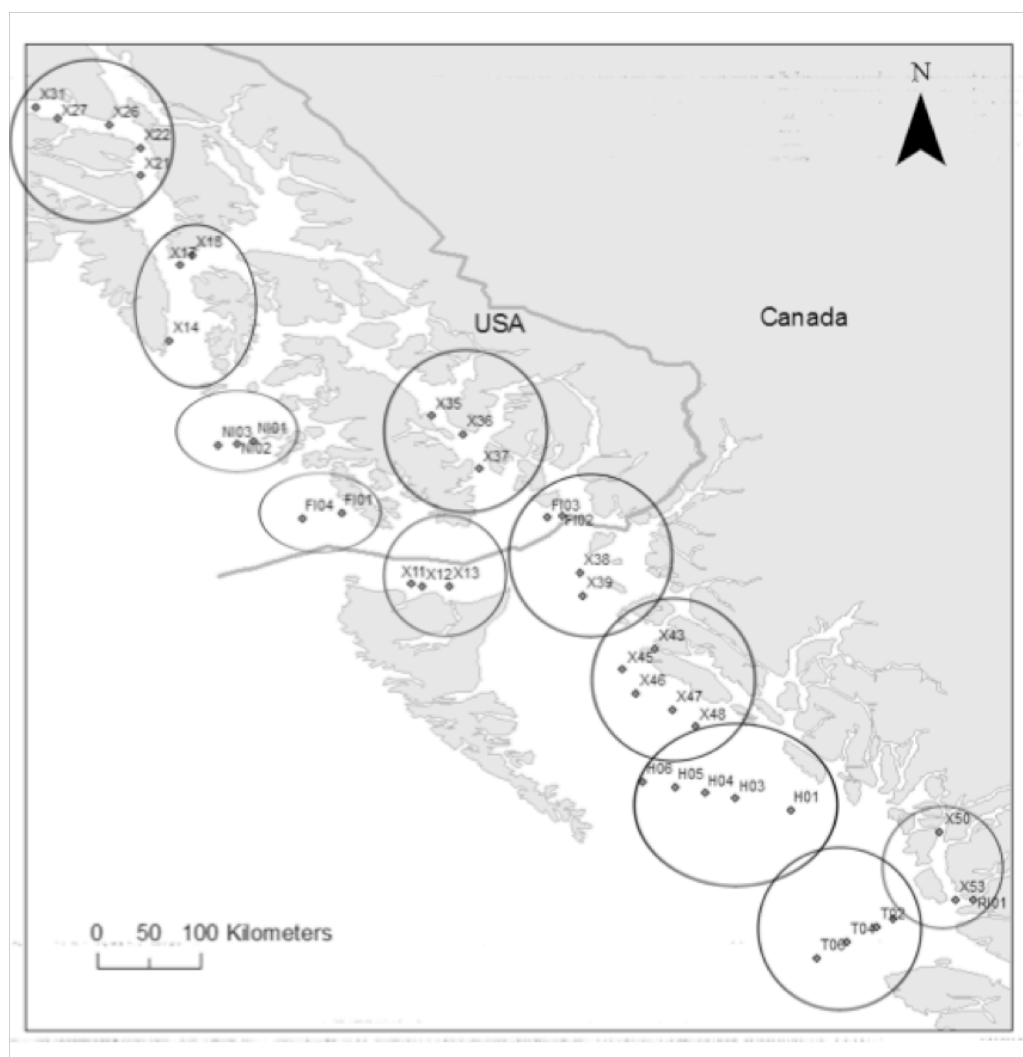


Figure 2.2.3. Sample map showing 'sub-regions' used for isotope baseline and as a random effect in the linear mixed-effects model. This map shows the study area in fall 2000 with original station identification codes where fish were caught. Circled areas indicate sites that were combined to create a 'sub-region'. The same sub-regions were used in each year and season, although the numbers of fish caught at individual sites and within sub-regions varied among years.

The weight of fish was calculated by subtracting the weight of the stomach contents for each fish, so that the relative weight is not affected by the recent feeding activity of the fish. The length and weight of fish were then log-transformed and the relationship between weight and length was compared between species using an analysis of covariance (ANCOVA).

During the sampling process, it was observed that the egg sacs of the juvenile pink salmon females were consistently larger than the egg sacs of the juvenile female chum salmon. In order to confirm this observation, a subsample of the females from the year 2001 was randomly selected and the weight of the egg sac was determined as a percentage of body weight of the salmon. The sample included 45 chum salmon and 57 pink salmon. Welch's two-sample t-test was used to compare the mean egg sac weight (as a percent of body weight) between juvenile pink salmon and chum salmon.

2.2.5.3 Determining the effect of CPUE on juvenile salmon size

The mean length of fish in relation to the abundance of juvenile pink salmon and chum salmon was tested by performing a linear regression on the mean fork-length (averaged first by tow) of each year, species, and region versus the mean \log_e CPUE. The CPUE for pink salmon and chum salmon was combined for this test. In order to create a factor estimating the availability of prey with respect to the density of salmon, the CPUE was divided by the zooplankton density (large size class). The mean fork-lengths were then regressed against this metric in the same manner as was done with the CPUE. When determining the \log_e of values, the function 'log1p' was used in R in cases when any of the values to be transformed were less than 1 but greater than zero. This ensured that none of the resulting \log_e values were negative.

2.2.5.4 Estimating juvenile salmon trophic position in different years and regions

The mean trophic positions of juvenile salmon were compared between species and years using a multi-factor ANOVA (each year was categorized as warm or cold, and odd or even). Before performing the ANOVA, the data were tested to ensure equality of variances and normality using the Fligner-Killeen and Bartlett tests. The north and south regions were considered separately in order to simplify the interpretation of the results. Tukey's honest significant differences were used to determine the years and regions in which the trophic positions of pink salmon and chum salmon were significantly different (adjusted $p < 0.05$) and to determine significant differences between warm and cold years and odd and even years.

2.2.5.6 Determining food source using $\delta^{13}\text{C}$

The corrected $\delta^{13}\text{C}$ of the fish was compared in a similar manner as the trophic positions. The $\delta^{13}\text{C}$ of fish was compared using a multi-factor ANOVA based on the species and the year that the fish were caught (each year was categorized as warm or cold, and odd or even). The north and south regions were considered separately. The data were tested beforehand to ensure equality of variances and normality using the Fligner-Killeen and Bartlett tests. Tukey's honest significant differences were used to again determine the years and regions in which the trophic positions of pink salmon and chum salmon were significantly different (adjusted $p < 0.05$) and to determine significant differences between years.

2.2.5.7 Estimating the effect of CPUE on niche overlap

In order to compare the combined trophic position and $\delta^{13}\text{C}$ among each of the years and between species, a multivariate analysis of variance (MANOVA) was performed to test for significant differences. The northern and southern regions were

analyzed separately in order to simplify the interpretation of the results. Figures were created, using R, in order to demonstrate the relative difference or similarity of the niches of pink salmon and chum salmon in each year and region. The difference between the mean niche of pink salmon and chum salmon in each year and region was measured using the Euclidean distance. When calculating the Euclidean distance, baseline-corrected $\delta^{15}\text{N}$ was used instead of trophic position, so that the units and scale of each axis would be analogous.

Regression analysis was performed to determine the relationship between the Euclidean distance and the \log_e -transformed mean total CPUE for a given year and region. Euclidean distance was also regressed against zooplankton density and the difference in mean length between the two species. As an indicator of the prey resources available to juvenile salmon, the zooplankton density (for the large size class) was divided by the CPUE. Regression analysis was performed to determine the relationship between Euclidean distance between the species and the combined CPUE and zooplankton density. Finally, regression analysis was performed comparing the CPUE and zooplankton density.

2.3. Results

2.3.1 Contrasting salmon abundance and zooplankton density in different years

The abundance of pink salmon and chum salmon was generally the highest in 2000: the greatest abundance observed was for pink salmon in the south (TD) in 2000 with a mean CPUE of 30.8 fish caught per 1.5 nautical miles (nmi), followed by chum salmon in the south in the same year with a mean CPUE of 22.5 fish per 1.5 nmi (Figure 2.3.1a). The abundance of both pink salmon and chum salmon was lowest in the north

(ACC) in 2004 with a mean CPUE of 0.2 chum salmon per 1.5 nmi and 0.9 pink salmon per 1.5 nmi.

Pink salmon were consistently more abundant than chum salmon except in the south in 2004, when there was a greater abundance of chum salmon. In even years there tended to be a greater abundance of fish in the south, and in odd years there was a greater abundance in the north (Figure 2.3.1b). When comparing an even, cool year (2000), to an even warm year (2004), the abundance of both pink salmon and chum salmon was greater in the cool year; this was observed in both the northern and southern regions. When comparing an odd, cool year (2001) to an odd, warm year (2005), the abundance was again greater in the cooler year, except in 2005 when there was a greater abundance of chum salmon in the north than there was in 2001, although the difference was small.

The confidence limits of the mean, determined using bootstrapping, were wide due to the large number of zeroes in the data set and the non-normality of the CPUE data. Using an ANOVA-like permutation test, significant differences were found in the combined CPUE of juvenile pink salmon and chum salmon between the north and south ($F = 9.5$, adjusted p -value = 0.004), between odd and even years ($F = 4.4$, adjusted p -value = 0.04), and between warm and cold years ($F = 7.0$, p -value = 0.006). A significant interaction was observed between the factor 'region' (north or south) and the factor 'odd/even year' ($F = 19.9$, adjusted p -value = 0.001).

The small size class of zooplankton was much more abundant than the larger size class (small = 6.12 ± 5.07 g 1000 m⁻³, large = 1.68 ± 2.00 g 1000 m⁻³) (Figure 2.3.2). The ANOVA showed a significant difference between the mean density of the small

size class of zooplankton in the north compared to the south ($F_{1,161} = 4.07$, $p = 0.045$), with the south having a higher average zooplankton density (north = 5.53 ± 5.13 g 1000 m⁻³, south = 7.02 ± 4.89 g 1000 m⁻³). There was a significant interaction between the factors “warm/cold year” and “odd/even year” ($F_{1,161} = 3.81$, $p = 0.05$) caused by the higher zooplankton density in both the south and north in the year 2005 (north, 2005 = 8.02 ± 6.76 g 1000 m⁻³, south, 2005 = 10.34 ± 5.38 g 1000 m⁻³).

Among the large size class of zooplankton, the ANOVA showed a significant three-way interaction between the factors ‘region’ (north/south), ‘warm/cold year’ and ‘odd/even year’ ($F_{1,158} = 5.72$, $p = 0.02$). This interaction was mainly a result of the low large-sized zooplankton mean density in the south in 2004 (0.71 ± 0.71 g 1000 m⁻³) and the high density in the north in 2004 (2.41 ± 1.33 g 1000 m⁻³).

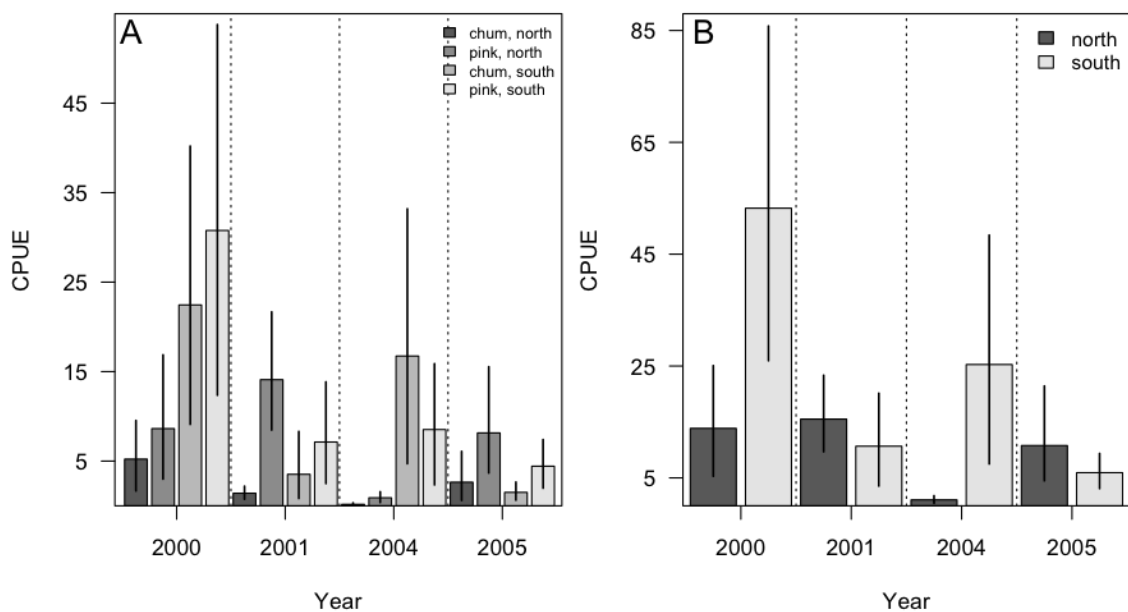


Figure 2.3.1. a) The catch per unit effort (CPUE) represented separately for each species, year and region (north or south). The error bars represent 95% confidence limits based on bootstrapping. b) The CPUE of pink salmon and chum salmon combined for each year and region.

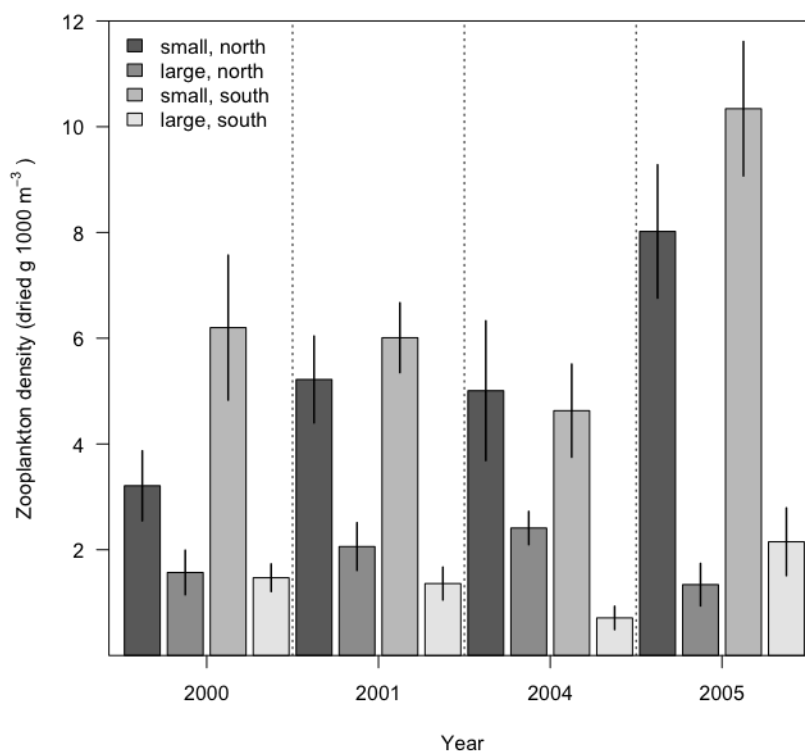


Figure 2.3.2. Zooplankton density for each size class, year, and region (north or south). The error bars represent standard error.

2.3.2 Variations in juvenile salmon length and weight

Juvenile chum salmon ranged in size from 164 mm to 273 mm, with a mean length of 222 ± 22 mm (standard deviation). Juvenile pink salmon ranged in size from 161 mm to 297 mm in length, with a mean length of 226 ± 32 mm (Figure 2.3.3). For a summary of mean lengths by year, region, and species, see appendix 1.

The mean size of pink salmon in the northern region was generally greater than the mean size of chum salmon (pink salmon: 235 ± 31 mm, chum salmon: 221 ± 22 mm, $t=2.3$, $df = 230$, $p = 0.009$), except in 2001 when the mean size of pink salmon (214 ± 31 mm) was similar to the mean size of chum salmon (217 ± 24 mm). In the south, the

mean size of pink salmon was smaller than chum salmon (pink salmon: 210 ± 26 mm, chum salmon: 221 ± 23 , $t = 3.7$, $df = 230$, $p = 0.0003$), though the difference was more pronounced in the cooler years (2000, 2001) than in the warmer years (2004, 2005). In warm years, chum salmon in the south were larger in the odd year than the even year ($t = 2.87$, $df = 37$, $p = 0.007$), and pink salmon in the south were also larger in the odd year ($t = 2.53$, $df = 44$, $p = 0.01$). Pink salmon in the south in cold years were larger in the even year than the odd year ($t = 2.69$, $df = 44$, $p = 0.01$), while chum were similar in size in the odd and even cold years. The largest mean size for any group was pink salmon in the north in 2004 (247 ± 27 mm), and the smallest mean size for any group was for pink salmon in the south in 2001 (197 ± 20 mm) (Figure 2.3.3).

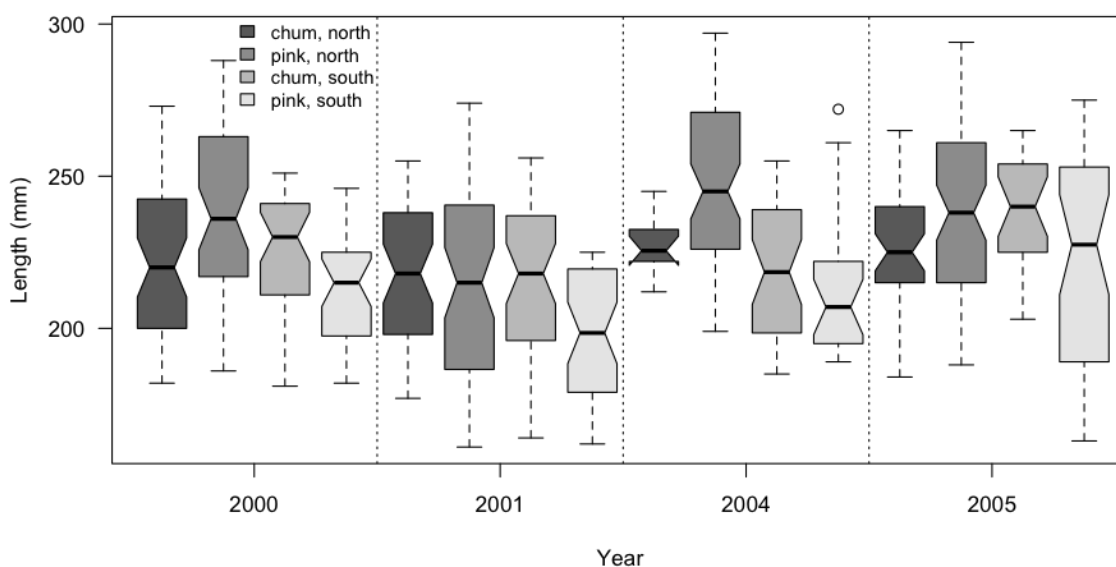


Figure 2.3.3. Distribution and median length (mm) of juvenile pink salmon and chum salmon in each year (2000, 2001, 2004, or 2005) and region (north or south). The darker grey boxes represent chum salmon and pink salmon in the north (respectively) and the lighter grey boxes represent chum salmon and pink salmon in the south.

2.3.3 Relationship between juvenile salmon weight and length

An analysis of covariance was applied to compare the weight to length relationship between species. The slopes of the regression lines for pink salmon and chum salmon were not significantly different (t -value = 0.11, df = 638, p -value = 0.91), however, the intercept was greater for chum salmon than for pink salmon (t -value = 14.58, df = 639, p -value < 0.0001) suggesting that juvenile chum salmon tend to be slightly heavier for a given forklength (Figure 2.3.4).

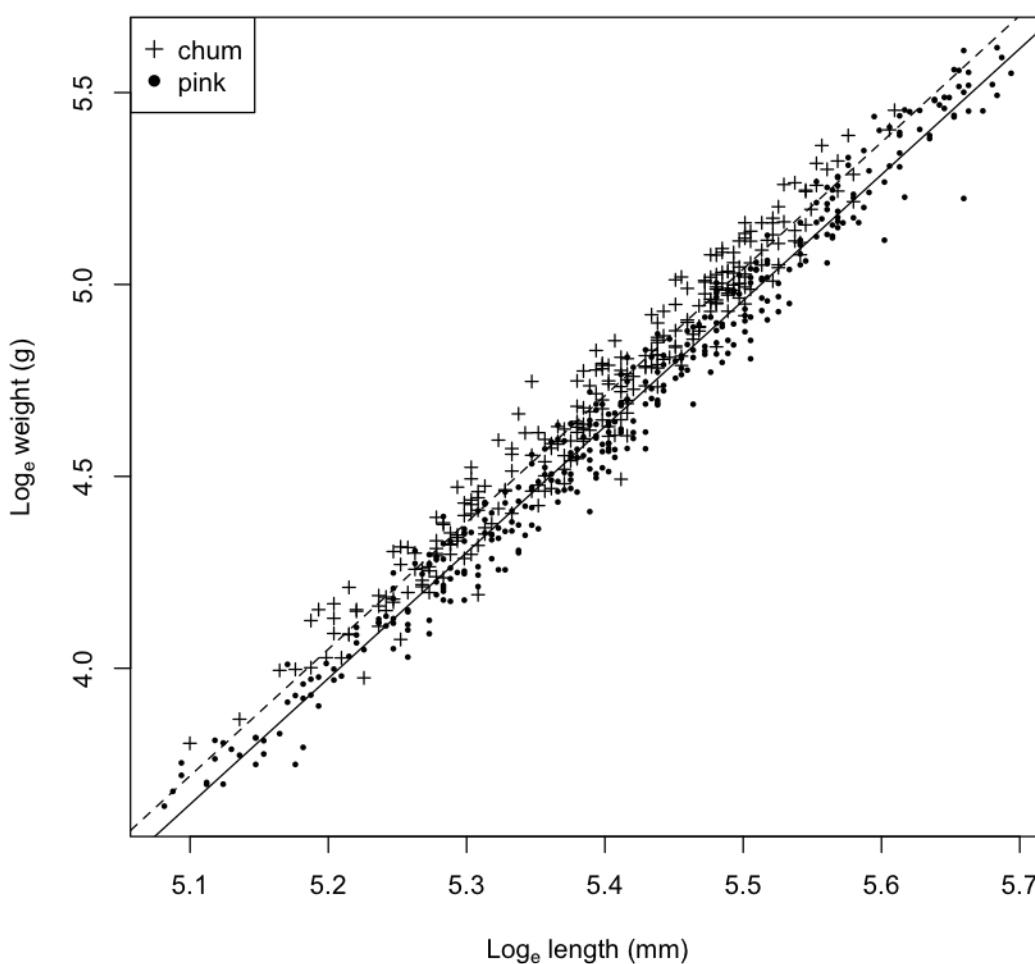


Figure 2.3.4. The natural logarithm of the weight in grams versus the natural logarithm of the length in millimetres for each sampled fish. The solid line is a regression line for relationship between weight and length for the pink salmon ($y = 3.29x - 13.12$), while the dashed line is that of the chum salmon ($y = 3.29x - 13.04$).

The mean weight of the female egg sac of pink salmon as a percentage of body weight was $0.25 \pm 0.09\%$ and the mean weight of the egg sac for chum salmon was $0.06 \pm 0.03\%$. The weight of the egg sac as a percentage of body weight was significantly higher in pink salmon ($t = 14.7$, $df = 72.6$, $p < 0.0001$).

2.3.4 The effect of juvenile salmon abundance on size

Regression analysis of the mean length of juvenile salmon and CPUE showed evidence that fork-length decreased with increasing CPUE ($R^2 = 0.24$, $df = 14$, $p = 0.05$) (Figure 2.3.5). When CPUE was divided by zooplankton density as a measure of the resources available to juvenile salmon, the relationship remained negative and the R^2 and p-values remained similar ($R^2 = 0.23$, $df = 14$, $p = 0.06$).

