

**The growth and diet composition of sockeye salmon smolts in Rivers Inlet, British
Columbia**

by

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Abstract

In the early life history of sockeye salmon smolts, prey availability (quality and quantity) and growth are strongly linked. During this critical period, when ~ 90% of their mortality occurs, they must attain a critical size at which they have sufficient energy stores to survive their long migration with little predation impact, leading to better survival and higher returns. To determine patterns of growth of out-migrating sockeye salmon and to link inter-annual variations in growth to diet and seasonality of the zooplankton community, seine netting and zooplankton tows were conducted in May-June 2008, 2009, and 2010 in Rivers Inlet, British Columbia, a fjord with estuarine circulation. Growth rate, condition factor and mass-length relationships were calculated from length and mass data obtained from fresh fish. Stomachs were analyzed for total prey composition in terms of biomass and abundance. Growth rates were faster in 2009 and 2010 than in 2008; however, the condition factor was highest in 2010, and similar in 2009 and 2008. Mass-length relationships indicated that sockeye smolts were significantly heavier per unit length in 2010 ($p < 0.05$). Bottom-up controls on spring productivity acting through environmental forcing such as temperature and advection may be responsible for the slower growth in the 2008 out-migrating population of sockeye salmon smolts. In 2008, quality and quantity of prey available may have not provided enough energy to maintain metabolism and to support rapid growth, possibly due to a mismatch in timing between spring productivity and the migration of the smolts.

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To Dad, with love.

Chapter 1: Introduction – The early life history of sockeye salmon smolts

British Columbia (BC), Canada, has ~2,700 km of coastline and an area of ~623,000 km², supporting ~10,000 unique spawning grounds for all five species of Pacific salmon, of which ~900 support sockeye salmon stocks (Henderson and Graham 1998). Historically, British Columbia contributed 25-40 million salmon, mostly pink and sockeye, to annual catches of salmonids in the North Pacific. This contribution declined from 14% to 8% of total Pacific Rim salmon production between the mid-1980's and mid-1990's, largely due to an increase in production of Alaskan and Japanese fisheries and the growing contribution of farmed Chinook and coho salmon (Henderson and Graham 1998). In BC, sockeye were the second most abundant salmon species, with ~80% of annual sockeye production originating from the Fraser River, Skeena River, Nass River, Rivers Inlet, Smith Inlet, and Barkley Sound systems (Figure 1; Henderson and Graham 1998). The Fraser River always produced the largest sockeye fishery, while the Skeena River and Rivers Inlet systems vied for the second largest (McKinnell et al. 2001).

Owikenno Lake, the main nursery lake of the Rivers Inlet sockeye population, has a maximum carrying capacity of 41,000 kg of sockeye fry annually (McKinnell et al. 2001). The lake is also the main freshwater source for the inlet, entering via the ~6.5 km long by ~100 m wide Wannock River and draining an area of ~3,970 km², representing 65% of the total catchment area (Figure 2; Hodal 2011). Three other freshwater sources are responsible for draining a total area of ~2,200 km² into the inlet (Hodal 2011). Sockeye spawning locations have been identified in a total of 12 tributaries, all of which are located within the Owikenno Lake catchment area (DFO 1996, DFO 1997). Seven of these tributaries are

responsible for 83% of sockeye escapement within the system (Nelson et al. 2003). Genetic analysis of sockeye from the seven main spawning sites exhibited no isolated populations, suggesting that gene flow and straying between the rivers is sufficient to treat Owikeno Lake sockeye as a single population (McKinnell et al. 2001, Nelson et al. 2003).

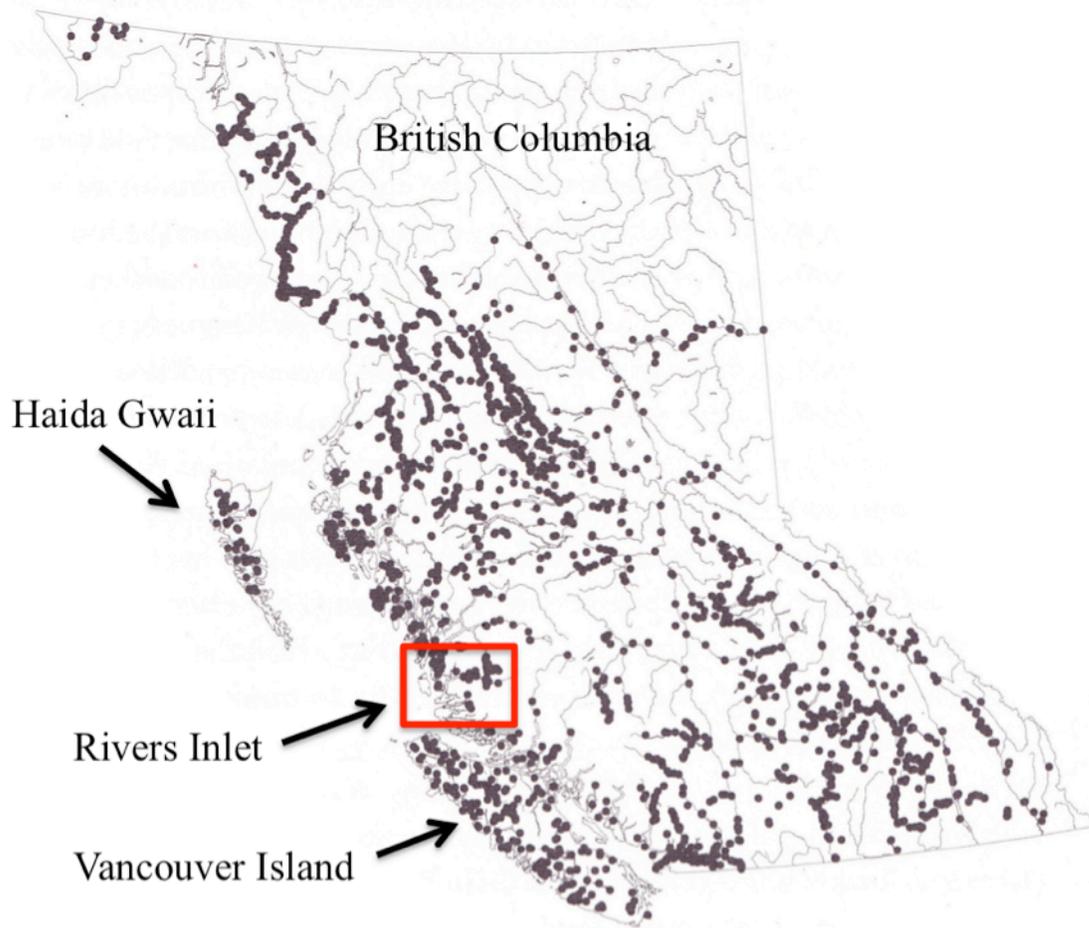


Figure 1: Map of British Columbia; dots indicate the historical spawning locations (~900) of sockeye salmon throughout the province. The fisheries associated with the Fraser River, Skeena River, and Rivers Inlet (red box) systems once produced the largest catches of sockeye salmon in British Columbia. Map from McPhail (2007).

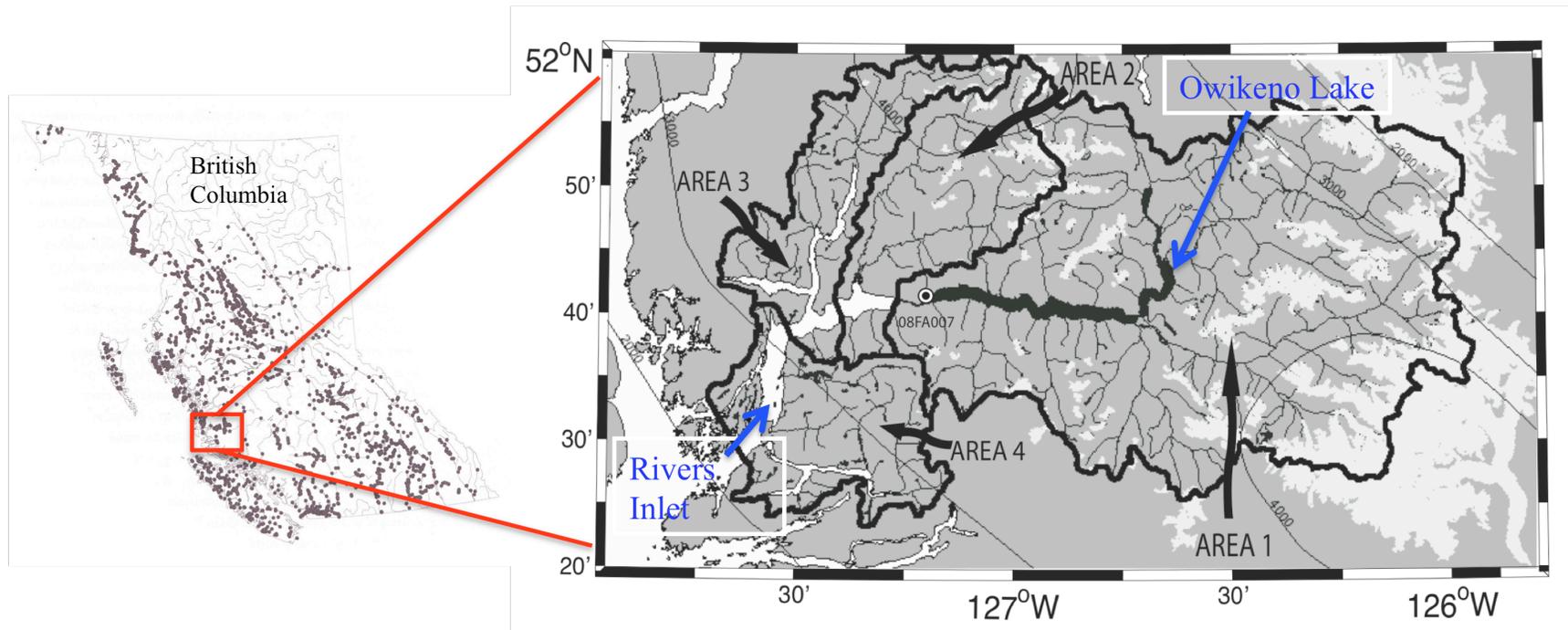


Figure 2: Outline of the four catchment areas draining into Rivers Inlet, including associated glaciers, rivers and annual precipitation averages (shown as isolines). The Owikeno Lake catchment (Area 1; Owikeno Lake is highlighted in black) drains an area of $\sim 3,970$ km². The other three catchment areas drain a total of $\sim 2,200$ km². Environment Canada maintains gauge 08FA007, which measures freshwater discharge from Area 1. Maps from McPhail (2007) and Hodal (2011).

Established in 1884, the Rivers Inlet commercial sockeye fishery supported up to 1900 gillnetters and 14 canneries for the first 90 years of the fishery, producing an average annual harvest of 808,000 fish, the largest fishery on the Central Coast (e.g. Wood 1970, DFO 1997, Nelson et al. 2003, Riddell 2004). Following a widespread change in fishing gear and low escapements in subsequent years (late 1950's to mid-1960's), concerns about recruitment overfishing led to a reduction in fishing area and number of allowable fishing days per week (Walters et al. 1993). At the time, optimal escapements were estimated to be 60-80% of the total return, or 400,000–600,000 fish (Wood 1970, Walters et al. 1993); however, several assessments of stock and recruitment data indicated that the optimum number of spawners needed to maximize average annual catch could be anywhere from 250,000 to 1.5 million fish (Walters et al. 1993, McKinnell et al. 1998). Continuing suspicion of recruitment overfishing in the late 1970's coupled with low escapements and large variations in catch led to the implementation of an experimental adaptive management plan to determine the optimal number of sockeye escapements, with the hope that an increase in the total number of spawners would lead to higher total production (Walters et al. 1993). The plan effectively closed the Rivers Inlet fishery for 8 years (1979-1988), allowing < 3 fishing days per year for the first 5 years and limited fishing of 1-2 days per week for the last 3 years (Walters et al. 1993). Results indicated that optimum escapement was 400,000 and concluded that an unidentified factor, possibly linked to poor marine survival, was preventing higher recruitment (Walters et al. 1993). While escapements increased in the 1980's, the subsequent decline and collapse of the Rivers Inlet sockeye population in the early 1990's led to the total closure of the fishery in 1996 (McKinnell et al. 1998, Nelson et al. 2003). Following a record low return of 3,600 adults in 1999, returns have increased to ~124,000 fish but have

remained below the 200,000 minimum required to reopen the fishery (e.g. Rutherford and Wood 2000, DFO 2002, Holtby 2002, Riddell 2004, DFO 2011).

Sockeye are the most valuable commercial fishery in British Columbia and are important ceremonially and as subsistence to the First Nations communities (Pauley et al. 1989). They are also an important prey item for many species of higher trophic levels, including bears which can consume up to 30 adult sockeye a day and rely on salmon to fulfill 90% of their annual dietary needs (Temple 2005). Determining the causes behind the reduced run is therefore of significance to the entire Rivers Inlet ecosystem.

Leading hypotheses point to a change in the marine environment and subsequent reduction in early marine survival of sockeye salmon smolts as the cause of low adult returns. Every 20–30 years, a regime shift, or an abrupt and synchronous change in climate-ocean conditions known as the Pacific Decadal Oscillation (PDO) occurs, which closely follows trends in the marine survival of Pacific salmon populations (Hare and Mantua 2000). Changes in climate-ocean conditions include sea surface temperature (SST), sea pressure (Aleutian Low), sea surface salinity (SSS), and changes in productivity (Beamish et al. 1998, Hare and Mantua 2000, McFarlane et al. 2000). Beamish and Bouillon (1993) found that all-nation salmon catches from Asia (Japan, Russia) and North America (Canada, United States) have undergone abrupt fluctuations that correspond to known regime shifts. The overlapping distribution of these populations and their synchronous changes in abundance provided strong evidence that a common marine event in the North Pacific Ocean affected their survival (Beamish and Bouillon 1993). The 1976 regime shift was associated with an intense Aleutian Low, cooling of the Central North Pacific, and warming of the Northeast Pacific, which led to higher values of productivity. The 1989 weakening of the Aleutian Low and

warming of the Central North Pacific and Northeast Pacific produced a general, all-nation increase in abundance of salmon (Hare et al. 1999, Hare and Mantua 2000).

While trends in all-nation catch did follow the large-scale dynamics of the PDO, populations around the Pacific Rim were also affected on a national scale (Hare et al. 1999, Hare and Mantua 2000). In North America, the 1976 regime shift caused a decrease in abundance of Alaskan salmon populations and a parallel increase in West Coast (Washington, Oregon and California) populations (Hare et al. 1999). This pattern reversed with the 1989 PDO event, characterized by warmer SSTs, a weaker Aleutian Low, and increased stratification. Zooplankton production in Alaskan waters increased, while those in the West Coast region decreased. The inverse relationship in zooplankton population dynamics and its effect on sockeye survival established a case for climatic, bottom-up control on salmon production early in the marine phase of their life cycle (McFarlane et al. 2000).

Hare and Mantua (1999) found BC to be a transitional region between Alaska and the West Coast, with coho and Chinook stocks exhibiting similar trends to the West Coast populations, and sockeye, pink and chum stocks more closely related to the Alaskan populations (although the changes in abundance were weaker than those seen in Alaska). Beamish et al. (1998) and McFarlane et al. (2000) ruled out overfishing as a cause of the early 1990's collapse in BC salmon stocks, because the decline was synchronous across several fisheries. The focus shifted to the effect of changing environmental variables on salmonid survival (Beamish et al. 1998). In BC, the 1976 regime shift was associated with a more intense Aleutian Low and an increase in salmon abundance. The subsequent 1989 regime shift weakened the Aleutian Low and increased SST. The PDO also influenced local populations on a regional basis throughout the province. In the Strait of Georgia, Beamish et

al. (1998) noted more winter zonal winds, an earlier spring freshet (the influx of freshwater from glacial melt), higher sea level, lower winter SSS, and reduced productivity following the 1989 regime shift. The decline in productivity amongst the lower trophic levels (phytoplankton and zooplankton) and increase in the metabolic rate of the outmigrating smolts (en route to the open ocean) translated into higher rates of marine mortality during the salmonids' first winter at sea (Beamish et al. 1998). The shift in salmon abundance caused by environmental change was through a change in the production of the salmon's food supply and its effect on the smolts' growth (Beamish et al. 1998, Beamish and Bouillon 1993, McFarlane et al. 2000).

In Rivers Inlet, significantly reduced Wannock River discharge and higher SSTs in the Queen Charlotte Sound provided clear signals of the 1976 regime shift (McKinnell et al. 1998). Lower discharge rates were suggested as a possible cause for reduced circulation, lower primary production, and a more saline environment, potentially reducing the freshwater lens available for the smolts to use as a transition between the freshwater and saltwater environments (McKinnell et al. 1998). Following the 1989 regime shift, the Queen Charlotte Sound faced the warmest SSTs on record (McKinnell et al. 2001). Although mean SST had increased since 1976, it reached peak levels in the early 1990's and abated by 1999 (McKinnell et al. 1998, McKinnell et al. 2001). These SST anomalies were caused by the persistence of winter wind patterns maintaining the poleward flow of warmer southerly waters, particularly into April and August, and accounted for 53.2% of the variation in recruits per spawner (McKinnell et al. 2001). The influx of warmer water into the Queen Charlotte Sound also generated anomalies in SSS from 1992–1998, the most extreme of which coincided with the crashes in the Rivers Inlet sockeye salmon population (McKinnell

et al. 2001). A corresponding delay in transition from downwelling to upwelling conditions also diminished deepwater nutrient input and delayed primary production. The warmer waters were therefore expected to have created a situation of lower food resources and increased vulnerability to predators, as well as introducing higher metabolic demands on the migrating smolts, and all potentially contributing to the lower marine survival of sockeye smolts (McKinnell et al. 1998, McKinnell et al. 2001).

In light of the hypothesized bottom-up control on salmon production in Rivers Inlet, the Rivers Inlet Ecosystem Study (RIES), conducted between 2008 and 2010, specifically investigated the drivers of lower trophic level processes in this ecosystem. The initiation of spring productivity occurs when the combination of light and nutrients can support the rapid accumulation of phytoplankton. Specifically, a phytoplankton bloom occurs when growth rates exceed loss rates and an accumulation of biomass occurs (Tommasi et al. in press). In Rivers Inlet, the initiation of the spring phytoplankton bloom in 2008 (3-April) and 2009 (18-April) was the most sensitive to wind direction, with strong outflow winds transporting phytoplankton out of the inlet and inhibiting the development of the spring bloom (Wolfe 2010). The duration and termination of the spring bloom may be controlled by surface water residence time and the timing and extent of deepwater renewal (Hodal 2011). Residence time (the mean amount of time it takes for a parcel of water to exit an estuary) controls the persistence of materials in the system. For example, a low (shorter) residence time earlier in the spring would transport any initial phytoplankton biomass out of the inlet before a bloom could be established (Hodal 2011). A later and weaker deepwater renewal would decrease the supply of nutrients to the system, terminating the bloom and resulting in lower estimates of seasonal productivity (Hodal 2011).

Seasonally, the spring transition is the date on which the winter southwesterly winds change to summer northeasterly winds, reducing outflow events in the inlet (Wolfe 2010). Historically (1969-2008), a shift to low-pressure systems interacting with coastal regions along Vancouver Island has caused later spring transition dates. This delayed onset of the spring transition coincided with crashes in salmon populations, including the Rivers Inlet sockeye population. It has been hypothesized that, through delaying the spring bloom, the later spring transition may have reduced zooplankton production and thus reduced prey availability to the sockeye salmon smolts (Wolfe 2010). The spring transition also contributes to deepwater renewal in the system. The input of this deep, saltwater layer from the Queen Charlotte Sound provides and controls nutrient levels in the estuary, and a weaker or delayed renewal will lower nutrient supply rates and affect the duration of spring production (Hodal 2011). Surface residence times (the mean amount of time it takes for a parcel of water to exit an estuary) are also important in controlling the persistence of materials in the system (Hodal 2011). In this way, the timing of the seasonal freshet determined the termination of the initial spring phytoplankton bloom.

High rates of advective transport may produce a loss term for both phytoplankton and zooplankton abundance and biomass that would ultimately affect the amount of food available to the outmigrating smolts. The earlier increase in surface outflow seen in 2009 and the subsequent lower seasonal production may therefore have led to a lower marine survival of sockeye salmon smolts (Hodal 2011). Hodal (2011) converted a 49-year record of daily river discharge into surface residence times of the freshwater layer. Residence times averaged 7 days during periods of high discharge and 15 days in times of low freshwater influx. Hodal (2011) noted high inter-annual variability, but a long-term shift of ~10 days to

an earlier initiation of the freshet. This suggests an additional mechanism for long term declines in Rivers Inlet production, which coupled with a later spring transition, may have impacted the sockeye smolts' survival.

The importance of inlet productivity to sockeye remains questionable. Also, the estuarine use by sockeye smolts as grounds for foraging and growth is largely unknown. Recent tracking studies in the Fraser River system have shown that they make limited use of the estuary, preferring instead to rapidly continue their northward migration (Welch et al. 2011). Qualitative attempts of Buchanan (2006) estimated the residence time of sockeye smolts in Rivers Inlet to be ~2-3 weeks. Since Rivers Inlet smolts are smaller than average, they may be more vulnerable to changes in their physical environment, which would impact their growth and survival during the transition from freshwater to saltwater (McKinnell et al. 2001). The Rivers Inlet estuary is therefore hypothesized to be a crucial staging zone for the smolts, acting as a transition area to higher salinities and an important feeding ground, where the smolts can roughly double their mass during their migration to the open ocean (Buchanan 2006).

Climate-driven changes in the timing of the phytoplankton bloom affect zooplankton community composition. For example, zooplankton production is closely coupled with trends in the Aleutian Low (Beamish and Bouillon 1993). Production of calanoid copepods in the California Current increased during years of intense lows and decreased in years when the Aleutian Low weakened and SSTs rose (Beamish and Bouillon 1993). Similarly, chlorophyll *a* concentrations in Rivers Inlet accounted for at least 30% of the variation in zooplankton biomass between 2006 and 2007 (Tommasi et al. in press). The timing of the spring phytoplankton bloom is correlated with zooplankton biomass and the composition of the

zooplankton community (Tommasi et al. in press). Zooplankton biomass is positively correlated with fish growth rate and yield, and fish populations may act as a link between primary producers and higher trophic levels (Ottersen et al. 2010, Chick and Van Den Avyle 1999, Fortier et al. 1995).

The temporal lag between prey production and consumer requirement is critical, and established the foundation for the match-mismatch hypothesis (e.g. Cushing 1990, Beamish and Bouillon 1993, Cushing and Horwood 1994, Beamish et al. 1998, Beamish and Mahnken 2001, Durant et al. 2007). A variety of environmental conditions may determine the initiation date and intensity of the phytoplankton bloom, setting up the composition and timing of the increase in abundance of the juvenile salmonids' prey. If this later coincides with the outmigration of the juvenile salmonids, their growth will be well supported (a match). Alternatively, a delayed spring bloom and subsequent altered zooplankton community, in terms of timing, quality (composition) and quantity, will affect juvenile growth, mortality, and overall survival (a mismatch; Cushing 1990, Cushing and Horwood 1994, Anderson and Hinrichsen 1996, Beamish and Mahnken 2001). The life stage just after marine entry may be a food sensitive critical period in which 90% of the sockeye population mortality occurs (e.g. Bollens et al. 1992, Simenstad et al. 1982, Straty and Jaenicke 1980). Two mechanisms control the mortality of smolts in their early life stages: 1) risk of predation upon marine entry, and 2) a failure to reach a critical size during their first marine summer (Beamish and Mahnken 2001). The match-mismatch hypothesis has recently been expanded to include the juvenile critical period hypothesis, in which the failure of the salmonids to reach a certain size by their first marine winter decreases their vitality (Beamish and Mahnken 2001). The size they attain is thought to be a function of environmental conditions controlling the quality

and quantity of prey availability during their outmigration (Beamish and Mahnken 2001). In Rivers Inlet, zooplankton were the main prey of sockeye smolts (Buchanan 2006). A change in the timing of the phytoplankton bloom may therefore affect the prey available for smolts entering the marine environment, subsequently affecting their feeding success (Cushing 1990, Cushing and Horwood 1994, Fortier et al. 1995, Chick and Van Den Avyle 1999).

The main aims of this thesis were: 1) to determine the spatial and temporal variability in growth of sockeye smolts, 2) to characterize the diet composition of sockeye smolts in a coastal fjord and 3) to describe the relationship between growth and feeding ecology throughout the inlet phase of their early marine life history.

Chapter 2: Estuarine growth of sockeye salmon smolts

2.1 Introduction

Changes in the marine environment may impact the ability of sockeye smolts to gain the energy and mass necessary for their survival. Sockeye have a highly variable life history pattern. Many populations remain in the nursery lake for up to two years, growing to a size at which they are less susceptible to predation upon their outmigration (Pauley et al. 1989). In Rivers Inlet, however, the majority of sockeye salmon spend one winter in Owikeno Lake before migrating to the marine environment, despite their small size at the end of this growth period (Gilbert 1915, Foskett 1958, McKinnell et al. 1998, 2001). The oligotrophic environment and density-dependent growth limit resources available to them during their freshwater residence time (Gilbert 1915, Foskett 1958, McKinnell et al. 1998, 2001). Historically, hypotheses predicted that these limited resources resulted in slow growth and produced unusually small smolts. The smolts may have been adaptively constrained by their physiological development and underdeveloped for successful migration (Gilbert 1915, 1916, Foskett 1958, McKinnell et al. 1998, 2001). For example, the transition to salt water may be more difficult for smolts of a smaller size, due to their lower ability to tolerate higher salinities (McKinnell et al. 1998). However, despite their small size, Rivers Inlet produced one of the largest sockeye runs on the Central Coast of British Columbia for the first 90 years (1884-1974) of the commercial fishery (Henderson and Graham 1998, McKinnell et al. 2001). In addition, the cohort of smolts with the smallest average size produced the largest catch on record for this stock (McKinnell et al. 2001).

McKinnell and Lundqvist (2000) investigated the importance of fry size in relation to adult recapture rates in hatchery released Atlantic salmon. They found a significant positive correlation between the fry size and survival rates in any one year class (McKinnell and Lundqvist 2000). Absolute size of a population may fluctuate between years; however, these variations are a response to environmental change and the instability of the marine environment, and have little influence on the survival of a single year class (McKinnell and Lundqvist 2000). Relative size of a fish within a specific cohort affects marine survival because larger fish within that cohort may incur survival advantages. In the case of sockeye smolts, a larger fish may face decreased risk of predation, a smoother transition from fresh to salt water, and have a heightened ability to maintain metabolic function throughout its first marine winter (Beamish and Mahnken 2001). A larger fish may also have an advantage in foraging success. Conversely, a smaller fish may face more intense competition for prey resources, an increased risk of predation, and may fail to reach the critical size necessary for winter survival (Beamish and Mahnken 2001).

In Rivers Inlet, the consistent average juvenile abundance in the lake phase and the relatively stable lake environment do not explain the decline in adult returns, and suggest that the early marine environment is key to the survival of sockeye smolts to adulthood (McKinnell et al. 1998, 2001). Local biological and physical conditions (e.g. prey availability, sea surface temperature and salinity), coupled with the physiology, growth, and feeding ecology of the smolts are critical in regulating sockeye smolts' growth and survival during the estuarine phase of their early life history (McKinnell and Lundqvist 2000, McKinnell et al. 2001, Tucker et al. 2009). The specific aims of this chapter are to: 1) to

describe the spatial and temporal distribution of the sockeye smolts, and 2) to determine the growth and condition of the smolts during their migration through the estuary.

2.2 Methods

The RIES occurred over three years (2008, 2009, and 2010) in Rivers Inlet, and sampling was conducted between late April and early July during this time. These sampling surveys were designed to overlap with the expected period of migration of sockeye smolts through the inlet. In 2008 and 2009, a total of five surveys were conducted fortnightly for approximately two months (Table 1). At some locations, seining was reset or terminated due to weather, mechanical issues, or strong tidal currents that made sampling more difficult (Appendices A, B, and C). For example, in 2010, an additional survey was conducted to compensate for weather and mechanical problems that hindered sample collection during the 19-June survey. The 19-June and 27-June surveys were spaced 8 days apart, and the 27-June and 5-July surveys were eight days apart, but all other 2010 surveys occurred fortnightly.

Table 1: Survey number and its corresponding date for each sampling year.

Year	Survey No.					
	1	2	3	4	5	6
2008	29-Apr	11-May	28-May	10-Jun	25-Jun	N/A
2009	1-May	17-May	31-May	15-Jun	29-Jun	N/A
2010	6-May	19-May	4-Jun	19-Jun	27-Jun	5-Jul

A total of 10 sites were surveyed, spaced along the length of Rivers Inlet (~45 km by ~3 km), to provide representative sampling from head to mouth and to determine the distribution of the smolts throughout the inlet (Figure 3). At the Dawsons, Bosquet and Dimsey sites, two sets were conducted, to determine the preference of migrating smolts for near-shore versus offshore environments, giving a total of 13 sites sampled per survey (Buchanan 2006). Sockeye smolts in Rivers Inlet also have two possible outmigration routes: 1) a southern route out of the main Rivers Inlet channel into the Queen Charlotte Sound, or 2) down the Darby Channel, a narrow, shallow passage along the north of the inlet that is separated from the main channel by a series of islands. Darby Channel enters into Fitz Hugh Sound, which is relatively protected from wind and swell in comparison to Queen Charlotte Sound. Smolts may preferentially use this latter route because it empties into these calmer, more sheltered waters (Buchanan 2006). Sites were chosen along both channels to determine the extent that smolts prefer one or the other.

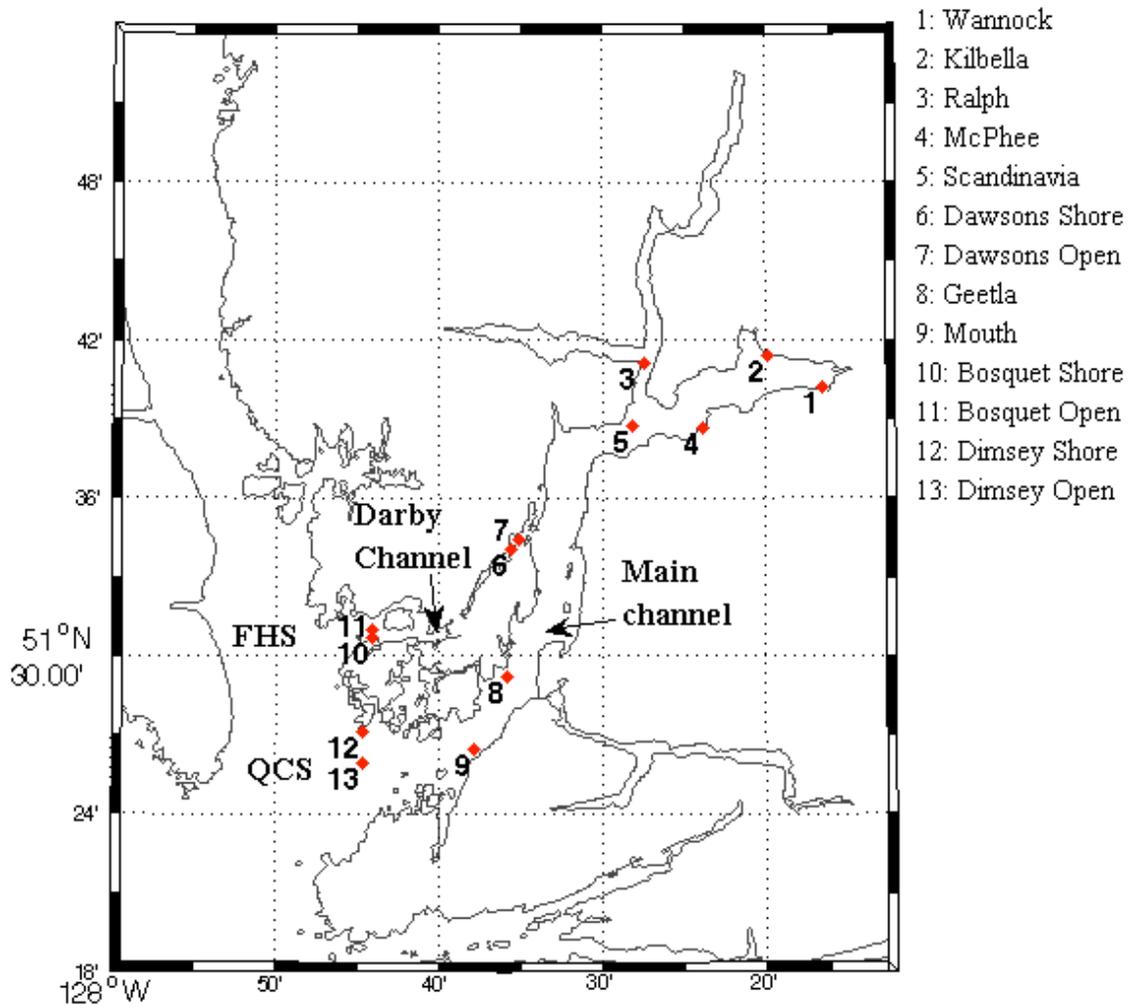


Figure 3: Map of Rivers Inlet. Arrows indicate two possible outmigration routes for the sockeye smolts: 1) down the more protected Darby Channel into the Fitz Hugh Sound (FHS), or 2) through the main channel into the Queen Charlotte Sound (QCS). Red dots indicate the location of the 13 seining stations sampled fortnightly from late April to early July in 2008, 2009, and 2010. The legend represents each station number and its corresponding name.

All fish samples were collected with a 364 m long by 29 m deep seine net, provided by the Department of Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC. The small mesh size (2.5 to 3.75 cm) and 0.6 cm knotless bunt were imperative for the unbiased collection of smolts spanning all size classes (Buchanan 2006). The seine net was deployed to a depth of approximately 30 m off the MV *Western Bounty*, a 16 m fishing vessel owned and operated by the Wuikinuxv First Nations of Rivers Inlet. Fish captured were kept in a live tank for identification and enumeration before preservation or release. Approximately 10-15 sockeye per set (when available) were frozen for later analyses.

Frozen sockeye were processed in the lab. Specimens were defrosted, weighed (grams wet weight to the nearest 0.001) and measured for standard (fork) and total length (mm to the nearest 0.05). The stomach was removed and preserved in formalin, and the specimen re-weighed. A tissue sample was collected for isotope analysis and the sagittal otoliths removed. A total of 717 sockeye were dissected in this manner (2008: n = 224; 2009: n = 232; 2010: n = 261).

Tissue samples for stable isotope analysis were dried for 24 hours at 50°C. These were then ground into a fine powder and stored in Eppendorf tubes prior to analysis of carbon and nitrogen stable isotope ratios. Samples were sent to IsoEnvironmental at Rhodes University in Grahamstown, South Africa, and run on a Europa Scientific Elemental Analyzer and a 20-20 Isotope Ratio Mass Spectrometer (IRMS). Standards used were refmix2 (beet sugar and ammonium sulfate) and a certified protein standard (Casein).

2.2.1 Data Analysis

Individual smolts were estimated to migrate through Rivers Inlet over a period of approximately two weeks (Buchanan 2006, K. Hyatt personal communication). Maximum growth rates were therefore calculated using 14 days as a proxy for estuarine passage time. Fish were separated by site and survey, and only those from the head (Wannock) and mouth (Bosquet Open and Bosquet Shore) of the inlet were used in growth rate calculations. In order to estimate mean length for these calculations, the lengths and masses of each individual fish were first compared to delta Carbon ($\delta^{13}\text{C}$) and delta Nitrogen ($\delta^{15}\text{N}$) stable isotope curves and any outliers identified and removed. Comparison with stable isotope signatures was done to ensure that the smolts used in the growth rate analysis exhibited an increase in trophic level from a mainly freshwater prey source to a marine foraging base. Only fish with a freshwater signature ($\delta^{13}\text{C} < -30 > -35$; $\delta^{15}\text{N} < 8 > 6$) from the head of the inlet were used for the starting lengths and masses, as they were assumed to be recent out-migrants from Owikeno Lake. The larger fish at the mouth exhibited an increase or plateau in marine signature ($\delta^{13}\text{C} < -25 > -20$; $\delta^{15}\text{N} < 12 > 9$), as they had spent more time in the inlet feeding on marine prey items. Initial length and mass (L_i and W_i) was averaged from sockeye smolts with freshwater signatures from the survey in which they first appeared at the head of the inlet. Final length and mass (L_1 and W_1) was averaged from smolts with marine signatures found at the mouth of the inlet from the subsequent survey. In 2008, a larger number of smolts appeared to exit via the main channel than in 2009 and 2010; therefore, estimates of final length and mass included sites representative of this route (Dimsey Open and Dimsey Shore).

Specific growth rates (SGR) were calculated from the natural log of the change in length (Hopkins 1992, MacFarlane 2010):

$$\text{SGR} = ((\ln(L_1) - \ln(L_i)) / (t-t_0)) \times 100 \quad (\text{Equation 1})$$

and the natural log of the change in mass (Hopkins 1992, MacFarlane 2010):

$$\text{SGR} = ((\ln(W_1) - \ln(W_i)) / (t-t_0)) \times 100 \quad (\text{Equation 2})$$

where SGR is the percentage change in length or mass, t is the estuarine residence time of the smolts, L_1 and W_1 are the mean length and mass at time t , and L_i and W_i are the initial mean length and mass.

Condition factor was calculated using Fulton's equation (Bolger and Connolly 1988):

$$K = 10^N(W) / L^3 \quad (\text{Equation 3})$$

where K is condition, W is mass (grams of wet weight) and L is length (mm) of the specimen, and N is a species specific scaling factor to bring the value of K closer to 1.00 ($N = 5$ for sockeye smolts; Hayden and Pinnix 2010, Morton and Routledge 2006).

Statistical analyses were performed using the SAS Institute's JMP 9. An ANCOVA tested for the significance of the interaction between log-transformed mass regressed on log-transformed length by year, as well as the significance of the interaction between site and survey (site survey) in terms of length and mass. If this interaction was not significant, then a one-way ANOVA was conducted for significant differences in the length and mass of the fish between sites and between surveys. Comparison of means using ANOM and Tukey-Kramer HSD tests determined the source of any significant differences. Since no sockeye smolts were caught during the first survey, analyses excluded the 29-April 2008, 1-May 2009, and 6-May 2010 sampling events. Due to their small sample sizes, the 11-May-2008 and 19-June-2010 surveys were also excluded from any statistical analyses.

2.3 Results

2.3.1 Spatial and temporal distribution of sockeye salmon smolts

The first seining in which sockeye smolts were found occurred on 11-May 2008, 17-May 2009, and 19-May 2010, corresponding to survey 2 in all years (Table 2). The abundance and spatial distribution of these first smolts varied between years. In 2008, only one smolt was caught at the head of the inlet (Wannock; Figure 3). In 2009, twenty initial smolts were caught at two locations in the upper inlet (Scandinavia and Ralph). The distribution in 2010 was wider, with a total of 483 smolts caught at several upper and mid-inlet locations (Wannock, Kilbella, McPhee, Dawsons Shore and Dawsons Open). Sampling during the 19-May 2010 survey was unsuccessful at four sites (Geetla, Mouth, Dimsey Shore, Dimsey Open); therefore, it is unknown whether the spatial distribution of the smolts extended into the lower inlet at this time.

In 2008, no smolts were collected at the Wannock site after 10-June, although they were still present throughout the remainder of the inlet (Appendix D). In 2009, smolts were caught at the Wannock location until 15-June (Appendix E). Sampling at the Wannock site was unsuccessful during the final survey on 29-June; however, smolts were distributed throughout the entire inlet at this time. In 2010, smolts were not found at Wannock after 19-May (Appendix F), but did maintain a presence throughout the entire inlet for the duration of the sampling season.

Table 2: Date, location, and number of the first sockeye smolts caught in each sampling season.

Year	Survey date	Distribution	No. smolts
2008	11-May	Wannock	1
2009	17-May	Scandinavia	19
		Ralph	1
2010	19-May	Wannock	48
		Kilbella	365
		McPhee	2
		Dawsons Shore	3
		Dawsons Open	65

2.3.2 Inter-annual abundance and catch per unit effort (CPUE)

The total number of sockeye smolts collected in 2008 was 3385 individuals in 71 sets, with an average catch per unit effort (CPUE) of 47.68 individuals per set. In 2009, a total of 1263 smolts were caught in 66 sets, with an average CPUE of 19.14 individuals per set. Sockeye smolts caught during the 2010 season totaled 1713 in 65 sets, and the average CPUE was 26.35 individuals per set. Catch frequency, or the percentage of successful sets divided by the total number of sets conducted per survey, indicated higher numbers of smolts throughout the 2008 season (Figure 4). Although the first occurrence of smolts was a week earlier in 2008 (Table 2), the wider distribution of smolts on first occurrence in 2009 and 2010 indicated that these runs were further advanced and probably had similar timing to 2008. The peak in the number of smolts collected during an individual survey also occurred earlier in the season in 2008 than in 2009 and 2010.

Total sockeye caught per survey and CPUE per survey varied between years (Figures 5 and 6). In 2008, the largest total number of smolts sampled from an individual survey was 2262 smolts on 10-June. The largest number of smolts found in 2009 occurred on 31-May at 580, and in 2010 on 4-June at 900 smolts. The largest catch totals corresponded to the highest

CPUE of 174.00 and 69.23 individuals per set in 2008 and 2010, respectively. The highest CPUE in 2009 occurred on 15-June at 45.91 individuals per set. In 2010, the low catch on 19-June was most likely due to a small sample size, as only two sets were conducted before mechanical error prevented further seining.

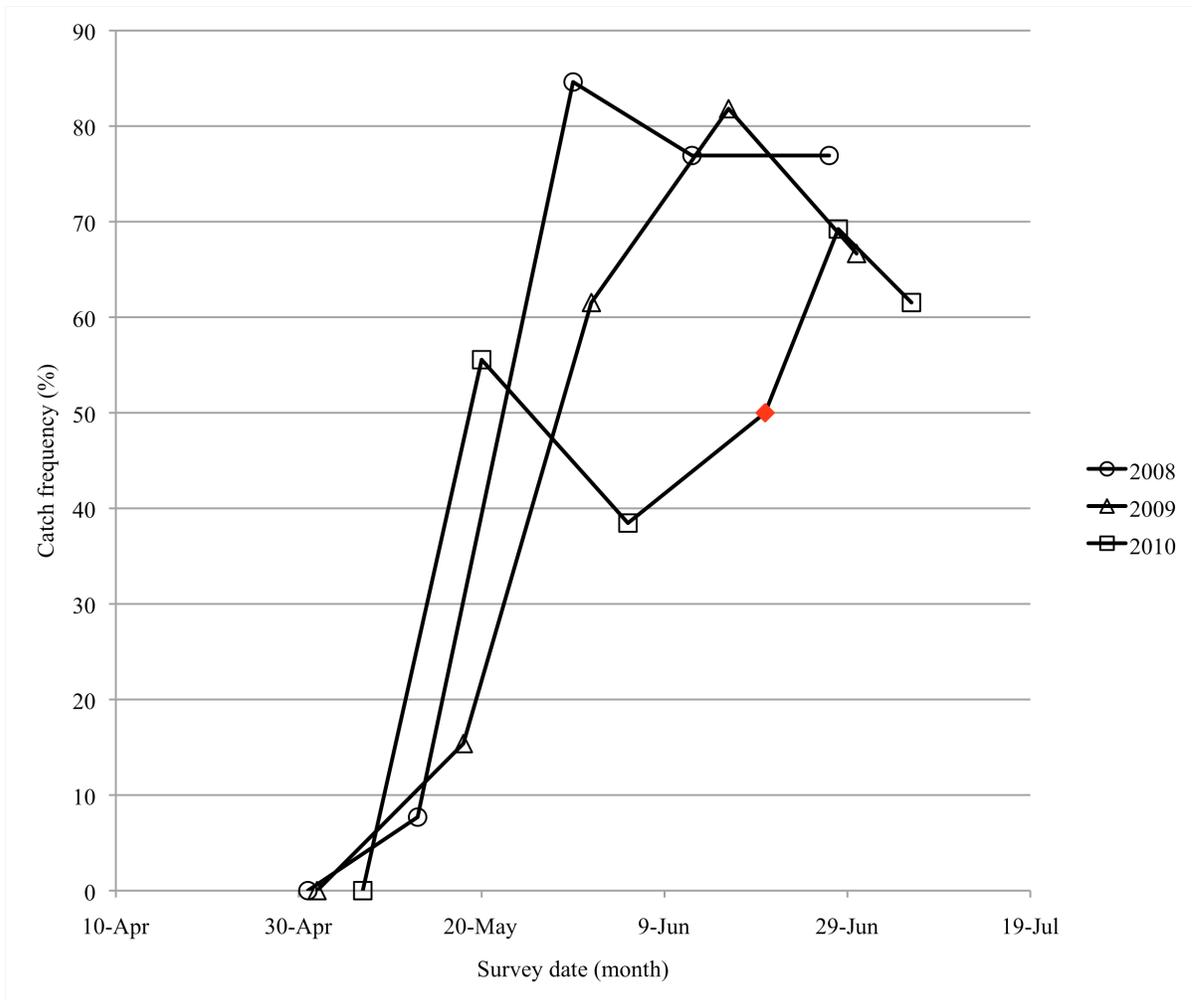


Figure 4: Catch frequency of smolts throughout the sampling seasons. The 2008 season had the largest total number of smolts caught and an earlier peak in migration. The red diamond indicates that only two sets were completed on the 19-June 2010 survey.

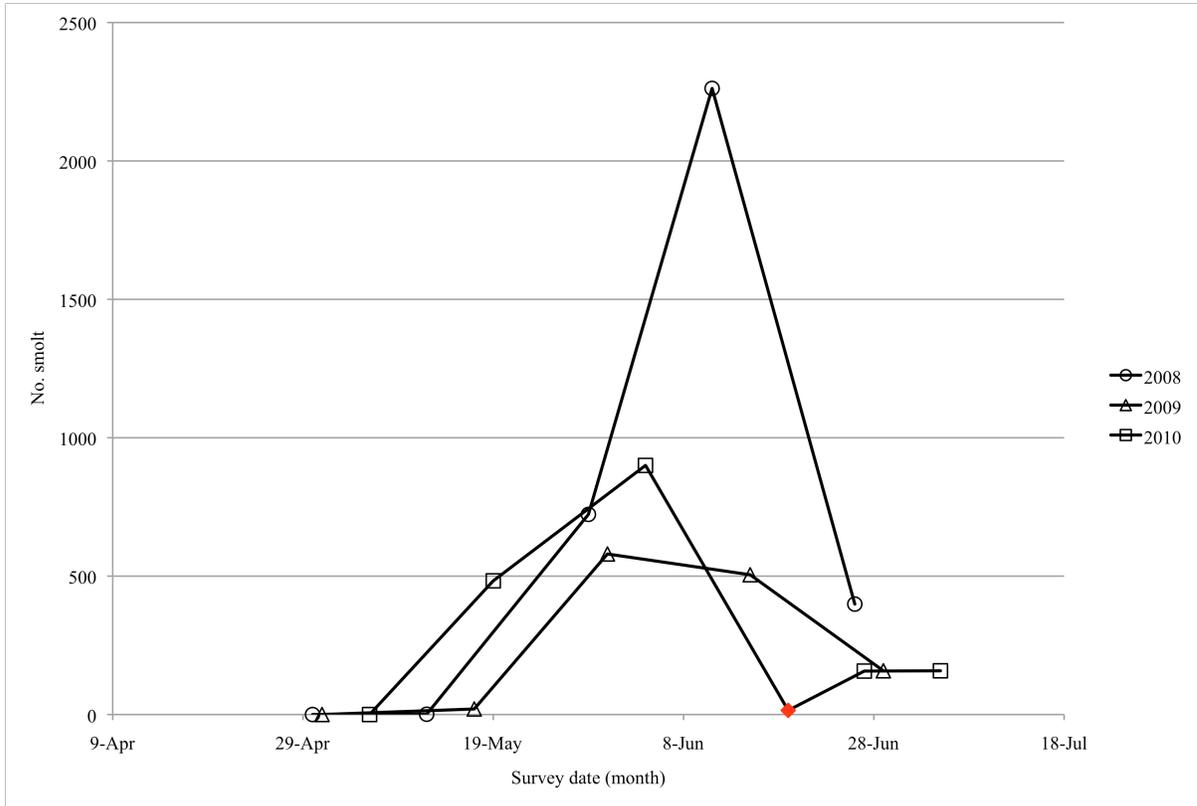


Figure 5: Total number of sockeye caught per survey in the 2008, 2009, and 2010 sampling seasons. The red diamond indicates that only two sets were completed on the 19-June 2010 survey.

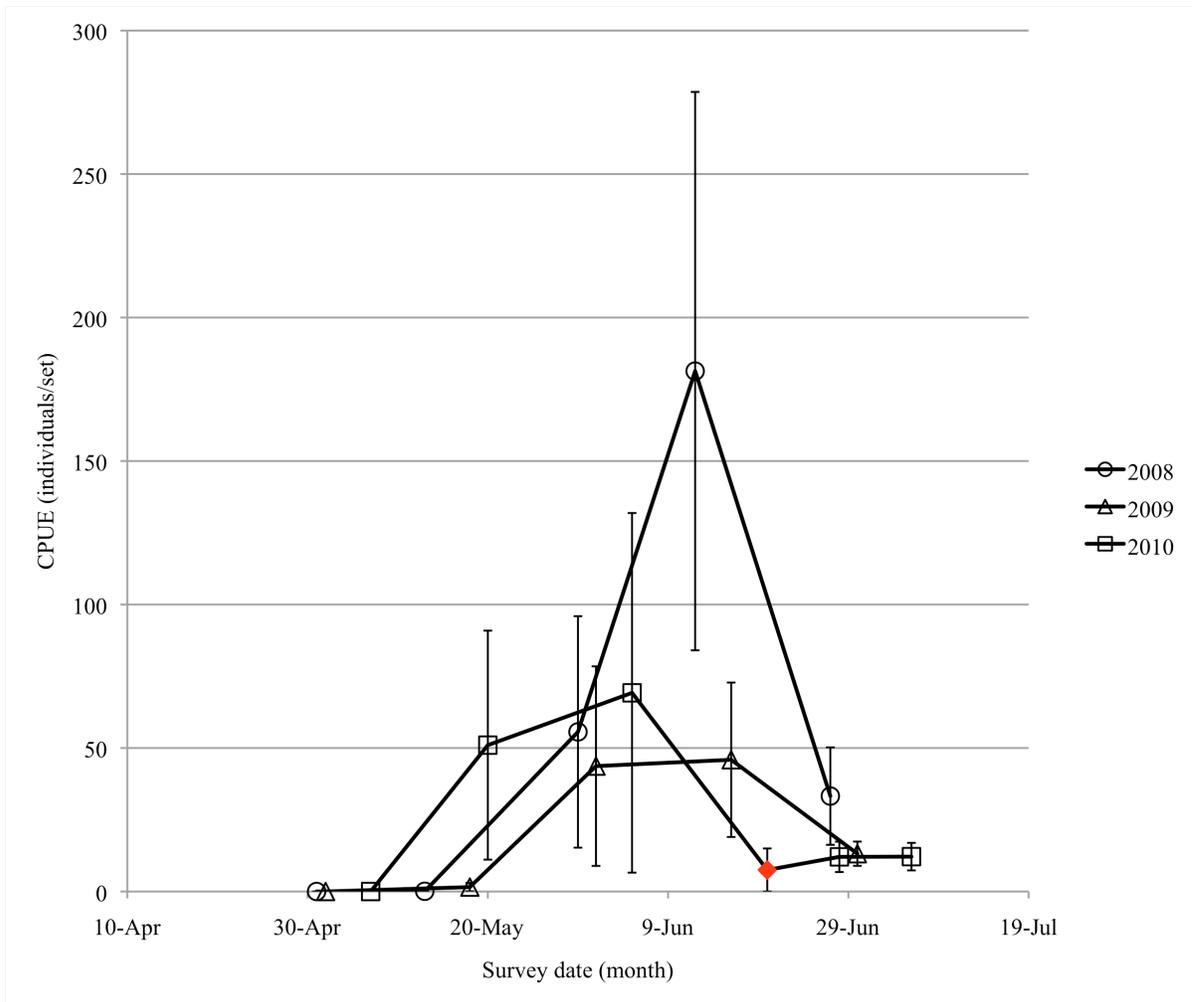


Figure 6: Mean catch per unit effort (CPUE; individuals per set) for each survey in the 2008, 2009, and 2010 sampling seasons. Vertical bars show standard error of the mean CPUE per survey. The red diamond indicates that only two sets were completed on the 19-June 2010 survey.

2.3.3 Ocean entry routes

In 2008, 43% of sockeye smolts migrated down the main channel, whereas in 2009 and 2010 only 12% and 7%, respectively, utilized the main channel (Table 3), although the total number of smolts found in 2008 was still higher in Darby Channel than the main channel. In 2009 and 2010, the majority of the smolts seemed to exit via the Darby Channel, as more smolts were collected at sites chosen to represent this alternative migratory pathway (Bosquet Shore, Bosquet Open). Smolts from all three years were caught in higher numbers at near-shore versus offshore locations.

Table 3: Yearly differences in the numbers of smolts caught exiting the inlet through two possible outmigration routes: 1) the Darby Channel and 2) the main channel.

			Year		
		Site	2008	2009	2010
Migratory route	Darby Channel	Dawsons Shore	229	49	836
		Dawsons Open	1078	144	125
		Bosquet Shore	151	297	95
		Bosquet Open	41	55	58
		Total	1499	545	1114
	Main channel	Geetla	373	0	17
		Dimsey Shore	446	49	36
		Dimsey Open	239	6	15
		Mouth	84	18	15
		Total	1142	73	83

2.3.4 Growth and condition of sockeye salmon smolts

Size distributions were relatively similar for 2008 and 2009, with a slightly wider range in 2010 (Table 4; Figures 7, 8, and 9). Mean standard length (fork length; L_F) varied between years, with the smallest observed in 2009 and the largest in 2010. Trends in mean mass exhibited similar patterns to those of length (Figures 7, 8, and 9). An ANOVA of log transformed mass regressed on log transformed length grouped by year indicated that individuals in the 2010 ($R^2 = 0.91$; slope = 0.31) cohort of sockeye smolts were significantly heavier per unit length ($F = 54.35$; $p < 0.0001$) than the 2008 ($R^2 = 0.91$; slope = 0.21) and 2009 ($R^2 = 0.89$; slope = 0.21) smolts (Figure 10).

Table 4: Sample size, range of size, mean size and ± 1 standard deviation for smolts from each sampling year.

Year	Sample size	Length range (mm)	Mean length (mm)	Mass range (g)	Mean mass (g)
2008	218	60 – 100	74 ± 9.6	1.9 – 7.8	4.9 ± 2.1
2009	231	50 – 100	73 ± 9.0	2.0 – 17.4	4.6 ± 2.0
2010	261	50 - 130	86 ± 15.3	1.5 – 26.9	9.3 ± 5.0

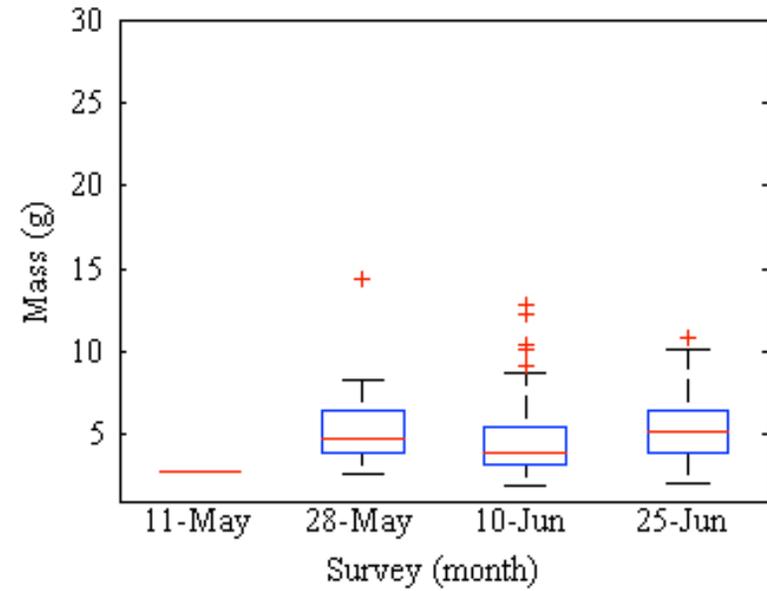
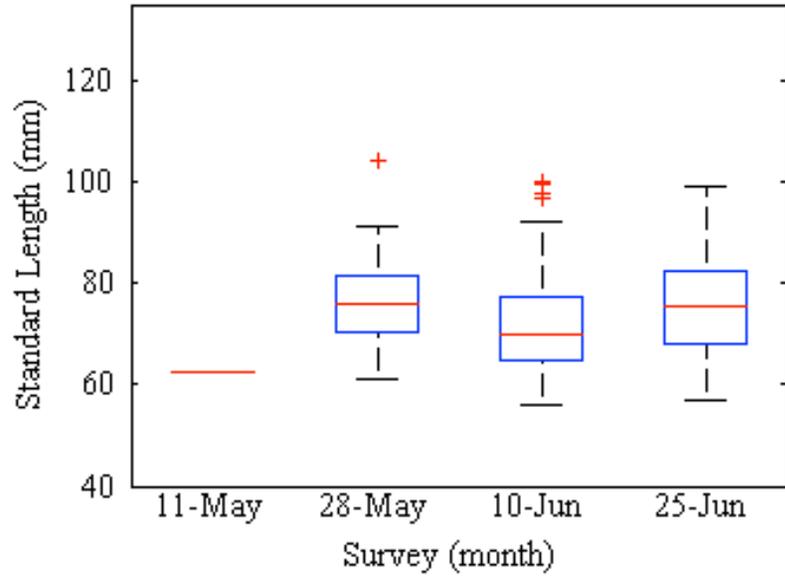


Figure 7: Box plots of length (mm) and mass (g) by survey for 2008. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. Only one fish was caught in survey 2.