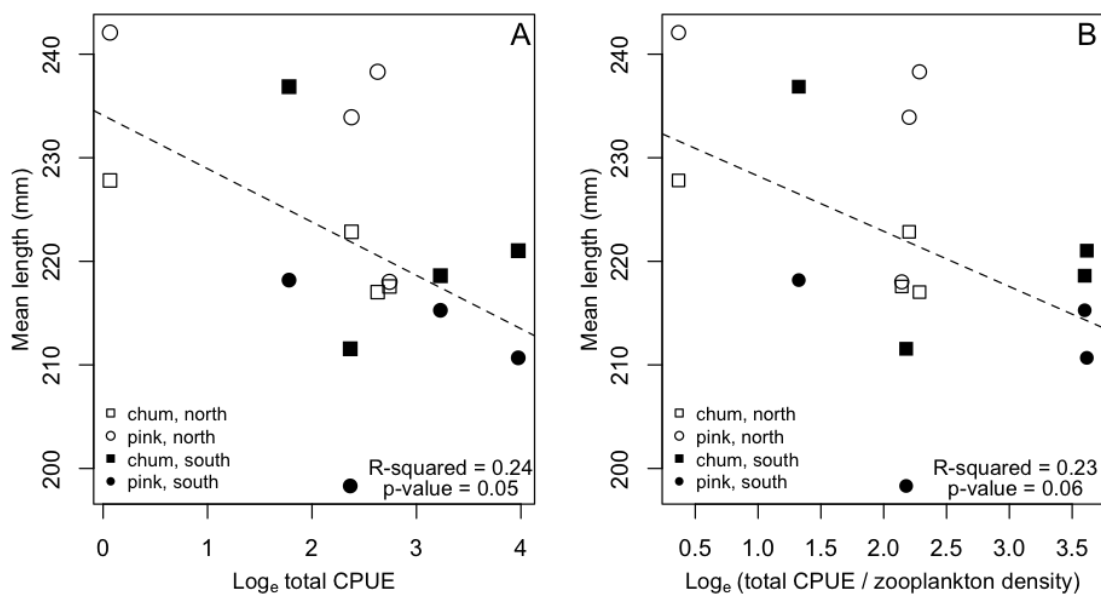


Figure 2.3.5. The relationship between the mean fork-length of pink salmon and chum salmon and the log_e CPUE (plot A) and the log_e of the result of the CPUE divided by the zooplankton density ($\text{dry g } 1000 \text{ m}^{-3}$) (plot B) within each region.

2.3.5 Juvenile salmon trophic positions in different years and regions

The trophic position of pink salmon and chum salmon tended to be higher in the south. In addition, the trophic position was higher in even years in the southern region. Chum salmon tended to have a higher trophic position than pink salmon, except for in the north in the warmer years.

The nitrogen isotope signatures of juvenile chum salmon ranged from 11.6‰ to 14.0‰ with a mean of $12.8‰ \pm 0.5‰$ (standard deviation), and ranged from 11.3‰ to 14.0‰ for pink salmon with a mean of $12.5‰ \pm 0.5‰$. For a summary of the mean and standard deviation by year, region and species, see appendix 1. The nitrogen isotope signature of zooplankton ranged from 7.4‰ to 12.2‰ with a mean of $10.4‰ \pm 0.9‰$, for a summary of zooplankton isotope signatures see appendix 1.

The mean trophic position of chum salmon, using zooplankton as a baseline, ranged from 2.2 to 3.2, with a mean of 2.7 ± 0.2 . The trophic position of pink salmon, again using zooplankton as a baseline, ranged from 2.2 to 3.1, with a mean of 2.6 ± 0.2 (Figure 2.3.6a). The trophic position of salmon in the south was consistently higher than the trophic position of salmon in the north ($F_{1, 241} = 204.9$, $p < 0.0001$), and this difference was more pronounced in the even years.

An ANOVA showed that the significant factors affecting the trophic position in the northern region included the species of salmon ($F_{1, 145} = 7.2$, $p = 0.008$), whether the year was warm or cold ($F_{1, 145} = 26.1$, $p < 0.0001$), and whether the year was odd or even ($F = 9.0$, $p = 0.003$). Significant interactions occurred between the factors “species” and “warm/cold year” ($F_{1,145} = 9.4$, $p = 0.002$) and between the factors “warm/cold year” and “odd/even year” ($F_{1,145} = 4.7$, $p = 0.03$).

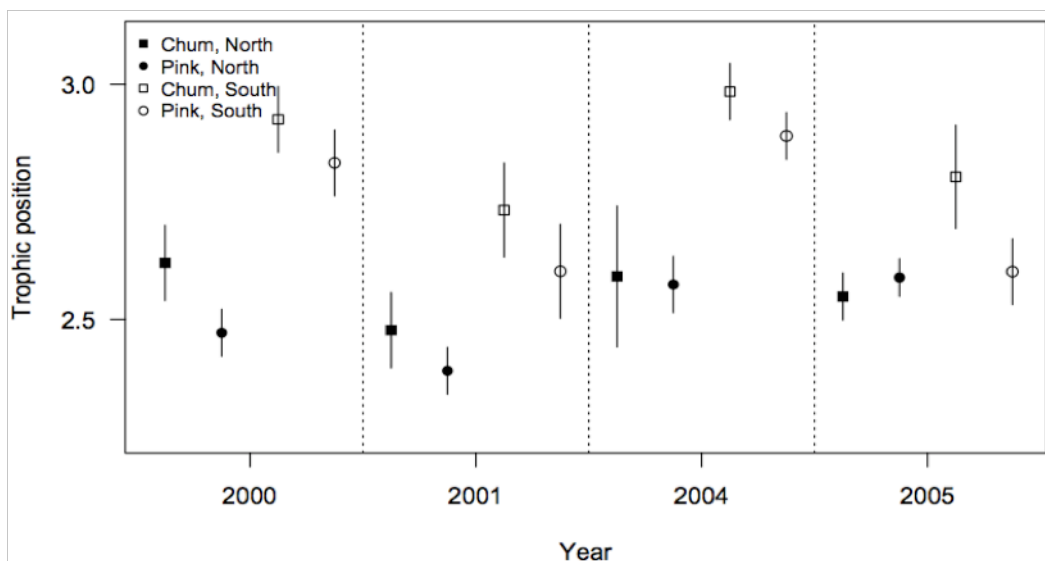


Figure 2.3.6. Trophic positions of juvenile pink salmon and chum salmon in each of the years and in both the northern and the southern regions. The error bars represent the 95% confidence intervals.

Tukey's Honest Significant difference test showed that the trophic position of salmon in the north was significantly lower in the year 2001 than in the other years ($p = 0.002$). The trophic position of pink salmon in the north in cold years was significantly lower than the trophic position of pink salmon in the north in warm years ($p < 0.0001$). Also in the north, the trophic position of pink salmon was significantly lower than the trophic position of chum salmon in cold years ($p = 0.0005$), but not in warm years ($p = 0.96$) (Figure 2.3.6).

An ANOVA showed that the significant factors affecting the trophic position of salmon in the southern region included the species of salmon ($F_{1,90} = 17.2$, $p < 0.0001$), and whether the year was odd or even ($F_{1,90} = 58.1$, $p < 0.0001$). Neither the warm-cool year factor ($F_{1,90} = 0.1$, $p = 0.7$), nor the interaction terms were significant in the south.

Tukey's Honest Significant difference test showed that the trophic position of chum salmon in the south was significantly higher than the trophic position of pink

salmon in the south ($p < 0.0001$), and that the trophic position of both pink salmon and chum salmon in the south was higher in even years than in odd years ($p < 0.0001$) (Figure 2.3.6).

2.3.6 Juvenile salmon food source based on $\delta^{13}\text{C}$

In the northern region, $\delta^{13}\text{C}$ tended to be higher among juvenile pink salmon, except in 2005 when it was higher for juvenile chum salmon. In the southern region, $\delta^{13}\text{C}$ tended to be lower for juvenile pink salmon in cooler years, but the pattern was reversed in warmer years. In the cool years, $\delta^{13}\text{C}$ was lower in the even year, but no consistent pattern was observed between the even and odd years in warmer years.

The trophic- and lipid-corrected carbon isotope ratio for chum salmon ranged from -20.5‰ to -17.6‰ with a mean of $-19.1\text{‰} \pm 0.6\text{‰}$, and for pink salmon it ranged from -20.3‰ to -17.8‰ with a mean of $-19.0\text{‰} \pm 0.5\text{‰}$ (Figure 2.3.7). For a summary of the mean and standard deviation by year, region and species, see appendix 1.

For the northern region, the trophic-corrected $\delta^{13}\text{C}$ data did not have equal variances based on the Fligner-Killeen ($p = 0.007$) and Bartlett ($p = 0.006$) tests. Due to the uneven variances, a Kruskal-Wallis rank sum test was performed and significant differences were shown to exist (chi-squared = 42.9, $df = 3$, $p\text{-value} < 0.0001$). Despite the issue of unequal variances, an ANOVA and Tukey's Honest Significant difference test were performed in order to explore the differences that existed in the data, but with a note of caution to the reader due to the violation of assumptions. The ANOVA showed that the most significant factor affecting $\delta^{13}\text{C}$ in the northern region was whether the year was odd or even ($F_{1, 145} = 43.6$, $p < 0.0001$). Significant interactions occurred between the factors 'species' and 'odd/even year' ($F_{1, 145} = 15.9$, $p = 0.0001$) and there

was also a significant interaction between the factors “odd/even year” and “warm/cold year” ($F_{1, 145} = 15.4, p = 0.0001$).

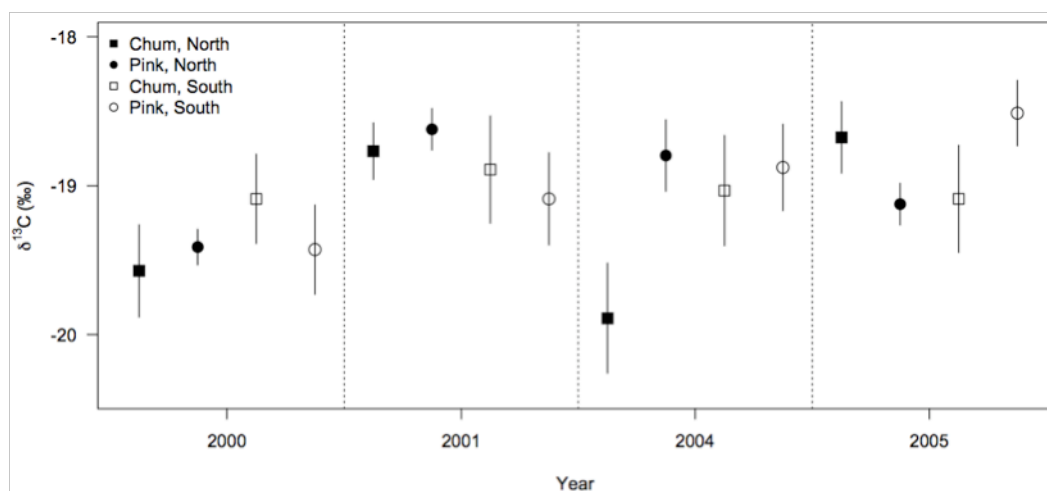


Figure 2.3.7. The mean $\delta^{13}\text{C}$ of pink salmon and chum salmon in each year and region. The error bars represent the 95% confidence limits.

The Tukey’s Honest Significant difference test showed that the trophic-corrected $\delta^{13}\text{C}$ of juvenile chum salmon in the north was significantly lower in even years ($p < 0.0001$). The trophic-corrected $\delta^{13}\text{C}$ of pink salmon in the north was significantly more negative in the year 2000 than it was in 2001 or 2004 ($p = 0.0005$), and was significantly more negative in 2005 than it was in 2001 ($p = 0.0008$). The mean $\delta^{13}\text{C}$ of chum salmon in the north in the year 2004 was significantly lower than the mean $\delta^{13}\text{C}$ of pink salmon ($p < 0.0001$), but in 2005 the $\delta^{13}\text{C}$ of chum salmon was significantly higher than the mean $\delta^{13}\text{C}$ of pink salmon ($p = 0.02$) (Figure 2.3.7).

An ANOVA showed that the significant factors affecting $\delta^{13}\text{C}$ in the southern region were whether the year was warm or cold ($F_{1, 90} = 7.2, p = 0.009$), and whether the year was odd or even ($F_{1, 90} = 4.3, p = 0.04$). A significant interaction occurred between the factors ‘species’ and ‘warm/cold year’ ($F_{1, 90} = 8.9, p = 0.004$).

The Tukey's Honest Significant difference test showed that the trophic-corrected $\delta^{13}\text{C}$ of chum salmon in the south was not significantly different between years. The trophic-corrected $\delta^{13}\text{C}$ of pink salmon in the south was significantly more positive in the year 2005 than it was in 2000 ($p = 0.0006$). The mean $\delta^{13}\text{C}$ of pink salmon and chum salmon were very similar to one another in the southern region every year except for 2005, when pink salmon had a higher mean $\delta^{13}\text{C}$, but this difference was not found to be significant ($p = 0.19$) (Figure 2.3.7).

2.3.7 Evidence for the effect of CPUE on niche overlap

The MANOVA performed on the combined trophic position and $\delta^{13}\text{C}$ of salmon in the northern region showed that all of the factors were significant. The factor “odd/even year” was the most significant ($F_{1, 145} = 21.9$, $p < 0.0001$), followed by the factor “warm/cold year” ($F_{1, 145} = 15.0$, $p < 0.0001$), and then the factor “species” ($F_{1, 145} = 4.0$, $p = 0.02$). There were significant interactions between the factors “warm/cold year” and “odd/even year” ($F_{1, 145} = 8.2$, $p = 0.0004$), the factors “warm/cold year” and “species” ($F_{1, 145} = 4.8$, $p = 0.009$), and the factors “odd/even year” and “warm/cold year” ($F_{1, 145} = 7.9$, $p = 0.0006$).

In the southern region, the MANOVA showed that all of the factors were again significant. The factor “odd/even year” was again the most significant ($F_{1, 90} = 28.7$, $p < 0.0001$), followed by the factor “species” ($F_{1, 90} = 9.0$, $p = 0.0003$), and then the factor “warm/cold year” ($F_{1, 90} = 4.2$, $p = 0.02$). The interaction term between the factors “warm/cold year” and “species” was also significant ($F_{1, 90} = 4.4$, $p = 0.02$).

The mean Euclidean distance between species in a given year and region was 0.58 ± 0.27 ‰. When calculating the Euclidean distance, baseline-corrected $\delta^{15}\text{N}$ was

used instead of trophic position, so that the units and scale of each axis would be analogous. The smallest Euclidean distance (suggesting the greatest niche overlap) between pink salmon and chum salmon (0.33 ‰) occurred in the north in 2001, and the largest Euclidean distance between species (1.09 ‰) occurred in the north in 2004. The Euclidean distance was also large in the south in 2005 (0.89 ‰) (Figure 2.3.8).

Regression analysis showed that there was not a significant relationship between the Euclidean distance between species and the difference in mean length (averaged first by tow) between species in a given year and region ($R^2 = 0.34$, $df = 6$, $p = 0.13$). This suggests that the difference in trophic niche between juvenile pink salmon and chum salmon cannot be predicted based on differences in size between the two species. A linear regression of Euclidean distance versus \log_e mean total CPUE found a significant negative relationship ($R^2 = 0.73$, $df = 6$, $p = 0.007$) between the two variables (Figure 3.9a). There was a significant positive relationship between Euclidean distance and the mean zooplankton density (dried g per 1000 m³) ($R^2 = 0.51$, $df = 6$, $p = 0.05$) (Figure 3.9b). When CPUE was divided by zooplankton density, there was a positive relationship with Euclidean distance ($R^2 = 0.68$, $df = 6$, $p = 0.01$) (Figure 3.9c). Finally, a negative relationship existed between the variables \log_e CPUE and zooplankton density, but the relationship was not significant at an α level of 0.05 ($R^2 = 0.47$, $df = 6$, $p = 0.06$) (Figure 3.9d).

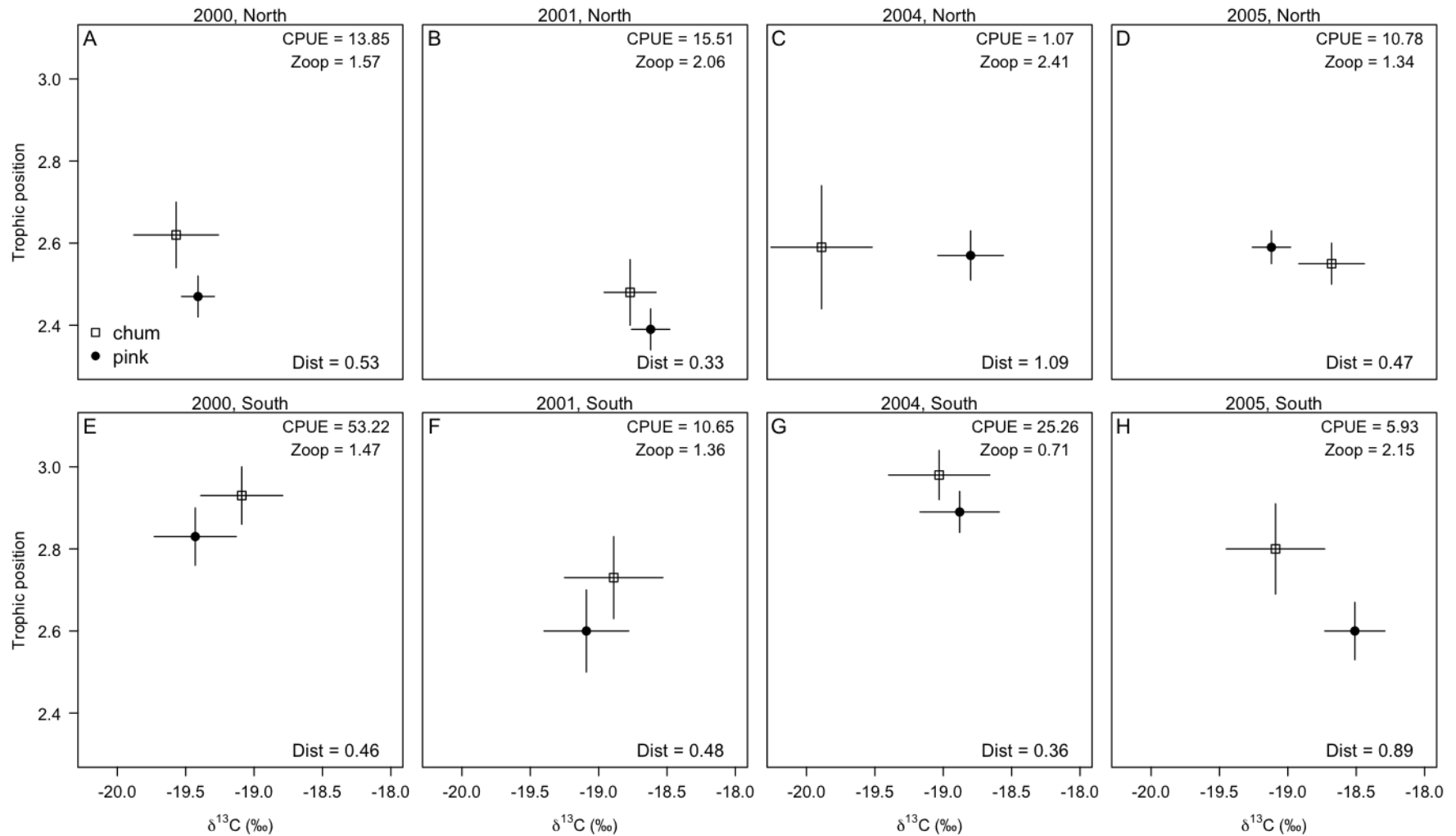


Figure 2.3.8. Mean trophic position versus the mean lipid- and trophic-corrected $\delta^{13}\text{C}$ of juvenile pink salmon and chum salmon in the northern and southern regions of the study area. Error bars represent 95% confidence limits. Figures A to D represent the northern region in the years 2000, 2001, 2004, and 2005, while figures E to H represent the southern region in the same years. The corresponding mean total CPUE and mean zooplankton density (dried g per 1000 m³) are included in the top right of each figure. Dist indicated in the bottom right of each graph represents the Euclidean distance (‰), calculated using the baseline corrected $\delta^{15}\text{N}$ and trophic corrected $\delta^{13}\text{C}$.

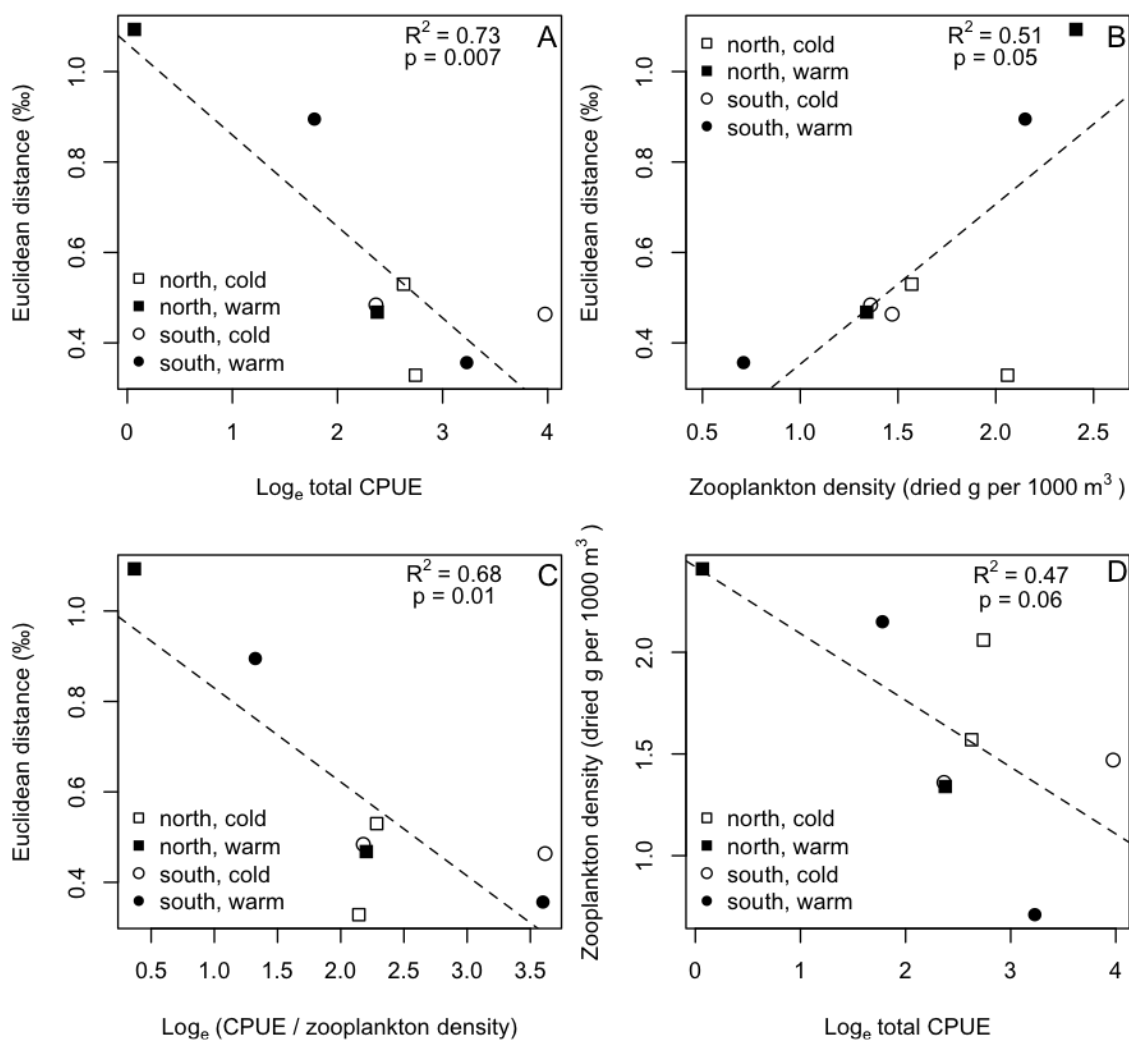


Figure 2.3.9. Relationships between Euclidean distance, zooplankton density, and CPUE.

Euclidean distance (‰) refers to the distance between pink and chum isotope signatures for a given year and region. Plot A represents the relationship between the Euclidean distance and total CPUE. Plot B represents the relationship between Euclidean distance and the mean zooplankton density (dried g per 1000 m^3). Plot C represents the relationship between Euclidean distance and the CPUE divided by the zooplankton density. Plot D represents the relationship between the mean CPUE and zooplankton density. The R^2 and p -values are given on each plot for a linear regression between the two variables, and dashed lines represent the slope of the regression.