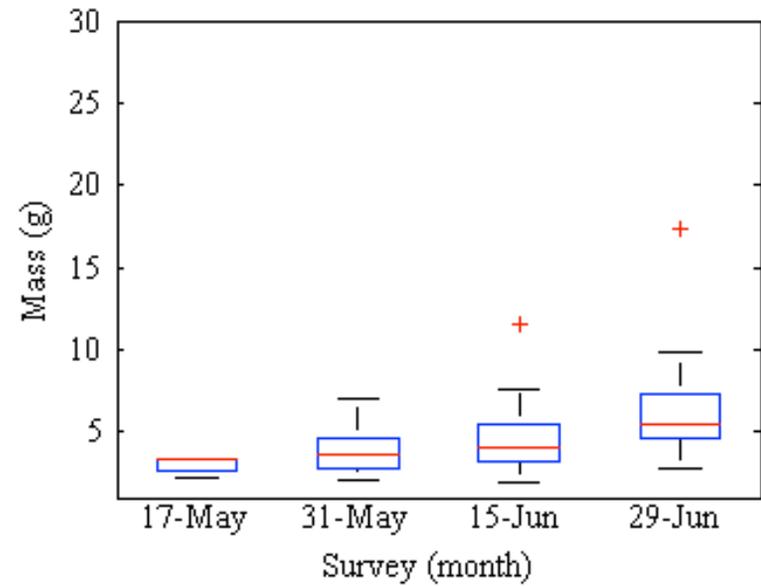
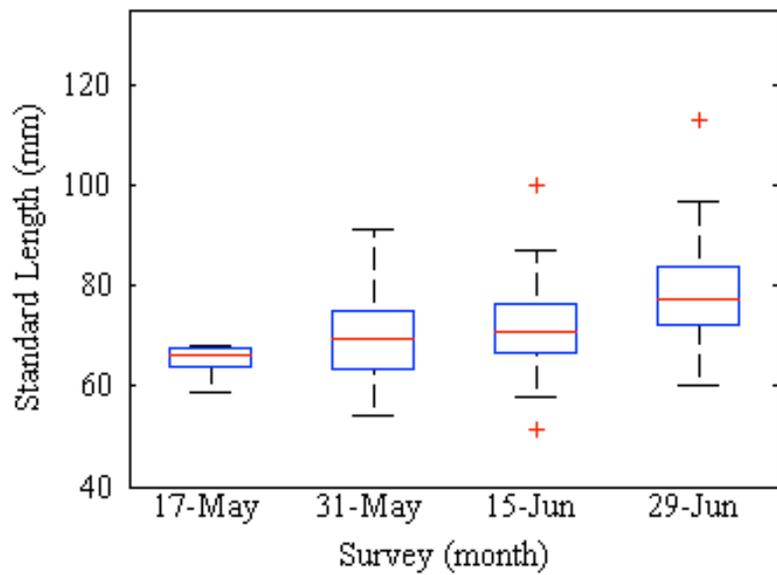


Figure 8: Box plots of length (mm) and mass (g) by survey for 2009. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. Smolts from the 29-June survey were significantly larger than smolts from the other surveys ($F = 26.97$; $p < 0.0001$).

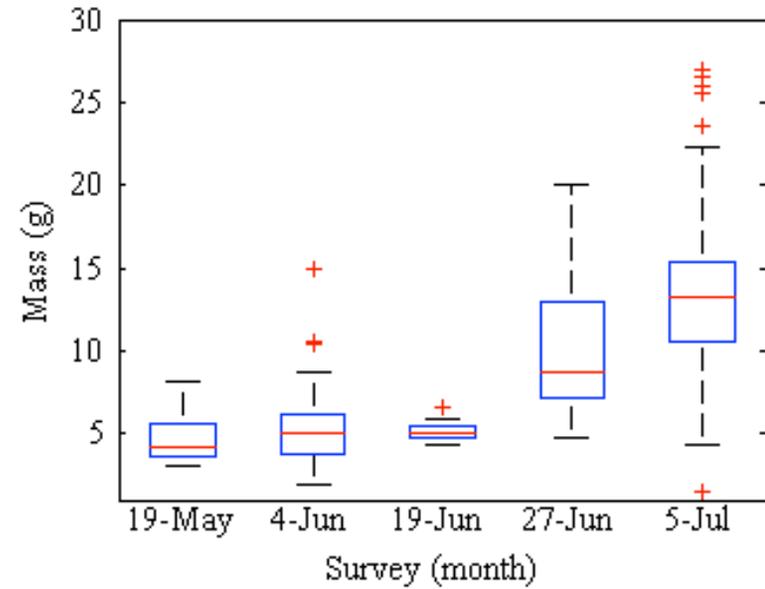
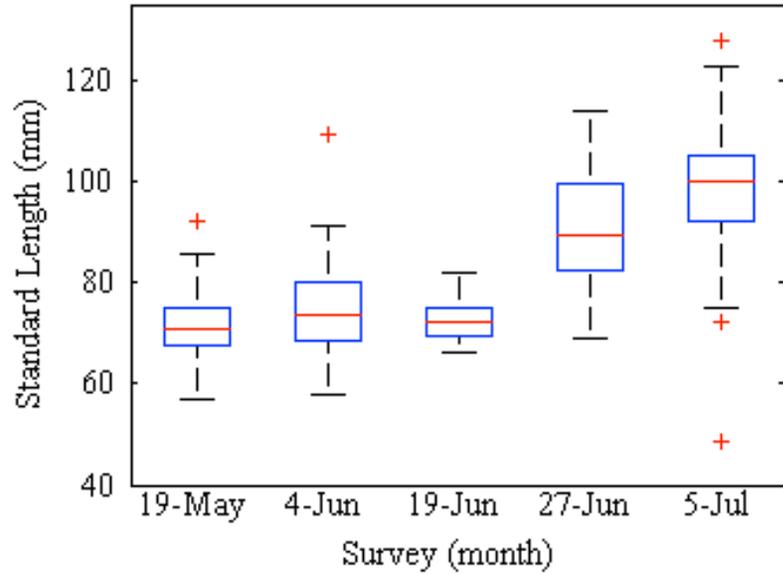


Figure 9: Box plots of length (mm) and mass (g) by survey for 2010. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. Only two sets were performed during the 19-June survey.

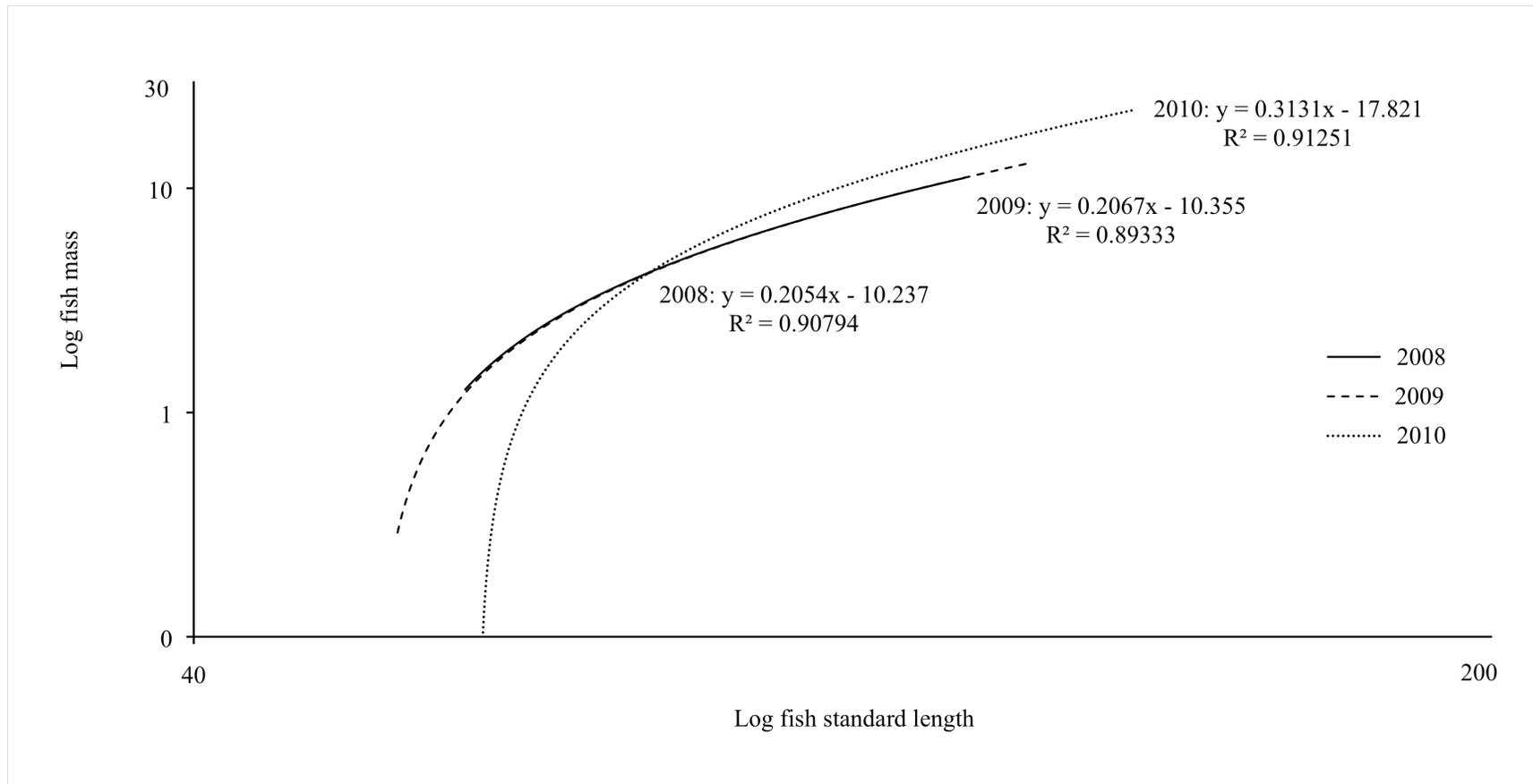


Figure 10: Log-transformed mass gain (g of wet weight) per unit length (mm) of sockeye smolts. An ANCOVA test for interactions between mass and length and for differences in slope by year revealed that smolts in 2010 were significantly heavier per unit length than in 2008 and 2009 ($F = 54.35$; $p < 0.0001$). The 2008 and 2009 cohorts were not statistically different.

Specific growth rates (SGR) of the sockeye smolts were the slowest in 2008, moderate in 2009, and the fastest in 2010 (Table 5). This trend was similar for both length (% of body length per day; % bl/day) and mass (% of body wet weight per day; % WW/day). SGR in 2008 was based on a small sample size, and is most likely an underestimate of actual growth throughout the inlet phase of the smolts' life cycle. Similarities in mass gained per unit length in the 2008 and 2009 seasons are not reflected in these calculations of growth rates, and may be due to an under or over estimation of residence time of the fish in the inlet (see discussion).

Mean condition factor (K) of smolts in 2008 was similar to the mean of the 2009 cohort (Figure 11), and both had a significantly lower condition index than the 2010 cohort ($F = 75.24$; $p < 0.0001$). According to the condition index of Barnham and Baxter (1998), the 2008 and 2009 cohorts were in “fair” to “good” condition, while the 2010 cohort was in “fair” to “excellent” condition

Table 5: Specific growth rates (SGR; % bl/day and % WW/day) for sockeye smolts, with linear growth in brackets (mm/day and g/day). Sample size (N), mean length (mm/day) and mean mass (g/day) and ± 1 standard deviation are shown for both the head (h) and the mouth (m) of the inlet. Due to the small sample size, SGR estimates for 2008 are likely underestimates.

Year	N (h)	N (m)	Mean length (h)	Mean length (m)	Mean mass (h)	Mean mass (m)	SGR (% bl/day)	SGR (% WW/day)
2008	3	36	71.50 ± 2.78	75.38 ± 9.87	4.10 ± 0.66	4.42 ± 2.51	0.59 (0.48)	1.69 (0.11)
	8	17	62.40 ± 2.80	74.67 ± 5.56	2.79 ± 0.15	4.58 ± 1.01	1.27 (0.88)	3.40 (0.13)
2009	8	13	66.70 ± 3.22	82.46 ± 6.76	3.41 ± 0.21	8.08 ± 2.41	1.50 (1.13)	5.92 (0.33)

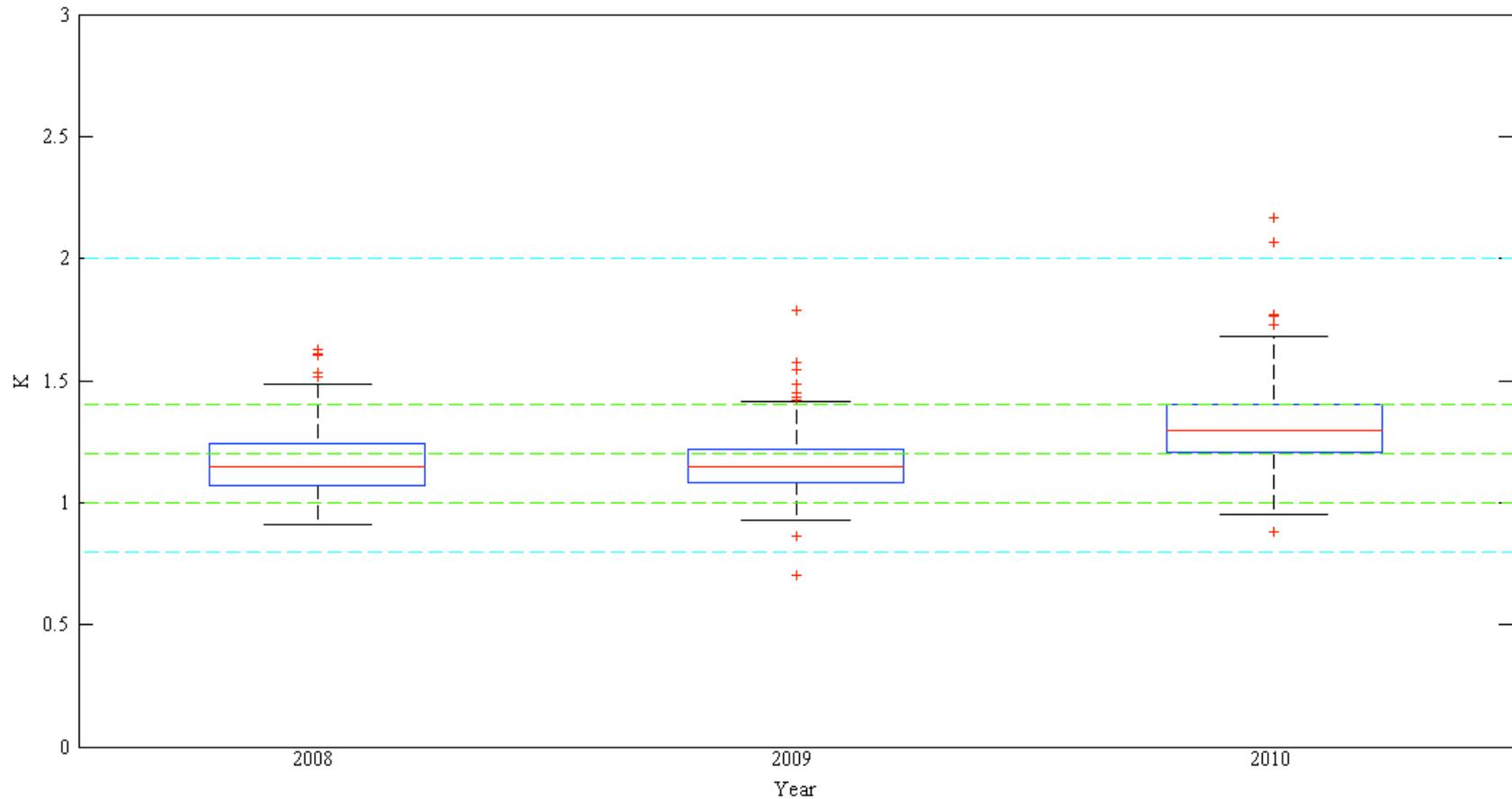


Figure 11: Condition factor (K) by year. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. After the condition index of Barnham and Baxter (1998), smolts above (> 2.0) or below (< 0.8) the dashed light blue lines are in exceptional or extremely poor condition, respectively. The dashed green lines indicate a change in condition index: Poor (0.8–1.0), Fair (1.0–1.2), Good (1.2–1.4), and Excellent (1.4–2.0). An ANOVA showed that the 2010 cohort had a significantly higher condition index than the 2008 and 2009 cohorts ($F = 75.34$; $p < 0.0001$).

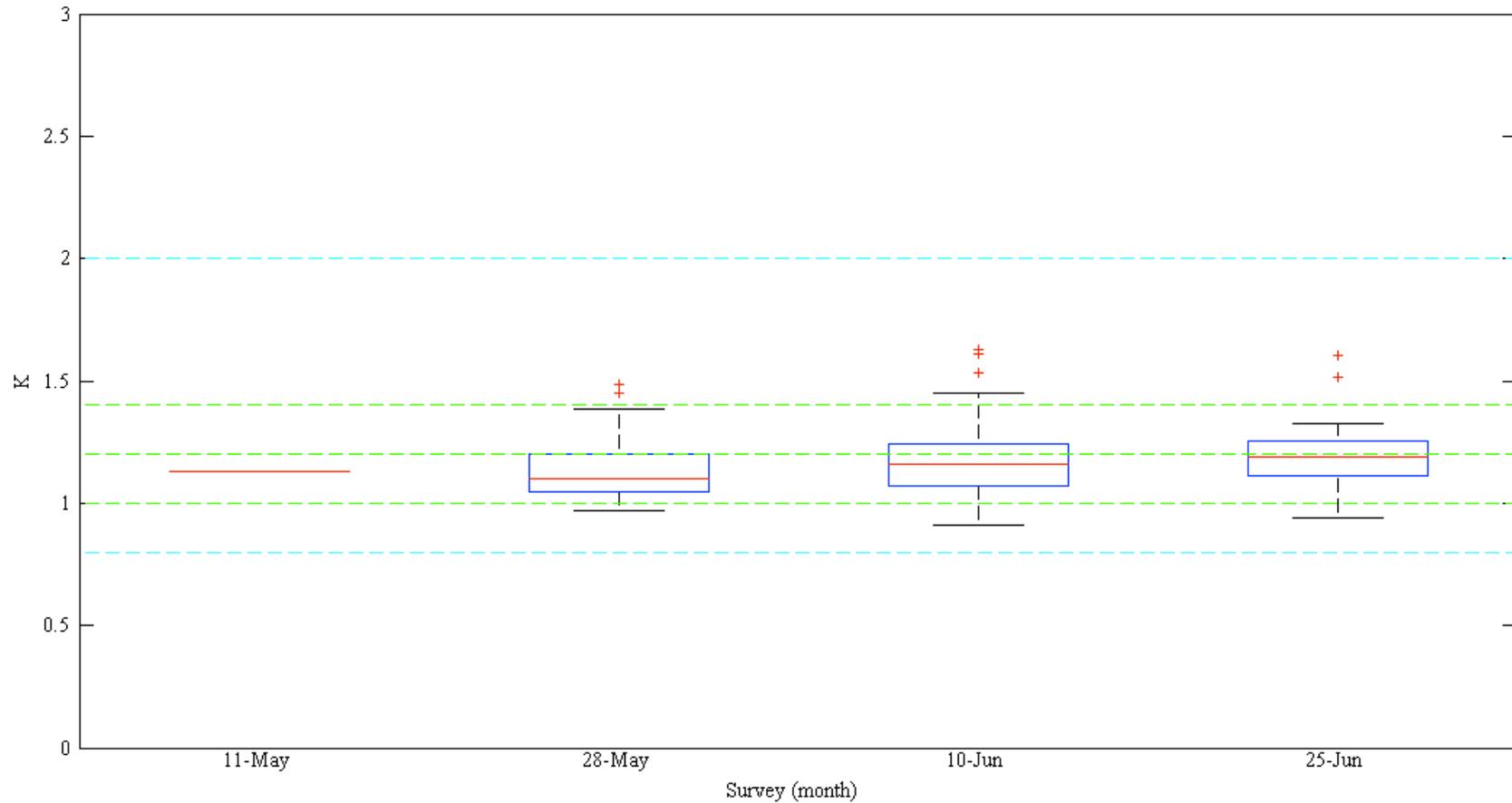


Figure 12: Condition factor (K) by survey of smolts caught in 2008. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. After the condition index of Barnham and Baxter (1998), smolts above (> 2.0) or below (< 0.8) the dashed light blue lines are in exceptional or extremely poor condition, respectively. The dashed green lines indicate a change in condition index: Poor (0.8–1.0), Fair (1.0–1.2), Good (1.2–1.4), and Excellent (1.4–2.0). Only one fish was caught during the 11-May survey.

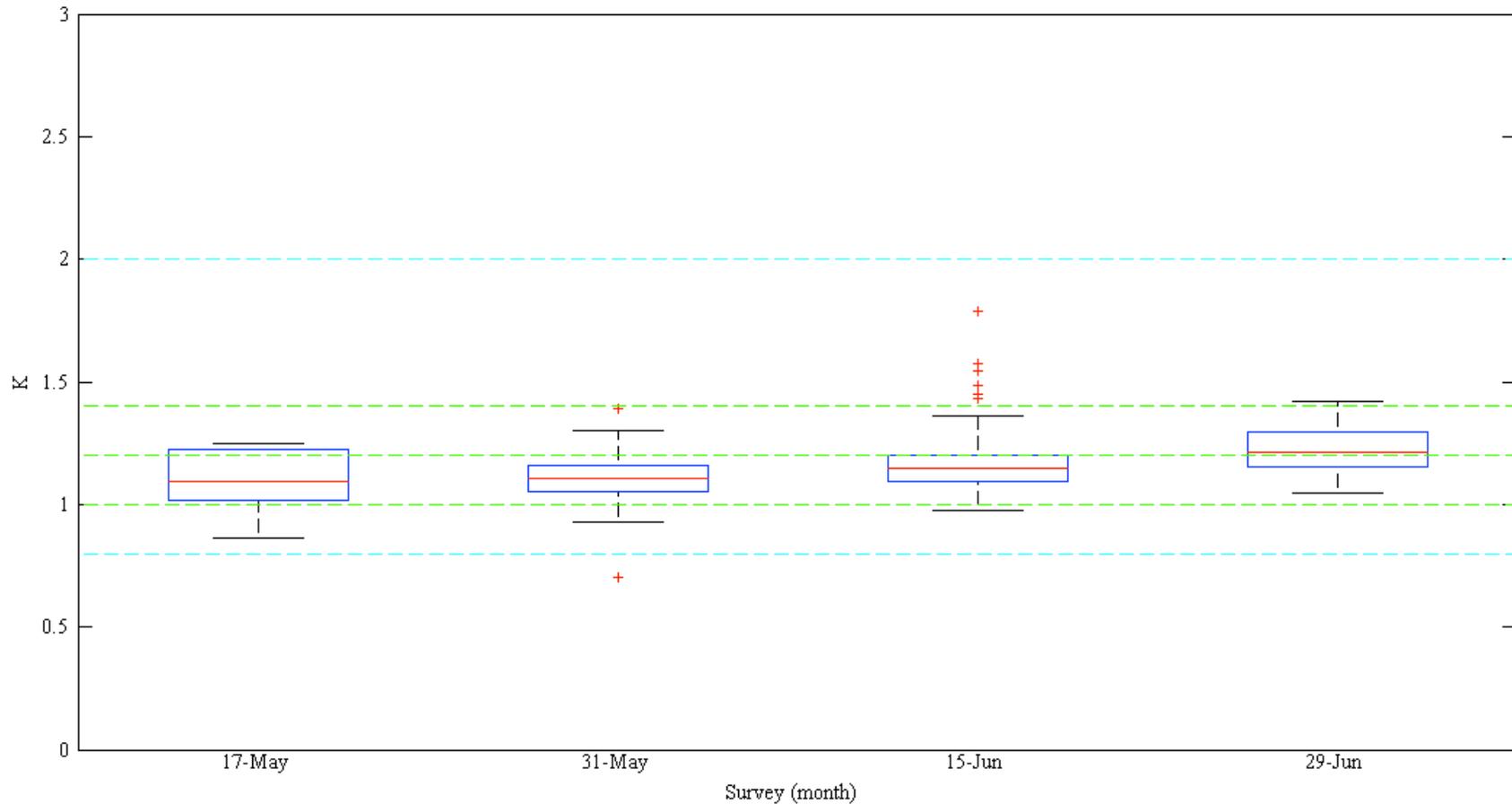


Figure 13: Condition factor (K) by survey of smolts caught in 2009. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. After the condition index of Barnham and Baxter (1998), smolts above (> 2.0) or below (< 0.8) the dashed light blue lines are in exceptional or extremely poor condition, respectively. The dashed green lines indicate a change in condition index: Poor (0.8–1.0), Fair (1.0–1.2), Good (1.2–1.4), and Excellent (1.4–2.0). Smolts caught on the 31-May and 29-June surveys in significantly different condition ($F = 17.46$; $p < 0.0001$).

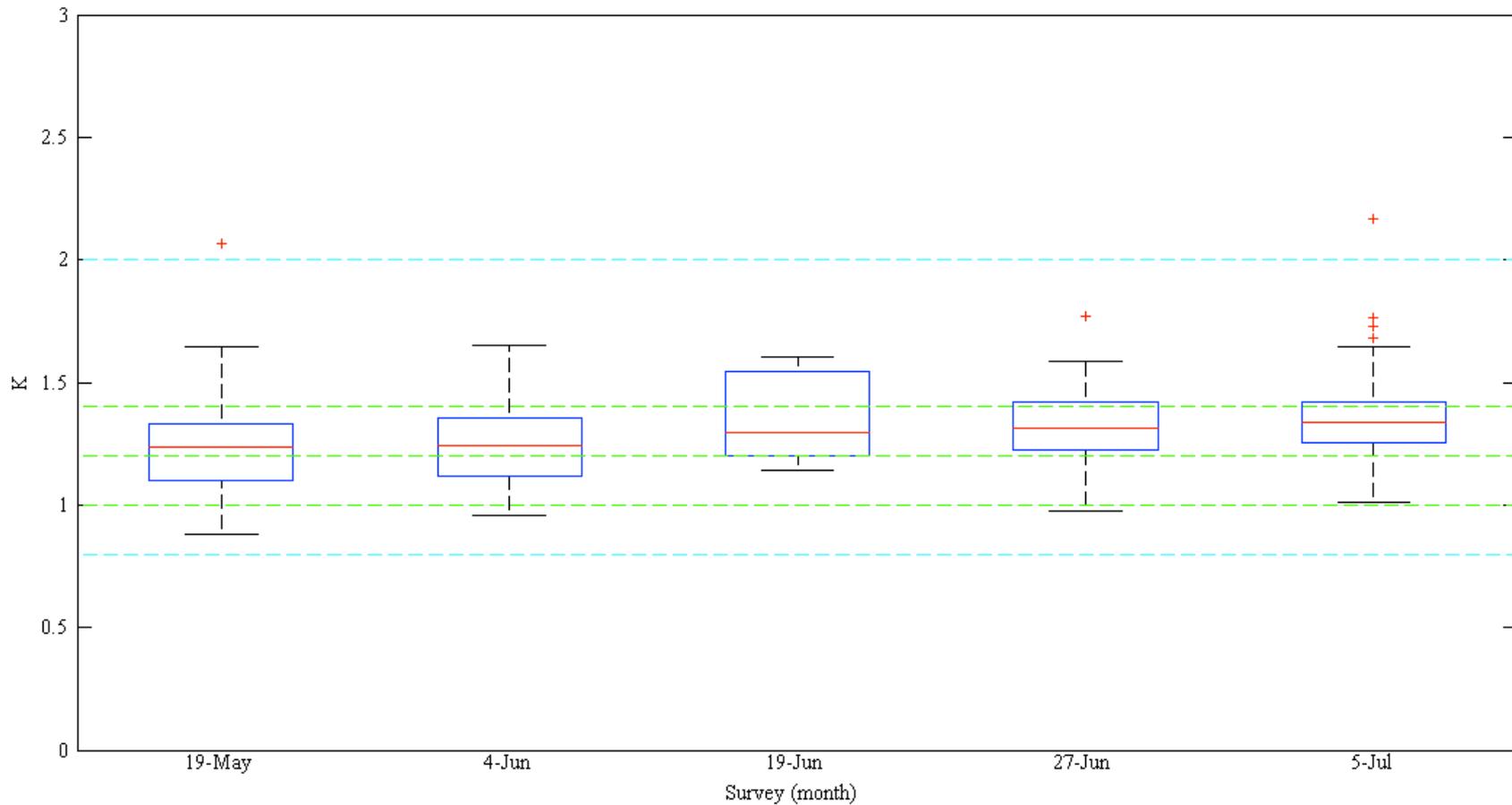


Figure 14: Condition factor (K) by survey of smolts caught in 2010. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. After the condition index of Barnham and Baxter (1998), smolts above (> 2.0) or below (< 0.8) the dashed light blue lines are in exceptional or extremely poor condition, respectively. The dashed green lines indicate a change in condition index: Poor (0.8–1.0), Fair (1.0–1.2), Good (1.2–1.4), and Excellent (1.4–2.0). Only two sets were performed during the 19-June survey. Smolts caught during the 19-May and 5-July surveys were significantly different ($F = 6.66$, $p = 0.0002$).

In 2008, 2009, and 2010, smolts of all sizes (length and mass) and condition were caught throughout the estuary, and there was a weak increase in size with movement down the inlet (Figures 15, 16, and 17). In 2008, fish caught at Bosquet Shore in survey 3 (Bosquet Shore 3), Dawsons Open 4, and Dawsons Shore 4 were significantly different in terms of length and mass from the other smolts ($F = 3.22$ and $F = 3.14$ for length and mass, respectively; $p < 0.0001$). Condition index was significantly different for fish from Mouth 4, Kilbella 3, Bosquet Shore 4, Dawsons Shore 3, and Scandinavia 3 ($F = 3.56$; $p < 0.0001$).

In 2009, significant differences in length were found for Mouth 5, Scandinavia 5, Dawsons Open 5, McPhee 3, and Wannock 4 ($F = 9.71$; $p < 0.0001$). The interaction of site survey was not significant for mass and condition index. A one-way ANOVA indicated that the smolts from Wannock and Mouth were significantly different in terms of mass between sites ($F = 8.44$; $p < 0.0001$), and smolts from the 29-June survey were significantly different from the other surveys ($F = 26.97$; $p < 0.0001$). Smolts from Dawsons Shore, Dawsons Open, Dimsey Shore and Dimsey Open were in significantly different condition than those from other locations ($F = 5.64$; $p < 0.0001$), and smolts caught on the 31-May and 29-June surveys were also significantly different ($F = 17.46$; $p < 0.0001$).

In 2010, Geetla 6, Ralph 6, Scandinavia 6, Wannock 2, Kilbella 2, Dimsey Shore 3, and Kilbella 6 were significantly different in terms of length ($F = 26.32$; $p < 0.0001$). In terms of mass, Geetla 6, Kilbella 2, and Wannock 2 were significantly different ($F = 17.56$; $p < 0.0001$). There was no significant site survey interaction for condition index. Smolts from Wannock, Ralph, Bosquet Shore, Geetla, and McPhee had a significantly different condition index ($F = 2.85$; $p = 0.0011$), and smolts caught during the 19-May and 5-July surveys were also significantly different ($F = 6.66$, $p = 0.0002$).