2.4. Discussion

The purpose of this study was to examine the feeding habits and trophic interactions of juvenile pink salmon and chum salmon in the coastal marine environment, and to compare these patterns between years of contrasting ocean conditions and salmon abundance. Contrary to expectations, I discovered that the trophic position of pink salmon and chum salmon was greatest in the southern region in even years when the abundance of juvenile salmon was also the highest. The trophic position was generally higher among chum salmon, and pink salmon in the southern region tended to have a more offshore-based diet in cooler years than in warm years. I found evidence that in warm years, the niches of juvenile pink salmon and chum salmon were more similar when abundance was high, and less similar when abundance was low.

This discussion will focus first on the size and abundance of pink salmon and chum salmon in the years and regions that were sampled. Next, this discussion will cover the effect of the region, abundance of salmon, and ocean conditions on the trophic level and food source of juvenile salmon. Finally, the discussion will focus on changes in the degree of niche overlap between pink salmon and chum salmon in years of contrasting ocean conditions.

2.4.1 Evidence of a density effect on the size of juvenile salmon

I expected that there would be increased abundance in even years in the southern portion of the study area (TD) due to the large number of juvenile pink salmon that leave the Fraser River in even years (Neave 1952). This expectation was met, as, in even years, there seemed to be a greater abundance of salmon in the southern portion of the study area. This suggests that the higher abundance of pink salmon leaving the Fraser River in even years did indeed contribute to the higher abundance of juvenile

pink salmon in the southern region in even years in this study. It is interesting to note though, that chum salmon were also more abundant in even years in the southern region, so the increased abundance is not due solely to Fraser River pink salmon.

The abundance also tended to be greater in the cooler years. This may suggest that the survival of juvenile salmon in the freshwater and coastal marine environments is improved when temperatures are closer to the historically average temperatures, such as the juveniles encountered in 2000 and 2001, as opposed to the more anomalously warm conditions observed in 2004 and 2005. There was a record return of over 20 million pink salmon to the Fraser River in 2001, which would represent the same cohort that left in 2000, when conditions were relatively cool (Beamish 2002). It was estimated that fewer than 10 million spawners returned in 2005 from the cohort that left in the warm year, 2004; this was lower than the average return of pink salmon to the Fraser, which is usually between 12 and 15 million spawners (Pacific Salmon Commission 2009). Mueter et al. (2002) also found that among the southern populations of pink salmon, chum salmon, and sockeye salmon, returns improved when juveniles entered the ocean in cooler years. The improved returns from juvenile cohorts that enter the ocean in cooler years in southern regions may be due to improved early marine survival resulting from an abundance of higher quality prey; it may also result from the reduced probability of a timing mismatch between juvenile salmon and their preferred prey (Mackas et al. 2007).

I expected that increased abundance would cause a density effect and that salmon would be smaller in years when there was greater abundance. It appears that the density of juvenile salmon does affect the size, since the mean size was negatively

correlated with the abundance of salmon. This was especially evident in the north in 2004 when very few salmon were caught and the average size for both pink and chum was relatively large. This conclusion is supported by the findings of other research (Ruggerone & Nielsen 2004), but it is also possible that the reduced CPUE and greater length may in fact reflect a shift in the timing of ocean entry, growth, and departure for the open ocean. The year 2004 was warm and plankton blooms occurred earlier than normal (DFO 2005), and warmer river temperatures may also have encouraged earlier departures of salmon into the coastal marine environment. These fish may then have grown faster and left the coast earlier than in other years, which would explain the small number of fish present and their larger size, as opposed to providing evidence of density-dependent growth.

It was observed that pink salmon in the north tended to be larger than chum salmon, especially in 2000 and 2004, while chum salmon tended to be larger than pink salmon in the south, especially in the cool years 2000 and 2001. This might suggest that there is a difference in mean time of emergence between the two species, with pink salmon in the north hatching and leaving the freshwater environment earlier than chum salmon, and the opposite pattern in the south. It is also possible that the differences in size between pink salmon and chum salmon point to evolutionary differences among the mix of populations sampled in the northern and southern regions. However, growth is a very plastic trait among salmon (Weatherley & Gill 1995), so it may be that conditions simply favoured the growth of pink salmon in the north and chum salmon in the south.

2.4.2 Enhanced trophic position in the south and when competition is high

I expected that the trophic position of pink salmon and chum salmon would increase when conditions were better. Notably, I expected that conditions would be

better in the northern region due to the presence of lipid-rich zooplankton prey (Lee et al. 2006), and because this area is further from the edge of the habitat range of pink salmon and chum salmon (Mueter et al. 2002). I also expected that conditions in the south would be improved in the cooler years due to increased mixing of the water column (Gargett 1997) and an influx of lipid-rich zooplankton (Trudel et al. 2007). Furthermore, I expected the trophic position of salmon to be reduced in even years in the south when abundance, and therefore competition, was high. Contrary to these expectations, the trophic position of juvenile salmon was actually higher in the southern region than in the north. The trophic position was also higher in even years in the southern region, when the abundance of juvenile salmon was high as well as warm years in the northern region. This pattern suggests that the trophic position of juvenile salmon might, in fact, increase under conditions of lower prey quality and increased competition, especially in the southern portion of the study area.

The higher mean trophic position displayed in the southern region might be due to a longer food chain in the south, perhaps with a greater abundance of smaller zooplankton species, and may indicate greater omnivory among zooplankton in the north (Peterson & Fry 1987). It is also likely that the trophic position of zooplankton does not predict its quality as a prey item. For example, many gelatinous zooplankton are carnivorous, but are not high in lipids and are generally a nutritionally poor food source (Davis 1993). Jennings et al. (2001) found that trophic position tends to increase with size within a species, but not always among species. There may be some omnivorous or carnivorous zooplankton species within which trophic position is related to prey size and therefore quality, but there is no evidence that higher trophic position

among zooplankton indicates higher quality prey. Therefore, a higher trophic position among juvenile salmon could, in some instances, be the result of eating poorer quality prey. This could also explain the higher trophic position of juvenile pink salmon and chum salmon the south in even years, when the abundance of fish in the south was highest. Perhaps the increase in trophic position among salmon in even years in the south reflects a greater reliance on nutritionally poor, carnivorous gelatinous zooplankton species. Furthermore, in limited observations of the stomach contents of both juvenile pink salmon and chum salmon in this study, the presence of gelatinous zooplankton species was detected, including cnidarians, ctenophores, and pteropods (*Limacina sp.*). There was also a large quantity of unidentifiable stomach contents, which could further suggest the presence of gelatinous zooplankton since this type of prey is difficult to identify and quickly digested (Arai et al. 2003).

While the trophic position among juvenile salmon was higher in the south in even years, juvenile chum salmon were not larger in the south in even years, and juvenile pink salmon in cold years were larger in the even year (2000), but smaller in the warm even year (2004). Therefore there is no consistent evidence that pink salmon and chum salmon were larger in the south in even years, which suggests that they did not benefit in the form improved growth as a result of eating prey of a higher trophic position. This further suggests that trophic position among these juvenile salmon may not be a reflection of prey quality.

The trophic position of chum salmon tended to be higher than pink salmon, except in the north in the warmer years. If gelatinous zooplankton are a more important prey item for chum salmon (Black & Low 1983, Tadokoro et al. 1996), and those

zooplankton are, in fact, of a higher trophic position than other important zooplankton prey, then this might explain the trend. Conversely, higher trophic positions might be evidence of different rates of accumulation of isotopes into the muscle tissue of juvenile pink salmon and chum salmon. It could also indicate a consistent trend in the prey preference of chum salmon, but of a prey type other than gelatinous zooplankton that has not been identified previously. An alternative explanation could be that an increase in competition for prey causes juvenile salmon to become more piscivorous, despite the increased risk of preying upon larger, harder to catch prey, and that this causes the increased trophic position among juvenile salmon under poorer feeding conditions. Density-dependent foraging time among juvenile marine fishes provides evidence that increased competition for prey resources can lead to increased foraging time (Walters & Juanes 1993). Increased foraging time increases the risk of predation, which suggests that competition encourages riskier feeding behaviours.

The higher mean trophic position exhibited in the south was due in part to generally higher baseline isotope signatures among the zooplankton sampled in the northern region. It is possible that the baseline used may not be an ideal reflection of the true baseline for the salmon. These salmon might have migrated recently from a more southern area, or the baseline isotope signature may have shifted suddenly before the sampling occurred. Isotope turnover in fish muscle tissue can take several months (Buchheister & Latour 2010) but depends on the size of the fish and how quickly it is growing (Weidel et al. 2011), so the isotope signatures of fish may reflect an earlier baseline isotope signature and not a lower trophic position. In order to determine an ideal baseline isotope signature to use, one would need to know the river where the

salmon originated, the speed and direction of migration, the rate of tissue turnover, and a time-series of zooplankton isotope signatures leading up to the time when fish were caught. Also, the trophic position calculated was often lower than three, but these salmon most likely would have a true trophic level of 3 or higher since they eat a variety of zooplankton, many of which are carnivorous (Brodeur et al. 2007). The trophic positions calculated should therefore be considered as relative rather than absolute trophic positions.

Despite some of the issues outlined concerning the isotope baseline, I believe the conclusion that salmon display a higher trophic position in the southern region is still valid, although it is possible that the difference in trophic position may be overestimated. Because these salmon are juveniles, they are growing quickly and incorporating the new baseline signature quickly into their muscle tissue. Pink salmon and chum salmon smolts weigh 0.2 to 0.4 grams when they enter the ocean (Quinn 2005) whereas the mean weight of the sampled pink salmon and chum salmon in the fall was 121 grams, so salmon had grown to more than 400 times their initial weight. Tissue replacement would occur rapidly as juvenile salmon grew, and at the time of capture tissue turnover would be occurring at a rate of approximately 0.01% per day, with a half-life of 70 days (Weidel et al. 2011).

2.4.3 Evidence for a more offshore-based food source in cooler years

In the south, pink salmon tended to have lower $\delta^{13}\text{C}$ than chum salmon in the cooler years, and higher $\delta^{13}\text{C}$ in the warmer years, whereas the $\delta^{13}\text{C}$ of chum salmon remained relatively constant. This might indicate that pink salmon are relying more on a food chain that originates from offshore waters in the cooler years, and from nearshore

waters in the warmer years. In warmer years there is more stratification of the water column (Whitney et al. 2005); this may have caused pink salmon to rely more heavily on nearshore nutrients in the warmer years, since less offshore nutrients would be introduced through the mixing of the water column. The same pattern did not occur among chum salmon, which may indicate that there was a certain feeding behaviour among chum salmon, or perhaps a favoured prey item, that masked or eliminated the isotopic effect of an increase in offshore nutrients.

The warm-year versus cold-year effect observed among pink salmon in the southern region is especially interesting in light of the work published by Kline et al. (2008). They found that marine survival increased in years when juvenile pink salmon diets were supplemented by a carbon source with depleted carbon isotope signatures, suggesting an influx of zooplankton with oceanic origin (Perry et al. 1999). In my study, the pink salmon in the south had low $\delta^{13}\text{C}$ signatures in the year 2000, and returned in great numbers in the year 2001 (Beamish 2002). This suggests that a similar phenomenon may have occurred among the fish I sampled as occurred with juvenile pink salmon in Kline's study in Prince William Sound, Alaska.

In the northern region, the carbon isotope signature of pink salmon did not change much from year to year, while the $\delta^{13}\text{C}$ of chum salmon appeared to be more negative in even years. Since a lower $\delta^{13}\text{C}$ can result from a greater proportion of nutrients from offshore waters (Perry et al. 1999, Miller et al. 2008), the changes in the carbon isotope signature might be related to changes in downwelling in the Alaska Coastal Current, or perhaps increased runoff from the land, which would increase terrestrial nutrients in the water. The fact that the pink salmon do not appear to be

affected by this same force suggests that it may relate to the feeding behaviour of chum salmon in the north. In the year 2004, when the greatest difference between pink salmon and chum salmon $\delta^{13}\text{C}$ is observed, chum salmon are also much smaller than pink salmon, which could have reduced the variety of prey to which they had access. Perhaps in this year they were limited to smaller, more offshore species due to their smaller size.

2.4.4 Competition increases niche overlap

My results indicate that for a given length, chum salmon tend to be heavier than pink salmon, while pink salmon have much larger egg sacs than chum salmon. These two findings suggest that, despite the similarity in their appearance at this early life-stage, pink salmon and chum salmon are physiologically distinct. Their innate physiological differences might result in different behaviours and dietary needs, which would suggest that juvenile pink salmon and chum salmon inhabit somewhat different ecological niches despite sharing the same habitat.

The combined trophic position and $\delta^{13}\text{C}$ of salmon shows that the trophic niche of the two species tends to overlap, though not always in a consistent manner. Whereas chum salmon tend to be at a slightly higher trophic position, there was no consistent difference in the $\delta^{13}\text{C}$ of the two species. I expected that the niches of pink salmon and chum salmon would overlap more when conditions were poor and when abundance was high. This appeared to be accurate because as CPUE increased, the distance between the niches of the two species decreased, indicating greater overlap when salmon abundance is high. When CPUE was divided by zooplankton density as a measure of available resources, there was a positive relationship between available prey resources

and Euclidean distance. This supports the hypothesis that it is increased competition for fewer resources that leads to the increased overlap of the niches of juvenile pink salmon and chum salmon. Perhaps when competition is greater for fewer prey items, both species will become less selective and incorporate a greater proportion of less favourable prey items into their diets. In the south in 2004 when abundance was high, the niches of pink salmon and chum salmon were similar and the trophic positions of both pink salmon and chum salmon were also very high, so perhaps both species increased their reliance on lower quality though more carnivorous prey, such as gelatinous zooplankton.

In the regions and years when the difference in niche between pink and chum were greatest (2005 south, 2004 north), the zooplankton density was also high. It might be that increased prey availability leads to greater niche differentiation between juvenile pink salmon and chum salmon. The zooplankton density was somewhat negatively correlated to the abundance of salmon, so it is possible that salmon reduce zooplankton density by feeding on the zooplankton, or that the density of zooplankton observed was unrelated to the abundance of salmon.

2.4.5 Conclusion

Welch and Parsons (1993) used stable isotopes to determine that pink salmon and chum salmon occupy a different niche as adults in the open ocean, while several other isotope studies found no such differentiation (Johnson & Schindler 2009). Fewer isotope studies have focused on juvenile pink salmon and chum salmon, but my results suggest that the degree of niche differentiation among juvenile salmon may be the result of a complex interplay between ocean conditions, prey availability, and the abundance of competitors. This conclusion supports findings based on stomach content analysis of

juvenile pink salmon and chum salmon (Brodeur et al. 2007). What is most apparent is that the niches of pink salmon and chum salmon are not static but change from year to year and region to region. Despite this dynamic nature of the niche of pink salmon and chum salmon, overall their niche tends to remain similar to each other, and they most likely will compete for the same resources and be affected similarly by changing ocean conditions.

If there is an increase in gelatinous zooplankton in the Pacific Ocean as climate change continues, a phenomenon that has been observed in other parts of the ocean (Brodeur 1999, Atkinson et al. 2004, Richardson 2008), then chum salmon might be the beneficiaries of this shift, while other species that are less well-adapted to this type of prey may begin to decline. An interesting next step in this research would be to determine the degree to which juvenile pink salmon and chum salmon depend on gelatinous zooplankton, and at what stage in their ontogeny a shift to this type of prey might occur.

Table 2.2. Summary of mean $\delta^{15}\text{N}$ data and the mean baseline corrected trophic levels for each year, region, and species. The column entitled ' $\delta^{15}\text{N}$ (‰)' reports the mean raw nitrogen isotope ratio. The column entitled 'drying method correction $\delta^{15}\text{N}$ (‰)' reports the nitrogen isotope signature after the correction was applied to samples that were oven-dried. The column 'trophic position' gives the mean trophic position calculated as described in the methods section. Each column labelled 'SD' gives the standard deviation of the mean in the preceding column.

Year	Region	Species	$\delta^{15}\text{N}$ (‰)	SD	Drying method correction		Trophic position	SD
					$\delta^{15}\text{N}$ (‰)	SD		
2000	North	Chum salmon	12.40	0.49	12.29	0.46	2.62	0.15
		Pink salmon	11.94	0.41	11.86	0.38	2.47	0.10
		Chum salmon	12.99	0.39	12.85	0.36	2.93	0.14
	South	Pink salmon	12.30	0.40	12.20	0.38	2.83	0.13
		Chum salmon	12.96	0.31	12.96	0.31	2.48	0.16
		Pink salmon	12.41	0.30	12.41	0.30	2.39	0.13
2001	North	Chum salmon	12.94	0.34	12.94	0.34	2.73	0.16
		Pink salmon	12.37	0.46	12.37	0.46	2.60	0.22
		Chum salmon	12.66	0.59	12.66	0.59	2.59	0.20
	South	Pink salmon	12.57	0.30	12.57	0.30	2.57	0.13
		Chum salmon	12.99	0.44	12.99	0.44	2.98	0.09
		Pink salmon	12.58	0.32	12.58	0.32	2.89	0.06
2004	North	Chum salmon	12.81	0.28	12.81	0.28	2.55	0.10
		Pink salmon	12.99	0.29	12.99	0.29	2.59	0.10
		Chum salmon	13.36	0.31	13.36	0.31	2.80	0.17
	South	Pink salmon	12.74	0.57	12.74	0.57	2.60	0.14

Table 2.3. Summary of mean $\delta^{13}\text{C}$ data before and after corrections for each year, region, and species. The column entitled ' $\delta^{13}\text{C}$ (‰)' reports the mean raw carbon isotope ratio. The column entitled 'drying method correction $\delta^{13}\text{C}$ (‰)' reports the carbon isotope signature after the correction was applied to samples that were oven-dried. The column 'lipid corrected $\delta^{13}\text{C}$ ' gives the mean carbon isotope signature after lipid correction calculated as described in the methods section, and the column 'trophic-corrected $\delta^{13}\text{C}$ ' reports the final carbon isotope signature as described in the methods section. Each column labelled 'SD' gives the standard deviation of the mean in the preceding column.

Year	Region	Species	$\delta^{13}\text{C}$ (‰)	SD	Drying method correction $\delta^{13}\text{C}$ (‰)	SD	Lipid corrected $\delta^{13}\text{C}$ (‰)	SD	Trophic level corrected $\delta^{13}\text{C}$ (‰)	SD
2000	North	Chum	-18.86	0.58	-18.84	0.55	-18.95	0.55	-19.57	0.58
		salmon								
		Pink								
	South	Chum	-19.08	0.43	-18.89	0.27	-18.94	0.26	-19.41	0.27
		salmon								
		Pink								
2001	North	Chum	-18.04	0.53	-18.04	0.53	-18.16	0.53	-19.09	0.58
		salmon								
		Pink								
	South	Chum	-18.43	0.55	-18.46	0.55	-18.59	0.55	-19.43	0.56
		salmon								
		Pink								
2004	North	Chum	-18.11	0.37	-18.11	0.37	-18.29	0.36	-18.77	0.41
		salmon								
		Pink								
	South	Chum	-18.10	0.37	-18.10	0.37	-18.23	0.36	-18.62	0.39
		salmon								
		Pink								
2005	North	Chum	-17.97	0.55	-17.97	0.55	-18.16	0.56	-18.89	0.59
		salmon								
		Pink								
	South	Chum	-18.30	0.57	-18.30	0.57	-18.49	0.57	-19.09	0.63
		salmon								
		Pink								
2004	North	Chum	-19.07	0.52	-19.07	0.52	-19.30	0.50	-19.89	0.49
		salmon								
		Pink								
	South	Chum	-18.03	0.48	-18.03	0.48	-18.22	0.50	-18.80	0.51
		salmon								
		Pink								
2005	North	Chum	-17.80	0.63	-17.80	0.63	-18.05	0.60	-19.03	0.55
		salmon								
		Pink								
	South	Chum	-17.77	0.38	-17.77	0.38	-17.99	0.34	-18.88	0.36
		salmon								
		Pink								
2005	North	Chum	-18.05	0.47	-18.05	0.47	-18.13	0.47	-18.68	0.51
		salmon								
		Pink								
	South	Chum	-18.39	0.34	-18.39	0.34	-18.53	0.31	-19.12	0.36
		salmon								
		Pink								
2005	North	Chum	-18.18	0.66	-18.18	0.66	-18.28	0.64	-19.09	0.57
		salmon								
		Pink								
	South	Chum	-17.84	0.40	-17.84	0.40	-17.91	0.40	-18.51	0.43
		salmon								
		Pink								

Table 2.4. Summary of mean zooplankton isotope data for each year and region. The column entitled ' $\delta^{15}\text{N}$ (‰)' reports the mean nitrogen isotope ratio. The column entitled ' $\delta^{13}\text{C}$ (‰)' reports the mean carbon isotope ratio. The column entitled 'Lipid corrected $\delta^{13}\text{C}$ (‰)' reports the mean carbon isotope ratio after lipid correction. Each column labelled 'SD' gives the standard deviation of the mean in the preceding column.

Year	Region	$\delta^{15}\text{N}$ (‰)	SD	$\delta^{13}\text{C}$ (‰)	SD	Lipid corrected $\delta^{13}\text{C}$ (‰)	SD
2000	North	10.30	0.37	-20.76	0.86	-19.55	0.88
	South	9.52	0.78	-19.78	1.18	-18.84	1.19
2001	North	11.04	0.66	-19.54	1.38	-17.88	1.39
	South	10.59	0.70	-18.84	1.44	-17.66	1.45
2004	North	10.65	0.63	-19.30	1.66	-17.68	1.68
	South	10.12	0.85	-20.00	1.37	-18.88	1.37
2005	North	10.98	0.35	-20.05	0.57	-19.19	0.60
	South	10.73	0.65	-20.38	0.93	-19.45	0.95

Chapter 3:

Ontogenetic niche shift among juvenile pink salmon and chum salmon in years of contrasting ocean conditions

Abstract

An ontogenetic niche shift can include changes in morphology, habitat, and feeding behaviour, and as an organism grows it may undergo such a shift. Juvenile pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), the most abundant species of Pacific salmon, experience a period of rapid growth during their first summer at sea, and the purpose of this paper is to determine how the food sources and trophic positions of these species change during that time. Understanding the foodweb dynamics of juvenile salmon in the coastal marine environment is important because a large proportion of the overall mortality of salmon is thought to occur during their first summer at sea. I also explored how the ontogenetic niche shift of juvenile pink salmon and chum salmon is affected by contrasting ocean conditions, which is important in understanding how climate change may affect the feeding behaviour and, ultimately, survival of Pacific salmon.

I hypothesized that juvenile salmon would shift their diet to a more offshore-based foodweb as they grew, but that the shift would be stronger in cool years due to improved feeding conditions. I expected that the shift would be weaker in warm years, especially in the south, when the ocean exhibits a shift to less nutritious prey species, and when a timing mismatch between salmon and their prey may occur. I also hypothesized that the trophic position of juvenile salmon should increase with size, as larger salmon have access to larger and higher trophic level prey. Finally, I also

hypothesized that zooplankton in the northern region would be more lipid-rich and, as a result, salmon in the north would display higher lipid content than salmon in the south.

My results show that the ontogenetic shift from summer to fall among juvenile salmon includes a shift to a more offshore-based diet and a higher trophic position. In the northern region the shift to an offshore food source was more pronounced, while in the south the shift to a higher trophic position was more pronounced. There was no evidence that the ontogenetic shift was smaller in warm years, but in warm years fish displayed a higher trophic position and appeared to eat from a more nearshore food source. Zooplankton was more lipid-rich in the northern region, but this did not translate into a clear pattern in energy density among juvenile salmon. In general, the trophic position of fish increased with size, but the relationship was more common among pink salmon and in the fall. I suggest that juvenile salmon in the south and in warm years may rely more heavily on higher trophic level prey, while salmon in the north might rely on prey that is lipid-rich but of a lower trophic position.

3.1. Introduction

3.1.1 Ontogenetic niche

An ontogenetic niche shift can include changes in the morphology of an organism, its feeding behaviour and habitat, as well as the competitors and predators with which it interacts (Werner & Gilliam 1984). Such shifts occur when an organism moves to a new habitat, when the available prey changes, or when the morphology of an organism changes, such that it has access to different prey. As an organism grows, it will have access to a wider variety of prey items, and while some species will continue to feed on smaller prey items while incorporating larger prey items, other species will display more discrete ontogenetic stages, abruptly shifting from one prey-type to another (Werner & Gilliam 1984).

Juvenile pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) enter the marine environment soon after emerging from the gravel, unlike other salmon species that tend to delay in lakes and rivers before smoltification. Because they leave freshwater so soon after emerging, they are quite small when they first enter the marine environment, and during their first summer and fall at sea they undergo rapid growth, growing to as much as 400 times their initial weight by the time fall arrives (Quinn 2005). It is unclear how the ontogenetic niches of juvenile pink salmon and chum salmon change during their first summer at sea, during the period of rapid growth that occurs in the coastal marine environment.

3.1.2 The diet of juvenile pink and chum salmon

Diet studies of juvenile salmon can help to clarify the nature of the ontogenetic niche shift that occurs during the first summer and fall at sea. Pink salmon and chum

salmon have been found to feed during the day on highly visible prey (Landingham et al. 1998, Armstrong et al. 2005). In July in the Gulf of Alaska, juvenile pink salmon fed mainly on larvaceans (tunicates), pteropods (*Limacina helicina*), and euphausiids. In September and October the diet of juvenile pink salmon was composed mainly of hyperiid amphipods, large copepods, large pteropods (*Clio pyramidata*), and larval or juvenile fishes. It was observed that as juvenile pink salmon increased in size, their diet consisted of a greater percentage of larger prey organisms (Healy 1991, Boldt & Haldorson 2003, Armstrong et al. 2005). Pink salmon smaller than 150 mm in length consumed prey that weighed less than 3 mg, while larger salmon consumed prey that weighed up to 16 mg (Boldt & Haldorson 2003).

In Northern British Columbia (BC) and Southeast Alaska, a diet study revealed that pink salmon and chum salmon relied heavily on euphausiids and hyperiid amphipods, and to a lesser extent, on other prey such as decapods, copepods, larvaceans (tunicates), and fish (Brodeur et al. 2007). However, Brodeur et al. (2007) did not find consistent differences in the diets of pink salmon and chum salmon from the early to the late summer. The diet of chum salmon tends to be similar to that of pink salmon, but chum salmon have been found to rely more heavily on gelatinous zooplankton such as larvaceans and salps (Sturdevant et al. 2004).

3.1.3 The implications of juvenile salmon size and growth

As juvenile salmon grow, their changing morphology (such as increased speed and larger gape size) gives them access to larger prey (Brooks & Dodson 1965). Larger prey tends to be a more efficient prey choice, offering more calories within a single prey item (MacArthur & Pianka 1966), while capturing many small prey items requires more energy expenditure by the predator (Pazzia et al. 2002). Within a species, larger

individuals tend to be of a higher trophic position (Jennings et al. 2001). Hence, if as they grow juvenile salmon select larger individuals within a prey species, this would result in an increase in trophic position as salmon get larger.

Growth in the first months at sea will determine how early in the season juvenile salmon have access to larger, more efficient prey. This is important because it is thought that a large proportion of the mortality that occurs in the marine environment happens in the first few months, and that this mortality may be growth dependent (Parker 1968, Francis & Hare 1994). It has been suggested that salmon must attain a critical size during their first summer at sea because larger salmon are less likely to be preyed upon and more likely to have stored enough fat to survive the winter (Beamish & Mahnken 2001, Farley et al 2011). Even a slight delay in early marine growth may have magnified effects on the overall growth of salmon due to the delay of these diet shifts (Aydin et al. 2005). Juvenile salmon growth has been linked to prey biomass and quality, and the abundance of competitors (Perry et al. 1996, Mathiesen et al. 2007, Trudel et al. 2007). The quality of the prey available varies not only as a function of prey size (Pazzia et al. 2002), but also as a function of lipid content (Trudel et al. 2002). Ocean conditions will play a large role in determining the prey quantity and quality available to juvenile salmon, which will in turn determine the growth and survival of salmon entering the ocean in a given year (El-Sabaawi et al. 2009).

3.1.4 The effect of ocean conditions on the ecology of juvenile salmon

It has been suggested that productivity, and, thus, prey quantity, may increase in warmer years in the Alaska Coastal Current system (ACC) due to increased downwelling and cyclonic winds that lead to an increase in advection of oceanic plankton into nearshore areas. Conversely, productivity further south in the California

Current System (CCS), is suggested to decrease in warm years due to decreased upwelling (Gargett 1997, Mueter et al. 2002). Warmer temperatures lead to increased stratification of the water column; in the ACC, which is light-limited, this allows phytoplankton to remain in the euphotic zone longer, resulting in increased primary production. In the CCS, which is not light-limited, increased stratification and reduced mixing of the water column results in lower nutrient availability, which reduces primary productivity (Gargett 1997).

Along the southern BC coast, warmer years have been linked to an influx of lipid-poor southern zooplankton species (Mackas et al. 2004, Hooff & Peterson 2006). Such an influx has been suggested to create conditions of poor quality food, especially along the west coast of Vancouver Island, which could potentially lead to reduced growth and delayed ontogenetic niche shifts among juvenile pink salmon and chum salmon. Conversely, in cooler years, the growth and survival of juvenile salmon along the south and central coasts of BC may improve as a result of a greater abundance of lipid-rich zooplankton species (Trudel et al. 2007).

When warm temperature anomalies occur in the coastal marine environment of the North Pacific Ocean, it causes a shift in the timing of plankton blooms, which may in turn create a temporal mismatch between predators and their prey (Mackas et al. 2007). Such a temporal mismatch could lead to poor feeding conditions for juvenile salmon in years when sea surface temperatures are abnormally warm (Winder & Schindler 2004, Mackas et al. 2010). Conditions resulting in a greater abundance of high quality prey available to juvenile salmon should lead to improved growth and

earlier ontogenetic niche shifts among juvenile salmon in the coastal marine environment.

Competition with other juvenile salmon will also determine the accessibility of high quality prey. Pink salmon and chum salmon are the most abundant species of salmon in the Pacific, and the abundance of these two species may drive the level of competition that individual salmon face in the coastal marine environment (Ruggerone et al. 2010). The majority of pink salmon that leave the Fraser River do so only in even years (Neave 1952, Beamish et al. 2010). This 2-year cycle causes large fluctuations in the abundance of salmon in the Strait of Georgia, and, as pink salmon migrate north throughout the summer, may also contribute to the abundance of salmon along the central and northern coasts of BC.

3.1.5 Modeling ontogenetic niche shifts using stable isotope signatures

Stable isotopes of carbon (^{13}C) can be used to determine the food sources of consumers (Peterson & Fry 1987). For example, due to biogeochemical differences, offshore oceanic systems tend to be depleted in heavy isotopes of carbon (more negative $\delta^{13}\text{C}$), while nearshore systems tend to be relatively enriched in heavier ^{13}C (less negative $\delta^{13}\text{C}$) (Perry et al. 1999, Miller et al. 2008). The trophic position of a consumer can be inferred from the stable isotope signature of nitrogen ($\delta^{15}\text{N}$), because heavy isotope enrichment occurs in a predictable manner from one trophic level to the next in marine foodwebs (Peterson & Fry 1987, Post 2002) by a process known as trophic discrimination. Many studies have used this phenomenon to determine the relative trophic position of consumers to each other (ie. Kaeriyama 2004, Welch & Parsons 1993), but have done so without first determining the baseline signatures of primary

consumers. The lack of an isotopic baseline limits the degree to which trophic positions can be reliably compared among seasons, regions, and years, because the baseline can vary depending on biogeochemical processes, such as nitrogen fixation and recycling, that affect $\delta^{15}\text{N}$ at the base of the foodweb (Post 2002, Matthews & Mazumder 2003).

Stable isotopes represent a time-integrated signature of assimilated diet, and can eliminate some of the bias inherent in gut-content analysis (such as variability in the time of sampling, short-term or anomalous changes in feeding patterns, or varying rates of digestion for different prey items) (Peterson & Fry 1987). Stable isotopes can thus be used to determine the general characteristics of the ontogenetic shift that occurs among juvenile salmon from summer to fall, and how the food source and trophic position of fish changes in relation to their size as well as the season. Another benefit of performing stable isotope analysis is that the carbon to nitrogen ratio (regardless of isotope signature) can be used as a proxy for lipid content and energy status in aquatic organisms (McConnaughey & McRoy 1979, Post et al. 2007). The lipid content of both prey and consumers can contribute to a greater understanding of how the energetic condition of the predator may change in relation to the quality of the prey.

3.1.6 Purpose / predictions

The objective of this study is to determine how the ontogenetic niche of juvenile pink salmon and chum salmon shifts during their first months at sea, and how this changes in years of contrasting ocean conditions and salmon abundance. When juvenile salmon initially emerge, they still carry the marine isotope signature of the parent fish (Doucett 1999), but, due to their rapid growth at this stage, the juvenile would quickly take on a more 'nearshore' isotope signature. The offshore marine environment tends to be more enriched in ^{15}N than the terrestrial environment, and estuaries and the nearshore

environment receive greater inputs from the terrestrial environment and therefore have a more 'terrestrial' isotope signature (Schoeninger & DeNiro 1984). As juvenile salmon leave the estuaries and nearshore environment, I anticipate that their tissues would turn over to reflect an increasingly offshore marine foodweb; therefore, I hypothesize that the nitrogen isotope signature of salmon muscle tissue would be higher in the fall. I also expect that the nitrogen isotope signature will increase due in part to the increasing trophic position of the juvenile salmon as they grow (Peterson & Fry, 1987), but carbon stable isotopes will help to confirm the increasing reliance on offshore food sources. The offshore environment is depleted in ^{13}C , so I anticipate that the summer carbon isotope signature of fish would be more positive than the fall isotope signature (Perry et al. 1999).

Anomalously warm temperatures can cause juvenile salmon to emerge from the freshwater environment earlier in the year (Murray & McPhail 1988), but can also cause a timing mismatch between juvenile salmon and their prey (Aydin et al. 2005). As a result, I hypothesize that in warm years the ontogenetic shift from summer to fall would be diminished due to poor early feeding conditions, so there would be less of a difference in the ontogenetic niche and size of juvenile salmon between summer and fall in warmer years. I anticipate that this diminished-shift effect would be more pronounced in the south than in the north, as the shift from northern to southern zooplankton species has been reported to occur to a greater degree in the southern end of the transition zone between the California Current System (CCS) and the Alaska Coastal Current (ACC) (Mackas et al. 2010). I also hypothesize that this diminished niche-shift effect would be stronger in the south in even years, when there is more competition for

prey resources due to a greater abundance of juvenile pink salmon migrating north from the Fraser River (Neave 1952).

As salmon grow larger, they have access to larger and higher trophic level prey (Boldt & Haldorson 2003); therefore I hypothesize that there would be a positive correlation between the size and trophic position of juvenile pink salmon and chum salmon. I anticipate that this effect would be stronger in the south, where zooplankton tends to be depleted in lipids compared to the north (Lee et al. 2006); as a result, larger prey would be more important for continued growth in the south, whereas in the north the quality of a prey item may not be as strongly linked to its size (and therefore trophic position). In order to test this hypothesis, I will also use the carbon to nitrogen ratio of the zooplankton samples to test the assumption that zooplankton in the north are indeed more lipid-rich than those in the south. Finally, I expect that feeding on lipid-rich prey will contribute to an increase in the fat stored by juvenile salmon, and so I expect there to be a positive relationship between the energy density of juvenile salmon and the energy density of zooplankton.

3.2. Methods

3.2.1 Study area

The study area extends northward from the northern tip of Vancouver Island to the southern end of Southeast Alaska (Figure 3.2.1). This area represents the southern portion of the downwelling domain of the Alaska Coastal Current (ACC) and also a transition zone that occurs between the ACC and the upwelling domain of the California Current System (CCS) (Ware & MacFarlane 1989).

3.2.2 Sampling design

Juvenile salmon were collected in the study area in the summer (June/July) and the fall (October/November) of 2000, 2001, 2004, and 2005. Based on BC lighthouse data available from Fisheries and Ocean Canada (<http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm>) the mean sea surface temperatures were relatively cool in the spring and summer of the years 2000 and 2001, and were relatively warm in the spring and summer of the years 2004 and 2005 (Figure 3.2.2). The years 2000 and 2001 corresponded to a cool/negative phase of the Pacific Decadal Oscillation (PDO), while 2004 and 2005 corresponded to a warm/positive phase of the PDO.

The years 2000, 2001, 2004, and 2005 were chosen not only for the contrast in ocean conditions, but also in order to sample from an odd and even year in both warm and cold conditions. Due to the dominance of odd-year spawners that arrive in the fall, the majority of juvenile pink salmon leave the Fraser River in even years rather than odd years (Neave 1952), so there would have been a greater abundance of juvenile pink salmon entering the Strait of Georgia from the Fraser River and migrating northward in 2000 and 2004. This odd-year dominance pattern does not hold for many rivers north of the Fraser (Riddell & Beamish 2003), so the overall abundance of juvenile pink salmon in the study area, which is north of the Strait of Georgia, is not necessarily greater in even years.

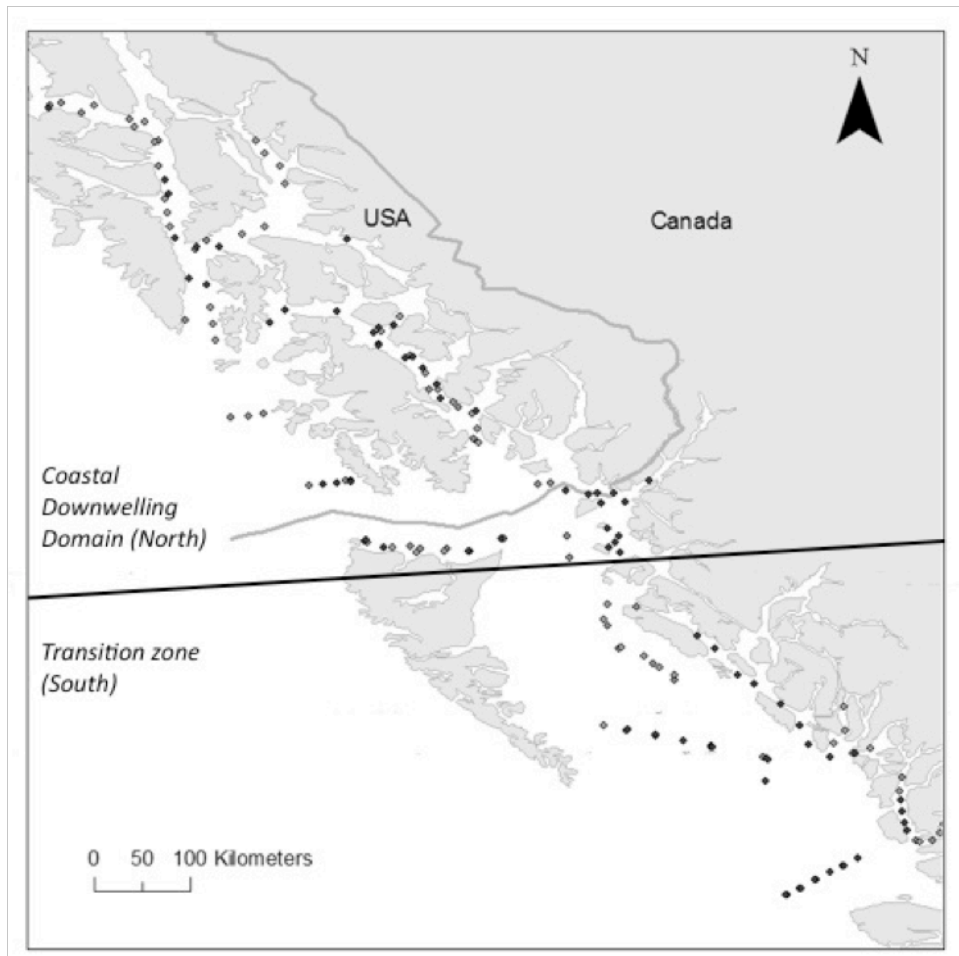


Figure 3.2.1. The study area, which extends from the northern tip of Vancouver Island north to Southeast Alaska. Points represent sample sites, although some did not have any fish. For the purposes of this study, the ‘northern’ region includes the sites along the northern edge of the Haida Gwaii, and all of the sites further north. The regions are based on the fisheries production domains of the North East Pacific (Ware & MacFarlane 1989); the northern region corresponds to the coastal downwelling domain of the Alaska Coastal Current, and the southern region corresponds to the transition zone between the Coastal Downwelling and Coastal Upwelling Domains.

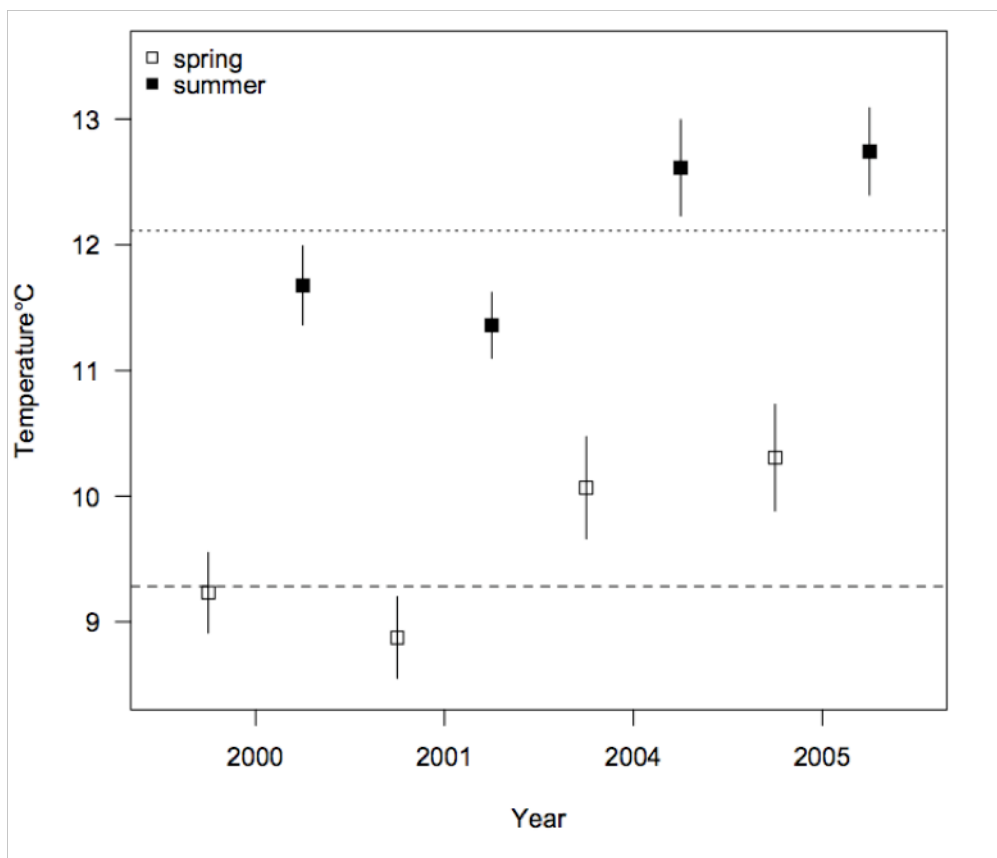


Figure 3.2.2. The mean sea surface temperature for each season and year studied. The points represent the mean temperature for the 3 months leading up to the sampling period. Unfilled squares represent ‘spring’ (April, May, June) and filled squares represent ‘summer’ (July, August, September). Bars represent the standard error of the mean, and the dashed horizontal line represents the mean ‘spring’ temperature for the years 1999 to 2009 and the dotted horizontal line represents the mean ‘summer’ temperatures for the same years. The sea surface temperature data are collected daily at five lighthouse stations within the study area. The lighthouse stations included were Langara Island, Bonilla Island, McInnes Island, Pine Island, and Egg Island.

3.2.3 Sample collection

Juvenile salmon were collected using a rope trawl with an opening 28 m wide and 16 m deep, towed at the surface at approximately 5 knots for 30 minutes. Fish forklength (mm) and wet weight (g) were determined at sea and fish were then frozen

individually at -20°C in marked plastic bags for later analysis. Zooplankton were collected from vertical bongo tows using two 58 cm diameter Nitex nets, to a depth within 10 m of the ocean floor or to a maximum of 150 m deep. Zooplankton were separated into 4 size classes, weighed, dried, weighed again, and stored for further analysis. The two smaller size classes (0.25-1.0 mm and 1.0-1.7 mm) were retained, the smaller size class for stable isotope analysis, and the larger size class as an indicator of prey density.

3.2.4 Stable isotope analyses

The total number of fish retained for isotope analysis was 1039; of these there were 395 from summer tows, and 644 from fall tows. A sample of skinless, boneless, dorsal muscle tissue was removed from each fish posterior to the dorsal fin. Muscle samples and zooplankton samples were freeze dried using a Labconco FreeZone Freeze Dry System, except for muscle samples from the year 2000, which had been previously air dried at 65°C for 72 hours. All samples were then ground to a fine powder using a Heavy Duty Wig-L-Bug grinding mill, and the powder was precisely weighed to a thousandth of a milligram and packed for analysis with a Thermo Delta IV Isotope Ratio Mass Spectrometer.

Stable isotope ratios are reported using the delta notation, which expresses isotope ratios relative to an international standard, air N₂ for nitrogen and Vienna Pee Dee Belemnite for carbon, and is defined as follows:

$$(1) \quad \delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000\text{‰}$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. Laboratory protocols included running one standard for every 11 samples, as well as repeating one out of every 11 samples. The standard

deviation of the measurements of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was $\pm 0.2\text{‰}$ based on repeated measurements of laboratory standards and $\pm 0.3\text{‰}$ based repeated measurement of samples of muscle tissue from the same fish.

In order to determine the effect of oven drying on the isotope signature of the samples as opposed to freeze-drying them, the muscle samples of 60 fish were divided and one half was oven-dried while the other half was freeze-dried. There was a small but consistent difference between the isotope signatures of freeze-dried and oven-dried samples (approximately 0.25‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), so a linear model derived from the subset was used to correct the isotope signatures of all of the oven-dried samples within the study. The best model ($\text{adj } R^2 = 0.95$, $F = 541.1$ on 2 and 56 DF, $p\text{-value} < 2.2\text{e-}16$) for correcting the carbon stable isotope signature was as follows:

$$(2) \quad \text{Corrected } \delta^{13}\text{C} = -4.2 + 1.0 * \delta^{13}\text{C of oven dried sample} + 1.35 * \text{C:N ratio}$$

Where C:N ratio refers to the ratio of carbon to nitrogen. The best model ($\text{adj } R^2 = 0.90$, $F = 504.9$ on 1 and 56 DF, $p\text{-value} < 2.2\text{e-}16$) to correct the nitrogen stable isotope signature was the following:

$$(3) \quad \text{Corrected } \delta^{15}\text{N} = 0.57 + 0.95 * \delta^{15}\text{N of oven dried sample}$$

Oven-drying muscle samples appeared to have little effect on the C:N ratio in most cases, but there were a greater number of outliers among the oven-dried samples where the C:N ratio was anomalously high. In these cases the freeze-dried sample C:N ratio was consistently lower. The C:N ratio of oven-dried samples was corrected according to the following model ($\text{adj } R^2 = 0.44$, $F = 46.0$ on 1 and 56 DF, $p\text{-value} < 8.0\text{e-}09$):

$$(4) \quad \text{Corrected C:N ratio} = 2.36 + 0.28 * \text{C:N ratio of oven dried sample}$$

Because this model was not able to predict the C:N ratio of freeze-dried samples as

accurately as the previous models (for ^{15}N and ^{13}C), and because most C:N ratios were very similar among salmon caught in the same year and region, the correction was applied only when the C:N ratio of an oven-dried muscle sample was more than 1 standard deviation from the mean. As a result, this correction was applied only to 36 out of 328 oven-dried samples.