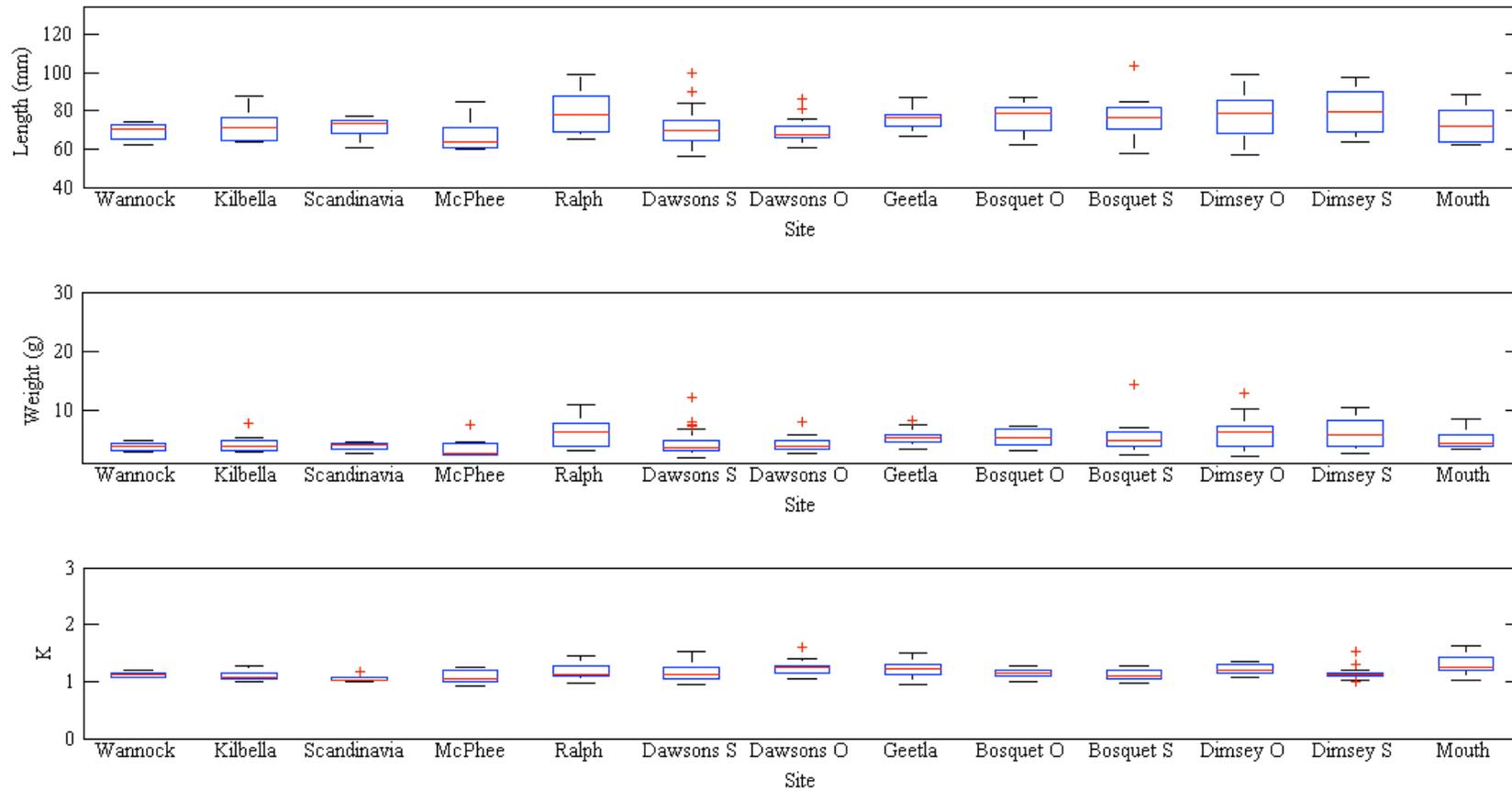


Figure 15: Length (mm), mass (g) and condition factor (K) by site of smolts caught in 2008. Sites followed by an S or an O represent Shore and Open, respectively. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles.

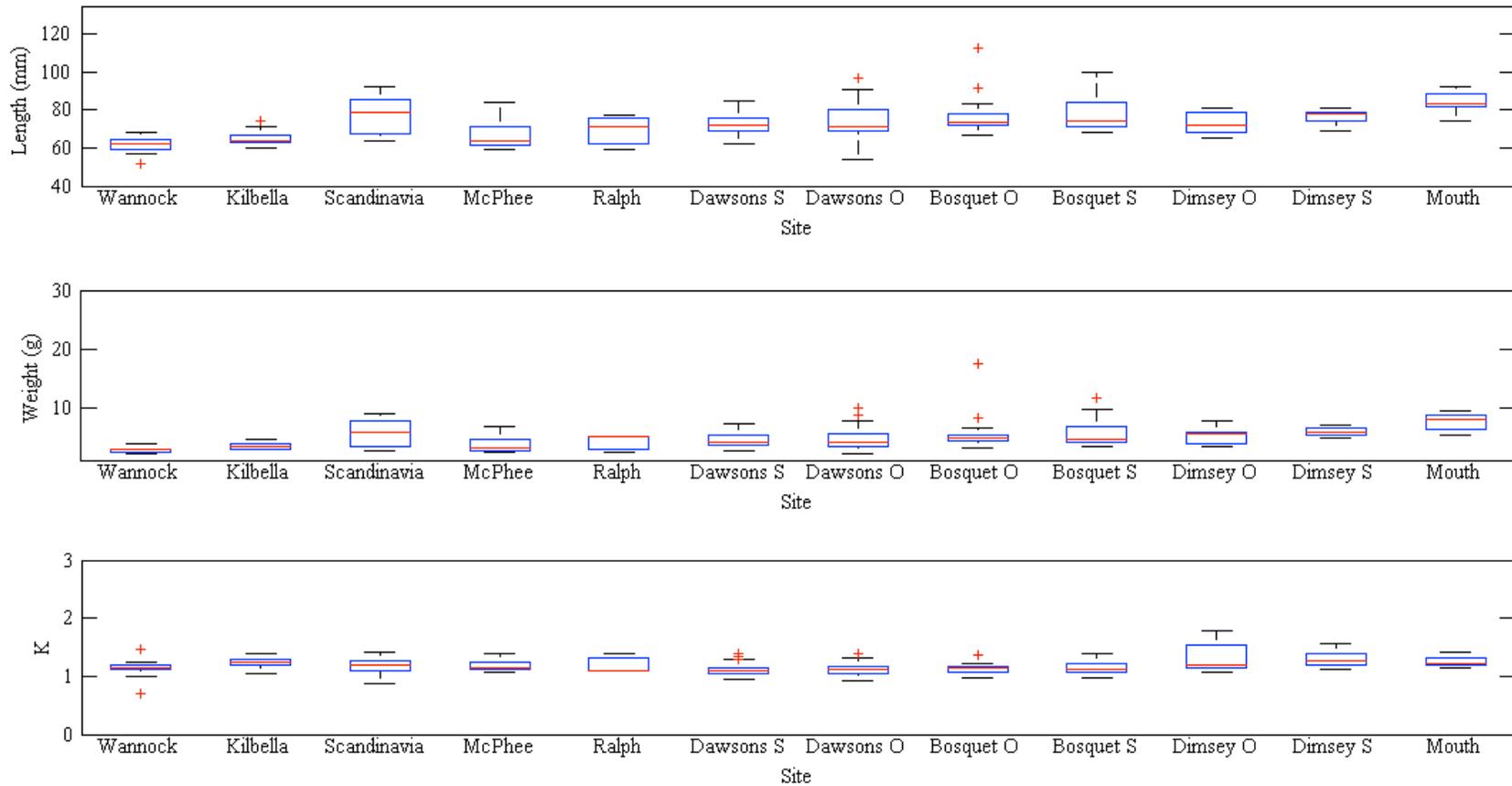


Figure 16: Length (mm), mass (g) and condition factor (K) by site of smolts caught in 2009. Sites followed by an S or an O represent Shore and Open, respectively. No smolts were found at Geetla. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentile. Smolts from Wannock and Mouth were significantly different in terms of mass ($F = 8.44$; $p < 0.0001$), and smolts from Dawsons Shore, Dawsons Open, Dimsey Shore and Dimsey Open were in significantly different condition than those from other locations ($F = 5.64$; $p < 0.0001$).

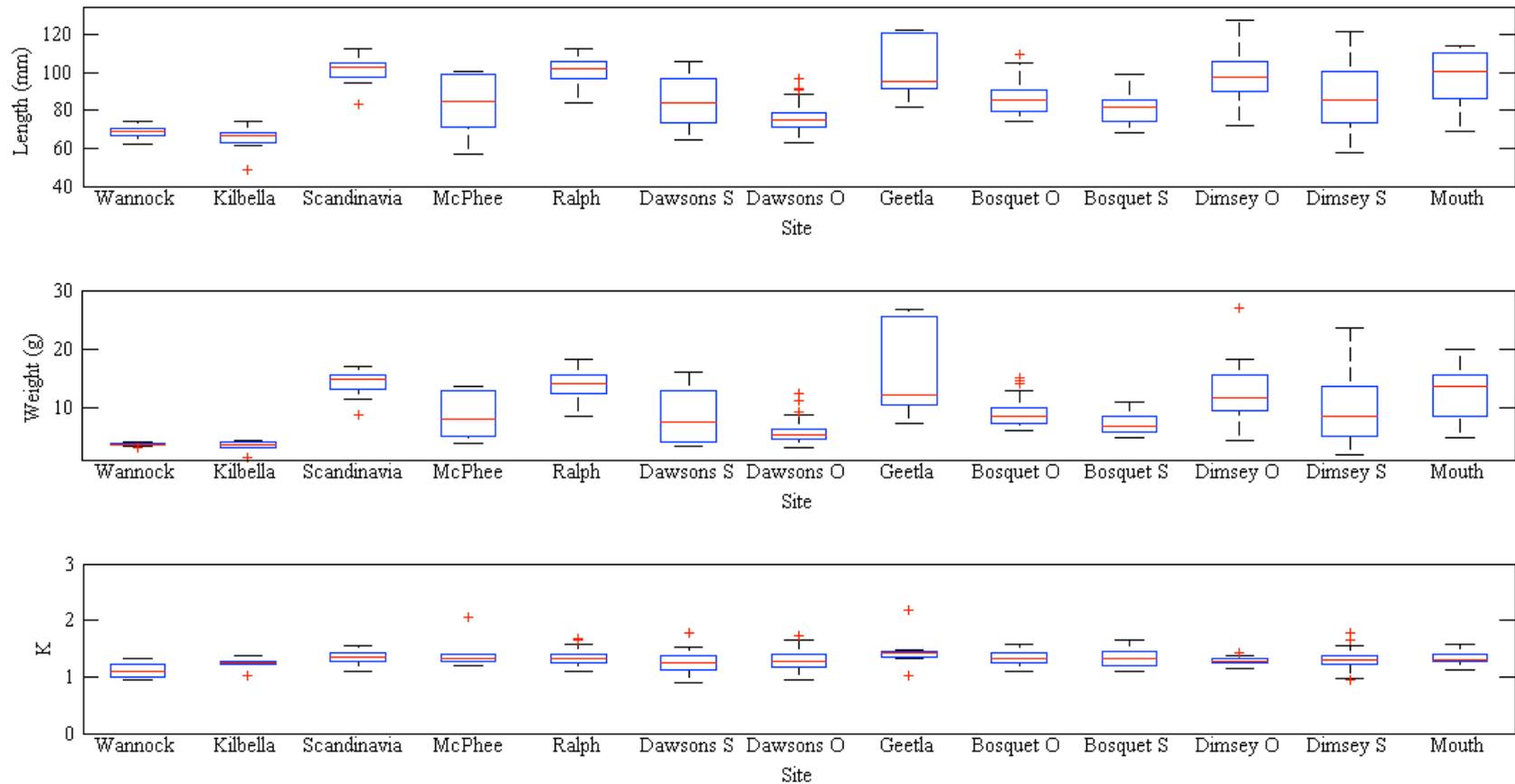


Figure 17: Length (mm), mass (g) and condition factor (K) by site of smolts caught in 2010. Sites followed by an S or an O represent Shore and Open, respectively. Whiskers indicate minimum and maximum values. The red crosses are outliers, and the red line represents the median of the samples. The blue box indicates quartiles, or the 25th (lower part of box) and 75th (upper part of box) percentiles. Smolts from Wannock, Ralph, Bosquet Shore, Geetla, and McPhee were in significantly different condition than smolts from other locations ($F = 2.85$; $p = 0.0011$)

2.4 Discussion

Mortality due to overfishing has been eliminated as a cause of the sharp decline in sockeye abundance in many BC systems (Beamish et al. 1998, McFarlane et al. 2000). In Rivers Inlet, where sockeye fisheries have been closed since 1996, the stocks have not rebounded to historical levels, leading researchers to conclude that climate conditions and not overfishing were primarily responsible for the decline in sockeye abundance (McKinnell et al. 1998, 2001, Friedland 2000, Farley Jr. et al. 2007). The growth and survival of sockeye smolts in several systems has been linked to the early marine stage of their life history (Friedland 2000, McKinnell et al. 2001, Beamish et al. 2004). Since Owikeno Lake fry are amongst the smallest in BC, they are especially vulnerable to changes in their environment (Gilbert 1915, Foskett 1958, McKinnell et al. 2001). Environmental changes, such as temperature, salinity, ocean upwelling, freshwater discharge, and the timing of the plankton bloom, are all expected to affect the migration, growth rate and survival of smolts through direct effects on their metabolism and indirect effects via bottom up controls (e.g. Beamish and Bouillon 1993, Beamish et al. 1998, Friedland 2000, McFarlane et al. 2000, Farley Jr. et al. 2007, Farley Jr. and Trudel 2009).

Environmental conditions may also affect the timing of the smolts' entry into the estuary. Physical and biological conditions in the freshwater phase, including temperature, river flow, photoperiod, and food supply, act as environmental cues for smolts to initiate their downriver migration, and a shift in these cues would affect the timing of estuarine entry (Crozier et al. 2008, Scheurell et al. 2009). The exact entrance date of the smolts into Rivers Inlet could not be determined, but may have varied between years. In 2008, the first observed

smolt was 60 mm in length and was at the head of the inlet. In 2009 and 2010, the first smolts were between 60-90 mm and were already caught midway down the inlet.

Although age-1+ smolts, the most common in BC, are estimated to be between 80-100 mm and approximately 5 g at marine entry, the Owikeno Lake fry face harsh freshwater conditions that inhibit their growth during the lake phase, and they therefore need to grow faster in the inlet to reach the average size of smolts from other BC systems (Pauley et al. 1989, McKinnell et al. 2001). In 2008, 2009, and 2010, despite a general increase in mean size, the smaller sizes persisted in the inlet through the end of the seining season. There are three possible explanations for this phenomenon: 1) the later migration of smaller size classes of smolts, consistent with the hypothesis of Tucker et al. (2009), in which several groups of sockeye emerge into the inlet at different times throughout the season, with the larger fry migrating earlier than the smaller fry, 2) within season variation in growth rates, or 3) the comingling of different stocks from other nursery lakes at the mouth of Rivers Inlet that pass by the inlet on their northward migration. Beamish et al. (2003) found a reduction in the size of sockeye smolts with time in the Strait of Georgia. He proposed that the early emigration of larger fish and the later emergence of smaller migrants hide the growth of the smolts as they migrate (Beamish et al. 2003). On the other hand, growth may also be masked by the mortality of smaller fish (Farley Jr. et al. 2007, Tucker et al. 2009). In Rivers Inlet, the consistent presence of smolts at Kilbella later in the sampling season could provide further evidence for this phenomenon. However, the Kilbella River and Chuckwalla River drain into Kilbella Bay at this location, and the possibility of a sockeye rearing lake that produces a later run of smolts than the main Owikeno Lake cohort should not be ruled out (Britton and Marshall 1980). This is supported by the stable isotope data, as differences in feeding

regimes from sockeye smolts caught at the Ralph and Kilbella locations were evident from their elevated tissue isotopic levels (unpublished data). This could indicate the presence of several smaller runs from different freshwater sources, and warrants further examination. Regardless of their freshwater source, a later run of smaller smolts and a masking effect may lower the mean values of length and mass used to calculate the change in size class from the head to the mouth of the inlet, potentially resulting in an under-estimation of growth rate during the estuarine outmigration.

Specific growth rate (SGR) in Rivers Inlet in terms of length (% body length/day) and mass gain (% WW/day) was the slowest in 2008, moderate in 2009 and the fastest in 2010. Since a total of four smolts were caught at the head of the inlet in 2008, the SGR for this season was most likely an underestimate. Estimates of 1.69, 3.40 and 5.92% WW/day in 2008, 2009, and 2010, respectively, were comparable to growth rates found in other studies. Buchanan (2006) estimated that sockeye smolts in Rivers Inlet experienced an approximate doubling in mean mass during their outmigration, resulting in a 3-5% increase in WW/day. The SGRs were also within the range of growth rates found for chum and pink salmon smolts (-0.7 to 7% WW/day) fed on different ration regimes (Koeller and Parsons 1977, LeBrasseur 1969). Growth rates of chum and pink smolts tend to be higher than those of sockeye smolts, and at the end of the summer chum and pink smolts are found with similar body sizes as sockeye, despite having started the season with smaller body masses (Brett and Shelbourn 1975, Farley Jr. et al. 2005). The SGRs fell outside the range found by Fisher and Percy (1988) for coho salmon smolts (2.2-2.3% WW/day). Farley Jr. and Trudel (2009) estimated growth rate potential for sockeye salmon smolts to be -0.39 to 0.69% WW/day for smolts averaging 74.0 g, and 1.01% WW/day for smolts averaging 110 g. The growth rate of

sockeye smolts has also been reported as -0.19 to 3.55% WW/day and as 5-15% WW/day on varying food rations (Brett and Shelbourn 1975, Brett 1976).

According to the condition index of Barnham and Baxter (1998) for salmonid fishes, the average condition of the 2008 and 2009 cohorts was “fair” ($K = 1.00-1.20$), and the average condition of the 2010 population was “good” ($K = 1.20-1.40$). Salmonids in moribund condition tend to have a longer, more slender body and less flesh than those in an average or healthy state. The “good” condition in 2010 was attributed to the heavier body mass per unit length compared to the other sampling years. Wood (1970) calculated the condition index of sockeye fry in Owikeno Lake for the brood years 1959–1966. Condition over all eight years averaged “fair” ($K = 1.09$), and remained within this boundary for all but two brood years. In 1966, sockeye fry were considered to be in “poor” condition ($K = 0.99$) and in 1964 they were in “good” condition ($K = 1.26$). In 2008 ($K = 1.12$), 2009 ($K = 1.14$), and 2010 ($K = 1.12$), recent entrants into Rivers Inlet (smolts caught at the Wannock site, just post-marine entry) had an average “fair” condition index. Although slightly higher than those found by Wood (1970), the similar average condition might indicate that feeding conditions and physical properties in the lake have remained relatively stable over time. This supports the hypothesis established by McKinnell et al. (1998) that the survival of sockeye in Rivers Inlet is related to a change in the early marine environment, and not a freshwater cause. The similarity in the mean condition index between years also suggests that differences in this study were attributed to growth after entry into the inlet.

In 2008 and 2009, values found for the condition of Rivers Inlet smolts were comparable to the borderline “poor” to “fair” condition ($K = 1.00 \pm 0.072$) found by Farley Jr. et al. (2005) in the Southern Bering Sea, Alaska for larger sockeye smolts ($L_F = 188.4$

mm; WW = 75.6 g). The 2010 cohort was in slightly better condition than those from the Southern Bering Sea. Hayden et al. (2010) found that the condition of Chinook, coho and steelhead smolts in Trinity River, California, generally increased over the sampling season, averaging “poor” to “fair” condition ($K = 0.90-1.20$). Fisher and Pearcy (1988) described a “fair” to “good” ($K = 1.02-1.35$) condition index for coho smolts. The wide range of condition within and between seasons and the differences in growth rates between years may be attributed to factors such as age, muscular development, season, fat reserves, productivity, temperature, river flow, prey availability (quality and quantity) and foraging success (Barnham and Baxter 1998, Farley Jr. et al. 2005, Hayden and Pinnix 2010).

Mass-length relationships depend on the fish condition and generally the heavier fish of a given length will be in better condition (Abowei 2010, Offem et al. 2009). If the slope b of a mass-length relationship $W=aL^b$ is equal to 3, the small and large specimens have the same form and condition. If b is greater than 3, the larger specimens are more stout, and if b is less than 3, the fish become more slender as they grow (Froese 2006, Offem et al. 2009). In Rivers Inlet, mass-length regressions had slopes $b = 2.94$ (2008), $b = 3.00$ (2009) and $b = 3.05$ (2010). All slopes were close enough to 3 to assume smolts in Rivers Inlet underwent isometric growth and maintained dimensional equality (Offem et al. 2009). Growth in mass and length was significantly lower in 2008 and 2009 than 2010, indicating that the 2010 cohort was heavier per unit length than in the previous sampling years. Condition was also better in 2010, supporting the hypothesis that growth and condition are coupled (Farley Jr. et al. 2007). The similar mass gain per unit length in 2008 and 2009 was supported by the similar mean condition between years; however, it was not reflected in the SGR calculations.

Changes in growth rate of sockeye smolts may be a physiological response to changes in the environment. Sockeye salmon smolts respond behaviorally (migration time, migration route, and feeding behavior) to varying environmental cues during their outmigration, so as to maximize their growth and survival potential (Tucker et al. 2009, Harvey and MacDuffee 2002). It is possible that environmental factors in 2008 caused the smolts to exit the inlet faster and consequentially at a smaller size, which would present as a slower growth rate. Similarly, in 2010, the smolts may have faced optimal environmental conditions in the inlet, and their behavioral response could have been to remain in the inlet for a longer period of time than in previous seasons. This longer estuarine passage time would allow them exploit prey resources and grow to a larger size, presenting as faster growth. Passage time may also change throughout the season, depending on variation in these environmental factors.

No formal studies have been conducted in Rivers Inlet to determine the passage time or the extent of estuarine usage of the sockeye salmon smolts. Based on qualitative attempts to follow peak abundances through Rivers Inlet, Buchanan (2006) found average speeds of the outmigrating smolts to be 1.9-2.9 km/day. This translated into migration times of ~23 days at 1.9 km/day and ~15 days at 2.9 km/day. A more recent study by Welch et al. (2011) utilized acoustic telemetry and the Pacific Ocean Shelf Tracking array (POST) to monitor the outmigration speed of sockeye smolts through the Fraser River watershed and out the Strait of Georgia, British Columbia, a total distance of ~800 km (400 km downriver and 400 km through the Salish Sea out of the Strait of Georgia). The sockeye smolts showed sustained swimming and directed migration, traveling the distance from the point of marine entry to the open ocean in ~22 days. Mean travel time for smolts ranging from 130-250 mm in length was 14 km/day with an average speed of 1 body length per second (bl/s). The swimming

speed of 1 bl/s was consistent with theoretically optimal speeds of 0.80-2 bl/s (Hinch et al. 2006, Welch et al. 2011). Smolts smaller than 130 mm could not be tracked due to size limitations of the acoustic tag, and this estimate is therefore representative of a larger, stronger smolt (> 130 mm) than those typically found in Rivers Inlet. If they traveled at a rate of 14 km/day, the smolts would reside in Rivers Inlet for ~3 days. If the smolts traveled at a mean swimming speed of 1 bl/s, their average speed of migration would correspond to 6.3-7.5 km/day in 2008, 2009, and 2010. Assuming sustained swimming, smolts would exit the inlet in 6-7 days.

Wood et al. (1993) estimated downstream travel time of sockeye smolts from Great Central Lake and Sproat Lake, and through Alberni Inlet and Barkley Sound, Vancouver Island, British Columbia. They travelled a total estimated distance of 94.9 km and 77.8 km, respectively, 70 km of which were in marine waters. Migration times in the marine phase averaged 1.9 km/day (April-May, Alberni Inlet) and 1.6 km/day (May-June, Barkley Sound). At a steady migration rate of 1 km/h, the smolts could have exited Barkley Sound in < 3 days, a speed consistent with the near physiological maximum of 5-7 bl/s, or 1.3-2.0 km/h (Brett 1965). Instead, they remained in the study area for 6 weeks. Wood et al. (1993) suggested his results may be an underestimation of the migration speed of sockeye smolts, and could not rule out estimates of 6-7 km/day found for sockeye smolts from Fraser River, British Columbia (Groot and Cooke 1987). The estimated travel times of Wood et al. (1993) would translate into migration times of ~23 days at 1.9 km/day and ~27 days at 1.6 km/day in Rivers Inlet.

Peterman et al. (1994) simulated the migration of sockeye smolts through the Strait of Georgia, British Columbia. The model tested migration rates of 40 mm/s, 80 mm/s, 240

mm/s, and 0 mm/s (passive migration). At 40 mm/s, less than 1 bl/s, the migration time was comparable to field observations of ~24 days. In Rivers Inlet, smolts swimming at 40 mm/s, or < 1 bl/s, would travel through the inlet in ~14 days. It would take ~7 days if they were migrating at 80 mm/sec, comparable to estimates using swimming speeds of 1 bl/sec. Sockeye smolts traveling at 240 mm/s, or ~3 bl/s, would exit the inlet in ~3 days. Passive migration should also be considered, as the physiological preferences of the smolts for certain temperatures, salinity and surface current patterns, as well as physical conditions in the study area, cannot be ruled out as factors that may determine the migration time and route of the smolts (Peterman et al. 1994).

Each season may also have a different migration rate, depending on physical factors such as river flow, surface winds, and temperature, or the amount of prey available to the smolts (Brett 1976, Peterman et al. 1994, Duffy 2009). For example, the residence time of the surface freshwater layer in Rivers Inlet averaged 7 days and 15 days during periods of high and low river discharge, respectively (Hodal 2011). In 2008 and 2009, discharge rates were highly variable, creating an alternating pattern of 1–2 weeks of high river flow rates followed by a period of low flow (Hodal 2011). In 2010, river flow remained relatively stable and was lower than in the previous sampling years. The timing of the high flow events corresponding to the smolts' outmigration was different between years, with the highest discharge values seen in late May and mid-June in 2008 and 2009, respectively. Smolts entering the estuary during a high flow event may travel through the inlet at a faster speed than those entering during a low flow event, as the large volume of freshwater entering via the Wannock River may advect the smolts through the estuary more rapidly. Smolts entering during low flow events may be subjected to reduced passive transport, and may therefore take longer traveling

through the inlet to the open ocean. A change in flow rate throughout the period of estuarine migration may also impact the migration time of the smolts on a cohort-to-cohort basis, causing migration times to change within a given season. Based on the estimates from other studies and surface water residence time in Rivers Inlet, migration times of ~7 days to ~27 days should not be dismissed without further consideration. However, adjusting the migration time in growth rate calculations did not change the trend of low growth rates in 2008, moderate growth rates in 2009, and fast growth rates in 2010.

Larger smolts are predicted to have higher survival rates and are more able to maintain metabolic function during their first marine winter (Beamish et al. 2004, Farley Jr. et al. 2007). In Rivers Inlet, the 2010 population could return in higher abundances than in the previous two years, given their larger size as they exited the inlet. Condition is an indicator of well-being and degree of adaptability to marine conditions; smolts with a high condition factor may have faced abundant prey availability throughout their migration through the estuary (Offem et al. 2009). Foerster (1968) hypothesized that three factors control the growth rates of smolts during their ocean residence: 1) the amount of food available to the salmonids, 2) water temperature, and 3) the degree of competition for food and the size of the feeding salmon. Various physical and biological factors, including prey availability, prey composition, temperature, salinity, and freshwater discharge are known to exert bottom-up controls on fish populations, and may be responsible for the inter-annual differences in growth and condition seen in 2008, 2009, and 2010 in Rivers Inlet (e.g. Pauley et al. 1989, McKinnell et al. 1998, Friedland 2000, Harvey and MacDuffee 2002, Farley Jr. et al. 2007). These would largely impact the metabolism and prey parameters of the sockeye smolts, affecting growth through energy supply and the smolts' activity levels (Brett 1976).

Larger fish deplete their energy reserves more slowly than smaller fish. If the amount of energy required for metabolism is larger than the amount gained from prey species, sockeye smolts may experience negative growth, reducing their ability to reach a critical size before winter (Beamish et al. 2004). Establishing the importance of prey quality and quantity to the growth rate potential and subsequent survival of sockeye salmon smolts is imperative to effectively managing stocks now and in the future.

In conclusion, the 2008 smolts used the main channel more than the smolts from 2009 and 2010. In all three years, there was a general increase in size with movement down the inlet and between surveys. The 2008 and 2009 cohorts were relatively similar in terms of mass, length and condition, whereas the 2010 cohort had a significantly larger mean size and higher condition index. The lower growth rates in 2008 and 2009 may have been a function of variations in the diet composition (quality and quantity) affecting the prey resources available to the smolts, coupled with higher river flow rates and advective transport of the smolts out of the inlet at a smaller size.

Chapter 3: Seasonal diet composition of sockeye salmon smolts

3.1 Introduction

Early life history stages are thought to be the critical period in determining the survival of salmonids in marine waters (Hartt 1980, Pearcy 1992). During their early marine entry period, the highest growth rates are usually accompanied by ~90% mortality (Pauley et al. 1989). Causes of this rapid growth and high mortality are variable and unpredictable (Simenstad et al. 1982, Straty and Jaenicke 1980). Beamish and Mahnken's (2001) critical size and critical period hypothesis proposed that the majority of marine mortality of salmonids occurs in two phases: 1) natural mortality related to predation upon marine entry and 2) a failure to reach a critical body size that allows the salmonids to maintain metabolic function and survive their first marine winter. Salmon smolts are thus required to maintain a minimum growth rate during their first summer at sea (critical period) in order to reach a body size necessary for survival (critical size). Larger individuals have a lower mass specific energy requirement, and can therefore allocate more energy to survival than smaller individuals (Beamish et al. 2004). A balance between feeding rates and food requirements is therefore crucial for the salmon smolts to maintain growth during their first marine summer (Healey 1980).

Salmonids travel across many different habitats throughout the duration of their life cycle. Their migration from freshwater through estuarine and coastal ecosystems to the open ocean challenges them with a wide variety of unfamiliar feeding habitats and prey types (Beacham 1986). Carlson (1976) found that the food resources available to fish in their early

marine life influence growth and condition, and may directly (starvation) or indirectly (reduced fitness) affect survival. Hartt (1980) and Straty and Jaenicke (1980) hypothesized that the type of food available had a major impact on the growth of sockeye smolts in Bristol Bay, Alaska. As a result of poor prey resources, smolts grew slowly until reaching more profitable feeding grounds (Hartt 1980).

Oceanographic conditions and feeding conditions could account for changes in behavioral patterns of out-migrating salmonids between years (Hartt 1980, Eggers 1980). Healey (1980) and Farley Jr. et al. (2005) proposed that the distribution of salmon smolts in coastal waters was related to SST and prey availability. For example, the rapid migration of sockeye smolts through estuarine environments may be delayed by high prey availability and greater foraging success. To maximize exploitation of food resources, salmon smolts may linger in areas with optimal foraging conditions, where they feed for longer periods or move into alternative habitats to enhance their growth (Eggers 1980, Simenstad et al. 1982, Hartt 1980, Straty and Jaenicke 1980). They may also leave the estuary prematurely or endure periods of low food ration upon depletion of the available resources in the pelagic foraging zone (Healey 1980). The drawback to this plasticity in their life history is the potential for higher vulnerability to predation and mortality (Eggers 1980, Crozier et al. 2008). The findings of Perry et al. (1996) supported the hypothesis of Farley Jr. et al. (2005), in that condition factor, feeding intensity and growth potential were positively correlated for pink and chum smolts off Vancouver Island. Low prey levels were consistent with food limitation and subsequent reduced growth efficiencies, indicating that variations in zooplankton abundance and biomass may drive estuarine migration time, foraging success and growth potential of salmonids (Straty and Jaenicke 1980, Perry et al. 1996, Crozier et al. 2008).

Other mechanisms controlling the metabolism, growth and survival of salmon smolts include sea surface temperature (SST), osmotic stress (salinity), and pelagic productivity (Pearcy 1992, Beamish and Mahnken 2001). For example, temperature fluctuations may influence zooplankton community formation during spring production, affecting the type (quality and quantity) of prey available to the salmonids (Straty and Jaenicke 1980, Pearcy 1992). A shift in the timing of spring production may also cause a mismatch between the peak in prey items and the timing of the smolts' migration, potentially creating situations of poor foraging success, due to reduced smolt-prey encounter rate that may be further complicated by the quality of the zooplankton prey (Cushing 1990, Cushing and Horwood 1994). In order to maintain rapid growth rates, salmon smolts need to develop successful foraging techniques while transitioning between environments and adapting to changing biotic and abiotic conditions (Brodeur 1990).

The feeding ecology of salmonids is consistent with the optimal foraging theory, in that the low diversity of prey items found in the diet composition suggests preferential feeding on certain taxa associated with the vertical distribution of the salmonids (Healey 1982, Brodeur et al. 2003). Despite the availability of a wide foraging base, salmon smolts consistently select prey that are the most energetically beneficial for the maintenance of their growth and function, such as larger and more visually obvious items, or those with minimal avoidance capabilities (Healey 1982, Simenstad et al. 1982, Brodeur et al. 2003). Several studies have shown that copepods and fish are their preferred prey items, but that smolts also consume amphipods, cladocerans, decapods, euphausiids, insects, and pteropods (e.g. Straty and Jaenicke 1980, Healey 1982, Simenstad et al. 1982, Beamish et al. 2003). The observed low variation in the diet composition and persistence of certain taxa in the fish stomach

throughout the season imply that the size, behavior and caloric content of prey items (e.g. zooplankton community composition) may be the key predictors of fish growth and survival potential (Healey 1980, Straty and Jaenicke 1980, Pearcy 1992). The morphological and energetic limitations in foraging capacity during their early life history may also drive the salmonids' preference for certain prey items (Simenstad et al. 1982). When optimal prey are not available, the opportunistic nature of their feeding behavior provides salmonids with the ability to exploit a wide variety of prey items from a broad foraging base, including smaller or less energetically rich zooplankton (Straty and Jaenicke 1980). It is this opportunism that allows salmon smolts to adapt their feeding strategy in response to the seasonality of the zooplankton community (LeBrasseur 1969, Straty and Jaenicke 1980, Pearcy 1992).

The aim of Chapter 3 was to study the spatial and temporal variability in the diet composition (abundance and biomass) of sockeye salmon smolts in relation to the zooplankton community composition. Environmental variables (temperature, salinity, river discharge, and photoperiod) that may impact the zooplankton community composition or the metabolic function of the smolts were also examined for their influence on the diet composition.

3.2 Methods

Fish were sampled and preserved as per the methodology described in Chapter 2. Preserved stomach samples were cut open and the contents removed. The stomach lining was weighed and discarded. Stomach contents were identified, enumerated, and measured for length (to the nearest 0.05 mm). They were then classified according to three digestive stages: fresh, partially digested, and digested. The fresh category contained almost intact, identifiable prey items. The partially digested stage consisted of a more compacted food bolus with prey items that were in varying stages of digestion, but that were still identifiable and measurable. The digested stage was comprised of a dense bolus of well-digested, predominantly unidentifiable content. Contents were weighed (to the nearest 0.001 g), when possible, on a Fisher Scientific accuSeries accu-413 balance (max: 410 g; d = 0.001 g). Given this precision, the mass of individual prey items lighter than 0.001 g could not be accurately recorded. In this case, the total mass of all prey items was recorded, either as a whole or as the sum of the mass of each digestion stage. Reconstructed biomass measurements (see below) were used to calculate the contribution of each individual prey item to the total mass of the stomach contents.

The average length for each species identified was averaged and the dry weight (DW; mg) of individual prey items was reconstructed from averaged literature values (Ricciardi and Bourget 1998, Brey 2001, Cauffopé and Heymans 2005), or from known length to weight relationships (regressions or ratios of length:DW; M. Galbraith unpublished data). DW was converted to wet weight (WW; mg) using species-specific conversion factors from literature (Appendix G). DW for prey items that could not be identified to a species level (due to digestion stage) was averaged from the DW of species within that category. For

example, the DW of unidentified copepods was estimated from the average DW of all copepod species (*Calanus marshallae*, *Metridia pacifica*, *Neocalanus plumchrus*, *Pseudocalanus* spp.) identified in the stomach contents. General conversion factors for that taxon were used to convert the DW to WW. The WW was then multiplied by abundance to obtain an estimate of prey biomass.

For comparative purposes, prey items in the stomachs and zooplankton in the water column were combined into the following taxonomic categories (Appendix G): Amphipoda, Bivalvia, Cirripedia, Cladocera, Copepoda, Crustacea, Decapoda, Euphausia, Jellyfish, “other”, Pisces, Pteropoda and Salps. Diet data were expressed as frequency of occurrence (% of stomachs) and contribution to total abundance (% contribution to total number of items in the diets) and biomass (% mg WW of diet contents) of prey items.

In addition to seine net surveys, bio-oceanographic surveys were completed in all years, occurring fortnightly in 2008 and 2009, and monthly in 2010, for a total of 27 surveys at 28 stations (Figure 18). A SeaBird Electronics 25 Conductivity, Temperature and Depth logger (CTD) was deployed to 50 m at UCTD (CTD only) stations, and to ~10 m from the bottom at all other stations. No UCTD stations were sampled in 2008. The bio-oceanographic stations were in close proximity to the seine stations, and the surveys generally occurred within a few days of each other. In 2009 and 2010, physical parameters of the water column were recorded simultaneously with each seine set. An RBR-CTD was deployed to 30 m, the effective depth of the seine net, and recorded temperature, salinity, turbidity, and fluorescence. In 2009, no data were available after 31-May, due to mechanical problems with the RBR. River flow measurements were recorded daily by Environment Canada, and are

available on the Environment Canada website (<http://www.wateroffice.ec.gc.ca>). Photoperiod was calculated using code derived for the Matlab program (Forsythe 1995).

Zooplankton tows were also conducted during the bio-oceanographic surveys, from ~10 m above the bottom (to a maximum depth of 300 m) to the surface (Figure 18). D. Tommasi analyzed these samples for species abundance and biomass. M. Galbraith and D. Tommasi also analyzed surface zooplankton data (0-10 m), collected during the bio-oceanographic surveys in 2008 (25-May) and 2010 (19-May and 23-June), for species abundance and biomass. Surface data were unavailable for the 2009 sampling season.

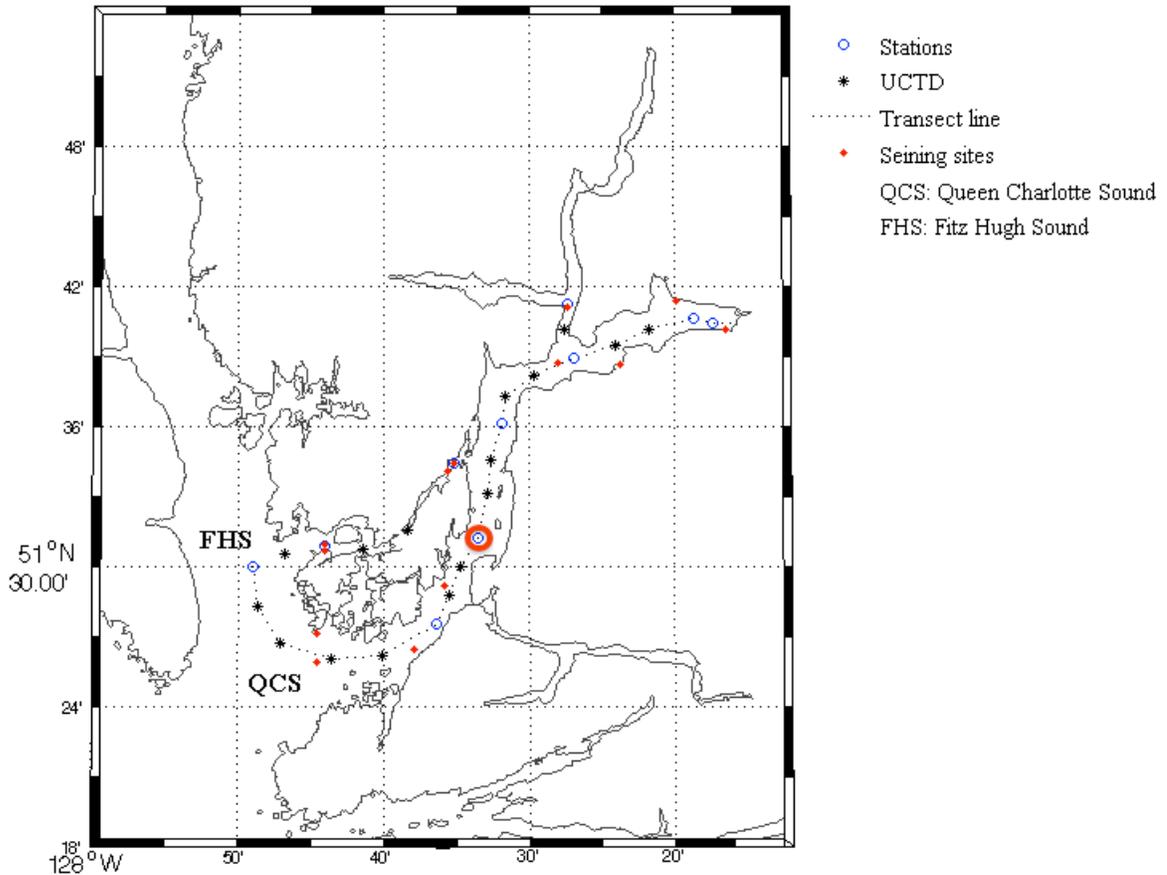


Figure 18: Map of Rivers Inlet, showing the transect followed during the bio-oceanographic surveys, in which physical and biological sampling were carried out. Stations included a variety of measurements, such as zooplankton hauls and CTD casts. The UCTD sites were stations in which only a CTD cast was conducted, and these were not sampled in 2008. Red dots indicate the location of the seining stations. The red circle marks the location of DFO2, from which environmental data used in the BioEnv procedure were collected.

3.2.1 Analysis of spatial and temporal variability in the diet composition

Since one set per site was performed during a survey was conducted at a different site, references to fish caught within a set and at a site are synonymous and will be referred to as “site” sampling. Two methods tested the similarity between samples (fish) at various levels using Primer-E v. 6.1.12. First, a matrix of log-transformed ($\log_{10}(x+1)$) prey abundance data was created to reduce the effects of extreme prey numbers. The data were then pooled by site to determine the spatial variation in stomach contents. The survey and year in which the seining event occurred were held constant. A Bray-Curtis resemblance matrix was created for each site, calculating the similarity of fish diets from a site. The average similarity between these concurrently caught fish was used as the percent similarity within sites. A SIMPER analysis provided the dissimilarity between sites, and was used to calculate the percent similarity ($100 - \%dissimilarity$) between sites from the same survey. A similar method was used to investigate the temporal aspects of sample variability (within and between survey and year), with either site and year or survey and year held constant.

The second method was used to measure variability in the diet similarity at either the site or the survey level. For this, all fish caught at one site during all surveys within a year, and all fish caught during a particular survey (seasonal variability) within a year, were pooled together and treated as described above.

Based on these results, a YearSurveySite factor was created and resemblance matrices formed for diet abundance and biomass, in which each stomach sample became a value averaged from the diet composition of all the fish in one set. A group-average cluster analysis created unique groupings based on these matrices, and samples were considered to be part of a specific cluster if they were $\geq 40\%$ similar. SimProf determined which clusters were

significantly different ($p < 0.05$) based on diet composition. A SIMPER analysis determined the indicator taxa within clusters, as well as the percent contribution of each taxon to the similarity within or the dissimilarity between clusters.

Environmental data (temperature, salinity, and fluorescence) obtained by CTD and RBR were extracted and analyzed using specialized code for the Matlab program (M. Wolfe personal communication). The data from DFO2 were then integrated and averaged over the top 30 m (Figure 18). The DFO2 site was chosen as it was assumed to be representative of the dynamics throughout the entire inlet, and 30 m was the sampling depth of the seine net. In 2008 and 2009, environmental data were collected within a few days of the seining survey, and it was thought that the dynamics of the inlet would not change dramatically within that short time frame. In 2010, data from the bio-oceanographic cruises were used when available and in close proximity to the seining surveys. When these data were unavailable or occurred > 5 days from the seining events, integrated and averaged 30 m RBR data collected during the seine net surveys were averaged across all sites and used in lieu of the CTD.

RBR data from each seining site were also used as the primary environmental variables, integrated and averaged over the top 30 m. When these data were unavailable, CTD data from DFO2 were used. In 2008, the RBR was not deployed, so all environmental data were from the CTD. Fluorescence parameters were tested when RBR data were available for the 2009 and 2010 seasons. Fluorescence has been included, but has not been calibrated to bottle chlorophyll data. Turbidity was excluded due changes in scaling that occurred in mid-sampling season.

The environmental dataset was then transferred into Primer-E v. 6.1.12, combined into a YearSurveySite matrix and normalized, in order to compare values with different units

of measurement. The BioEnv procedure generated a Spearman Rank correlation coefficient between the abiotic environmental variables and the biotic diet data, to determine which physical variables best explained the clusters formed by the diet cluster analysis. The BioEnv procedure was also run using CTD data with a 2-week time lag, to determine the extent to which pre-existing environmental variables affected the diet composition of the outmigrating sockeye smolts. Variables with the strongest correlation were tested with the RELATE permutation test, which uses 999 permutations to test for the significance ($p < 0.05$) of the relationship between the abiotic variables and diets. These tests assessed the physical explanations behind the diet composition.

The selectivity index, E (coefficient of selectivity; %), was calculated using Ivlev's formula (Pakhomov and Shumatova 1992):

$$E = (r_i - p_i) / (r_i + p_i) \quad (\text{Equation 4})$$

where r_i (%) is the relative abundance of a particular prey item in the diet, and p_i (%) is the relative abundance of that item in the zooplankton community.

3.3 Results

3.3.1 Similarity comparisons by catch statistics

Dietary similarity based on prey abundance within a site during a specified survey and year was at least 15% greater than the similarity between sites and surveys (Figure 19). Therefore, a YearSurveySite factor was assigned to each sample, averaging values for fish from each site, but keeping them temporally distinct from other samples caught at the same site in a different survey and year.

The second method yielded a 6% difference between the within sites and within surveys comparison (Figure 20). These both were at least 7% higher than similarity between surveys. Similarity within years and between years was at least 21% greater than these comparisons. Despite the higher percentage similarities, the trend of decreasing similarity with increasing temporal resolution and the larger standard deviations computed with this method justified the use of the YearSurveySite factor as a representation of the diet composition.

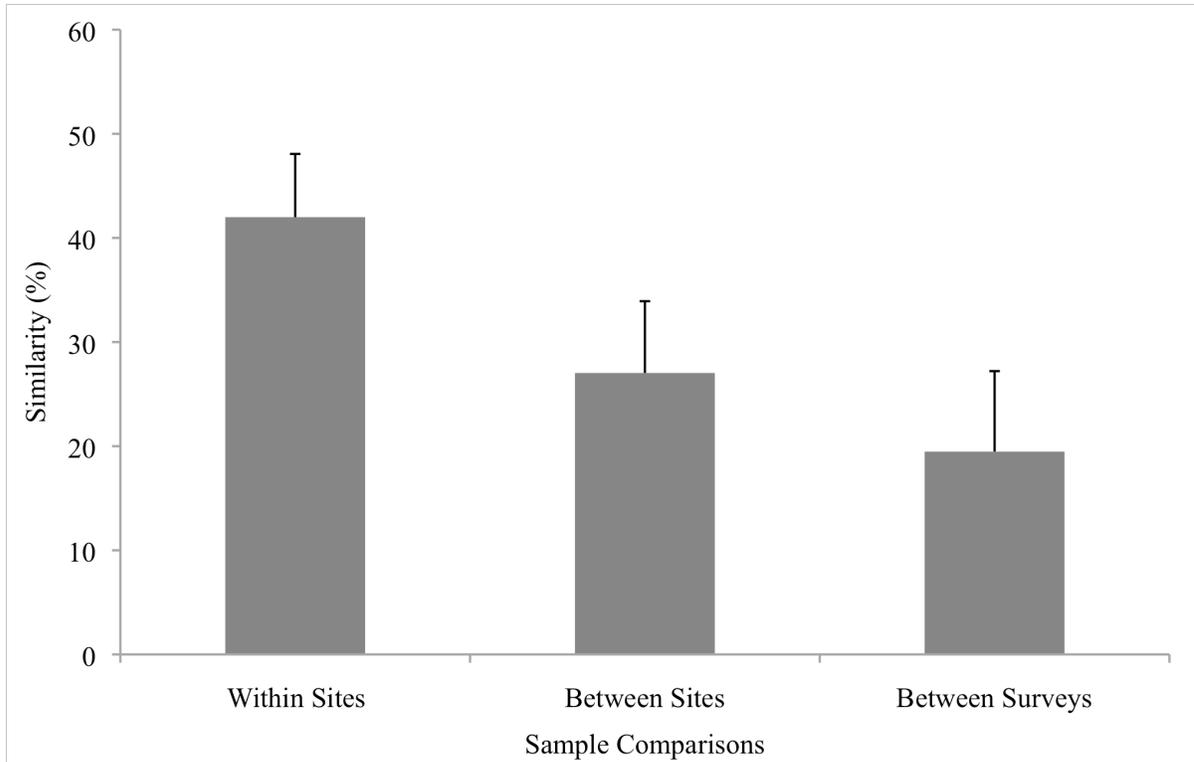


Figure 19: Average similarity (%) of smolts' diets within and between sites, and between surveys, based on Bray-Curtis similarities of prey abundance data. In all cases similarity levels were calculated across all three years; error bars indicate ± 1 standard deviation.

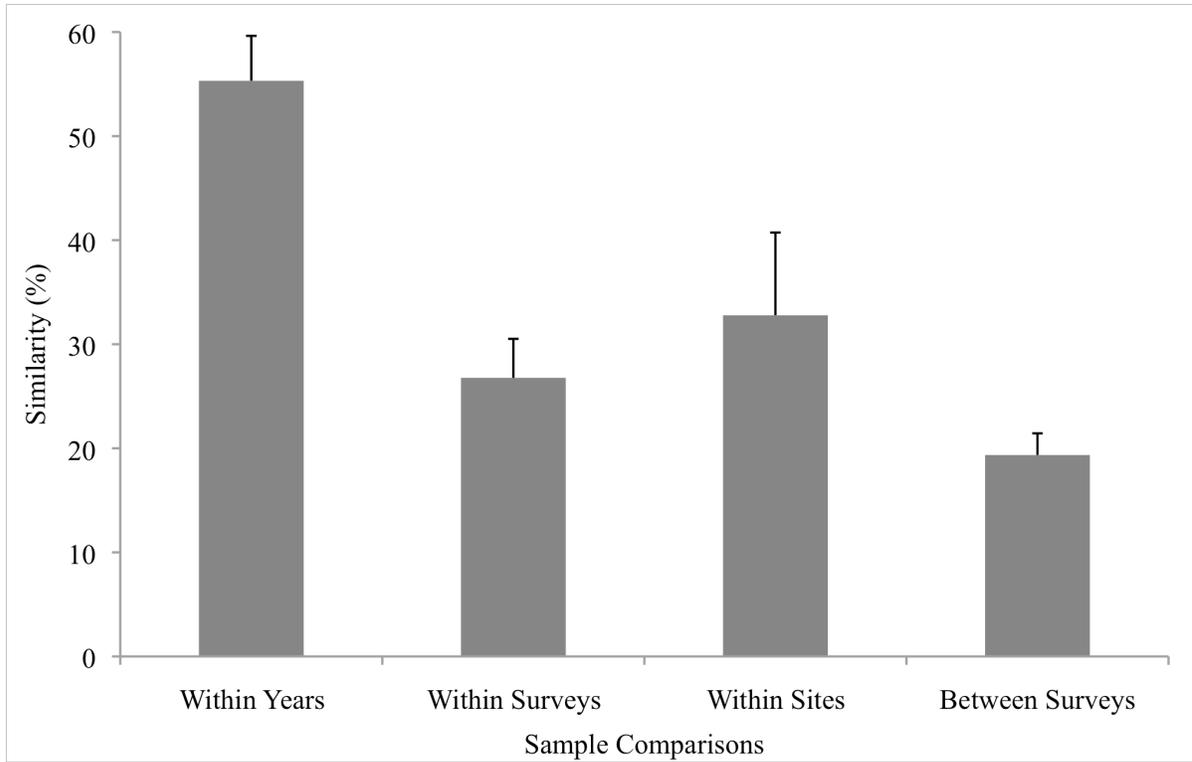


Figure 20: Average similarity (%) of samples from pooled sites or surveys based on Bray-Curtis similarities of prey abundance data. In all cases similarity levels were calculated across all three years; error bars indicate ± 1 standard deviation.

3.3.2 Diet composition of sockeye salmon smolts

The diet of sockeye salmon smolts was composed of thirty-seven taxa that varied in frequency of occurrence, abundance, and biomass between years (Appendix H). The most important groups in terms of abundance were Cladocera, Cirripedia and Bivalvia. In terms of biomass, Cirripedia, unidentified Pisces and *Calanus marshallae* were the main contributors. The main contributors to the diet composition will be described in more detail below. Of the three years, 2008 had the most diverse dietary composition, with 33 of the 37 taxa present in at least one sample. Only 27 taxa were found in 2009, exhibiting the lowest diversity between the years. 30 taxa were found in 2010 stomachs. *Calliopus* spp., Clupeiformes, *Cyphocaris* spp., Gadiformes, and Polychaeta were unique to 2008, and Siphonophora occurred only in samples from the 2010 cohort.

In all years, only 2-4% of all stomachs analyzed were empty (Table 6). Mean abundance (number of prey items per stomach), mean biomass (mg of WW), relative percentage of empty stomachs and mean gut fullness indexes (GFI, %) varied between the three sampling years (Tables 6 and 7). Stomachs from 2008 had a significantly lower mean abundance than 2009 and 2010 ($F = 14.54$; $p < 0.0001$). Mean mass of the food bolus did not vary significantly between years. Nevertheless, in 2008 mean mass and GFI were higher than in 2009 and 2010, while fish in 2009 had the highest mean prey abundance of the three years (Tables 6 and 7). In 2010, mean GFI was the lowest of the three years and was significantly lower than the mean GFI in 2008 ($F = 7.89$; $p = 0.0004$).

Table 6: Number of stomachs analyzed, mean abundance of prey items and ± 1 standard deviation, abundance range, and relative percentage of empty stomachs for sockeye salmon smolts collected in 2008, 2009, and 2010.

Year	No. stomachs analyzed	Mean abundance per stomach	Abundance (range)	% Empty stomachs
2008	180	26 \pm 49	1-503	3
2009	112	116 \pm 216	1-1378	4
2010	107	106 \pm 200	1-1017	2

Table 7: Number of stomachs analyzed, mean biomass (mg WW) and ± 1 standard deviation, and biomass range (mg WW) of prey in the stomachs. Mean gut fullness index (GFI, %) and ± 1 standard deviation, and GFI range (%) of sockeye smolts per sampling year.

Year	No. stomachs analyzed	Mean biomass per stomach (mg)	Biomass (range, mg)	Mean GFI per stomach (%)	GFI (range, %)
2008	180	80.31 \pm 101	0.08-621	1.52 \pm 1.63	0-10.55
2009	112	59.18 \pm 116	1.09-731	1.25 \pm 1.45	0-6.83
2010	107	63.31 \pm 101	0.05-519	0.87 \pm 0.62	0-2.56

In all three years, Cirripedia, Insecta and Cladocera were present in 83% of the stomachs (Appendix H). Cladocera, Cirripedia, and Bivalvia contributed 75% to total abundance. Cirripedia, fish (unidentified and Clupeiformes) and Copepoda (unidentified and *Calanus marshallae*) composed 61% of the total biomass (Appendix H).

In 2008, fish (unidentified and Clupeiformes) and crustaceans (unidentified and *Themisto pacifica*) occurred most frequently (Appendix H). There were no Cladocera, *Euphausiacea calyptopis*, *Euphausiacea furcilia* or Siphonophora present. Crustaceans (Cirripedia, Cladocera), Bivalvia and Insecta were the most frequent prey items in 2009. There were no *Calliopus* spp. Clupeiformes, *Cyphocaris* spp., Gadiformes, *Hyperiidæ* spp., Polychaeta, *Primno* spp., *Pseudocalanus* spp., Siphonophora or *Thysanoessa* spp. found in

the 2009 stomachs. In 2010, crustaceans (Cladocera and Cirripedia) and Bivalvia were the most frequent prey items in the diets. No *Calliopus* spp., Clupeiformes, *Cyphocaris* spp., unidentified *Euphausiidae*, Gadiformes, Isopoda or Polychaeta were present.

In terms of numbers, crustaceans (Cladocera and Cirripedia), Bivalvia and Pteropoda composed 51, 77 and 84% of the abundance of prey items in 2008, 2009 and 2010, respectively (Appendix H). Other prey items contributed to < 10% of the total abundance of diets in all three years.

In terms of biomass, fish (unidentified and Clupeiformes) contributed to 35% to the mass of the food bolus in 2008, while crustaceans (Cirripedia and Copepoda) were the most important prey items in 2009 and 2010, composing 53-54% of the total diet biomass. The remaining prey items found in the stomachs individually composed < 10% of total diet biomass in all three sampling seasons (Appendix H).

For additional analyses, prey items were further grouped into thirteen categories, encompassing the diversity of the zooplankton community composition (see methodology). Cirripedia, Copepoda, Amphipoda, Pteropoda, fish and unidentified crustaceans composed > 80% of prey items in the 2008 diet abundance and biomass (Figures 21 and 22). In 2009, > 70% of the diets were comprised of Cladocera and Cirripedia. In 2010, Cladocera, Cirripedia, Bivalvia and Amphipoda accounted for > 70% of the abundance and biomass of prey items (Figures 21 and 22).