Lipids are depleted in ^{13}C compared to muscle tissue, so it is important to correct the $\delta^{13}\text{C}$ based on the lipid content of the tissue sample (McConnaughey & McRoy 1979). Because juvenile salmon tend to have relatively low lipid content ($\approx 3\%$ in my data, based on carbon to nitrogen ratios as per Post et al. 2007) and their lipid content is not highly variable, lipid correction makes little difference to the fish $\delta^{13}\text{C}$ signature (Post et al. 2007). Marine zooplankton tend to have slightly higher lipid content ($\approx 12\%$ in my data). Hence, in order to be consistent, the $\delta^{13}\text{C}$ of all samples (both zooplankton and fish) were corrected mathematically based on the C:N ratio, which was determined during mass spectrometer analysis. The formula for lipid correction based on C:N ratio for aquatic organisms is as follows (Post et al. 2007):

$$(5) \quad \delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$$

Correcting $\delta^{13}\text{C}$ in this manner also allows for consistency between this paper and other recent studies of the isotopic characteristics of Pacific foodwebs such as Johnson and Schindler (2009) and Kline (2010).

Because juvenile salmon are migratory, the baseline isotope signatures were averaged over the sub-region where salmon were caught. Sub-regions were determined based on geographic proximity of sampling locations (Figure 3.2.3); the similarity of sampling sites based on oceanographic indicators was also taken into consideration.

These oceanographic indicators included sea surface temperature, sea surface salinity, proximity to shore, and depth. These indicators were reviewed and sites that were both highly anomalous as well as devoid of pink salmon or chum salmon were dropped from the average baseline calculation. The trophic position of fish was determined following Vander Zanden & Rasmussen (1999). The formula is as follows:

$$(6) \quad \text{Trophic position} = [(\delta^{15}\text{N}_{\text{salmon}} - \delta^{15}\text{N}_{\text{zooplankton}}) / 3.4\text{‰}] + 2$$

The baseline-corrected $\delta^{15}\text{N}$ value is divided by 3.4‰ because this is the average trophic discrimination factor from one trophic level to the next among marine organisms (Vander Zanden & Rasmussen 2001), and 2 was added because zooplankton are assumed to represent the second trophic level. Although it is an oversimplification to assume that all zooplankton of the small size class are primary consumers (Kling et al. 1992), it is necessary for my purposes because of the massive time and expertise that would be required to separate, identify, and analyze each zooplankton sample. Furthermore, I used bulk zooplankton because assemblages of species are not consistent and baseline species may vary among regions and between years.

3.2.5 Statistical Analysis

All statistical analyses were performed with the statistical package R (R Development Core Team 2009). Based on the previously described sampling design, the salmon caught were grouped based on the species, the year they were collected, and whether they were collected in the northern portion or the southern portion of the study area.

3.2.5.1 Estimating the abundance of juvenile salmon

The catch per unit effort (CPUE) was calculated for each tow using the following formula:

$$(7) \quad \text{CPUE} = [\text{number of fish caught} / \text{tow distance (nautical miles)}] \times 1.5 \text{ nautical miles}$$

Multiplying by 1.5 nautical miles standardizes the CPUE so that it is consistent with recent studies that report abundances of juvenile Pacific salmon, such as Fisher et al. (2007) and Tucker et al. (2009).

The CPUE for each year and region (north or south) of the study area was determined by estimating the mean CPUEs for that year, region and species. Because the data were not evenly distributed and because many sampling sites yielded no fish and thus a value of zero, bootstrapping was used to estimate confidence limits for the mean catch per unit effort (Efron 1981). The abundance of juvenile pink salmon and chum salmon will initially be reported separately, but for the majority of the discussion will be considered together in order to better represent the overall density of juvenile salmon. The combined juvenile pink salmon and chum salmon mean CPUE and confidence limits were calculated in the same manner as the separated CPUE values. The combined values for CPUE were compared between years and regions using an ANOVA-like permutation test. This is an alternative to a parametric Analysis of Variance (ANOVA) or Kruskal-Wallis test with fewer assumptions about the data and the distribution of the test statistic (Good 1993). Data was permuted 10,000 times in order to create an empirical distribution of the F-statistics, and to determine an adjusted p-value of the original data set.

3.2.5.2 Linear mixed-effects modeling to estimate differences in trophic niche

Linear mixed-effects models were used to determine the effect of independent fixed variables on the dependent variables. Linear mixed effects models allow for the inclusion of random effects in the model, which can help to avoid pseudoreplication (Zuur et al. 2009). The independent fixed variables included in the model were the factors ‘warm/cold year’, ‘odd/even year’, ‘season’ (summer/fall), ‘species’ (pink salmon/chum salmon), and ‘region’ (north/south). The nested random effects included were ‘tow’ and ‘sub-region’ (tow being nested within sub-region), and in this case ‘sub-region’ refers to a group of tows within relatively close proximity. These are the same sub-regions on which the average isotopic baseline was calculated (Figure 3.2.3).

The dependent variables investigated using the model were the length of fish, the $\delta^{15}\text{N}$, the $\delta^{13}\text{C}$, the trophic level of fish, as well as the C:N ratio of zooplankton and fish. The model was run twice for the isotope signatures, trophic level, and C:N ratio of fish, once with the length of fish included as an independent variable, and once without, in order to determine how the variation might be related to length, and whether statistically significant differences existed among groups regardless of the size of fish.

The function ‘lme’ was used from the R package ‘nlme’ (Pinheiro 2011), and the maximum likelihood (ML) method was used to fit the model, as opposed to the restricted maximum likelihood (REML) method, in order to allow comparisons between models (Crawley 2007). When higher-level interaction terms were not significant in the model, they were removed successively from higher order interactions (three-way interactions, for example) to lower order interactions. Successively simplifying the model ensures accurate p-values (Crawley 2007). In some cases, the model was applied only to one species, season, or region, in order to investigate specific relationships and

to simplify the interpretation of results (to avoid 4-way interactions, for example). In such cases, the applicable fixed-effect was also dropped from the model (ie. species, season, region). Models were checked by plotting the standardized residuals against the fitted values to ensure homoscedasticity, by ensuring that response variables were a reasonably linear function of the fitted values, and by checking that errors were reasonably normally distributed (Crawley 2007).

The zooplankton C:N ratio was investigated using a similar model, but the fixed-effect ‘species’ was not included, nor was the random effect ‘tow’, because chemical analysis was performed on bulk zooplankton samples from each bongo tow, so there was only one value for zooplankton C:N ratio per tow.

3.2.5.3 Estimating the trophic niche shift from summer to fall

The trophic shift between the summer and fall juvenile salmon populations was characterized by plotting the mean $\delta^{15}\text{N}$ against the mean $\delta^{13}\text{C}$ for each of the years, seasons, regions, and species. The difference in trophic niche was estimated by determining the Euclidean distance between the summer and fall positions for a given year/region/species. In order to determine if the magnitude of the trophic shift was related to the magnitude of change in juvenile salmon size, the Euclidean distance was regressed against the change in mean length from summer to fall. The Euclidean distance was also regressed against the summer and fall CPUE to determine if the magnitude of the trophic niche shift was related to the density of juvenile salmon. Finally, in order to determine the effect of the factors ‘region’, ‘species’, and ‘warm/cold year’ on the trophic niche shift from summer to fall, linear models were used which incorporated these independent variables with the 3 following dependent variables (a separate model was used for each dependant variable): Euclidean distance

between summer and fall, difference in $\delta^{15}\text{N}$ from summer to fall, and difference in $\delta^{15}\text{C}$ from summer to fall.

In order to determine how changes lower down the food web might affect the trophic shift of juvenile salmon, the trophic shift among the small zooplankton size class from summer to fall was examined. The mean $\delta^{15}\text{N}$ of zooplankton was plotted against the mean $\delta^{13}\text{C}$ for each of the years, seasons, and regions. The Euclidean distance between the summer and fall values was measured, and linear models were used to determine the effect of the factors 'warm/cold year' and 'region' on the Euclidean distance as well as the difference between the summer and fall $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The Euclidean distance and the difference between the summer and fall $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for zooplankton was regressed against the same measures for juvenile salmon in order to determine if the shift in zooplankton niche could predict the shift in juvenile salmon niche.

3.2.5.4 Determining the relationship between size and trophic position

Linear mixed-effect modeling was used to investigate the relationship between fish size and trophic position, and a series of linear regressions were also performed. For the linear regressions, separate analyses were performed for each year, region, season, and species, and Holm's correction was applied in order to account for the use of multiple tests (Holm 1979).

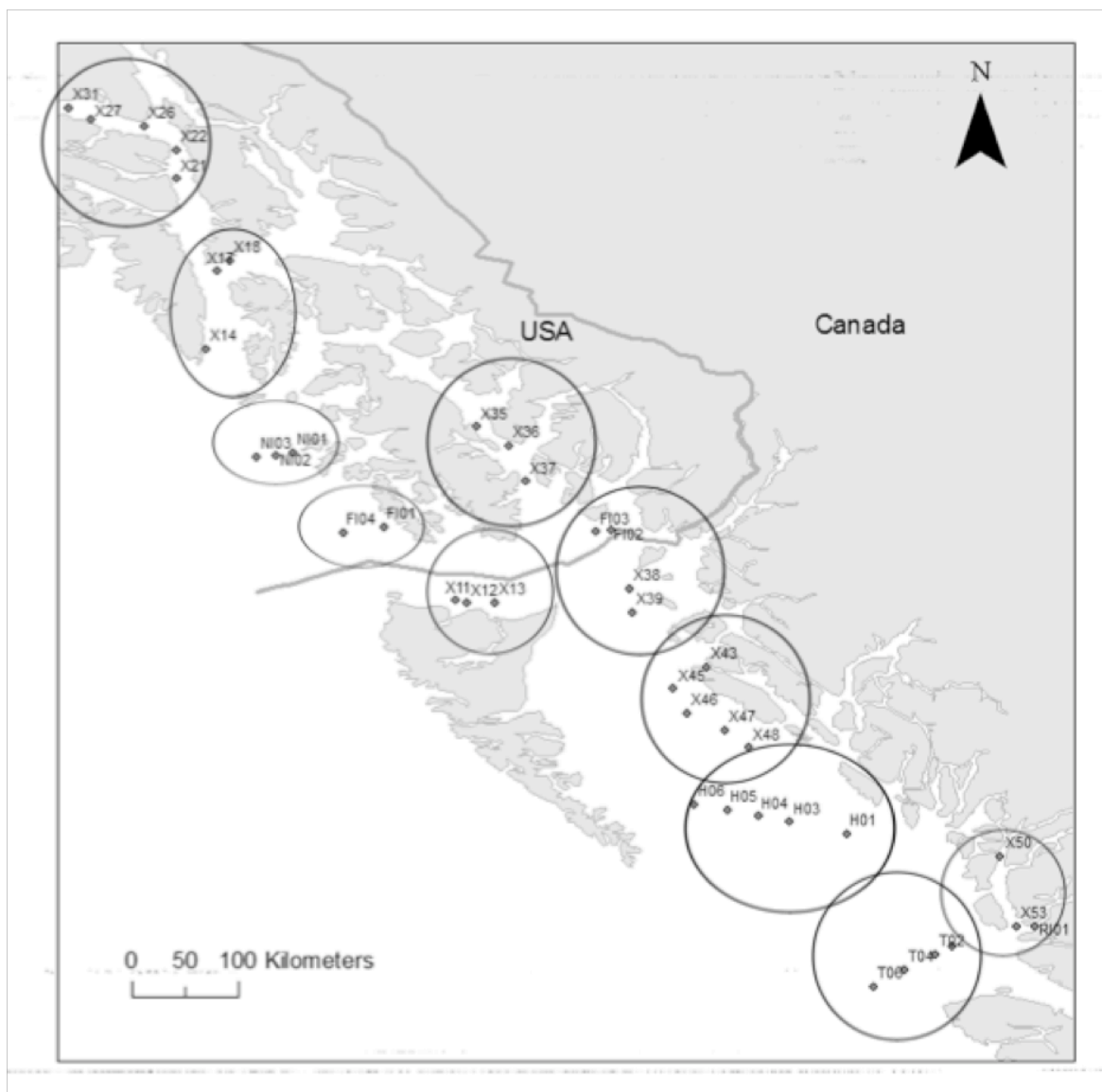


Figure 3.2.3. Sample map showing ‘sub-regions’ used for isotope baseline and as a random effect in the linear mixed-effects model. This map shows the study area in fall 2000 with original station identification codes where fish were caught. Circled areas indicate sites that were combined to create a ‘sub-region’. The same sub-regions were used in each year and season, although the numbers of fish caught at individual sites and within sub-regions varied.

3.3. Results

3.3.1 Juvenile salmon abundance in summer and fall

In the summer, the mean CPUE was higher in the south than in the north, and juvenile pink salmon were consistently more abundant than juvenile chum salmon (Figure 3.3.1a). In this study, the abundance of salmon caught in the summer was greater in warm years (161 fish per 1.5 nautical miles (nmi)) than cold years (6 fish per 1.5 nmi), and in the cool years the abundance was greater in the even year (2000) (19 fish per 1.5 nmi) than the odd year (1 fish per 1.5 nmi), while in the warm years the abundance was slightly greater in the odd year (2005) (181 fish per 1.5 nmi) than the even year (144 fish per 1.5 nmi) (Figure 3.3.1b). In cool years the abundance tended to be greater in the fall (22 fish per 1.5 nmi) than the summer (5 fish per 1.5 nmi), and in warm years the abundance was greater in the summer (161 fish per 1.5 nmi) than the fall (7 fish per 1.5 nmi) (Figure 3.3.1b/d).

In the fall, juvenile pink salmon were consistently more abundant than juvenile chum salmon (mean pink salmon CPUE: 10 fish per 1.5 nmi, mean chum salmon CPUE: 5 fish per 1.5 nmi) except for in the south in the year 2004, when there was a greater abundance of juvenile chum salmon. In even years in the fall, there tended to be a greater abundance of fish in the south (south: 45 fish per 1.5 nmi, north: 7 fish per 1.5 nmi), and in odd years there was a greater abundance in the north (south: 9 fish per 1.5 nmi, north: 13 fish per 1.5 nmi) (Figure 3.3.1d). When comparing an even, cool year (2000), to an even warm year (2004), the abundance of both pink salmon and chum salmon was greater in the cool year (even, cool: 31 fish per 1.5 nmi, even, warm: 5 fish per 1.5 nmi); this was true in the fall in the northern region and in the southern region (Figure 3.3.1d). When comparing an odd, cool year (2001) to an odd, warm year

(2005), abundance was again greater in the cooler year (odd, cool: 13 fish per 1.5 nmi, odd, warm: 9 fish per 1.5 nmi), except that in 2005 there was a greater abundance of juvenile chum salmon in the north than there was in 2001, although the difference was small (Figure 3.3.1d).

The confidence limits of the mean, determined using bootstrapping, were quite wide due to the large number of zeroes in the data set and the non-normality of the CPUE data. The permutation approach used to test for significance in this data helped to deal with the non-normality of the data. Using an ANOVA-like permutation test, significant differences in the combined CPUE of juvenile pink salmon and chum salmon were found between the north and south ($F = 17.4$, adjusted p-value < 0.0001), between warm and cold years ($F = 7.2$, adjusted p-value = 0.002), and between fall and summer ($F = 17.4$, adjusted p-value = 0.0002). Significant interactions were observed between the factor 'north/south' and the factors 'odd/even year' ($F = 4.4$, adjusted p-value = 0.03), 'warm/cold year' ($F = 14.3$, adjusted p-value < 0.0001), and season ($F = 20.7$, adjusted p-value < 0.0001). There was also a significant interaction between the factors 'warm/cold year' and 'season' ($F = 35.6$, adjusted p-value = 0.0001).

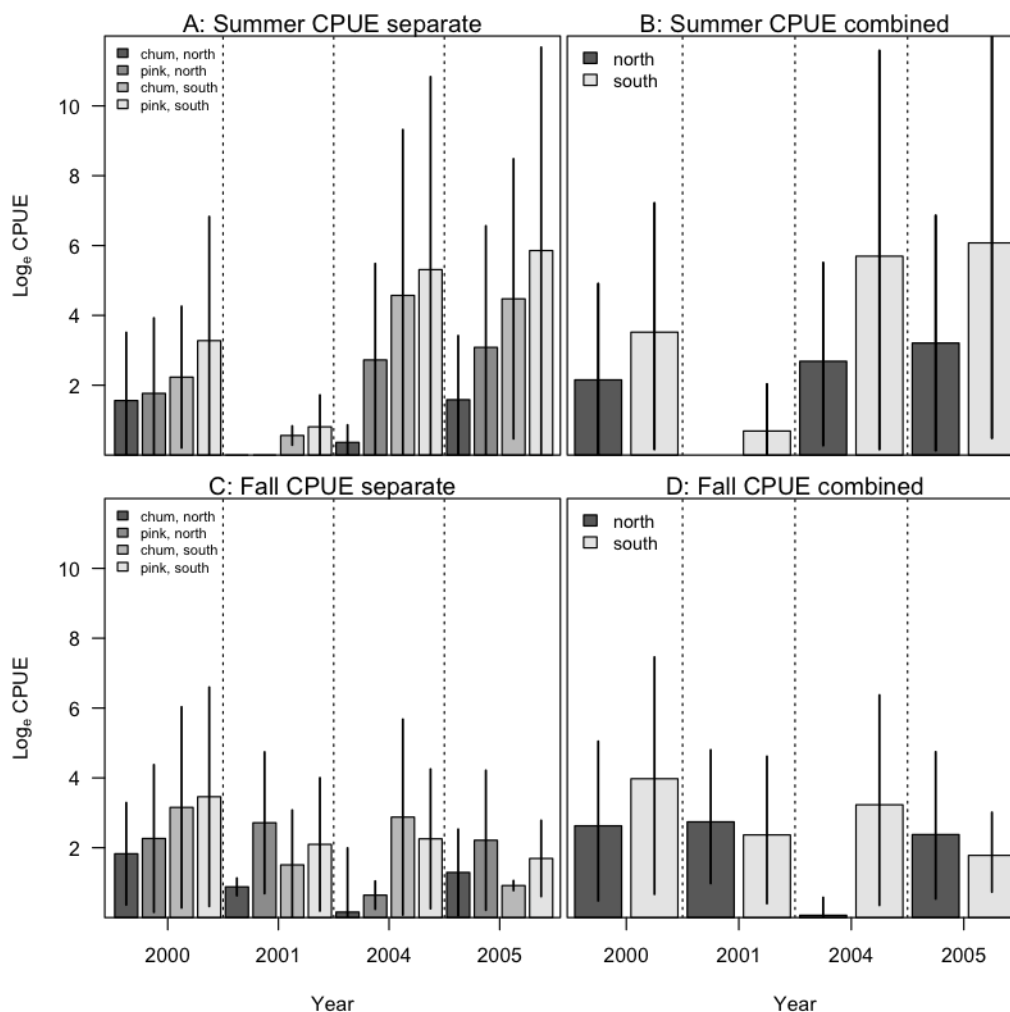


Figure 3.3.1. The mean \log_e CPUE in the summer versus the fall for juvenile pink salmon and chum salmon in the northern and southern regions in each of the sampling years. Error bars represent confidence limits for the mean CPUE. Panels 'A' and 'C' show mean CPUE for juvenile pink salmon and chum salmon separately in the summer and fall, respectively, in the north and south and in each of the sampling years. Panels 'B' and 'D' show mean CPUE for both species combined in the summer and fall, respectively, in the north and south and in each of the sampling years.

3.3.2 Increasing mean size of juvenile salmon from summer to fall

The mean size of juvenile pink salmon and chum salmon increased from 133 ± 17 mm (standard deviation) in the summer to 222 ± 23 mm in the fall (Figure 3.3.2). It

should be noted that lengths, weights, isotope signatures, trophic positions, and C:N ratios reported in the text of the results section are averaged first by tow to avoid pseudoreplication. The mean weight increased from $24 \pm 10\text{g}$ in the summer to $116 \pm 42\text{g}$ in the fall (Figure 3.3.3). Linear mixed effects (lme) modeling confirmed that the difference in length between seasons was highly significant ($t = 15.6$, $df = 295$, $p < 0.0001$). The lme showed a significant interaction between the region (north or south) and the species ($t = 3.3$, $df = 295$, $p = 0.001$) (Figure 3.3.4). This interaction was mainly driven by the differences between species in the fall; juvenile pink salmon tended to be larger than juvenile chum salmon in the north (pink salmon: 231 ± 26 mm, chum salmon: 220 ± 16 mm), and smaller than juvenile chum salmon in the south (pink salmon: 209 ± 23 mm, chum salmon: 222 ± 19 mm). In the summer, juvenile chum salmon tended to be larger than juvenile pink salmon regardless of the region (pink salmon: 129 ± 18 mm, chum salmon: 137 ± 15 mm) ($t = 2.9$, $df = 63$, $p = 0.006$).

The linear mixed effects (lme) model indicated an interaction for mean length between the variables “warm/cold year” and “odd/even year” ($t = 3.3$, $df = 295$, $p = 0.02$). This interaction was a result of the small size of salmon in year 2001 in both the fall and summer in the south, and in the fall among juvenile pink salmon in the north (no data is available for the size of juvenile salmon in the north in the summer of 2001 because no salmon were caught). Juvenile chum salmon were unusually large in the summer in the north in the year 2000 (159 ± 18 mm), which was a cool year, as well as in the south in the fall of 2005 (237 ± 15 mm), which was a warm year.

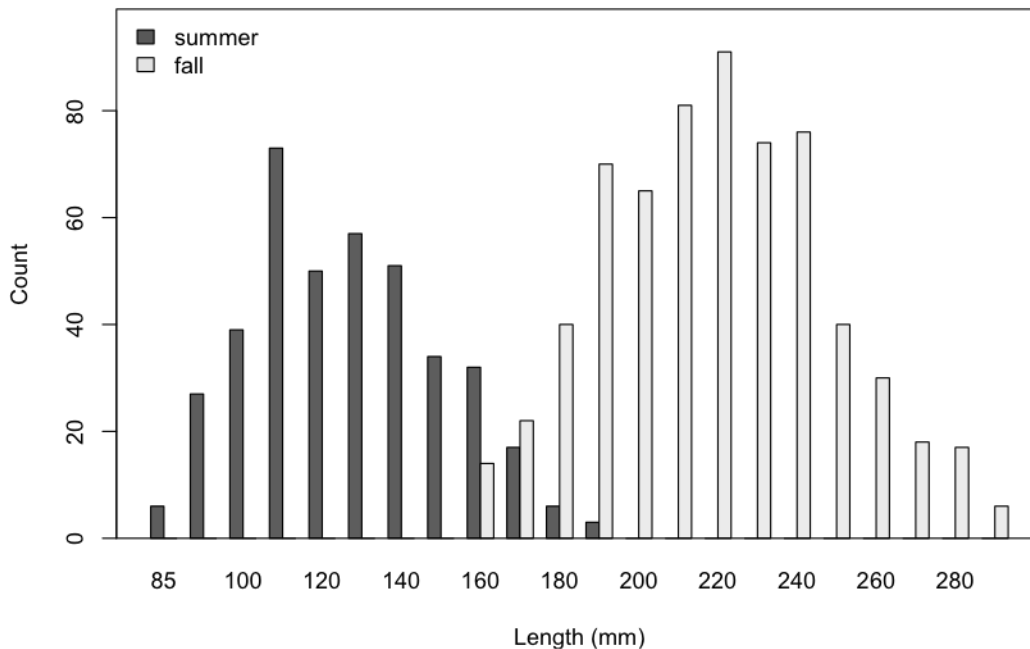


Figure 3.3.2. Distribution of length for all juvenile salmon caught in the summer versus the fall.

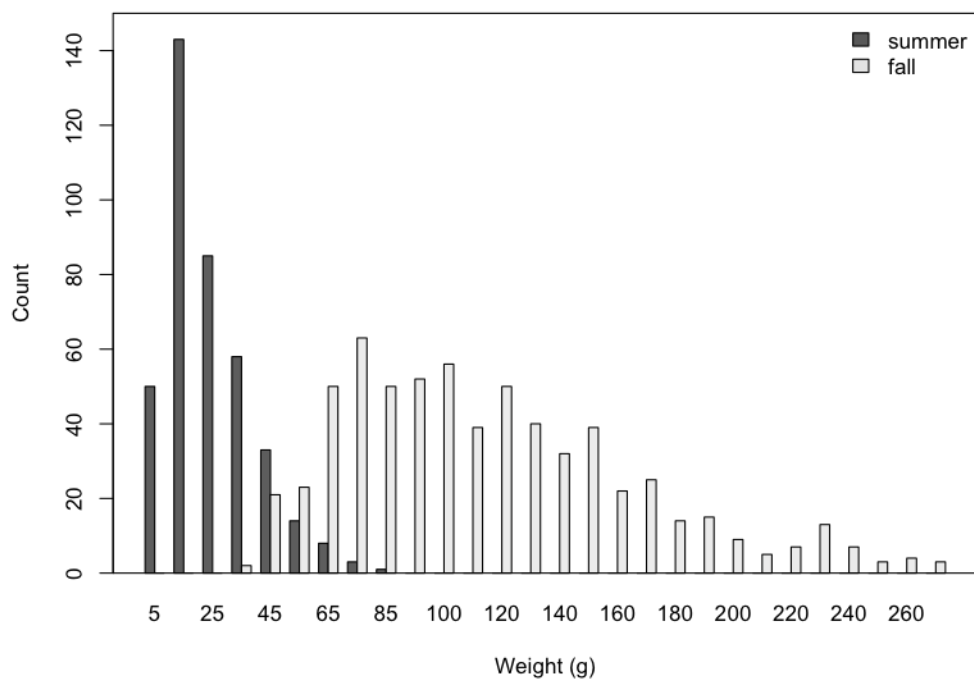


Figure 3.3.3. Distribution of weight for all juvenile salmon caught in the summer versus the fall.