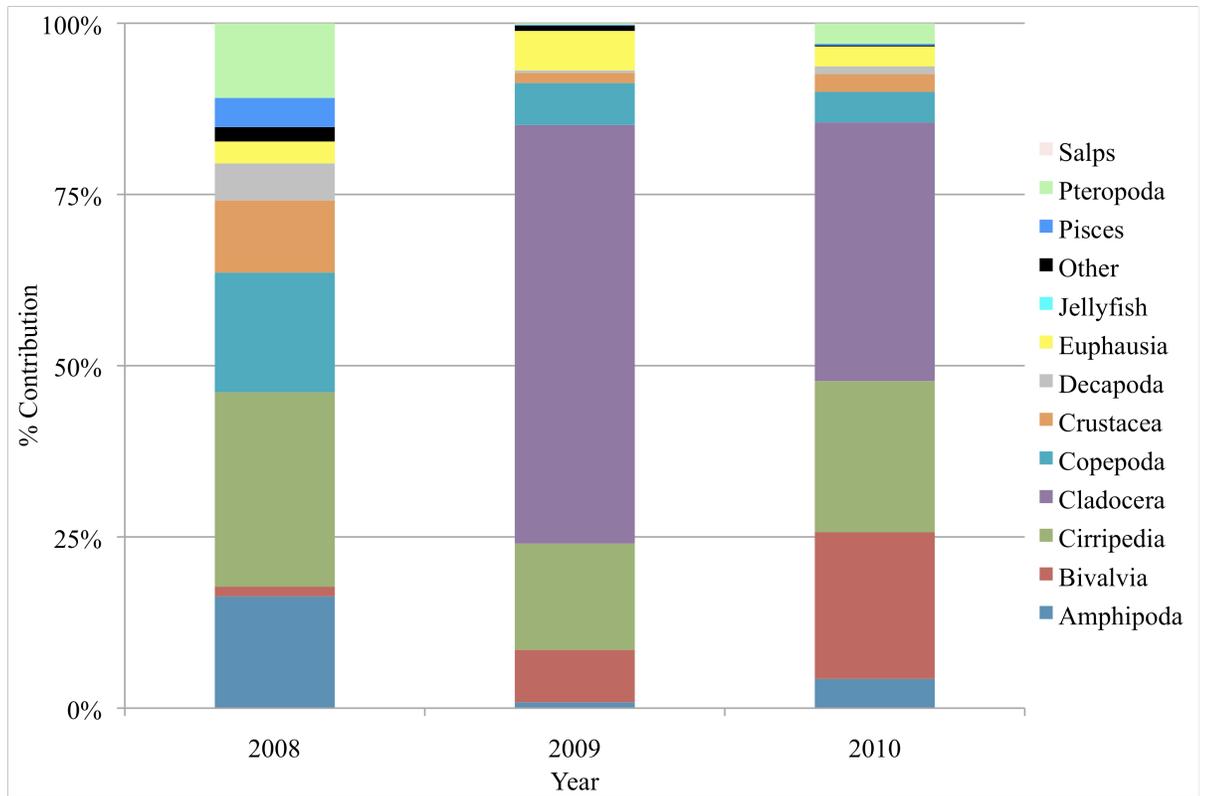


Figure 21: Percent contribution of prey taxa in each sampling year to total abundance of prey items in the diet of sockeye salmon smolts.

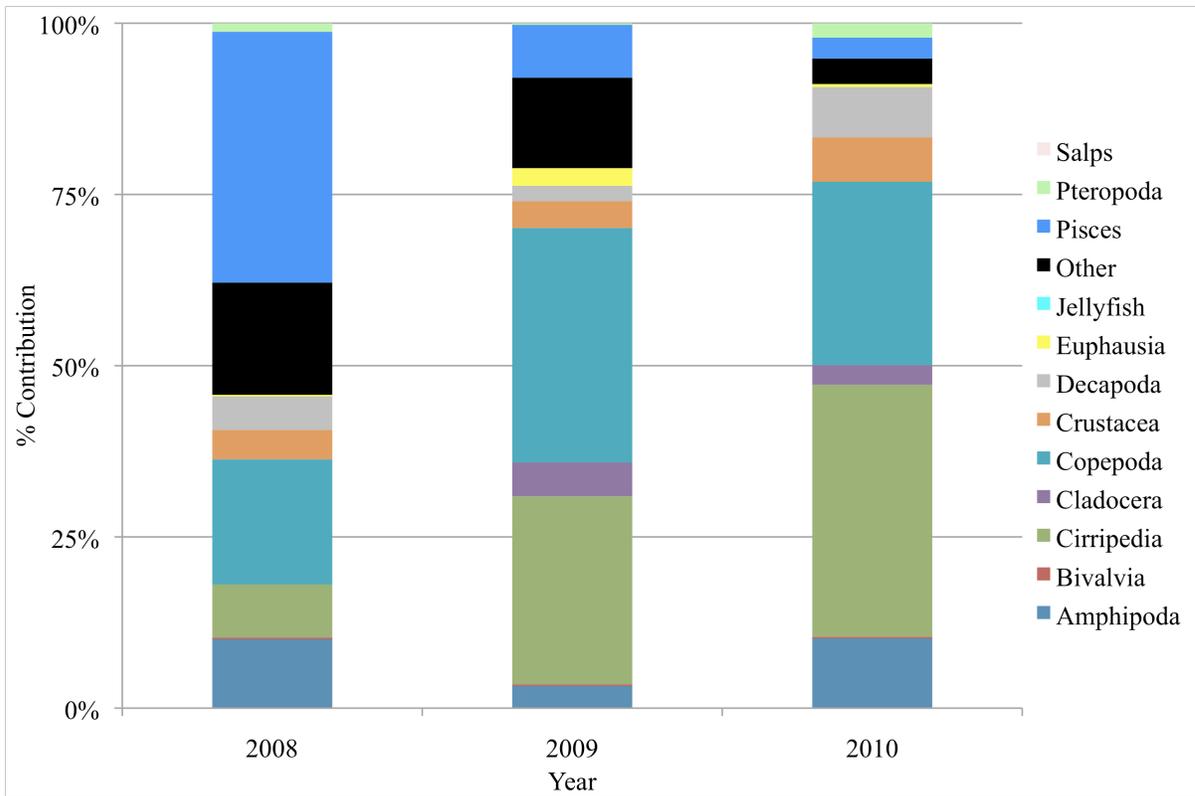


Figure 22: Percent contribution of prey taxa in each sampling year to total biomass (mg wet weight) of prey items in the diet of sockeye salmon smolts.

3.3.3 Zooplankton community composition in the water column (0-300 m)

The zooplankton community in May and June 2008, 2009, and 2010 from 0-300 m was subdivided into the same 13 taxa as the diet composition (Appendix I). Abundance was the highest in 2008 and lowest in 2010, and biomass was the highest in 2008 and the lowest in 2009 (Table 8). There were no significant differences in abundance or biomass of the zooplankton community between years.

The most frequent species / taxa found in 2008, e.g. *Limacina helicina*, *Microcalanus pusillus*, *Oithona* spp., *Oncaea borealis*, and *Pseudocalanus* spp., were encountered in all tows. In 2009, 100% of all samples contained Amphipoda, *Metridia pacifica*, *Oithona* spp., and *Pseudocalanus* spp. The 2010 samples all contained Copepoda, Copepoda nauplii, *Limacina helicina*, *Metridia pacifica*, *Microcalanus pusillus*, *Oithona* spp., Polychaeta, and Siphonophora.

In 2008, Copepoda and Pteropoda dominated zooplankton abundance (Figure 23). Copepoda accounted for 79% of the community abundance in 2009, while Copepoda and Pteropoda overwhelmingly dominated the zooplankton community in 2010. In all years, Pteropoda and Copepoda dominated the zooplankton biomass, contributing > 70% to the community biomass (Figure 24).

Table 8: Total abundance (ind. m⁻³) and biomass (mg m⁻³) and ± 1 standard deviation of the zooplankton community from 0-300 m in all three sampling seasons.

Year	Total abundance (ind. m ⁻³)	Total biomass (mg m ⁻³)	Mean abundance (ind. m ⁻³)	Mean biomass (mg m ⁻³)
2008	55,823 ± 11,156	5,265 ± 1,022	4,294 ± 11,156	405 ± 1,022
2009	44,749 ± 9,644	1,437 ± 162	3,442 ± 9,644	111 ± 162
2010	27,829 ± 5,036	2,300 ± 369	2,141 ± 5,036	177 ± 369

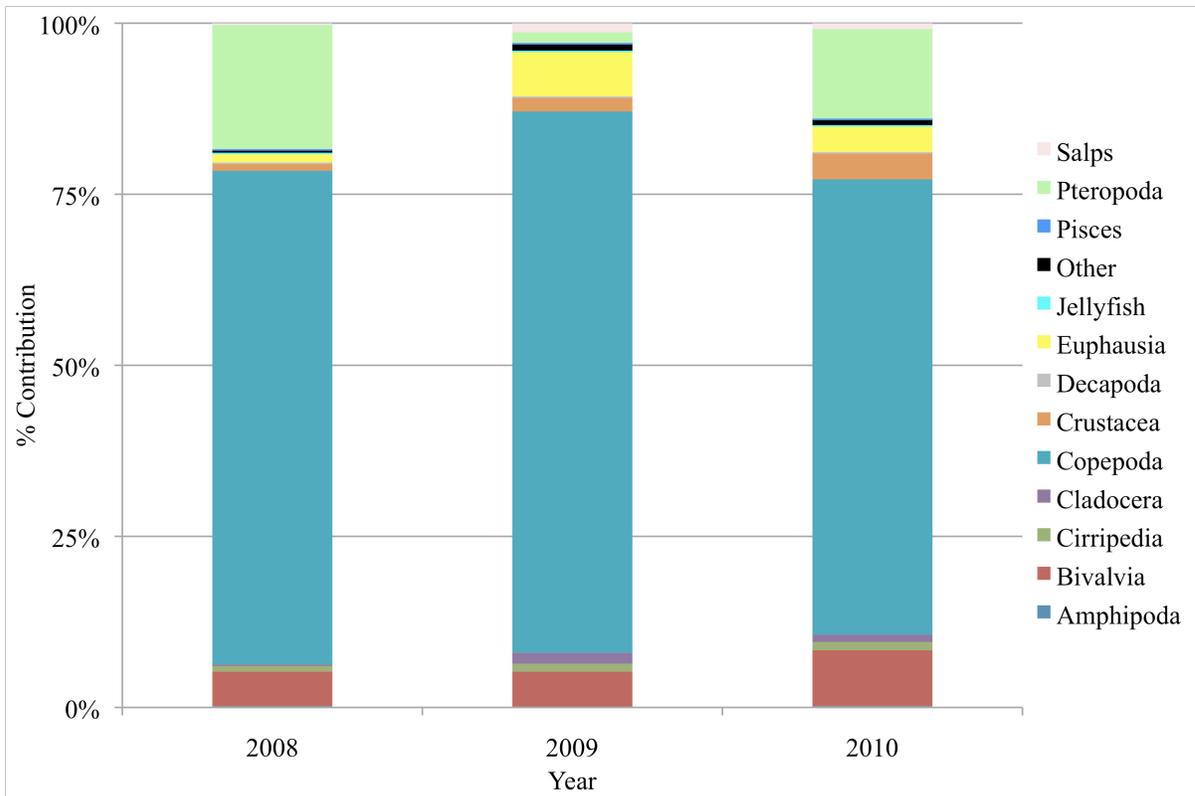


Figure 23: Percent contribution of zooplankton taxa in each sampling year to community abundance (0-300 m). Data provided by D. Tommasi (unpublished).

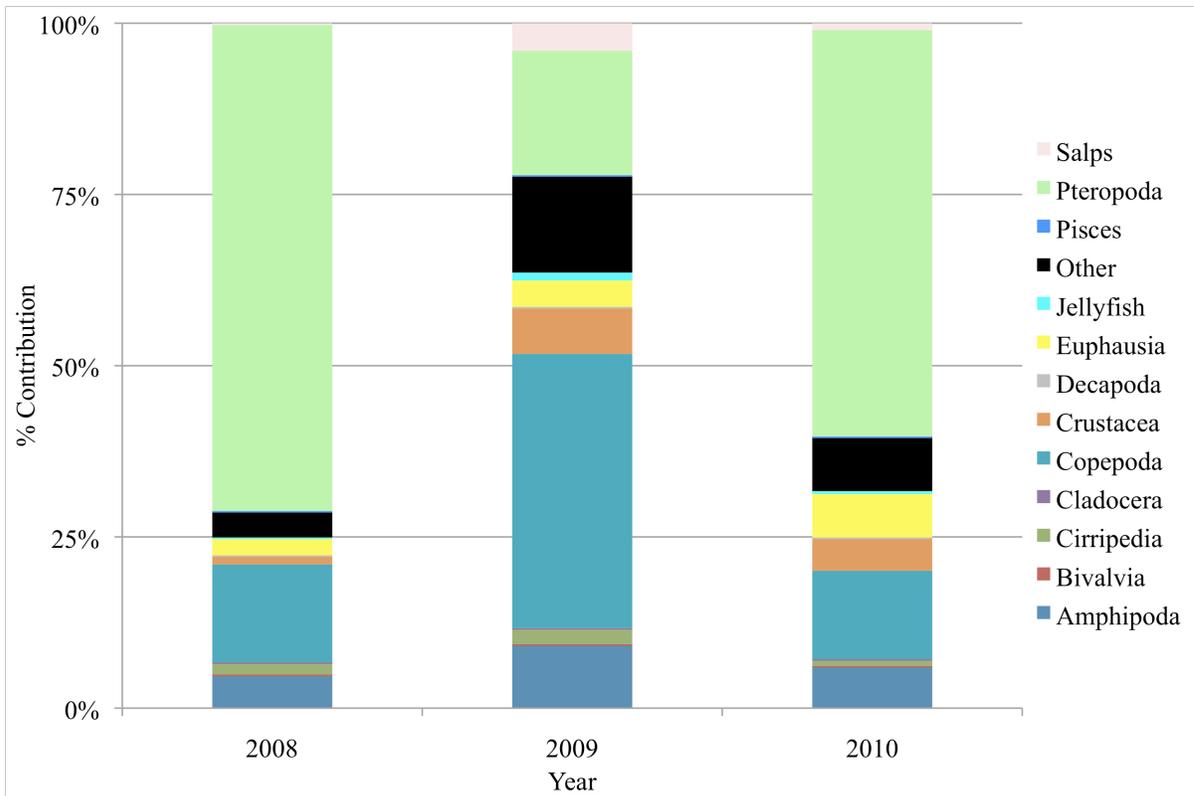


Figure 24: Percent contribution of zooplankton taxa in each sampling year to community biomass (0-300 m). Data provided by D. Tommasi (unpublished).

3.3.4 Surface zooplankton community composition (0-10 m)

Surface concentrations of zooplankton abundance and biomass were lower in 2008 than in 2010 (Table 9), although there were no significant differences between the years. In 2008, Copepoda, Cirripedia and Pteropoda dominated total daytime zooplankton abundances in the top ten meters of the water column, while only Copepoda strongly dominated the community at night (Figure 25). In 2010, Copepoda, Pteropoda, and Bivalvia accounted for ~85% of the total surface community (Figure 26). The dominating taxa during daytime were Copepoda, Pteropoda, and Bivalvia, while at night the first two groups contributed to 82% of the community.

Copepoda and Pteropoda were the most prominent contributors to the surface zooplankton biomass in both 2008 and 2010 (Figures 27 and 28). However, in 2008 Pteropoda and Cirripedia dominated the surface community during the day, while Copepoda, Pteropoda and Decapoda were the most significant taxa at night. In 2010, Copepoda and Pteropoda strongly dominated total biomass during both day and night (Figure 28).

Table 9: Total abundance (ind. m⁻³) and biomass (mg m⁻³) and ±1 standard deviation of the zooplankton community from 0-10 m in 2008 and 2010. Data was not available for 2009.

Year	Total abundance (ind. m ⁻³)	Total biomass (mg m ⁻³)	Mean abundance (ind. m ⁻³)	Mean biomass (mg m ⁻³)
2008	20,076 ± 1,160	1,178 ± 54	1,544 ± 4,182	91 ± 196
2010	132,752 ± 5,523	30,328 ± 1,558	10,212 ± 19,909	2,333 ± 5,618

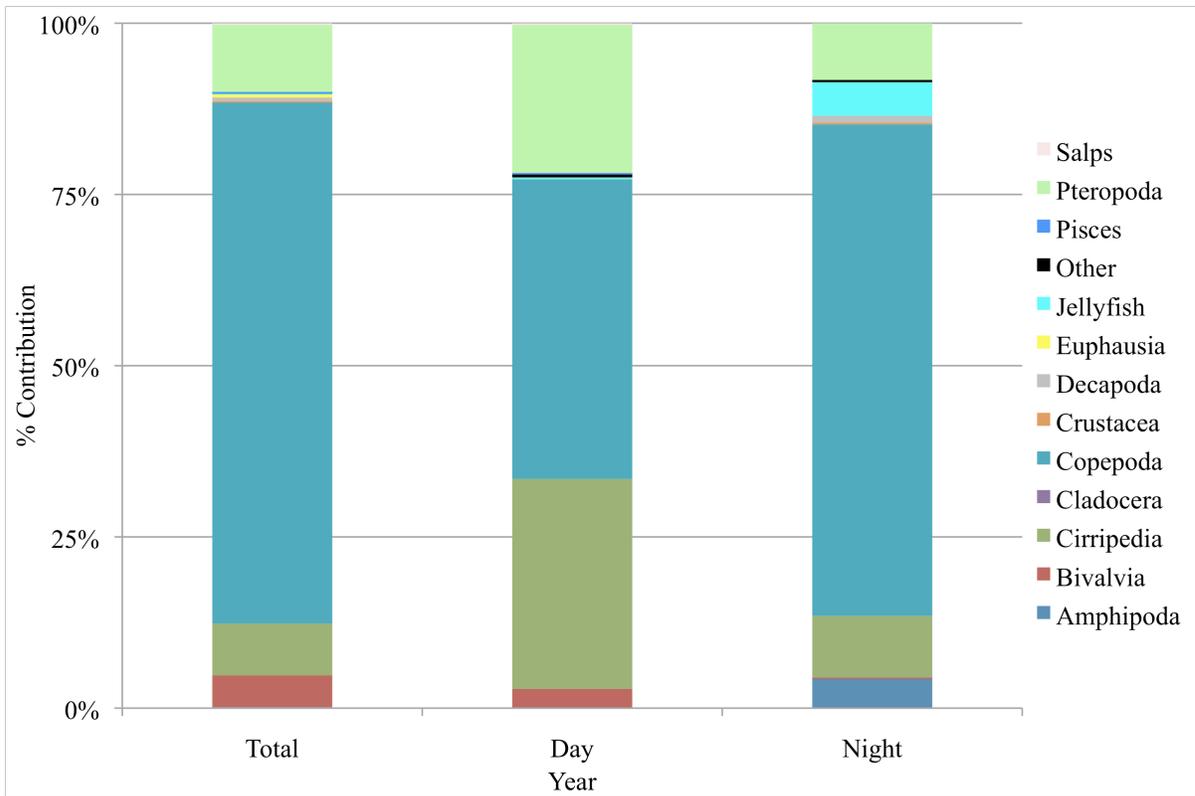


Figure 25: Percent contribution of zooplankton taxa to the 2008 surface community abundance (0-10 m). Data provided by M. Galbraith (unpublished).

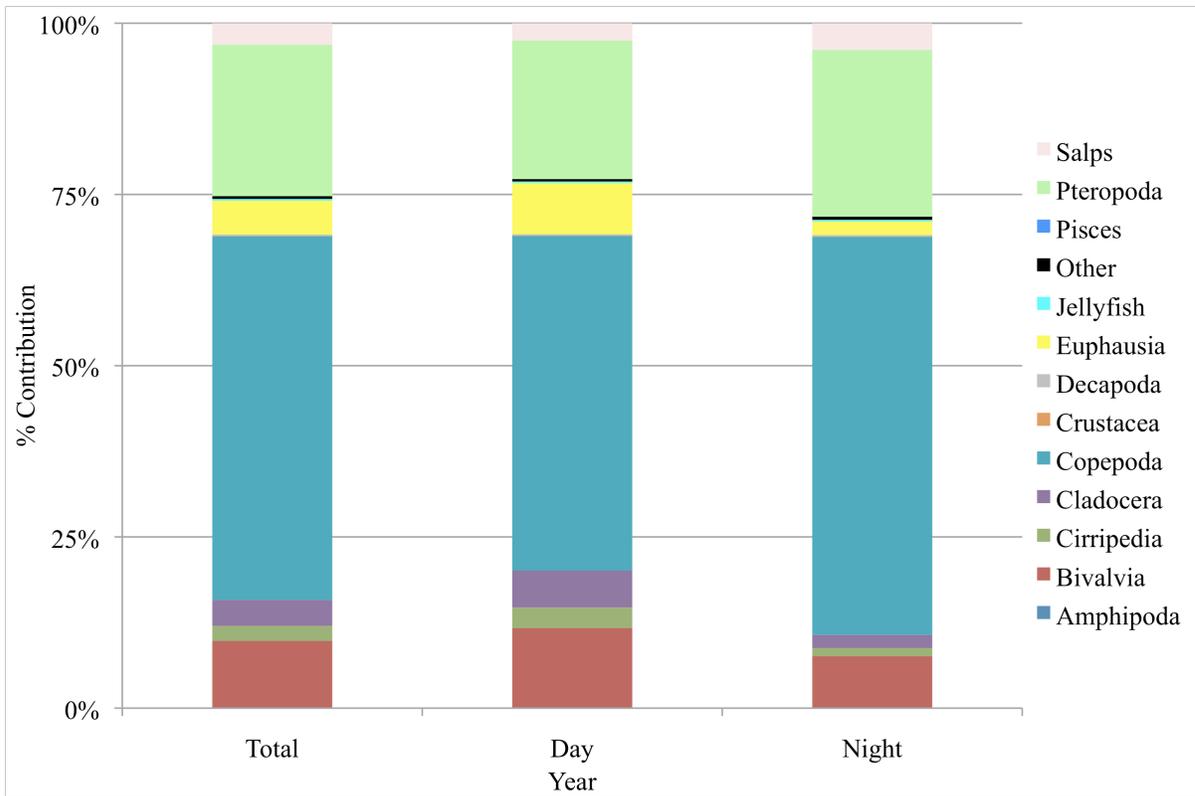


Figure 26: Percent contribution of zooplankton taxa to the 2010 surface community abundance (0-10 m). Data provided by D. Tommasi (unpublished).

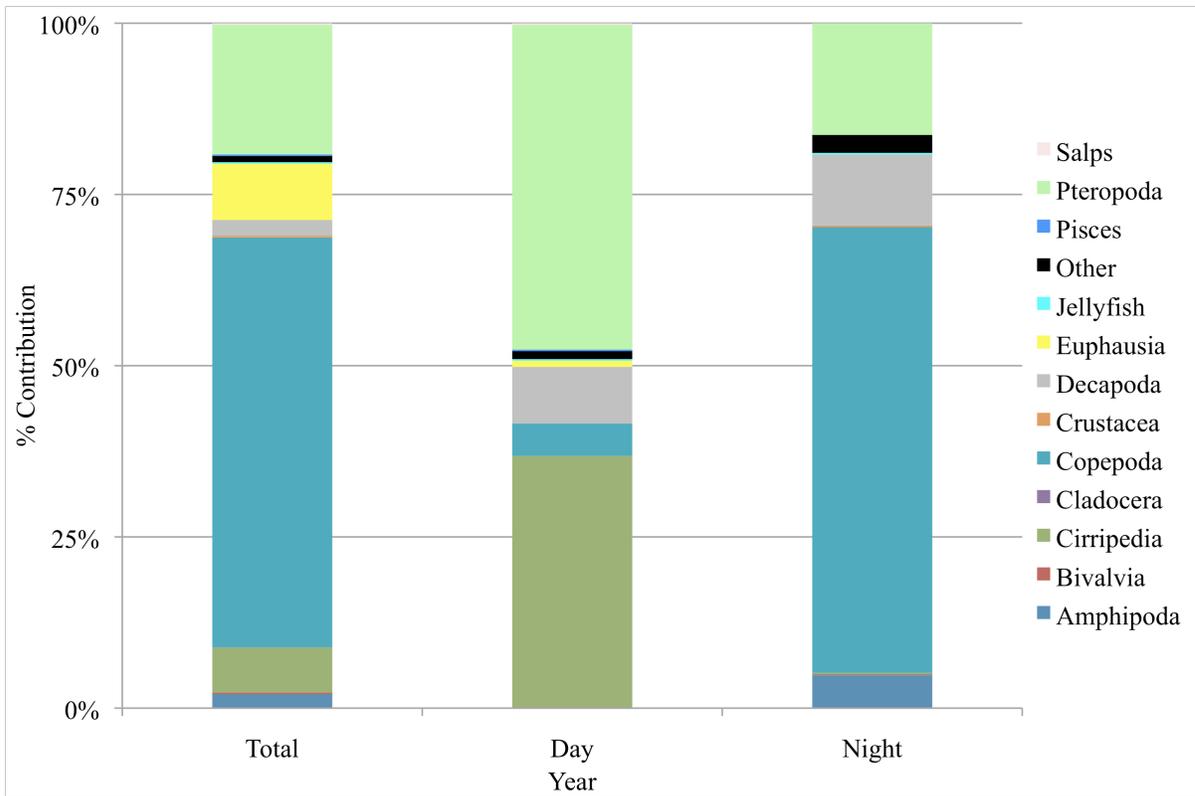


Figure 27: Percent contribution of zooplankton taxa to the 2008 surface community biomass (0-10 m). Data provided by M. Galbraith (unpublished).

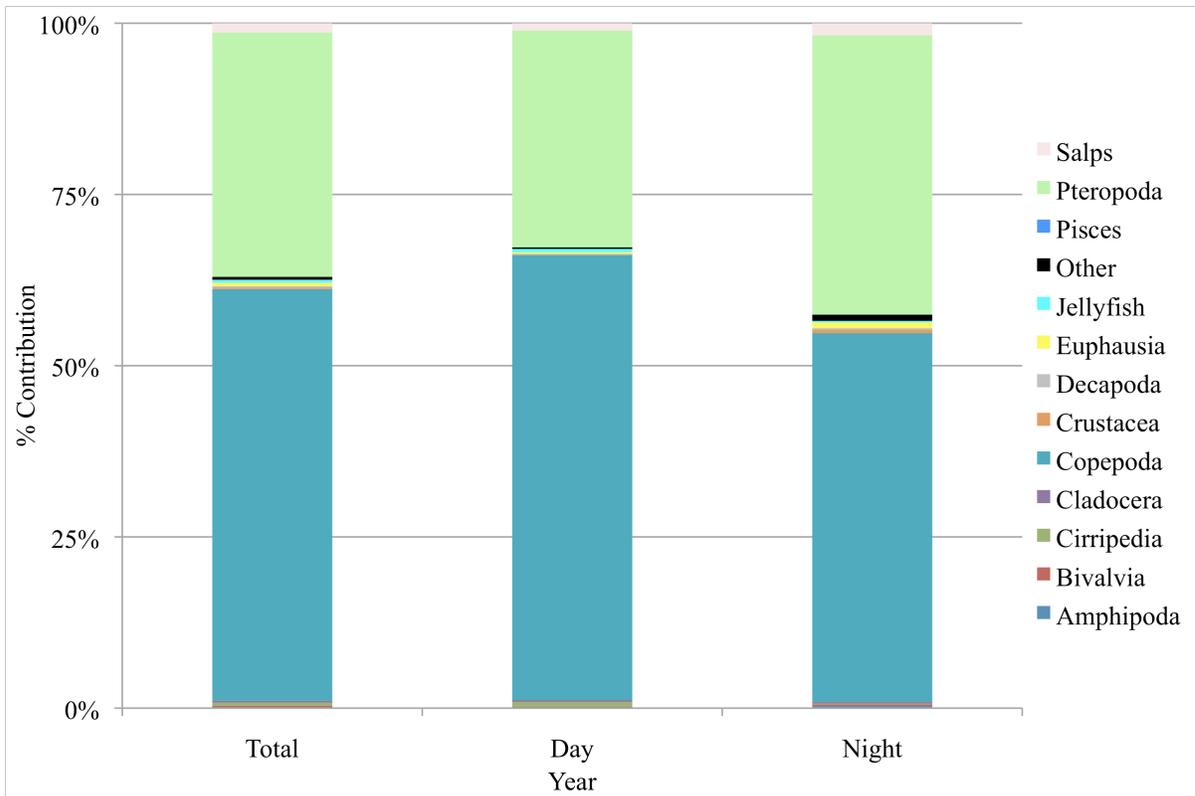


Figure 28: Percent contribution of zooplankton taxa to the 2010 surface community biomass (0-10 m). Data provided by D. Tommasi (unpublished).

3.3.5 Selectivity index for preferential prey items

The selectivity index ranked preference and avoidance of prey items into two categories: 1) highly (0.5 to 1.00) or moderately (0 to 0.5) preferred and 2) heavily (-1.00 to -0.5) or moderately (-0.5 to 0) avoided (Pakhomov and Shumatova 1992). Using zooplankton abundances from 0-300 m, selectivity calculations indicated that sockeye salmon smolts had high preference for Amphipoda, Cirripedia, Decapoda and Pisces in all three sampling seasons (Table 10). They heavily avoided Copepoda, Jellyfish, Pteropoda and Salps. Seasonally, the food preferences of the smolts exhibited opposite trends in 2008 compared to 2009 and 2010. In 2008, they highly selected for Crustacea and the “other” category, and exhibited moderate selection for Euphausiacea. Bivalvia and Cladocera were heavily avoided in 2008. In 2009 and 2010, smolts had a high preference for Cladocera and a moderate preference for Bivalvia, and moderately avoided Crustacea and Euphausiacea. The difference between 2009 and 2010 was in their preference for the “other” category as smolts moderately or heavily avoided it in 2009 and 2010, respectively.

Surface data from 2008 and 2010 indicate that sockeye smolts exhibited a high preference for Amphipoda, Cirripedia, Crustacea, Decapoda and Pisces (Table 11). They heavily avoided Copepoda, Jellyfish, and Salps. Food preferences exhibited opposite trends for the remaining taxa. The 2008 smolts highly selected for Euphausiacea, the “other” category and Pisces, while heavily avoiding Bivalvia and Cladocera. In 2010, smolts highly preferred Cladocera and moderately selected for Bivalvia, exhibiting heavy avoidance of Pteropoda and moderate avoidance of Euphausiacea and the “other” category.

Table 10: Selectivity index, used to determine the feeding preferences of sockeye salmon smolts for zooplankton taxa available in the entire water column (0-300 m). Positive values indicate preference for that prey (moderate: 0 to 0.5; heavy: 0.5 to 1.00) and negative values indicate avoidance (moderate: -1.00 to -0.5; heavy: -0.5 to 0).

Zooplankton Taxa	2008	2009	2010
Amphipoda	0.98	0.74	0.90
Bivalvia	-0.56	0.20	0.45
Cirripedia	0.94	0.86	0.90
Cladocera	-1.00	0.95	0.94
Copepoda	-0.61	-0.86	-0.87
Crustacea	0.81	-0.18	-0.21
Decapoda	0.97	0.63	0.94
Euphausiacea	0.38	-0.07	-0.14
Jellyfish	-1.00	-1.00	-1.00
Other	0.64	-0.12	-0.52
Pisces	0.97	0.89	0.97
Pteropoda	-0.25	-0.86	-0.63
Salps	-1.00	-1.00	-1.00

Table 11: Selectivity index, for the surface (0-10 m) zooplankton community. Positive values indicate preference for that prey (moderate: 0 to 0.5; heavy: 0.5 to 1.00) and negative values indicate avoidance (moderate: -1.00 to -0.5; heavy: -0.5 to 0). Surface data was unavailable for the 2009 sampling season.

Zooplankton Taxa	2008	2010
Amphipoda	0.98	0.98
Bivalvia	-0.53	0.37
Cirripedia	0.58	0.82
Cladocera	-1.00	0.82
Copepoda	-0.63	-0.85
Crustacea	0.97	0.92
Decapoda	0.92	0.94
Euphausiacea	0.65	-0.28
Jellyfish	-1.00	-1.00
Other	0.67	-0.14
Pisces	1.00	1.00
Pteropoda	0.04	-0.76
Salps	-1.00	-1.00

3.3.6 Cluster analysis of inter-annual abundance and biomass of prey items

Ten clusters characterized the abundance of the diet composition of the smolts, with four significantly different groups of clusters (Figure 29). Pisces was characteristic of group 1 (Cluster A; $p = 0.001$). Bivalvia, Cirripedia and Cladocera were indicators of group 2 (Clusters B and C; $p = 0.001$). Amphipoda, Copepoda, Crustacea, Decapoda and Pteropoda were indicators of Group 3 (Clusters D, E, F, G and H; $p = 0.001$), while Cirripedia and the “other” category were the distinguishing taxa of group 4 (Clusters I and J; $p = 0.001$).

Eight clusters characterized the biomass of the diet composition, with seven significantly different groups of clusters (Figure 30). Pteropoda was characteristic of group 1 (Cluster A; $p = 0.001$). Cirripedia was an indicator of group 2 (Cluster B; $p = 0.001$), and the “other” category of group 3 (Cluster C; $p = 0.001$). Crustacea was characteristic of group 4 (Cluster D; $p = 0.001$), while Cladocera and Pisces distinguished groups 5 (Cluster E; $p = 0.001$) and 6 (Cluster F; $p = 0.003$), respectively. Group 7 was characterized by Copepoda and Amphipoda (Clusters G and H; $p = 0.003$).

In terms of abundance and biomass, BioEnv using CTD data showed that $> 10\%$ of the variation between fish diets was based on correlations with temperature, salinity and a joint temperature-salinity effect (Tables 12 and 13). Both temperature and salinity were significantly correlated to the variation between diets. In term of variation in diet abundance using the RBR data, salinity contributed 4.5%, and in terms of biomass, salinity and a joint temperature-salinity effect contributed $> 10\%$. Salinity was significantly correlated to the variation in biomass. Results using a 2-week time lag showed that $> 10\%$ of the between diet variation in abundance and biomass was significantly correlated to temperature (Tables 14 and 15). In terms of biomass, 11% were related to a joint temperature-salinity effect.

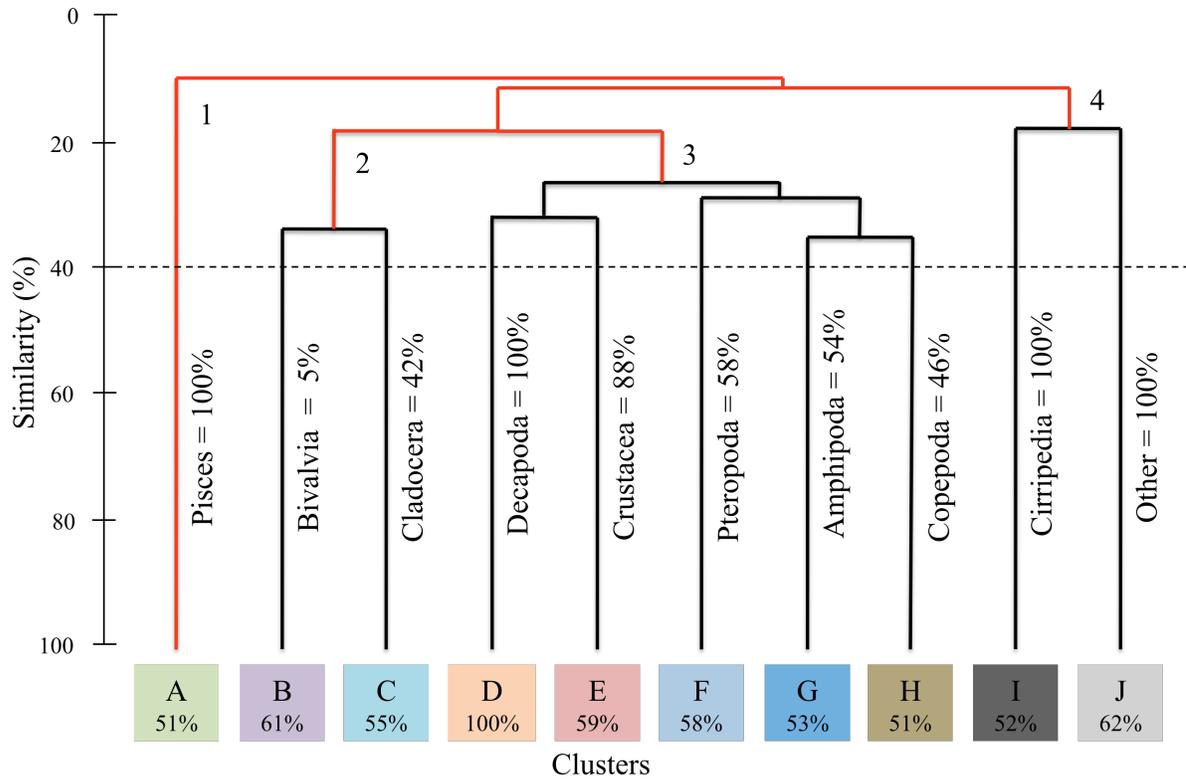


Figure 29: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey abundance found in the diet of sockeye salmon smolts. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance. D is an outlier with only one fish caught in the set.

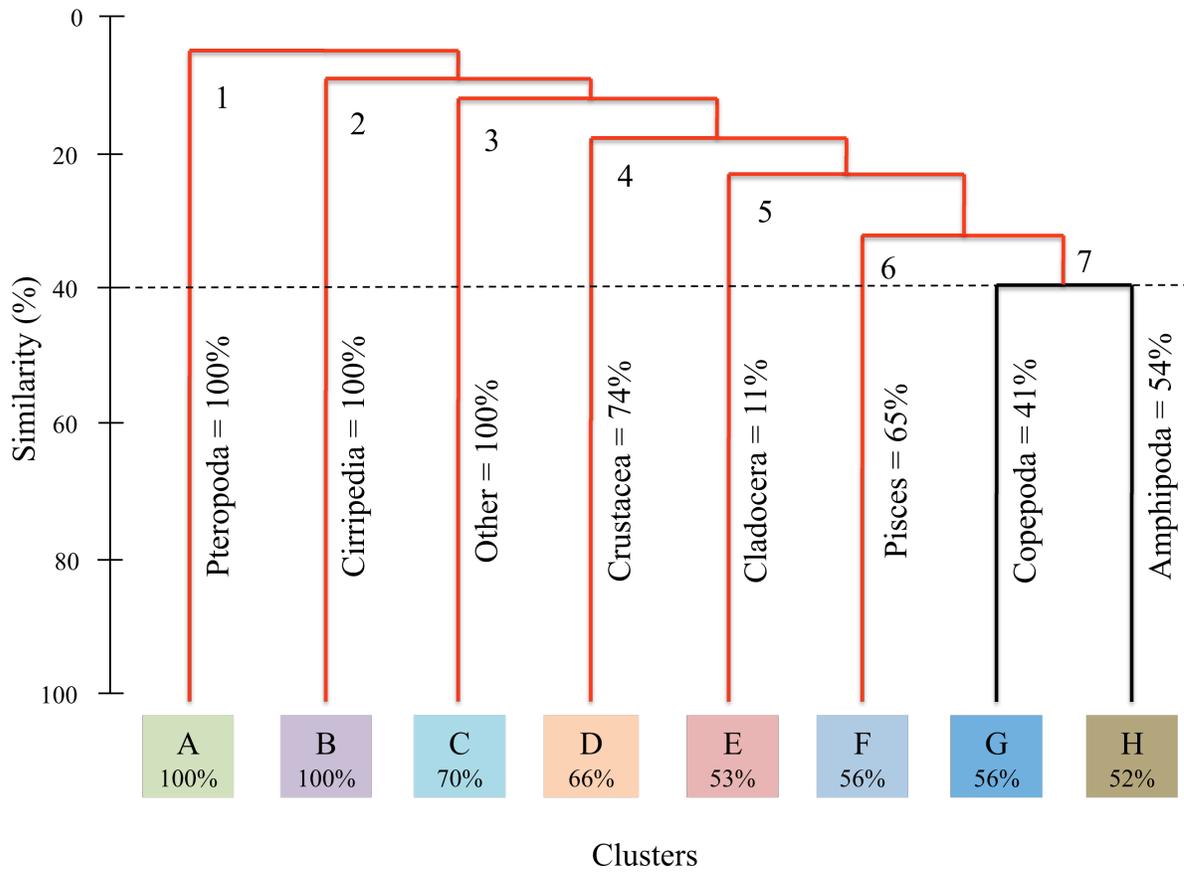


Figure 30: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey biomass found in the diet of sockeye salmon smolts. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance. A and B are outliers with only one fish caught in each set.

Table 12: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD and RBR to diet abundance data between years. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	CTD Contribution (%)	RBR Contribution (%)
	<i>14</i>	
Salinity	(p = 0.001)	4.5
Temperature-Salinity	11	
	<i>9</i>	
Temperature	(p = 0.009)	

Table 13: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD and RBR to diet biomass data between years. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	CTD Contribution (%)	RBR Contribution (%)
	<i>17</i>	<i>14</i>
Salinity	(p = 0.001)	(p = 0.007)
Temperature-Salinity	14	11
	<i>10</i>	
Temperature	(p = 0.005)	

Table 14: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to diet abundance data between years. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
	<i>10</i>
Temperature	(p = 0.01)

Table 15: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to diet biomass data between years. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
	<i>13</i>
Temperature	(p = 0.005)
Temperature-Salinity	11

3.3.7 Cluster analysis of intra-annual abundance and biomass of prey items

Based on prey abundance, diet composition in 2008 formed eight clusters in five significantly different groups (Figure 31). Group 1 (Cluster A; $p = 0.001$) was characterized by Cirripedia, while group 2 (Cluster B; $p = 0.008$) and group 3 (Cluster 3; $p = 0.03$) were distinguished by the “other” category and Pisces, respectively. Bivalvia was an indicator of group 4 (Cluster D; $p = 0.03$), and Amphipoda, Copepoda, Crustacea and Euphausiacea were indicators of group 5 (Clusters E, F, G and H; $p = 0.03$).

Based on prey biomass, the diet composition in 2008 formed seven clusters with only two significantly dissimilar groups (Figure 32). Group 1 was characterized by its low contribution to overall biomass (Cluster A; $p = 0.009$). Identifying taxa of group 2 were Amphipoda, Cirripedia, Copepoda, Crustacea, the “other” category and Pisces (Clusters B, C, D, E, F and G; $p = 0.009$).

BioEnv was run with CTD data only, as the RBR was not used in 2008. Photoperiod, a joint temperature-photoperiod effect, a joint salinity-photoperiod effect, and a joint temperature-salinity-photoperiod effect were responsible for $> 20\%$ of between diet variation in abundance and biomass (Tables 16 and 17). Photoperiod, temperature and discharge were significantly correlated to fish diet variation. A 2-week time lag showed that various joint effects of the four variables contributed to $> 13\%$ of the variation in abundance and biomass between diets, and temperature and salinity were significantly correlated (Tables 18 and 19).

In 2009, prey abundance data formed five clusters in three significantly dissimilar groups (Figure 33). Group 1 was identified by Cirripedia and Cladocera (Clusters A and B' $p = 0.001$). Group 2 was characterized by the “other” category (Cluster Cp = 0.005), and Copepoda and Crustacea characterized Group 3 (Clusters D and E; $p = 0.005$).

Biomass data in 2009 formed four clusters and three significant groupings (Figure 34). The distinguishing taxon of group 1 was the “other” category (Cluster A; $p = 0.01$) and Cirripedia of group 2 (Cluster B; $p = 0.02$). Copepoda and Crustacea were characteristic of group 3 (Clusters C and D; $p = 0.02$).

BioEnv using CTD data showed that photoperiod, a joint temperature-photoperiod effect, and temperature were responsible for $> 15\%$ of the variation in diet abundance (Table 20). In terms of biomass, $> 15\%$ of the variation was correlated to temperature, photoperiod, and a joint temperature-photoperiod effect and temperature-discharge effect (Table 21). RBR data revealed that photoperiod and photoperiod and discharge were responsible for $> 10\%$ of the variation in terms of between diet abundance and biomass, respectively. In terms of abundance and biomass, a 2-week time lag showed various joint effects of environmental variables contributing $> 28\%$ to the variation between fish diets, and temperature and discharge were significantly correlated (Tables 22 and 23). Despite only having an effect with another variable, salinity and photoperiod were also significantly related to the fish diet composition.

In 2010, six clusters based on abundance data formed five significantly dissimilar groups (Figure 35). Group 1 was identified by Pteropoda, Amphipoda and Copepoda (Clusters A, B and C; $p = 0.001$). Cirripedia characterized group 2 (Cluster D; $p = 0.001$), and Crustacea was the distinguishing taxon of group 3 (Cluster E; $p = 0.001$). Group 4 was identified by Bivalvia (Cluster F; $p = 0.003$), and Decapoda characterized group 5 (Cluster G; $p = 0.003$).

In terms of biomass, six clusters formed three significantly different groups in 2010 (Figure 36). Group 1 was identified by Pteropoda (Cluster A; $p = 0.001$). Crustacea was the

indicator taxon in group 2 (Cluster B; $p = 0.004$). Cirripedia, Copepoda, Pisces and Amphipoda characterized group 3 (Clusters C, D, E and F; $p = 0.004$).

BioEnv for CTD data from 2010 showed that a joint temperature-salinity effect and temperature-salinity-discharge effect explained up to 18% of the variation between diet abundance and biomass (Tables 24 and 25). Salinity, a joint salinity-discharge effect, and fluorescence collected by RBR explained up to 39% of the fish diet variation in terms of abundance and biomass. A 2-week time lag showed contributions of $< 4\%$ to between diet variation and there were no significant correlations between the environmental variables and the diet composition for either abundance or biomass (Tables 26 and 27).

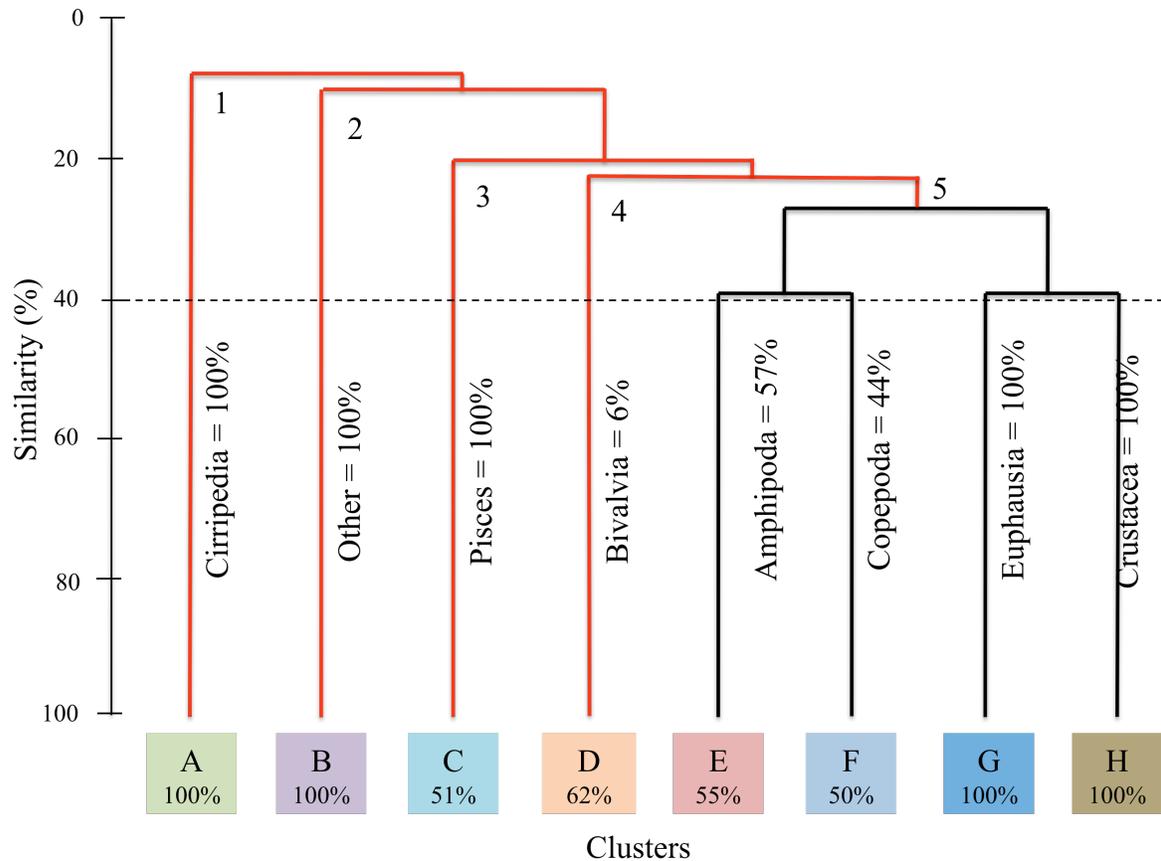


Figure 31: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey abundance found in the diet of sockeye salmon smolts in 2008. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance. A, B, G and H are outliers with only one fish caught in each set.

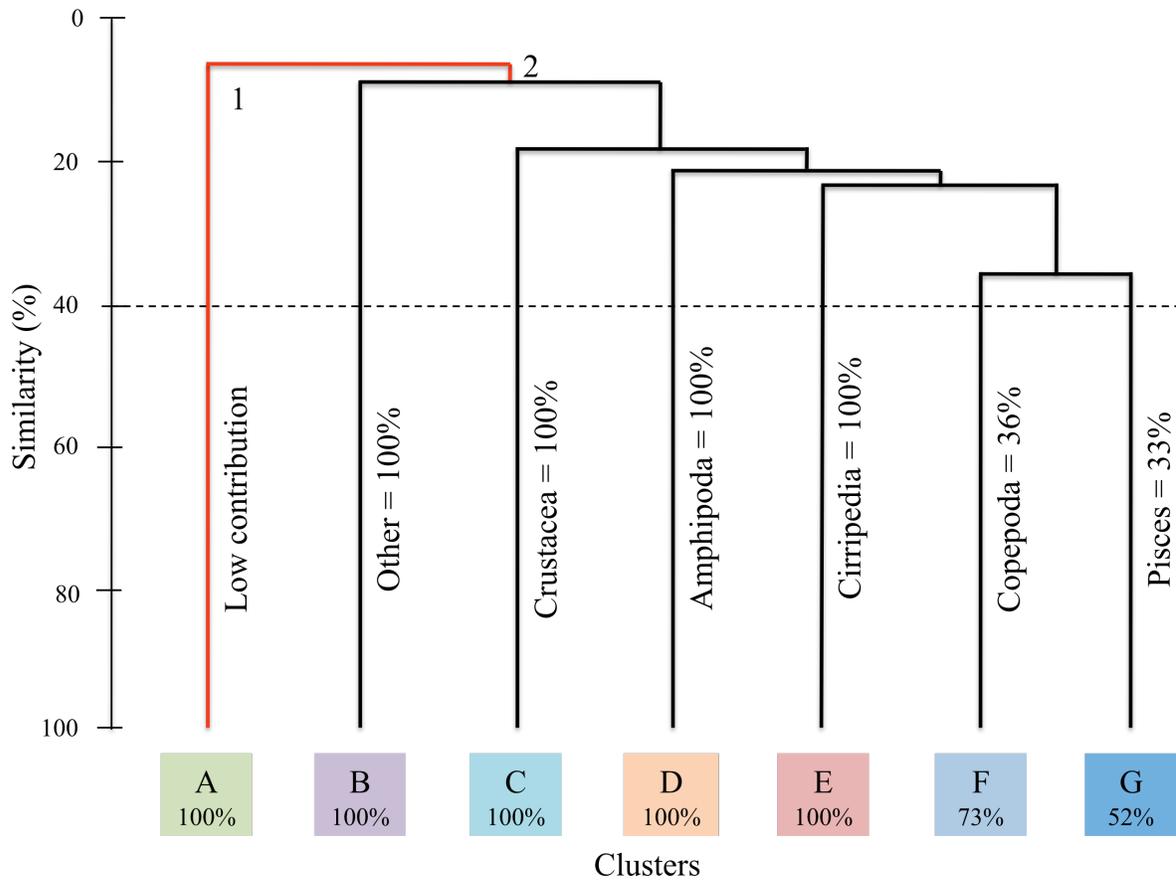


Figure 32: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey biomass found in the diet of sockeye salmon smolts in 2008. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance. A to E are outliers with only one fish caught in each set.

Table 16: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD to 2008 diet abundance data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets. The RBR was not used in 2008.

Variable	Contribution (%)
	25
Photoperiod	(p = 0.001)
Temperature-Photoperiod	25
Salinity-Photoperiod	25
Temperature-Salinity-Photoperiod	25
	24
Temperature	(p = 0.003)
	17
Discharge	(p = 0.002)
Temperature-Discharge	17
Salinity-Discharge	17
Temperature-Salinity-Discharge	17
Discharge-Photoperiod	16

Table 17: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD to 2008 diet biomass data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets. The RBR was not used in 2008.

Variable	Contribution (%)
	20
Photoperiod	(p = 0.009)
Temperature-Photoperiod	20
Salinity-Photoperiod	20
Temperature-Salinity-Photoperiod	20
	15
Temperature	(p = 0.03)
Discharge-Photoperiod	14
Temperature-Discharge-Photoperiod	14
Salinity-Discharge-Photoperiod	14
Temperature-Salinity-Discharge-Photoperiod	14
	11
Discharge	(p = 0.03)

Table 18: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to 2008 diet abundance data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
Temperature-Photoperiod	28
Salinity-Photoperiod	28
Temperature-Salinity-Photoperiod	28
Photoperiod	26
	25
Temperature	(p = 0.008)
Salinity	25
Temperature-Salinity	25
Discharge-Photoperiod	17
Temperature-Discharge-Photoperiod	17
Salinity-Discharge-Photoperiod	17

Table 19: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to 2008 diet biomass data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
	22
Temperature	(p = 0.01)
	22
Salinity	(p = 0.01)
Temperature-Salinity	22
Temperature-Photoperiod	22
Salinity-Photoperiod	22
Temperature-Salinity-Photoperiod	22
Photoperiod	20
Discharge-Photoperiod	13
Temperature-Discharge-Photoperiod	13
Salinity-Discharge-Photoperiod	13

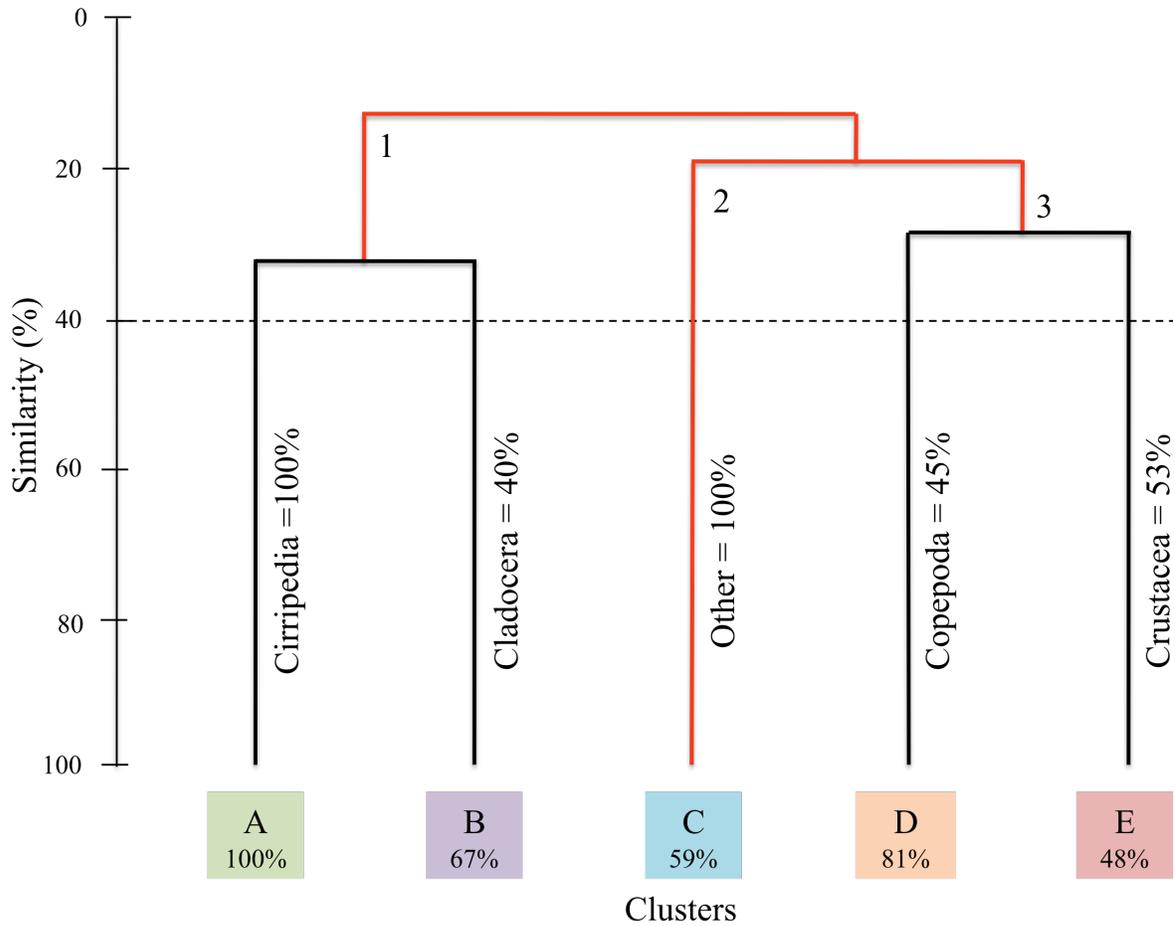


Figure 33: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey abundance found in the diet of sockeye salmon smolts in 2009. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance. A is an outlier with only one fish caught in the set.

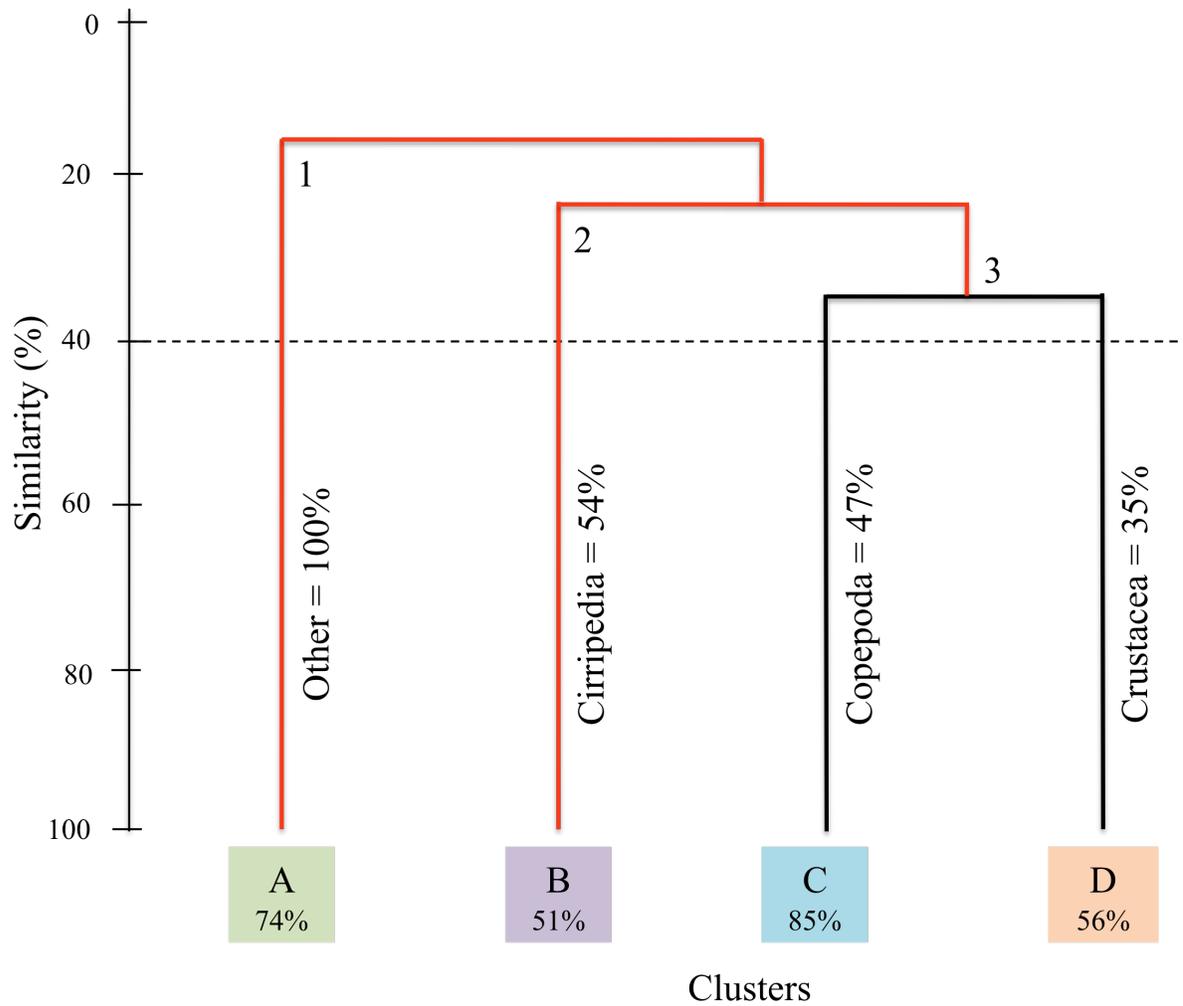


Figure 34: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey biomass found in the diet of sockeye salmon smolts in 2009. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance.