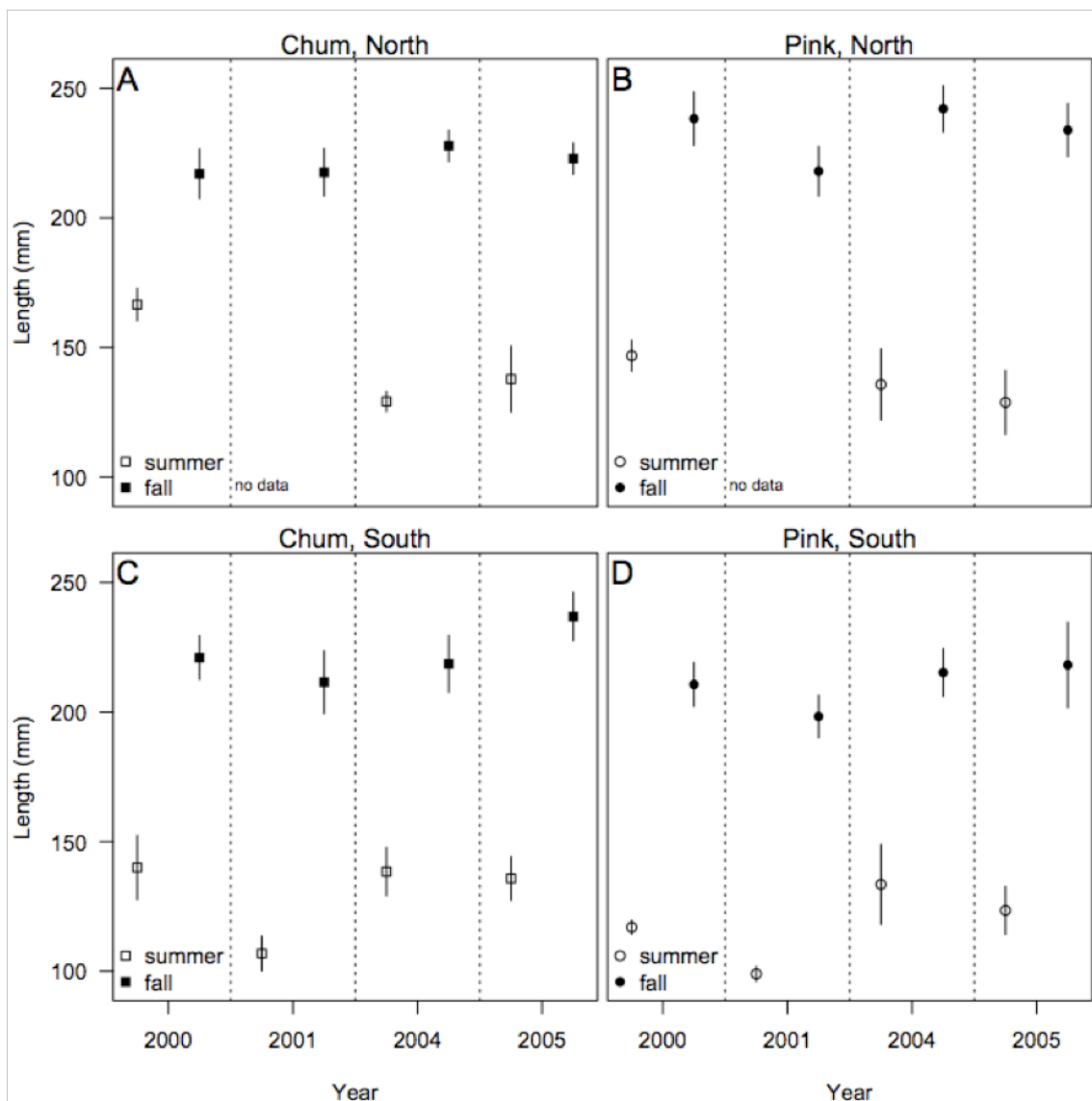


Figure 3.3.4. The mean length in the summer versus the fall for juvenile pink salmon and juvenile chum salmon in the northern and southern regions in each of the sampling years. The error bars represent the 95% confidence limits of the mean. Plots A and C represent juvenile chum salmon in the north and south, respectively, and plots B and D represent juvenile pink salmon in the north and south, respectively. No juvenile pink salmon nor juvenile chum salmon were caught in the north in the summer of 2001.

3.3.3 Juvenile salmon food source based on stable isotopes

The mean $\delta^{15}\text{N}$ of juvenile salmon muscle tissue was $12.5 \pm 0.5\text{‰}$, and was significantly higher in the fall than the summer (fall: $12.6 \pm 0.5\text{‰}$, summer: $12.2 \pm 0.5\text{‰}$, $t = 3.8$, $df = 289$, $p = 0.0002$), and length had a significant effect in the model ($t = 4.4$, $df = 713$, $p < 0.0001$). The species of fish was significant overall ($t = 5.0$, $df = 290$, $p < 0.0001$) with juvenile pink salmon having a lower mean $\delta^{15}\text{N}$ ($12.4 \pm 0.5\text{‰}$) than juvenile chum salmon ($12.7 \pm 0.5\text{‰}$). When length was included in the model the difference between juvenile pink salmon and chum salmon mean $\delta^{15}\text{N}$ was no longer significant in the south, where juvenile pink salmon tend to be smaller than juvenile chum salmon, but became significant in the northern region ($t = 2.1$, $df = 161$, $p = 0.04$).

Mean $\delta^{15}\text{N}$ was significantly higher in the warm years than cooler years (warm: $12.7 \pm 0.5\text{‰}$, cool: 12.4 ± 0.5 , $t = 2.8$, $df = 289$, $p = 0.005$). The difference remained significant in the south whether or not fish length was included in the model, but was not significant in the north when length was removed from the model (Figure 3.3.5c/d).

The factor 'odd/even year' was significant in the north ($t = 2.1$, $df = 161$, $p = 0.04$) with odd years having higher mean $\delta^{15}\text{N}$ (odd: $12.7 \pm 0.5\text{‰}$, even: $12.3 \pm 0.5\text{‰}$). The difference remained significant when length was removed from the model ($t = 6.0$, $df = 161$, $p < 0.0001$). In the south, the mean $\delta^{15}\text{N}$ was very low in the summer of 2001 ($11.6 \pm 0.5\text{‰}$) (Figure 3.3.5c/d). This difference was significant when length was not included in the model ($t = 4.0$, $df = 8$, $p = 0.004$), but became insignificant when length was included as fish were anomalously small in the summer of 2001 (mean length: $116 \pm 18\text{mm}$).

In the south, the year 2005 had the highest mean $\delta^{15}\text{N}$ values (summer: $12.3 \pm 0.3\text{‰}$, fall: $13.0 \pm 0.6\text{‰}$), which was significant in the lme ($t = 4.0$, $df = 289$, $p = 0.0001$). This difference was significant with or without length included in the model. In the north in 2005 the summer mean $\delta^{15}\text{N}$ was low among pink salmon (mean: $11.7 \pm 0.3\text{‰}$, $t = 7.1$, $df = 161$, $p < 0.0001$) (Figure 3.3.5c/d). Among juvenile chum salmon in the north in the fall the mean $\delta^{15}\text{N}$ was low in the year 2000 ($12.3 \pm 0.5\text{‰}$) ($t = 2.4$, $df = 84$, $p = 0.02$) (Figure 3.3.5a).

The mean lipid-corrected $\delta^{13}\text{C}$ of juvenile salmon was $-18.2 \pm 0.7\text{‰}$ (standard deviation). In summer the mean $\delta^{13}\text{C}$ was $-17.3 \pm 0.5\text{‰}$, which was significantly less negative than the mean fall value, $-18.4 \pm 0.6\text{‰}$ ($t = 6.0$, $df = 295$, $p < 0.0001$) (Figure 3.3.6). The mean carbon isotope signature was also more positive in warm years than cold years (warm: $-17.9 \pm 0.7\text{‰}$, cold: $-18.4 \pm 0.6\text{‰}$, $t = 2.7$, $df = 295$, $p = 0.007$). In the summer, odd years tended to have a lower $\delta^{13}\text{C}$ signature (odd: $-17.2 \pm 0.5\text{‰}$, even: $-17.5 \pm 0.5\text{‰}$, $t = 5.3$, $df = 295$, $p < 0.0001$); this was especially noticeable in the summer of 2001 (3.3.6c/d), when $\delta^{13}\text{C}$ was abnormally low ($18.1 \pm 0.8\text{‰}$) among both juvenile pink salmon and chum salmon in the southern region (no fish were caught that year in the northern region).

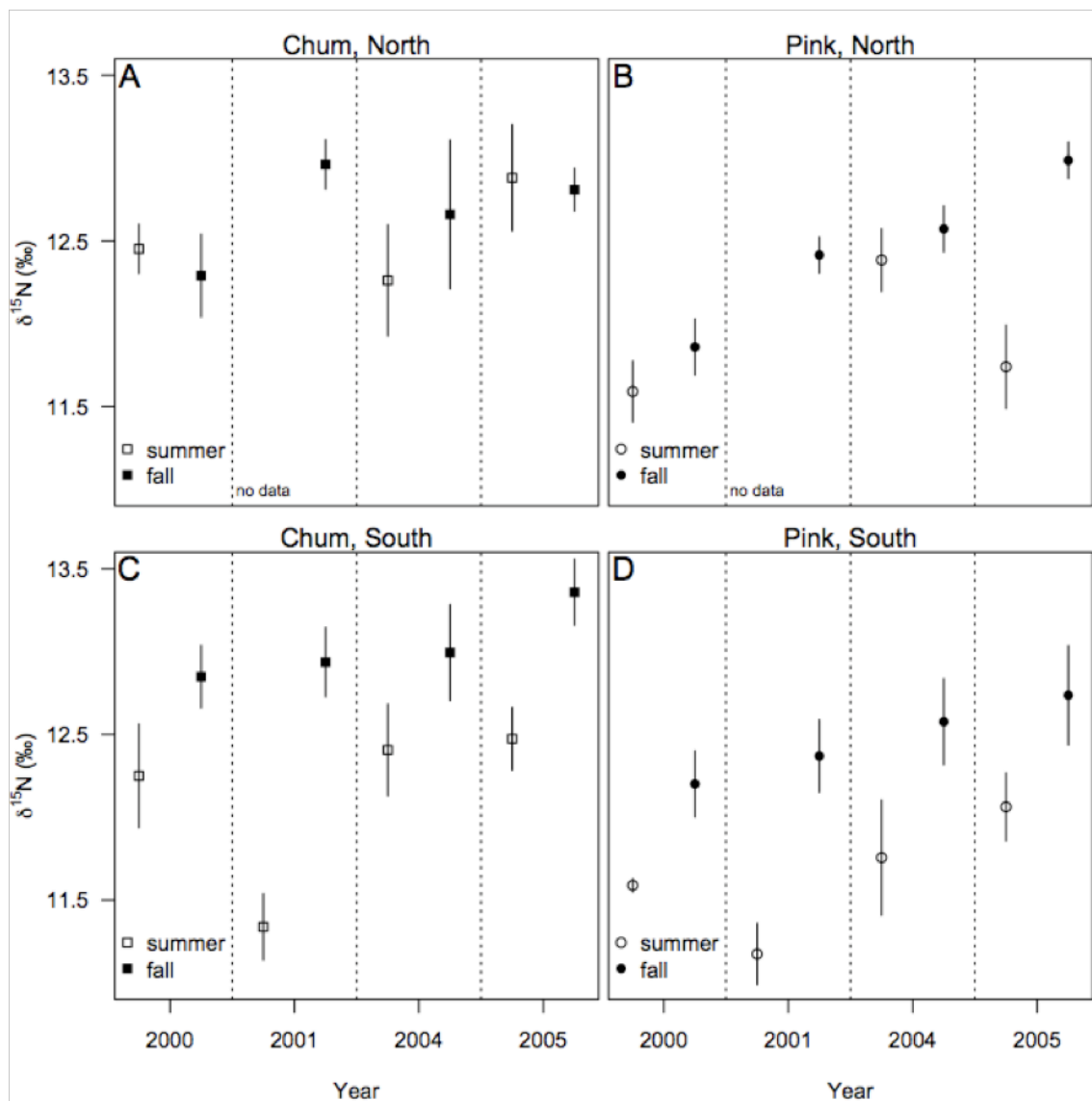


Figure 3.3.5. The nitrogen isotope signatures in the summer versus the fall for juvenile pink salmon and chum salmon in the northern and southern regions in each of the sampling years. The error bars represent the 95% confidence limits of the mean. Plots A and C represent juvenile chum salmon in the north and south, respectively. Plots B and D represent juvenile pink salmon in the north and south, respectively. No juvenile pink salmon nor chum salmon were caught in the north in the summer of 2001.

In the north, the difference between the mean $\delta^{13}\text{C}$ in fall and summer was generally quite pronounced (summer: $-17.2 \pm 0.4\text{‰}$, fall: $-18.5 \pm 0.5\text{‰}$, $t = 11.4$, $df = 288$, $p < 0.0001$), except among juvenile chum salmon in 2005, when there was no significant difference (summer: $-17.6 \pm 0.2\text{‰}$, fall: $-18.1 \pm 0.5\text{‰}$, $p = 0.1$) (Figure 3.3.6a). Among juvenile chum salmon in the south in the summer, $\delta^{13}\text{C}$ was significantly higher in warmer years (mean: $-17.0 \pm 0.4\text{‰}$, $t = 3.6$, $df = 60$, $p = 0.0006$) (Figure 3.3.6c). Among juvenile pink salmon in the southern region there was a significant difference between the fall and summer $\delta^{13}\text{C}$ in even years but not odd years ($t = 4.4$, $df = 26$, $p = 0.0002$). The mean value of $\delta^{13}\text{C}$ was also higher in warmer years (Figure 3.3.6d) (warm: $-17.7 \pm 0.5\text{‰}$, cold: $-18.5 \pm 0.6\text{‰}$), but this difference was only significant ($t = 4.9$, $df = 64$, $p < 0.0001$) if length was not included as a fixed effect in the model.

The change in trophic niche from summer to fall was estimated using the Euclidean distance between the mean summer and fall $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 3.3.7). The mean Euclidean distance was $1.31 \pm 0.51 \text{‰}$. The greatest shift (2.54‰) occurred between the summer and fall of 2004 among juvenile chum salmon in the north. The smallest shift occurred between summer and fall juvenile chum salmon in the north in 2005 (0.52‰).

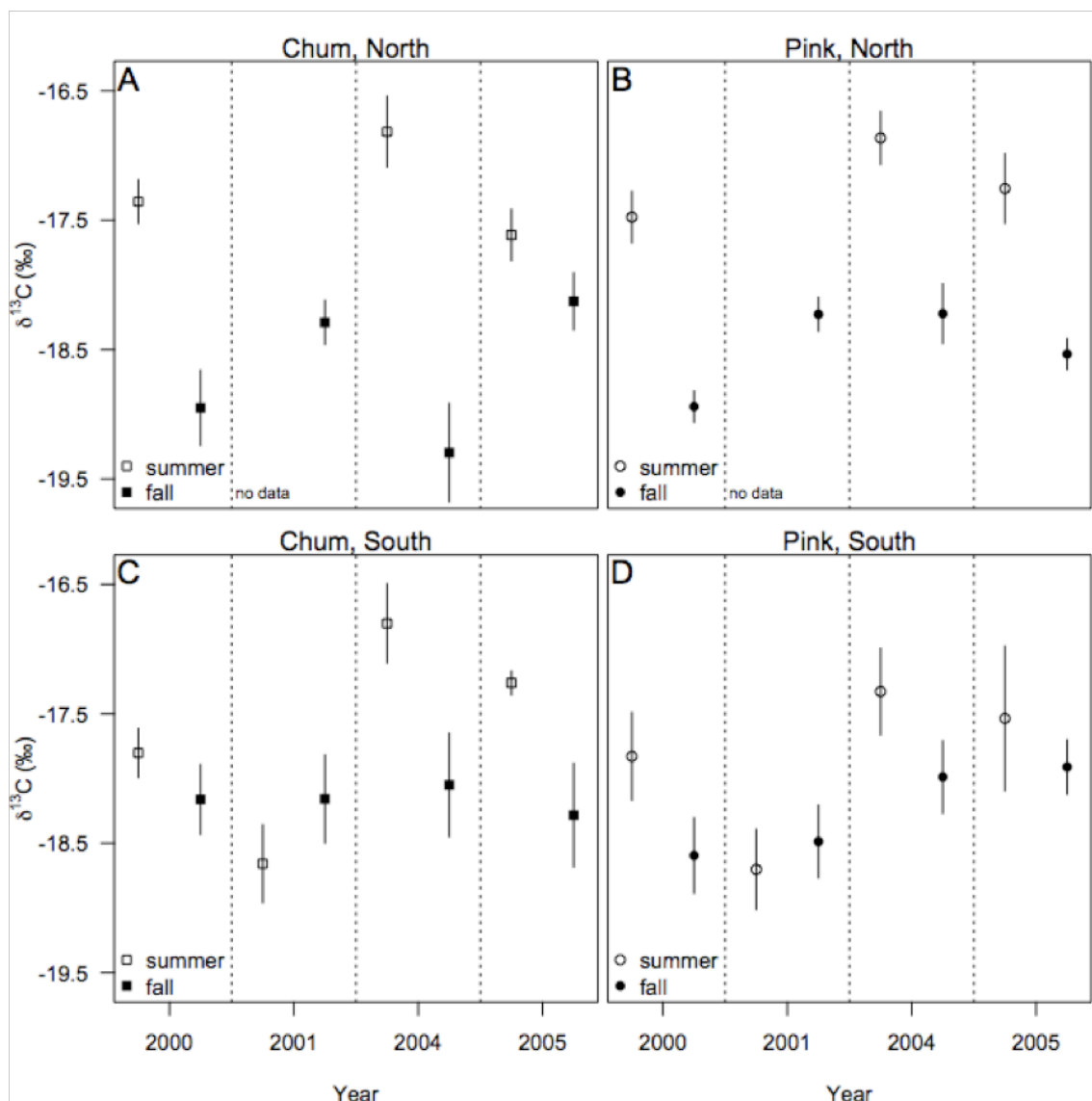


Figure 3.3.6. The carbon isotope signature in the summer versus the fall for juvenile pink salmon and chum salmon in the northern and southern regions in each of the sampling years. The error bars represent the 95% confidence limits of the mean. Plots A and C represent juvenile chum salmon in the north and south, respectively, plots B and D represent juvenile pink salmon in the north and south, respectively. No juvenile pink salmon nor juvenile chum salmon were caught in the north in the summer of 2001.

Regression analysis showed no significant relationship between Euclidean distance and the change in mean length from summer to fall of juvenile salmon ($R^2 = 0.04$, $df = 12$, $p = 0.5$), nor was there any significant relationship between Euclidean distance and summer or fall CPUE (summer: $R^2 = 0.07$, $df = 12$, $p = 0.4$, fall: $R^2 = 0.21$, $df = 12$, $p = 0.1$). Furthermore, there was no significant relationship between the difference in species mean $\delta^{15}\text{N}$ and the difference in mean length between species ($R^2 = 0.13$, $df = 6$, $p = 0.39$), nor was the difference in species mean $\delta^{13}\text{C}$ significantly correlated with the difference in mean length ($R^2 = 0.06$, $df = 6$, $p = 0.57$). Linear models showed that the factors 'species' and 'warm/cold year' had no significant effect on the Euclidean distance, the difference in $\delta^{15}\text{N}$ from summer to fall, nor the difference in $\delta^{13}\text{C}$ from summer to fall. The factor 'region' had no significant effect on the Euclidean distance ($t = 1.55$, $df = 12$, $p = 0.15$), but was a significant factor in the differences in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from summer to fall ($\delta^{15}\text{N}$: $t = 2.43$, $df = 12$, $p = 0.03$, $\delta^{13}\text{C}$: $t = 2.98$, $df = 12$, $p = 0.01$). The factor 'region' had opposite effects on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$; in the north, the mean difference in $\delta^{15}\text{N}$ from summer to fall was small (0.31 ± 0.50), while in the south it was larger (0.87 ± 0.36). Conversely, in the northern region, the mean difference in $\delta^{13}\text{C}$ was large (1.45 ± 0.63), while the difference in $\delta^{13}\text{C}$ from summer to fall in the south was smaller (0.47 ± 0.59).

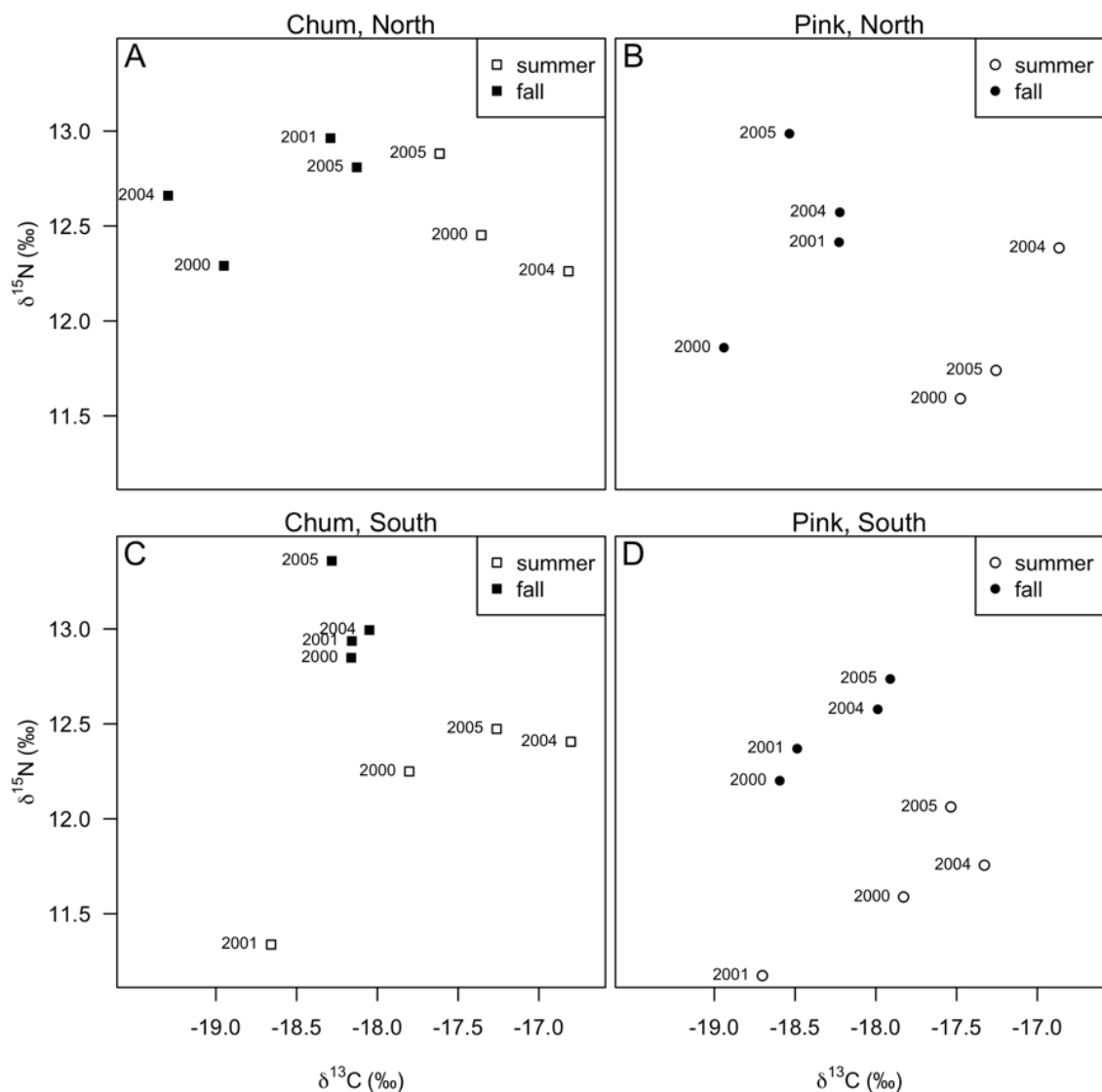


Figure 3.3.7. Mean $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for each year and season. Plots A and C represent juvenile chum salmon in the north and south, respectively, plots B and D represent juvenile pink salmon in the north and south, respectively. No juvenile pink salmon nor juvenile chum salmon were caught in the north in the summer of 2001.

The shift in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from summer to fall for zooplankton was similar to the shift observed among juvenile salmon (Figure 3.3.8). The mean $\delta^{15}\text{N}$ increased from summer to fall and the mean $\delta^{13}\text{C}$ decreased. Linear models showed no significant effect of region on the Euclidean distance between summer and fall zooplankton values,

or the differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from summer to fall (although the power of this test was lower than for juvenile salmon, since there were fewer values). The factor ‘warm/cold year’ was significant for the mean difference in $\delta^{13}\text{C}$ from summer to fall ($t = 2.78$, $df = 5$, $p = 0.04$), with the mean shift in cold years (-1.7 ± 0.3) being greater than the mean shift in warm years (-1.0 ± 0.3). Regression analysis showed no significant relationship between juvenile salmon and zooplankton for the Euclidean distance ($R^2 = 0.21$, $df = 12$, $p = 0.1$), difference in $\delta^{15}\text{N}$ from summer to fall ($R^2 = 0.01$, $df = 12$, $p = 0.7$), nor the difference in $\delta^{13}\text{C}$ from summer to fall ($R^2 = 0.02$, $df = 12$, $p = 0.5$). Salmon $\delta^{15}\text{N}$ was positively correlated with the zooplankton $\delta^{15}\text{N}$ ($R^2 = 0.22$, $df = 28$, $p = 0.01$), but there was no significant relationship between juvenile salmon $\delta^{13}\text{C}$ and zooplankton $\delta^{13}\text{C}$.

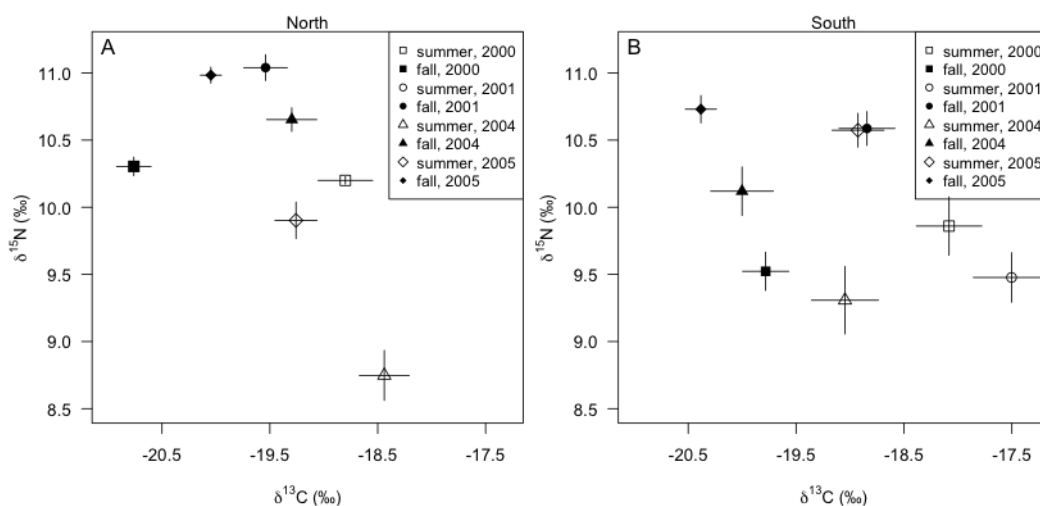


Figure 3.3.8. Mean zooplankton $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for each year and season. Plot A represents zooplankton in the north and plot B represents zooplankton in the south. Unfilled symbols represent the summer values and filled symbols represent the fall values. Error bars represent the standard error of the mean.

3.3.4 The relationship between juvenile salmon trophic position and size

Length was a significant factor the in the linear mixed effects model for trophic position ($t = 5.0$, $df = 641$, $p < 0.0001$). Linear regression was performed for each season, species, year, and region and, after correcting for the use of multiple tests, length and trophic level were found to be significantly correlated in 12 of the 30 groups tested. Of the 12 groups where length was significantly correlated, 9 were in the fall, and 8 of the 12 groups were among juvenile pink salmon, and 7 were in the northern region (Table 3.1).

Juvenile pink salmon tended to have a slightly lower trophic position than juvenile chum salmon (pink salmon: 2.6 ± 0.2 , chum salmon: 2.7 ± 0.2 , $t = 5.9$, $df = 284$, $p < 0.0001$), but when length was included in the model this difference was no longer significant. The mean trophic position in the southern region was significantly higher than in the north ($t = 5.3$, $df = 11$, $p = 0.003$), and this was significant whether or not length was included in the model (Figure 3.3.9, Figure 3.3.10).

In the south, the trophic position was lower in the summer than in the fall (summer: 2.6 ± 0.2 , fall: 2.8 ± 0.2 , $t = 3.1$, $df = 284$, $p = 0.003$), while in the north the trophic position of juvenile salmon was significantly higher in the summer, but only in the warm years ($t = 6.8$, $df = 158$, $p < 0.0001$). The mean trophic position in odd years (2.6 ± 0.2) was significantly lower than the mean trophic position in even years (2.7 ± 0.3) ($t = 2.6$, $df = 281$, $p = 0.01$). These remained significant when length was dropped from the model.

Table 3.1. Results from linear regression of the relationship between trophic position and length of juvenile pink salmon and chum salmon. A Holm's correction was applied to account for the use of multiple tests and the far right column indicates whether the relationship remained significant after the correction. Those groups where the relationship remained significant are highlighted in grey.

Species	Region	Year	Season	Intercept	Slope	R ²	df	p-value	significance ($\alpha = 0.05$)	Significant after Holm's correction?
chum salmon	north	2000	fall	1.84	0.0036	0.27	46	0.000	***	Y
			summer	-0.88	0.0232	0.66	3	0.09		N
		2001	fall	1.71	0.0032	0.25	41	0.001	**	Y
			summer	NA	NA	NA	NA	NA		NA
		2004	fall	4.64	-0.0090	0.23	10	0.12		N
			summer	2.37	0.0060	0.04	4	0.70		N
		2005	fall	1.91	0.0030	0.19	40	0.004	**	N
			summer	2.28	0.0051	0.27	26	0.004	**	N
	south	2000	fall	2.99	-0.0003	0.00	32	0.84		N
			summer	1.78	0.0067	0.59	16	0.000	***	Y
		2001	fall	1.72	0.0050	0.37	41	0.000	***	Y
			summer	2.19	0.0039	0.31	20	0.007	**	N
		2004	fall	2.73	0.0011	0.03	34	0.29		N
			summer	3.12	-0.0018	0.01	30	0.53		N
		2005	fall	3.99	-0.0053	0.17	20	0.06		N
			summer	2.22	0.0025	0.17	35	0.01	*	N
pink salmon	north	2000	fall	2.02	0.0019	0.19	49	0.001	**	Y
			summer	0.76	0.0126	0.46	6	0.07		N
		2001	fall	1.94	0.0021	0.21	53	0.000	***	Y
			summer	NA	NA	NA	NA	NA		NA
		2004	fall	2.11	0.0019	0.14	60	0.002	**	Y
			summer	3.30	-0.0018	0.06	32	0.15		N
		2005	fall	2.09	0.0022	0.26	63	0.000	***	Y
			summer	1.59	0.0078	0.37	26	0.001	**	Y
	south	2000	fall	2.70	0.0008	0.01	29	0.65		N
			summer	2.42	0.0009	0.01	13	0.68		N
		2001	fall	1.53	0.0056	0.23	38	0.002	**	Y
			summer	1.85	0.0073	0.15	18	0.09		N
		2004	fall	2.38	0.0025	0.20	20	0.04	*	N
			summer	2.55	0.0002	0.00	34	0.89		N
		2005	fall	2.16	0.0021	0.36	36	0.000	***	Y
			summer	1.75	0.0056	0.38	27	0.000	***	Y

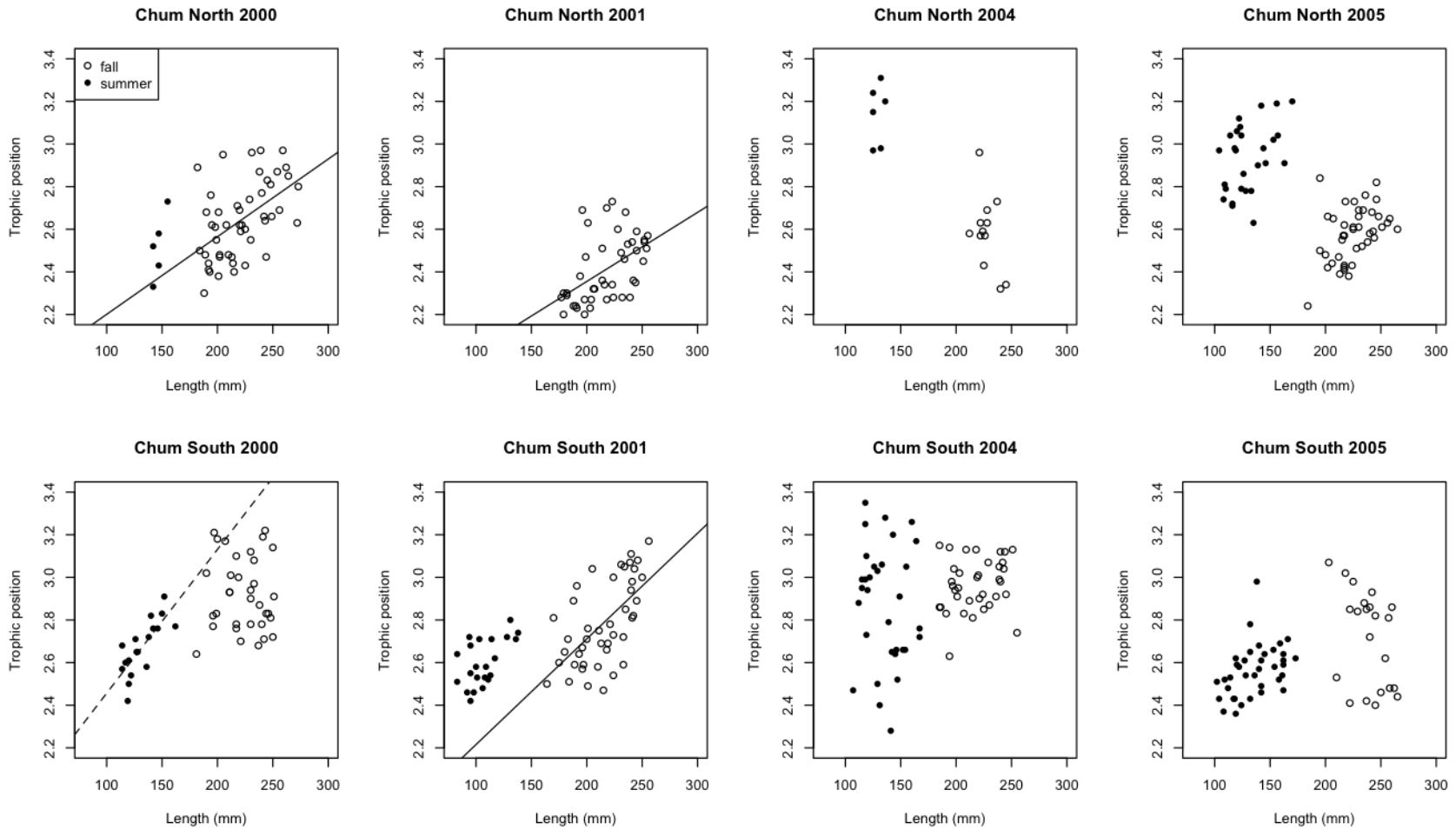


Figure 3.3.9. The trophic position versus the length of juvenile chum salmon in the summer and the fall in the northern and southern regions in each of the sampling years. When the relationship was significant ($\alpha = 0.05$), and remained significant after a Holm's correction, a trend line was added to the figure. Trend lines are separate for summer and fall, the trend line for the summer is a dashed line, and the trend line for the fall is solid.

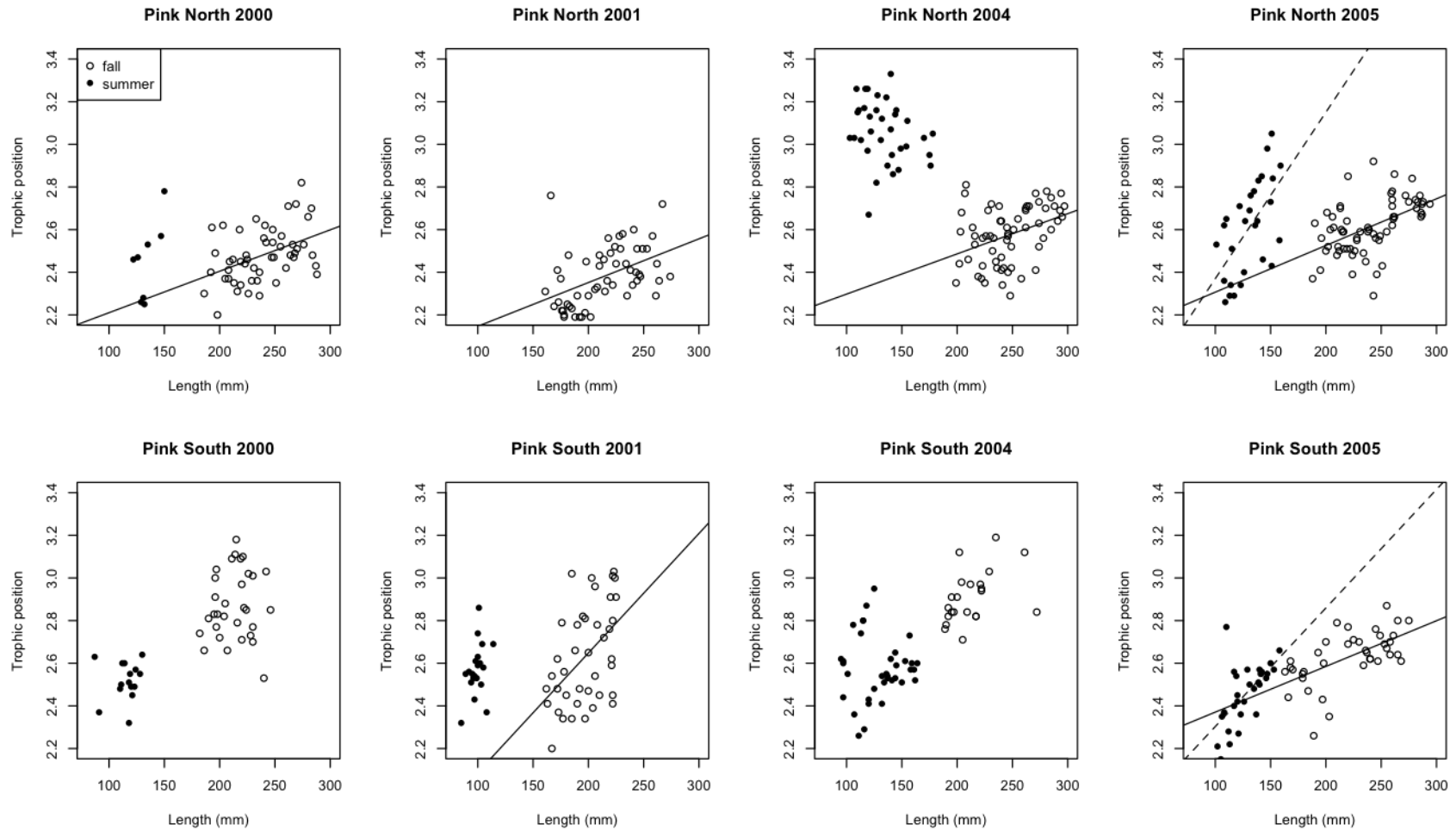


Figure 3.3.10. The trophic position versus the length of juvenile pink salmon in the summer and the fall in the northern and southern regions in each of the sampling years. When the relationship was significant ($\alpha = 0.05$), and remained significant after a Holm's correction, a trend line was added to the figure. Trend lines are separate for summer and fall, the trend line for the summer is a dashed line, and the trend line for the fall is solid.

3.3.5 Lipid content of juvenile salmon and zooplankton

The mean C:N ratio for juvenile salmon was 3.2 ± 0.1 . The factors 'season' and 'north/south' were not significant in the overall model although they remained in the model due to higher order interactions. There was a highly significant interaction between the factors 'warm/cold year' and 'odd/even year' ($t = 15.5$, $df = 289$, $p < 0.0001$), and this interaction was a result of the high mean C:N ratio in the year 2000, which was a cool, even year (3.28 ± 0.13) and 2005, which was a warm, odd year (3.25 ± 0.06), and the lower mean C:N ratio in the years 2001, a cool, odd year (3.18 ± 0.05) and 2004, a warm, even year (3.13 ± 0.06) (Figure 3.3.11). Regression analysis showed a slightly negative relationship between the mean fish C:N ratio and the mean zooplankton C:N ratio (slope = -0.06 , intercept = 3.5 , $R^2 = 0.17$, $df = 28$, $p = 0.02$). Regression analysis found no relationship between juvenile salmon C:N ratio and CPUE ($R^2 = 0.001$, $df = 28$, $p = 0.89$).

Among zooplankton, the mean C:N ratio was 4.7 ± 0.9 . The C:N ratio was generally higher in the northern region than the southern region (north: 5.0 ± 0.9 , south: 4.5 ± 0.6 , $t = 2.5$, $df = 9$, $p = 0.03$), and the lowest mean C:N ratio was observed in 2005 (4.3 ± 0.6) (Figure 3.3.12).

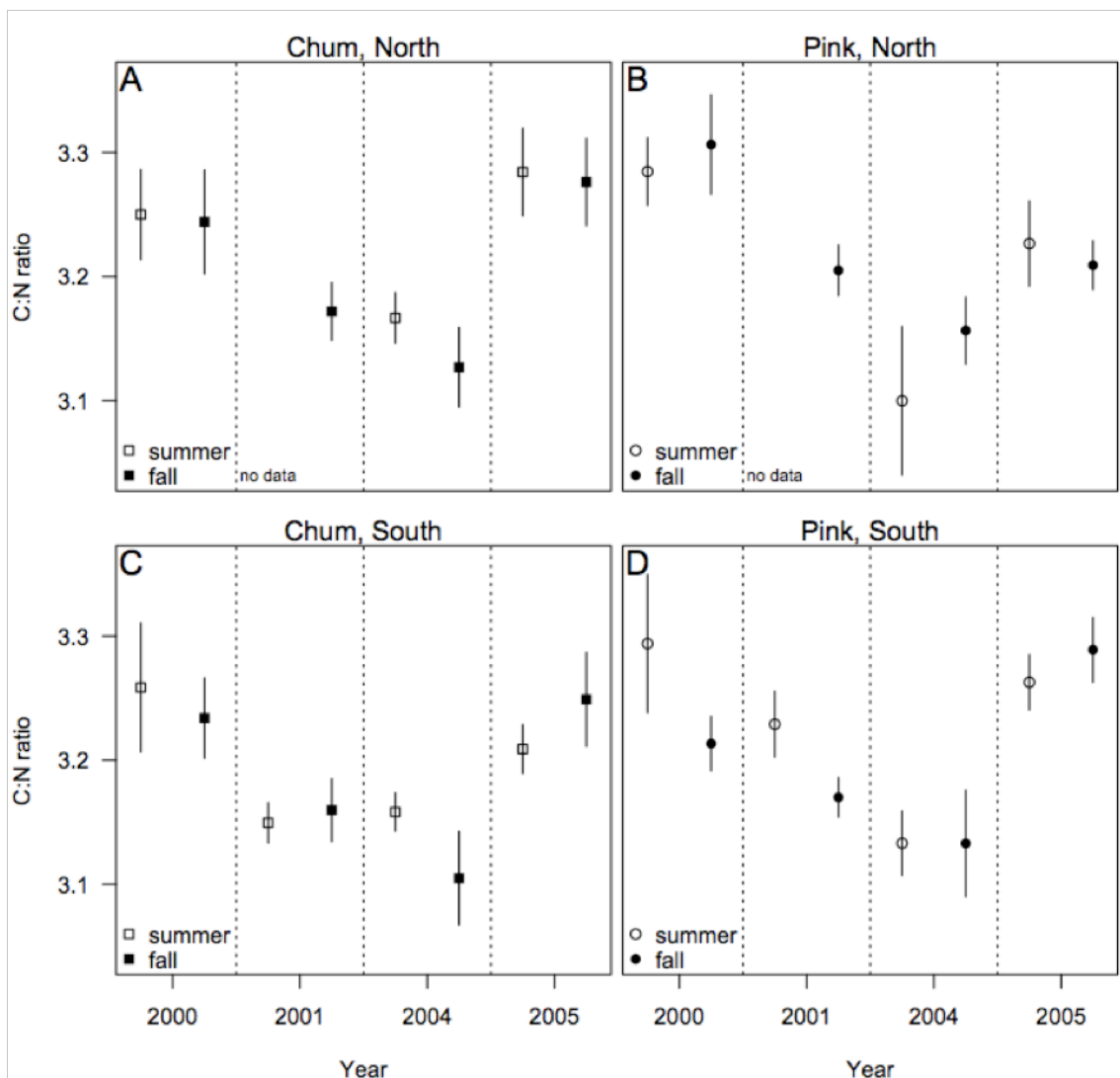


Figure 3.3.11. The C:N ratio (a proxy for lipid content) in the summer versus the fall for juvenile pink salmon and chum salmon in the northern and southern regions in each of the sampling years. The error bars represent the 95% confidence limits of the mean. Plots A and C represent juvenile chum salmon in the north and south, respectively, plots B and D represent juvenile pink salmon in the north and south, respectively. No juvenile pink salmon nor juvenile chum salmon were caught in the north in the summer of 2001.

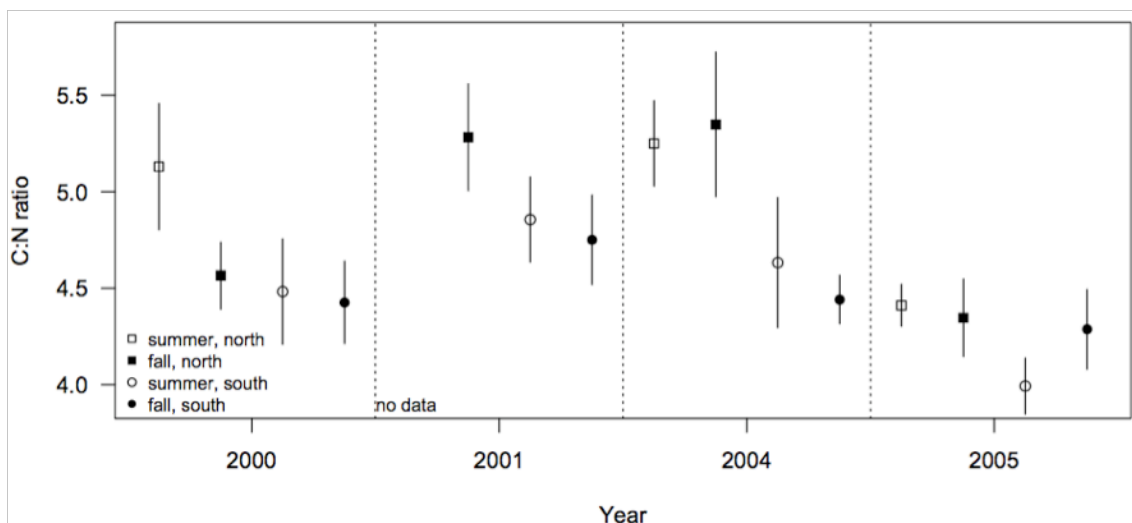


Figure 3.3.12. The carbon to nitrogen ratio (a proxy for lipid content) of zooplankton in the north and the south in the summer and fall in each of the sampling years. The error bars represent the 95% confidence limits of the mean.

3.4. Discussion

My intention was to determine how the ontogenetic niche of juvenile pink salmon and chum salmon shifts during their first months at sea, and how this changes in years of contrasting ocean conditions and salmon abundance. The results showed that juvenile salmon were much larger in the fall than the summer, as expected, growing in length from an average of 133 mm to 222 mm. Their weight increased from an average of 24 g to 116 g. The considerably larger size of juvenile salmon in the fall suggests that an ontogenetic diet shift may take place over the summer and into the fall.

3.4.1 Increased offshore-based food-source in the fall

I expected that juvenile salmon would display a more marine isotope signature in the fall because juveniles would be leaving the estuary and nearshore environment and eating from a more offshore-based foodweb. The marine environment tends to be more enriched in ^{15}N than the terrestrial environment (Schoeninger & DeNiro 1984), and $\delta^{15}\text{N}$

of predators reflects trophic position (Peterson & Fry 1987), hence, I expected the mean $\delta^{15}\text{N}$ to be significantly higher in the fall. The linear mixed effects model showed that there was an overall increase in $\delta^{15}\text{N}$ from summer to fall. The difference from summer to fall was more pronounced in the southern region than in the northern region. In the northern region there appeared to be a significant difference between the summer and fall $\delta^{15}\text{N}$ among juvenile pink salmon, especially in the year 2005, but not among juvenile chum salmon. In the south, there was a very large difference between the summer and fall $\delta^{15}\text{N}$ in the year 2001. This was a cold year and the fish in summer were unusually small, it is possible that fish emerged from the freshwater environment slightly later this year, as salmon are known to delay emerging in colder years (Murray & McPhail 1988). The late emergence would have resulted in later development and growth, which might have resulted in a greater reliance on a nearshore diet, causing the lower $\delta^{15}\text{N}$ in the south in the summer of 2001. They may have been more limited to smaller and lower trophic prey in this year due to their smaller size. The low $\delta^{15}\text{N}$ of salmon in the summer did not appear to affect the $\delta^{15}\text{N}$ of salmon in the fall, as it was not significantly lower in the fall of 2001.

Length had a significant effect on the $\delta^{15}\text{N}$ of juvenile salmon, as was expected since $\delta^{15}\text{N}$ also reflects the trophic position of a consumer. It is difficult to determine whether the increase in $\delta^{15}\text{N}$ was due in greater part to a shift from a nearshore to an offshore foodweb, or a switch from lower to higher trophic level prey. Since the carbon isotope signature has a smaller trophic discrimination factor (1‰ per trophic level), and trophic enrichment causes an increase in $\delta^{13}\text{C}$, while the offshore environment is depleted in ^{13}C (Perry et al. 1999), $\delta^{13}\text{C}$ can help to determine whether the difference in

$\delta^{15}\text{N}$ from summer to fall is based only on an increased trophic position of fish, or due in part to an increased reliance on an offshore foodweb.

Carbon isotopes were consistently lower among juvenile salmon in the fall than the summer, showing that a greater proportion of the juvenile salmon diet is from a marine-based foodweb in the fall. This confirms that the shift in $\delta^{15}\text{N}$ is due at least in part to an increased reliance on an offshore foodweb. The year 2001 in the south was an exception, when fall and summer $\delta^{13}\text{C}$ were not significantly different among either pink salmon or chum salmon.

The juvenile salmon niche-shift mirrored the shift that occurred among zooplankton from summer to fall. Generally, zooplankton $\delta^{15}\text{N}$ increased in the fall and $\delta^{13}\text{C}$ decreased, suggesting that the shift in the juvenile salmon food source is the result of the introduction of offshore-based nutrients into the coastal marine environment later in the summer and into the fall.

Overall, it appeared that in the south, there was a greater shift in juvenile salmon $\delta^{15}\text{N}$, while in the north the shift was more pronounced in juvenile salmon $\delta^{13}\text{C}$. This suggests that the ontogenetic shift in the north is based on an increased reliance on an offshore-based food web, and it might also suggest that there is a greater subsidy of nutrients coming from offshore in the north. In the southern portion of the study area, there was less of a shift in juvenile salmon $\delta^{13}\text{C}$, and more of a shift in juvenile salmon $\delta^{15}\text{N}$. This could be due in part to an offshore-based diet, but might also reflect a greater reliance on higher trophic level food among salmon in the south as they change ontogenetic niches.

The shift among zooplankton did not exhibit this regional effect; this suggests that the differences observed among juvenile salmon in the northern and southern regions may be more related to differences in the foodweb and the feeding behaviour of juvenile salmon than simply to a difference in the baseline isotope signatures. It is possible that the structure of the foodweb is different in the northern and southern regions, perhaps the greater shift in $\delta^{15}\text{N}$ in the south is due to a longer food chain in the south with a greater abundance of smaller zooplankton.

3.4.2 Ontogenetic shift is not diminished in poor conditions

I hypothesized that the ontogenetic shift from summer to fall would be diminished due to poor feeding conditions. I expected that there would be less of a difference in the ontogenetic niche and size of juvenile salmon between summer and fall in warmer years in the south. There was no strong evidence to support this hypothesis. Fish in warmer years were not significantly smaller than fish in cold years in the fall and the difference from summer to fall did not increase in colder years. There was no relationship between the magnitude of the trophic niche shift and the change in the size of juvenile salmon.

I had also hypothesized that increased density of juvenile salmon would lead to a reduced trophic niche shift among juvenile salmon from summer to fall. There was no relationship between the magnitude of the trophic niche shift and the abundance of juvenile salmon in either the summer or the fall. Furthermore, the magnitude of the shift that occurred among zooplankton from summer to fall also did not predict the magnitude of the shift among juvenile salmon.

The summer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ appeared to reflect a more nearshore diet among the juvenile salmon in the south in warm years. In warm years, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ tended to be higher than in cold years. This suggests that juvenile pink salmon and chum salmon are eating at a higher trophic level in warm years, but from a more nearshore-based foodweb. The zooplankton exhibited a stronger shift in $\delta^{13}\text{C}$ in cold years than warm years from a nearshore to an offshore signature, suggesting a greater influx of offshore nutrients in cold years that may contribute to improved survival among juvenile salmon (Kline et al. 2008).

3.4.3 Trophic position of juvenile salmon increases with size

As salmon grow larger, they have access to larger and higher trophic level prey (Boldt & Haldorson 2003); therefore I hypothesized that there would be a positive correlation between the size and trophic position of juvenile pink salmon and chum salmon. Using baseline corrected trophic position, as opposed to $\delta^{15}\text{N}$, ensures that the differences in trophic position are not simply due to isotopic changes at the base of the foodweb. Modeling showed that fish trophic position was significantly positively correlated with fish length, and a series of regressions showed that the relationship was significant in the fall among juvenile pink salmon in the north each year, and in the south in odd years. The relationship was also significant among juvenile chum salmon in the fall in the north in cold years, and in the south in 2001. Since the trophic position was more commonly related to length among juvenile pink salmon, this suggests that pink salmon are more likely than chum salmon to eat at a higher trophic position as their ontogeny changes. This finding might be related to the differences in feeding behaviour between pink salmon and chum salmon. Notably, chum salmon are known to rely more

heavily on gelatinous zooplankton (Sturdevant et al. 2004), and may supplement their diet with this prey item regardless of their size. This could dampen the relationship between their size and trophic position.

I also expected trophic position to be more strongly related to size in the southern region than the northern region, but there was no evidence to support this hypothesis. The mean trophic position of juvenile pink salmon and chum salmon in the fall was higher in the southern region than in the northern region, which may suggest that the trophic position of prey is more important in the south, whereas in the north the zooplankton are higher in lipids and therefore the prey quality is not as strongly linked to prey size and trophic position. This finding also shows that a similar pattern observed in $\delta^{15}\text{N}$ before correcting for the baseline was not simply due to a difference at the base of the food web, but most likely related to an actual difference in trophic position of fish.

3.4.4 Lipid-rich zooplankton suggest higher prey quality in the north

The C:N ratio was used to determine the relative lipid-richness of zooplankton in each year and region, and I hypothesized that zooplankton would be more lipid-rich in the north and in cooler years in the south. Zooplankton was significantly more lipid-rich in the northern region as well as in the south in the coolest year, 2001, but not the year 2000. This lends support to the hypothesis that zooplankton prey are of a higher quality in the northern portion of my study area.

I expected that lipid-rich zooplankton would lead to more energy-dense salmon, and that lower abundances of salmon would also result in more energy-dense salmon. There was no evidence to support a positive correlation between zooplankton lipid content and salmon energy density. The energy density of salmon was similar in the

northern and southern regions, and appeared to vary from year to year, while there was little difference between species and seasons. This might suggest that salmon in the northern portion of the study area have evolved to rely on more lipid-rich prey, and therefore it does not translate to greater energy density among juvenile salmon in the northern portion of the study area. There was no evidence of a relationship between the energy density of juvenile salmon and the abundance of juvenile pink and chum salmon. In warm years, the mean lipid content of salmon was higher in the odd year (2005), while in the cooler years the mean lipid content was higher in the even year (2000). Since this pattern was observed in both the northern and southern regions, it most likely is not related to the greater number of salmon leaving the Fraser River in even years.

3.4.5 Conclusion

A clear ontogenetic shift occurs among juvenile pink salmon and chum salmon from the summer to the fall in the coastal marine environment. Fish grow rapidly during this time, and their ontogenetic niche shifts to reflect an increasingly offshore-based diet. In the north, where zooplankton is more lipid-rich, the shift is more evident in a change in food source, it shifts from a nearshore to offshore-based diet. In the south, the shift is more evident in the change in trophic position; fish appear to eat at a higher trophic position in the fall. In warm years, the diet of salmon is more nearshore-based and the trophic position appears to be higher than in cool years. In general, the trophic position of fish increased with size, though the relationship appears to be stronger among juvenile pink salmon than chum salmon, and is not always consistent.

The data presented in this paper can be used to better understand the role of growth in ontogenetic niche, and can also help to understand some of the complex interactions between ocean conditions and the foodweb dynamics of juvenile salmon.

As ocean conditions continue to change and hatchery stocking of pink salmon and chum salmon continues, this information can be used to better understand and monitor changes in the ecology of juvenile salmon.

Appendix 2: Data summary for chapter 3

Table 3.2. Summary of mean juvenile salmon forklength and mean CPUE by year, region, species, and season. Forklength (mm) reports the mean length for salmon in each cohort. The column labelled 'SD' gives the standard deviation of the mean for the values in the preceding column. CPUE gives the mean and the following columns give the upper and lower confidence limits. The column entitled 'number of fish' reports the total number of fish sampled in each group. The column entitled 'number of tows' reports the total number after averaging fish of the same species caught in the same tow.

Year	Region	Species	Season	Length (mm)	SD	CPUE	CPUE lower limit	CPUE upper limit	Number of fish	Number of tows
2000	north	chum	fall	217.0	18.0	5.22	1.67	9.53	48	14
			summer	166.6	15.6	3.77	0.00	10.77	25	2
		pink	fall	238.3	23.2	8.63	2.99	16.87	51	20
			summer	146.8	15.9	4.85	0.00	13.50	28	2
	south	chum	fall	221.0	16.3	22.45	9.11	40.21	34	15
			summer	140.0	12.4	8.31	1.68	15.90	41	4
		pink	fall	210.7	15.8	30.77	12.36	53.77	31	14
			summer	117.0	2.7	25.44	3.68	60.33	29	4
2001	north	chum	fall	217.6	19.5	1.41	0.75	2.19	43	18
			fall	218.0	26.7	14.10	8.47	21.67	55	31
	south	chum	fall	211.6	20.1	3.52	0.83	8.32	43	11
			summer	106.8	15.7	0.75	0.00	2.06	22	3
		pink	fall	198.3	16.9	7.13	2.48	13.84	40	17
			summer	99.0	6.5	1.24	0.00	3.73	20	1
2004	north	chum	fall	227.8	8.1	0.17	0.05	0.33	12	7
			summer	129.2	4.8	0.44	0.00	1.04	6	2
		pink	fall	242.1	19.6	0.90	0.36	1.57	62	19
			summer	135.7	20.7	14.24	3.54	29.98	34	9
	south	chum	fall	218.6	16.4	16.74	4.71	33.19	36	9
			summer	138.4	14.0	95.70	13.36	210.58	32	9
		pink	fall	215.3	11.3	8.52	2.34	15.88	22	6
			summer	133.5	20.4	201.48	26.38	451.00	36	7
2005	north	chum	fall	222.8	12.8	2.64	0.62	6.08	42	18
			summer	137.8	15.6	3.88	0.32	10.12	28	6
		pink	fall	233.9	25.7	8.15	3.67	15.54	65	25
			summer	128.8	15.1	20.84	2.67	53.20	28	6
	south	chum	fall	236.9	14.8	1.50	0.62	2.64	22	10
			summer	135.8	11.1	86.66	37.68	141.60	37	7
		pink	fall	218.2	32.0	4.43	1.98	7.40	38	15
			summer	123.4	12.3	348.22	124.33	685.44	29	7

Table 3.3. Summary of mean juvenile salmon C:N ratio and lipid-corrected $\delta^{13}\text{C}$ data for each year, region, species, and season. Data was averaged first by tow, then by region (north or south). Each column labelled 'SD' gives the standard deviation of the mean in the preceding column.

Year	Region	Species	Season	C:N ratio	SD	Lipid corrected $\delta^{13}\text{C}$ (‰)	SD
2000	north	chum	fall	3.24	0.08	-18.95	0.55
			summer	3.25	0.09	-17.36	0.42
		pink	fall	3.31	0.09	-18.94	0.26
			summer	3.28	0.07	-17.48	0.52
	south	chum	fall	3.23	0.06	-18.16	0.53
			summer	3.26	0.05	-17.80	0.19
		pink	fall	3.21	0.04	-18.59	0.55
			summer	3.29	0.06	-17.83	0.34
2001	north	chum	fall	3.17	0.05	-18.29	0.36
			fall	3.21	0.06	-18.23	0.36
	south	chum	fall	3.16	0.04	-18.16	0.56
			summer	3.15	0.04	-18.66	0.71
		pink	fall	3.17	0.03	-18.49	0.57
			summer	3.23	0.06	-18.70	0.69
2004	north	chum	fall	3.13	0.04	-19.30	0.50
			summer	3.17	0.03	-16.82	0.34
		pink	fall	3.16	0.06	-18.22	0.50
			summer	3.10	0.09	-16.87	0.30
	south	chum	fall	3.10	0.06	-18.05	0.60
			summer	3.16	0.02	-16.80	0.46
		pink	fall	3.13	0.05	-17.99	0.34
			summer	3.13	0.03	-17.33	0.44
2005	north	chum	fall	3.28	0.07	-18.13	0.47
			summer	3.28	0.04	-17.61	0.24
		pink	fall	3.21	0.05	-18.53	0.31
			summer	3.23	0.04	-17.26	0.33
	south	chum	fall	3.25	0.06	-18.28	0.64
			summer	3.21	0.03	-17.26	0.12
		pink	fall	3.29	0.05	-17.91	0.40
			summer	3.26	0.03	-17.54	0.74

Table 3.4. Summary of mean juvenile salmon $\delta^{15}\text{N}$ and trophic position data for each year, region, species, and season. Data was averaged first by tow, then by region (north or south). Each column labelled 'SD' gives the standard deviation of the mean in the preceding column.

Year	Region	Species	Season	$\delta^{15}\text{N}$ (‰)	SD	Trophic position	SD
2000	north	chum	fall	12.29	0.46	2.62	0.15
			summer	12.45	0.37	2.52	0.15
		pink	fall	11.86	0.38	2.47	0.10
			summer	11.59	0.49	2.45	0.18
	south	chum	fall	12.85	0.36	2.93	0.14
			summer	12.25	0.31	2.71	0.11
		pink	fall	12.20	0.38	2.83	0.13
			summer	11.59	0.04	2.51	0.02
2001	north	chum	fall	12.96	0.31	2.48	0.16
			fall	12.41	0.30	2.39	0.13
	south	chum	fall	12.94	0.34	2.73	0.16
			summer	11.34	0.47	2.60	0.11
		pink	fall	12.37	0.46	2.60	0.22
			summer	11.17	0.42	2.57	0.12
2004	north	chum	fall	12.66	0.59	2.59	0.20
			summer	12.26	0.41	3.14	0.14
		pink	fall	12.57	0.30	2.57	0.13
			summer	12.38	0.28	3.06	0.11
	south	chum	fall	12.99	0.44	2.98	0.09
			summer	12.41	0.42	2.90	0.27
		pink	fall	12.58	0.32	2.89	0.06
			summer	11.76	0.46	2.59	0.11
2005	north	chum	fall	12.81	0.28	2.55	0.10
			summer	12.88	0.39	2.93	0.19
		pink	fall	12.99	0.29	2.59	0.10
			summer	11.74	0.31	2.55	0.20
	south	chum	fall	13.36	0.31	2.80	0.17
			summer	12.47	0.25	2.56	0.07
		pink	fall	12.74	0.57	2.60	0.14
			summer	12.06	0.27	2.44	0.08

Table 3.5. Summary of mean zooplankton C:N ratio, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data for each year, region, species, and season. Each column labelled 'SD' gives the standard deviation of the mean in the preceding column.

Year	Region	Season	C:N ratio	SD	$\delta^{15}\text{N}$ (‰)	SD	Lipid corrected $\delta^{13}\text{C}$ (‰)	SD	number
2000	north	fall	4.56	0.47	10.30	0.37	-20.76	0.86	29
		summer	5.13	0.28	10.20	0.03	-18.80	0.44	3
	south	fall	4.43	0.59	9.52	0.78	-19.78	1.18	30
		summer	4.48	0.34	9.86	0.53	-18.08	0.74	6
2001	north	fall	5.28	0.94	11.04	0.66	-19.54	1.38	46
	south	fall	4.75	0.65	10.59	0.70	-18.84	1.44	31
		summer	4.86	0.29	9.48	0.49	-17.50	0.94	7
2004	north	fall	5.35	1.34	10.65	0.63	-19.30	1.66	51
		summer	5.25	0.40	8.75	0.67	-18.44	0.84	13
	south	fall	4.44	0.30	10.12	0.85	-20.00	1.37	22
		summer	4.63	0.58	9.31	0.87	-19.05	1.08	12
2005	north	fall	4.35	0.59	10.98	0.35	-20.05	0.57	34
		summer	4.41	0.20	9.90	0.49	-19.26	0.71	13
	south	fall	4.29	0.66	10.73	0.65	-20.38	0.93	41
		summer	3.99	0.20	10.57	0.36	-18.93	0.68	8

Chapter 4: Conclusion

My research shows that the ecological niche of a population, based on their food source and trophic position, can change from year to year in a dynamic environment such as the Northeast Pacific Ocean. The niches of two concurrent and similar species appear to shift roughly in unison, although there was some evidence that the degree of overlap might be affected by an interplay between the density of organisms and the resources available. My evidence also confirms that the diet of a population will change to reflect an ontogenetic shift as the organisms of that population increase in size.

My results show that the niches of juvenile pink salmon and chum salmon appear to overlap in the coastal marine environment, and that the degree of overlap increases when the competition for resources increases. Further research would be needed to determine the cause, but I suggest that it is due to a combination of the prey species present, the level of competition between the two species, and the preferred prey of the two species.

Surprisingly, mean trophic position of juvenile pink salmon and chum salmon was higher in warm years, in the southern portion of the study area, and in years when salmon abundance was high. I suggest that this might be, in part, due to timing of emergence, and that the trophic position of prey may not reflect its quality, and also that the lipid content of zooplankton may be an important factor to consider when determining prey quality. Chum salmon have been found to rely more heavily on gelatinous zooplankton at various life-stages than do other salmon species (Sturdevant et al. 2004), and chum salmon in my study tended to display a higher trophic position than pink salmon. I suggest that some of the variation observed between species and among

regions and years might be related to different levels of reliance on gelatinous zooplankton. It is difficult to determine the importance of gelatinous zooplankton in the diets of salmon since this type of prey is digested quickly and hard to identify (Arai et al. 2003), but it may warrant further inquiry, especially as there is evidence that the amount of gelatinous zooplankton is increasing in the world's oceans (Brodeur 1999, Atkinson et al. 2004, Richardson 2008).

There appeared to be a greater input of offshore-based nutrients into the juvenile salmon diets in the coastal marine environment in cooler years in the southern region. Cooler temperatures can lead to decreased stratification of the water column, and in cooler years the California Current System tends to exhibit increased upwelling (Gargett 1997). It is possible that a combination of these factors lead to improved nutrient availability and mixing of the water column in the cooler years (Whitney et al. 2005), which might have contributed to improved survival of juvenile salmon in those years (Beamish 2002).

There was a distinct ontogenetic niche shift that occurred from the summer to the fall, which was apparent due to the larger size, higher trophic level, and more offshore-based food source of salmon in the fall than the summer. An interesting trend was observed in the ontogenetic niche shift of both species in the southern region versus the northern region. In the south, the niche shift was characterized by a shift in trophic position, while in the north the shift was characterized by a shift from a nearshore to an offshore-based diet. Trophic position was correlated with size in the fall in the north, but it appears that the diet in the fall in the north is not of a particularly higher trophic position than the summer. This difference might be related to differences in the

zooplankton assemblage in the north, as well as the more lipid-rich prey that is present in the northern region (Lee et al. 2006, this study).

There is still much to be learned about the diet of juvenile salmon in the coastal marine environment and how it relates to their survival. It is understood that juvenile pink salmon and chum salmon tend to feed on highly visible prey, which consists mostly of zooplankton and some fish (Landingham et al. 1998, Armstrong et al. 2005). Many of the favoured prey species of juvenile pink salmon and chum salmon have been identified, but there are many limitations to diet studies due to their restricted spatial and temporal scales.

Although stable isotope studies have limitations, they allow researchers to view the diets of organisms from a different and broader scale. The temporal scale offered through the use of isotope studies is much larger than the ‘snapshot’ offered through stomach content analysis. As more research is undertaken at a variety of scales and combining both stable isotope and diet studies, a clearer picture of the ecology of juvenile salmon will begin to emerge. As larger scale trends are observed, and explained through smaller scale, mechanistic studies, it may be possible to better predict the survival of salmon in the marine environment.

Better prediction and management of salmon stocks is a currently a topic of great interest to many Canadians. The prediction of sockeye stocks returning to the Fraser River was significantly overestimated in 2009, when only 1.4 million sockeye returned (Pacific Salmon Commission 2009), and the return was seriously underestimated in 2010, when 29 million sockeye unexpectedly returned (Pacific Salmon Commission 2010). Such erroneous predictions could create financial impacts on the fishing industry

and the communities that rely on it, but hopefully, with a better understanding of the ecology of juvenile salmon in the coastal marine environment, prediction methods will continue to improve.

Further research that would be of great value would be a wide scale investigation of the spatial and temporal stable isotope dynamics of zooplankton along the Pacific coast (research that has already begun), as well as an investigation into the speed at which isotopic turnover occurs in the tissues of quickly growing juvenile salmon. Pink salmon and chum salmon would be especially interesting to study in this context since the majority of their growth occurs in the marine environment, although a combination of observation and laboratory experiments would be necessary to draw robust conclusions for such a complex issue.

The data presented in this paper elucidate some interesting trends in the trophic and foodweb dynamics of juvenile salmon. The isotope signatures recorded can be added to the growing body of knowledge concerning isotope dynamics in nature, and can be used to compare with data concerning salmon in future years and in different regions, as well as with other species in the marine environment. Since there is little isotope data available for juvenile pink salmon and chum salmon from the coasts of northern British Columbia and Southeast Alaska, this study can act as a baseline for this area, and could be used in the future to identify major shifts in the feeding behaviours and trophic dynamics of juvenile pink salmon and chum salmon.

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