Table 20: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD and RBR to 2009 diet abundance data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	CTD Contribution (%)	RBR Contribution (%)
	<i>17</i>	<i>17</i>
Photoperiod	(p = 0.02)	(p = 0.009)
Temperature-Photoperiod	17	
	<i>15</i>	
Temperature	(p = 0.01)	
Temperature-Discharge	12	

Table 21: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD and RBR to 2009 diet biomass data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	CTD Contribution (%)	RBR Contribution (%)
	<i>15</i>	
Temperature	(p = 0.02)	
	<i>15</i>	<i>15</i>
Photoperiod	(p = 0.03)	(p = 0.02)
Temperature-Photoperiod	15	
Temperature-Discharge	15	
	<i>11</i>	<i>11</i>
Discharge	(p = 0.05)	(p = 0.04)

Table 22: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to 2009 diet abundance data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
Salinity-Discharge-Photoperiod	31
Temperature-Salinity-Discharge-Photoperiod	31
Salinity-Photoperiod	31
Temperature-Salinity-Photoperiod	31
	29
Discharge	(p = 0.003)
Salinity-Discharge	29
Temperature-Salinity-Discharge	29
Temperature-Discharge	29
	29
Temperature	(p = 0.001)
Discharge-Photoperiod	29
Salinity	(p = 0.01)
Photoperiod	(p = 0.01)

Table 23: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to 2009 diet biomass data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
Salinity-Discharge-Photoperiod	33
Temperature-Salinity-Discharge-Photoperiod	33
Salinity-Photoperiod	33
Temperature-Salinity-Photoperiod	33
Salinity-Discharge	32
Temperature-Salinity-Discharge	32
	31
Temperature	(p = 0.001)
	30
Discharge	(p = 0.001)
Temperature-Discharge	30
Discharge-Photoperiod	28
Salinity	(p = 0.004)
Photoperiod	p = (0.02)

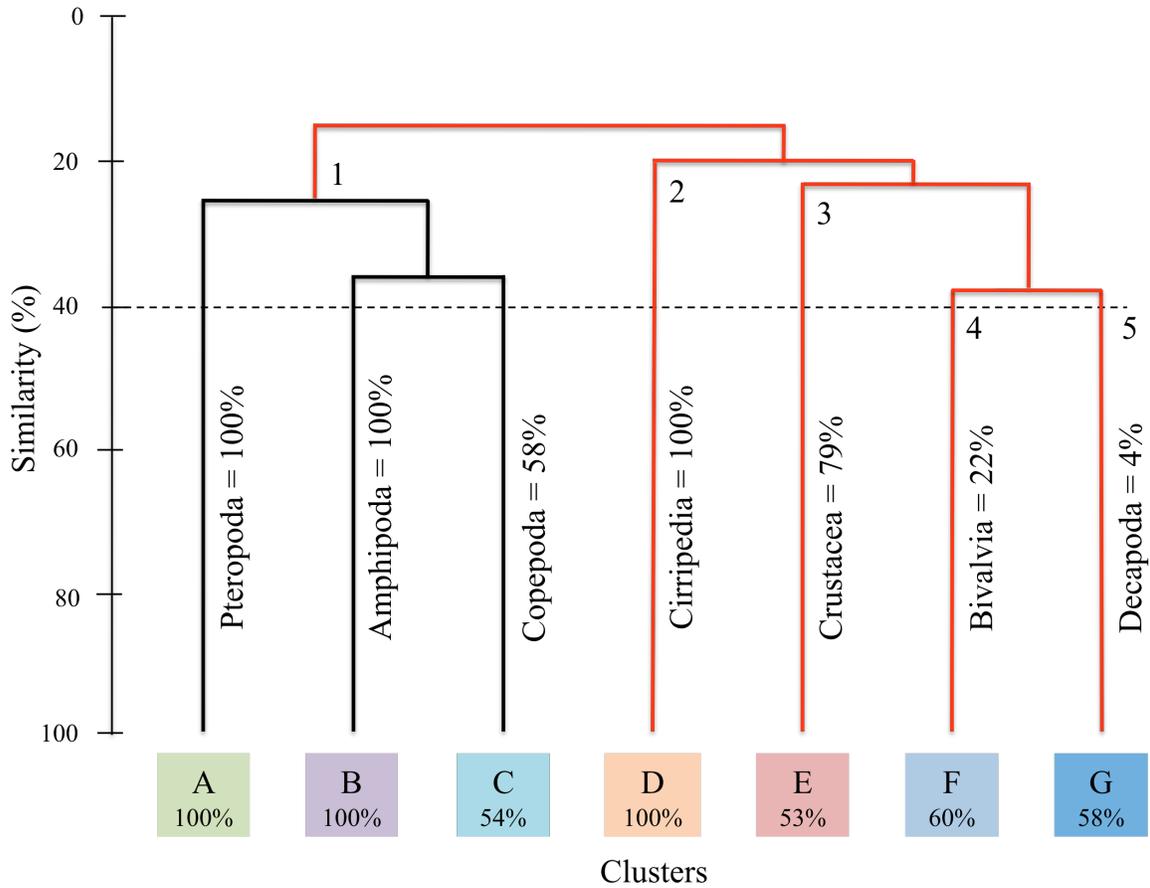


Figure 35: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey abundance found in the diet of sockeye salmon smolts in 2010. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance. A, B and D are outliers with only one fish caught in each set.

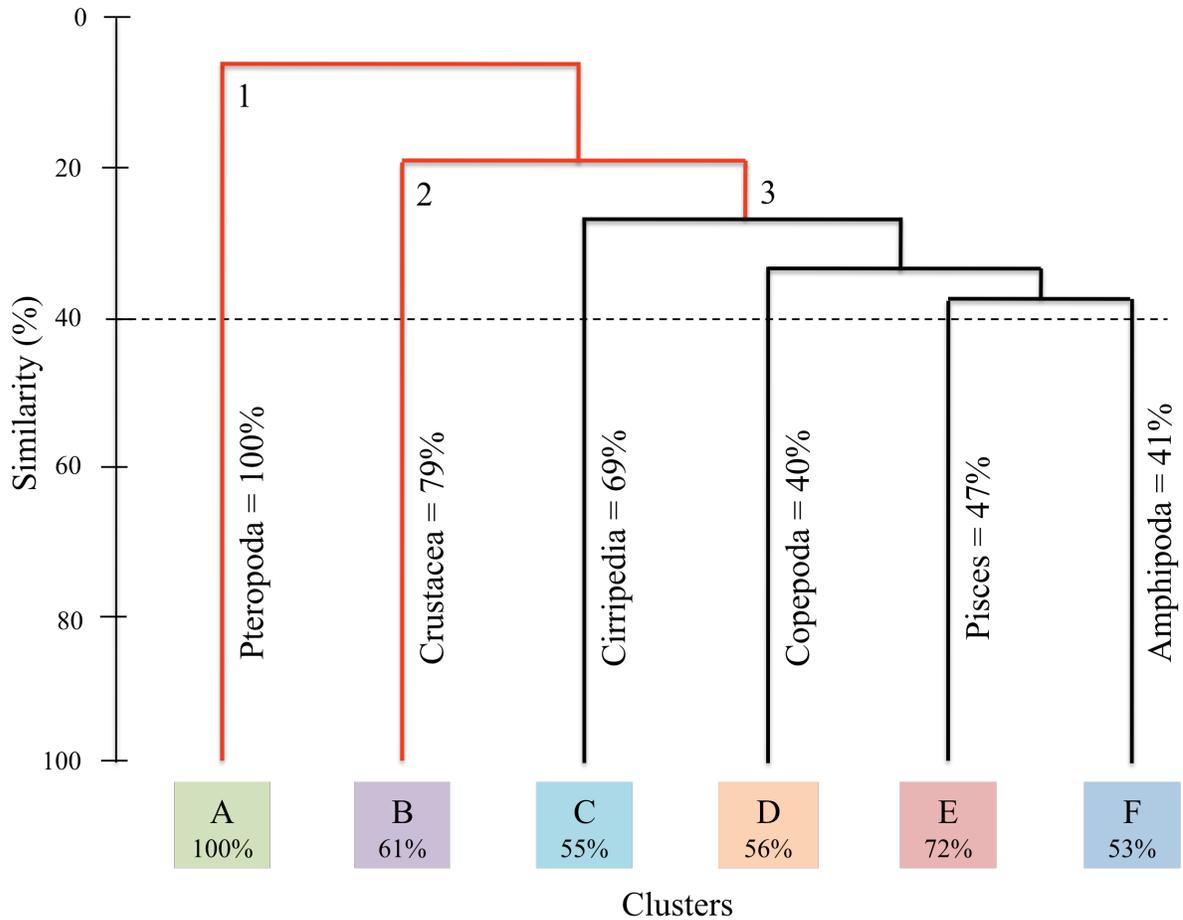


Figure 36: Hierarchical cluster based on group-average sorting of a Bray Curtis similarity matrix of prey biomass found in the diet of sockeye salmon smolts in 2010. The Y-axis indicates similarity between clusters, and the X-axis shows the clusters formed. The percentages below each letter represent the similarity within that cluster. Taxa listed are the indicator species that contributed the given percent to the total similarity within a cluster. Red lines indicate clusters identified as significantly dissimilar at the 5% significance level using a SimProf test, and the corresponding numbers represent groupings of clusters based on this significance. A is an outlier with only one fish caught in the set.

Table 24: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD and RBR to 2010 diet abundance data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect between the parameters listed. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Abundance Variable	CTD Contribution (%)	RBR Contribution (%)
		39
Fluorescence		(p = 0.04)
Temperature-Salinity	18	
Temperature-Salinity-Discharge	18	
	17	
Salinity	(p = 0.01)	13
Salinity-Discharge	17	13
Salinity-Photoperiod		11
Salinity-Discharge-Photoperiod		11

Table 25: Results of the BioEnv and RELATE comparing environmental parameters collected by CTD and RBR to 2010 diet biomass data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect between the parameters listed. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Biomass Variable	CTD Contribution (%)	RBR Contribution (%)
		36
Fluorescence		(p = 0.05)
Temperature-Salinity	17	14
Temperature-Salinity-Discharge	17	14
	17	20
Salinity	(p = 0.01)	(p = 0.02)
Salinity-Discharge	17	19
Salinity-Photoperiod		10

Table 26: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to 2010 diet abundance data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
Temperature	0.1

Table 27: Results of the BioEnv and RELATE using a 2-week time lag to compare environmental parameters collected by CTD to 2010 diet biomass data. Contribution (%) is the amount that the variable contributes to the variation between fish diets. Variable names linked by a hyphen represent a joint effect. Bold and italicized numbers are significantly correlated, with their associated p-value listed below % contribution in brackets.

Variable	Contribution (%)
Salinity-Photoperiod	4
Temperature-Salinity-Discharge-Photoperiod	4
Temperature-Salinity-Photoperiod	4
Temperature-Photoperiod	4
Temperature	3

3.4 Discussion

Sockeye smolts in Rivers Inlet, British Columbia were exposed to a diverse zooplankton prey field, here classified into thirteen main taxa. Inter-annual diet composition of the smolts varied substantially. Cluster analyses revealed that copepods were the only prey items that consistently contributed to similarities in prey abundance and biomass in the stomachs in all three years. In addition to copepods, in terms of abundance, amphipods, bivalves, and fish contributed the most to the similarities in 2008 diets. These were different from the 2009 samples, in which cladocerans, crustaceans and items in the “other” category contributed the most to similarities. In 2010, bivalves, crustaceans and decapods contributed the most to the similarities in the diets. In terms of biomass, fish contributed the most to the similarity in the 2008 diets. In 2009, Cirripedia, copepods, crustaceans, and the “other” category contributed the most to the similarity, while in 2010 amphipods, Cirripedia, copepods, crustaceans, and fish were responsible for the majority of similarity in diet composition.

The sockeye smolts selectively fed on this diverse array of zooplankton with varying intensity. In the 2008, 2009, and 2010 sampling seasons, they preferentially fed on amphipods, Cirripedia, decapods and fish. In years when they were abundant (2009 and 2010), the smolts also intently foraged for cladocerans. Previous diet studies in Rivers Inlet showed that the sockeye salmon smolts were feeding on small, neustonic species (Buchanan 2006). Buchanan (2006) only examined the cardiac portion of the stomach, and found that Bivalvia were the most numerous prey taxon, along with *Oikopleura*, *Evadne* and *Calanus* spp. Amphipoda and Euphausiacea only comprised 2.2-2.6% of the diet by abundance, but were the most energetically efficient in terms of energy expended for capture versus energy

derived from the prey (Buchanan 2006). As in the 2008, 2009, and 2010 sampling seasons, Buchanan (2006) found very few of these species in the zooplankton samples. No *Oikopleura* were present in the 2008, 2009, and 2010 stomachs. Several other studies also indicated that sockeye smolts preyed upon amphipods, Cirripedia, decapods and fish. However, in these studies, copepods were found to be the primary food items for sockeye salmon smolts (e.g. Straty and Jaenicke 1980, Healey 1982, Simenstad et al. 1982, Beamish et al. 2003).

Simenstad et al. (1982) proposed that inter-annual variations in diet composition could be attributed to inter-annual variability in the zooplankton community structure and a subsequent switch to a more energetically efficient foraging base. In the absence of preferred prey species, sockeye smolts would need to switch to an alternative food source to avoid starvation (Straty and Jaenicke 1980, Brodeur 1990). In Rivers Inlet, zooplankton abundance in 2008 was higher over the entire water column than in 2009 and 2010; however, zooplankton were in fact more abundant in the surface (0-10 m) in 2010 than in 2008. It is hypothesized that smolts reside within the surface freshwater layer, where salinities gradually increase with movement out of the inlet, allowing the recent outmigrants to physiologically adjust to areas of higher salinities. Preliminary experiments show that, when confined to a 0–6 m net, the majority of the smolts remain at around 4 m depth (Gerbrandt personal communication). However, the possibility that smolts are seeking out areas of neutral buoyancy when stressed cannot be ruled out as a factor in these experiments. If smolts reside within this freshwater surface layer, the greater variety in the diet composition in 2008 may be driven by the low prey availability in the top 10 m of the water column. Smolts would then need to exploit a wider range of prey taxa to meet their metabolic demands.

Despite the higher abundances and biomass of zooplankton in the 2010 surface tows, the community was largely dominated by copepods and pteropods, which, according to selectivity indexes, were not preferred prey items. Copepods in particular were also found in high concentrations throughout the entire water column, and were well represented in the diet composition. This apparent negative preference for copepods in general may actually represent positive selection for certain species of copepods (e.g. *Calanus marshallae*, *Metridia pacifica* and *Neocalanus plumchrus*), as results indicated that they did avoid the majority of the prey resources afforded to them by the larger copepod population. Preferences for certain prey items were examined on the level of taxon, in which the species of copepods, for example, that were present in the diets of the smolts were pooled and compared to all the species of copepods present in the zooplankton community. Selectivity preference may have changed for certain species of copepods if compared to the abundances of a specific species. In addition, selectivity indexes showed the preference of smolts for certain prey items assuming that every prey item present at any given time persisted in the water column throughout the entire season. The smolts would have unlimited access to a highly diverse foraging base and could select for optimal prey items. Since selectivity indexes show only inter-annual differences in seasonality of the zooplankton foraging base, they do not reflect changes in prey preference within a season, and may miss the finer details of the smolts' foraging behavior under conditions of dynamic prey composition. Another caveat of the selectivity indexes lies in the vertical distribution of the smolts. Since it currently remains unknown where they reside, their assumed vertical distribution is 30 m, the depth of the seine net. If this is true, selectivity indexes do not represent the true prey preferences of the smolts, as the zooplankton community within the upper 30 m of the water

column was not investigated in this study. However, the feeding behavior of the smolts in Rivers Inlet is also not known, and it may be that they undergo rapid feeding trips into another depth range before returning to an area of optimal environmental conditions (e.g. temperature and salinity), again highlighting the uncertainty in the prey resources available to the foraging smolts.

Selection for copepods, or any taxon, may be relative to the abundance of other taxa present in a similar spatial and temporal orientation. Intra-annual cluster analyses reflect a changing diet composition over time and space, representing the community of prey items available to the smolts within their vertical distribution. Support for the hypothesis that selectivity indexes miss the seasonality of the zooplankton community is evident in the fact that clusters in each sampling year were defined by similarities in copepod feeding. This may indicate a preference for copepods over other available prey items, or the persistence of copepods despite other seasonal changes in the foraging base. Copepods may also be more energetically beneficial to smolts, in terms of calories gained versus energy expended for capture. Also, while other prey items may be advected more quickly out of the inlet due to low surface freshwater residence times, those that undergo diel vertical migrations may have higher retention rates, as they are exposed to surface currents for a reduced period of time. If they were retained for longer in the inlet, smolts would encounter them at higher frequencies than other prey items that are rapidly advected of the inlet.

Size, behavior and caloric content of prey items may also drive the seasonal variation in diet composition, as smolts may respond to the changes in the energy benefits derived from their prey by altering their feeding behavior to exploit resources that will maximize their growth and function (Eggers 1980, Healey 1980, Straty and Jaenicke 1980, Pearcy

1992). In addition to copepods, cladocerans and bivalves composed a majority of the abundance of prey items in the diets in 2009 and 2010. Despite their presence in the diets, cladocerans and bivalves did not make a large impact on biomass; however, their numerical contribution indicated an abundance of cladocerans and bivalves in the water column at some point during the sampling season in 2009 and 2010, suggesting that these species may be highly seasonal and temporally variable. The contribution of cladocerans to group similarity in 2009 and bivalves in 2010 suggests they persisted in the inlet for a longer time period in these respective years. Cirripedia contributed to a majority of the abundance and biomass of the diets in 2009 and 2010. This indicated a high abundance and the potential to derive good energy benefits. In contrast, fish were not present in high abundances in any year, but did substantially contribute to the biomass of diets in 2008. Their low contribution to biomass in 2009 and 2010 may have been due to the presence of different species or different growth patterns of the larvae. While fluctuations in abundance and biomass did have an impact on the concentrations of food available to the smolts, it did not deter preferential feeding for certain items. For example, Cirripedia were the most abundant in diets in 2010, even though their relative abundance in the water column from 0-300 m was comparable to the abundances in 2008 and 2009. However, in surface zooplankton samples, Cirripedia were more abundant in 2008 than in 2010. Their lower abundances in the surface in 2010 did not cause the smolts to feed more intensely on alternative prey. The greater variety of prey items in the 2008 diet composition may be a consequence of reduced availability of zooplankton associated with the top 10 m of the water column and a subsequent switch to a more opportunistic foraging pattern, supporting the theory of Straty and Jaenicke (1980),

Simenstad et al. (1982) and Brodeur (1990), and highlighting the importance of the surface zooplankton community.

Foraging success is largely dependent on the abundance and biomass of the zooplankton community at the time of estuarine migration. Carlson (1976), Straty and Jaenicke (1980) and Perry et al. (1996) hypothesized that low prey levels coincided with food limitation, reduced growth potential, and a shorter estuarine migration time. In Rivers Inlet, estuarine migration time was calculated to be between one and three weeks. Differences in growth rates over this time may be an artifact of an altered estuarine residence time based on the quality and quantity of the prey community and environmental conditions. For example, in years with less prey available, smolts may spend less time in the inlet to reach more profitable feeding grounds over the continental shelf. In years of high prey abundance, their migration time may be slower, so as to exploit the prey resources available in the more protected waters of the inlet. In 2008, the apparent slower growth could simply be a faster migration time in response to reduced zooplankton abundance in the surface layer, faster advection of the smolts out of the inlet during periods of high river discharge, or suboptimal variations in temperature and salinity. It is possible that they traveled more quickly to the coastal waters of the Queen Charlotte Sound in response to poor feeding conditions. In contrast, the faster growth in 2010 could have been due to a longer estuarine migration time, in which the smolts exploited zooplankton resources and grew to larger sizes than in previous years, despite a foraging base dominated by negatively selected prey. Their longer estuarine migration time may have coincided with a change in the zooplankton community, in quality or quantity (e.g. an increase in biomass as the zooplankton grow or an increase in abundance

of more preferred prey items). However, these spatial and temporal aspects were not examined in relation to diet composition.

Variations in prey abundance, biomass and composition may also affect the route of the smolts as they migrate through the estuary (Hartt 1980, Eggers 1980, Pearcy 1992, Farley Jr. et al. 2005). In this study, seasonal sampling was designed to cover all potential exit routes from the estuary into the Queen Charlotte Sound or Fitz Hugh Sound. In 2008, more smolts were captured in the main channel after the fork with the Darby Channel than within the Darby Channel, especially earlier in the sampling season. An opposite trend was seen in 2009 and 2010. Diets in 2008 were also characterized by a wider range of prey taxa, most notably a higher biomass contribution of fish larvae. The differences in the diet composition may be related to the greater use of the main channel by 2008 smolts. However, there were no spatial or temporal differences in the diets of smolts caught in the Darby Channel or in the main channel after the fork with the Darby Channel. Therefore, it is unknown as to why the smolts may have altered their migration route, but it is hypothesized that they follow the temperature, salinity and foraging conditions (abundance of food available) to which they are most acclimatized during years of suboptimal environmental conditions (Straty and Jaenicke 1980, Hartt 1980, Eggers 1980, Pearcy 1992). Perhaps the smolts were changing their migration route in response to environmental variables or concentrations of zooplankton found in certain areas of the inlet, studies of surface zooplankton composition as well as localized temperature and salinity regimes would need to be conducted in order to find more conclusive evidence for this phenomenon. An examination of the effects of environmental changes on the zooplankton community and their indirect effects on the sockeye population

would also be an asset to explore the caveats of diet composition under changing climate conditions.

Environmental variables may also explain the differences in the diet composition of the smolts. BioEnv conducted with and without a 2-week time lag indicated that temperature and salinity had the biggest impact on the inter-annual similarity of the stomach composition of the sockeye salmon smolts. Temperatures integrated over 30 m remained below 10°C in all three years. Integrated salinity averaged around 30 in all years. Intra-annually, temperature, salinity, photoperiod and river discharge were significantly correlated to the diet groupings in 2008 and 2009. Discharge during the smolts' migration averaged 414 m³s⁻¹, 454 m³s⁻¹, and 377 m³s⁻¹ in 2008, 2009, and 2010, respectively, and photoperiod was ~16 hours a day. These higher discharge values in 2008 could contribute to the reduced prey availability in the surface layer in 2008, as well as the slower growth in 2008 and 2009 when compared to 2010. In 2010, salinity and fluorescence were the only statistically significant variables responsible for diet groupings, and no significant correlations were found with a 2-week time lag. Fluorescence data from the RBR (measured as a proxy for chlorophyll *a*) was responsible for > 30% of the variation in prey abundance and biomass in 2010, and is a known factor controlling the timing of the spring zooplankton bloom (Wolfe 2010). Since data gaps exist throughout the season, it is difficult to determine the actual influence it exerts over the cluster formation of the diets. A more accurate comparison would determine the effects that peaks in fluorescence have on the control of the timing of the zooplankton bloom and its community structure and biomass. The results of the BioEnv still leave > 60% of the diet variation unexplained. The environmental factors responsible for the diet groupings are controlled by climate forcing that may show local variation on an inter-annual basis,

affecting plankton (bottom-up) dynamics within the Rivers Inlet system (Wolfe 2010, Hodal 2011). Changes to these parameters may affect the timing of spring production, in turn affecting the timing of the zooplankton bloom and its composition, and potentially the quality of the prey available in the inlet for outmigrating smolts (Wolfe 2010, Tommasi et al. in press). Alterations to the abundance, biomass, or composition of the bloom, through, for example, warmer waters, high advective transport, or a mismatch in the timing of productivity and the smolts' migration, would influence the diet composition and feeding behavior of smolts and could account for the inter-annual differences in diet composition seen in Rivers Inlet in 2008, 2009, and 2010 (Cushing 1990, Wolfe 2010, Hodal 2011).

In order to further the understanding of the feeding ecology of sockeye smolts during their period of estuarine residence immediately after marine entry, future studies should determine the vertical distribution of smolts, allowing for a match with the zooplankton sampling to better reflect prey availability in the smolts' current feeding habitat. Feeding experiments may be useful to further the understanding of feeding dynamics of sockeye smolts, including their preferred prey species and alternate prey species chosen by the smolts under varying environmental conditions. Biomass and caloric content estimates for prey quality should be considered to determine the energy benefits of pursuing certain prey items. These should be compared to physiological regulations of sockeye salmon smolts to determine the energetic efficiency of optimal and opportunistic foraging behaviors during the outmigration period of their early life history.

In conclusion, the diet composition of the sockeye smolts was highly variable within and between years. No spatial or temporal trends in diet composition were found. Zooplankton abundance and biomass from 0-300 m was the highest in 2008. Within the top

10 m layer, however, the highest zooplankton concentrations were observed in 2010. Despite the smolts' apparent negative preference for copepods, they contributed largely to the diet, and cluster analyses revealed that copepods were responsible for most of the similarity between diets in each sampling season. Therefore, selectivity indexes do not reflect the seasonality of the zooplankton community and smolts may be feeding within a certain part of the water column that is not reflected in these indexes. Finally, although environmental variables (temperature, salinity, photoperiod and river discharge rates) accounted for up to 40% of the seasonality in the diets, > 60% of this variation remains unexplained.

Chapter 4: Conclusion

4.1 Bottom-up control on the growth of sockeye smolts

The growth of sockeye salmon smolts in Rivers Inlet, British Columbia varied substantially between the years 2008, 2009, and 2010. Growth was calculated in terms of specific growth rates (% of body length per day; % of body wet weight per day) based on a 14-day estuarine migration time. Smolts from 2010 were significantly heavier per unit length, appeared to grow faster and to be in better condition than those from 2008 and 2009. Mass gain per unit length was similar in 2008 and 2009, and growth appeared to be the slowest in 2008. New entrants into the estuary in all three seasons began with a “fair” condition index when caught near the Wannock River. These smolts had a slightly higher average “fair” condition factor than those seen in Owikeno Lake fry from 1959-1966, supporting the hypothesis that long-term changes have most likely occurred in the marine phase of their life cycle (Wood 1970, McKinnell et al. 1998). In 2008 and 2009, the smolts maintained this condition throughout the season. In 2010, their condition index increased to an average “good” condition. Smolts need to gain a critical size during their early marine life (just after marine entry) in order to maintain the metabolic demands of the first marine winter (Beamish and Mahnken 2001). The inability to attain the energy reserves required to survive the winter is associated with a lower condition index and an increased susceptibility to predators (Beamish and Mahnken 2001). It appears that smolts in 2010 utilized the inlet more extensively to grow and obtain a better condition before migrating to the coastal shelf waters. Establishing a performance index to compare the condition, fitness and health of smolts

would be beneficial to studies of the early life history phases of salmonids within and across systems (Hayden and Pinnix 2010).

Diet composition was highly variable on an inter-annual and intra-annual basis. The diets in 2009 and 2010 were more similar to each other than to 2008, when smolts had the most diverse diet composition. Despite this, the growth and condition in 2009 was more similar to that of 2008. BioEnv revealed that up to 40% of this variation was related to temperature, salinity, photoperiod, river discharge rates, or a joint effect of these variables. This leaves at least 60% of the variation in diet composition unexplained. One crucial aspect to the smolts' growth and survival during this critical early marine period is the match between zooplankton availability (quality and quantity) and the presence of outmigrating smolts in the inlet. The match-mismatch hypothesis of Cushing (1990) states that when fish enter the inlet during the period of prime prey productivity, it ensures their maximum exploitation of the foraging base. This theory has been expanded to include a match or mismatch between the gape width of predators (smolts) and the size of their prey (Fortier 1995, Duffy 2009). Populations have adapted their spawning times to reduce the possibility of a mismatch in timing between the migration of larvae or juveniles and peaks in prey abundance (Crozier et al. 2007). Environmental factors have been known to delay or expedite the initiation of spring production in Rivers Inlet, creating an increased potential for migrating juveniles to miss the peak in density and possibly experience altered community composition of their zooplankton prey (Cushing 1990, Wolfe 2010, Tommasi et al. in press). The combination of changes in spring productivity and the estuarine migration time of the smolts may account for the inter-annual variations in growth and condition. There is an indication that the timing of the zooplankton bloom is affected by the onset of the spring

phytoplankton bloom (Tommasi et al. in press). In 2008, the phytoplankton bloom occurred on 3-April. In 2009, this was delayed to 18-April, and in 2010 the bloom began on the 10-March (Wolfe 2010). The zooplankton bloom from April through June peaks (26-May 2008; 4-May 2009; 19-May 2010) after the peak in phytoplankton, and should correspond to the peak in fish migration (Cushing 1990). Smolts were first observed in the estuary in early May in 2008 and late-May in 2009 and 2010 (Figure 37). Their migration overlapped with peak zooplankton abundances (from 0-300 m and 0-10 m) in 2008 and 2010 (a match); however, in 2009 their migration occurred after an early peak in zooplankton abundance (a mismatch).

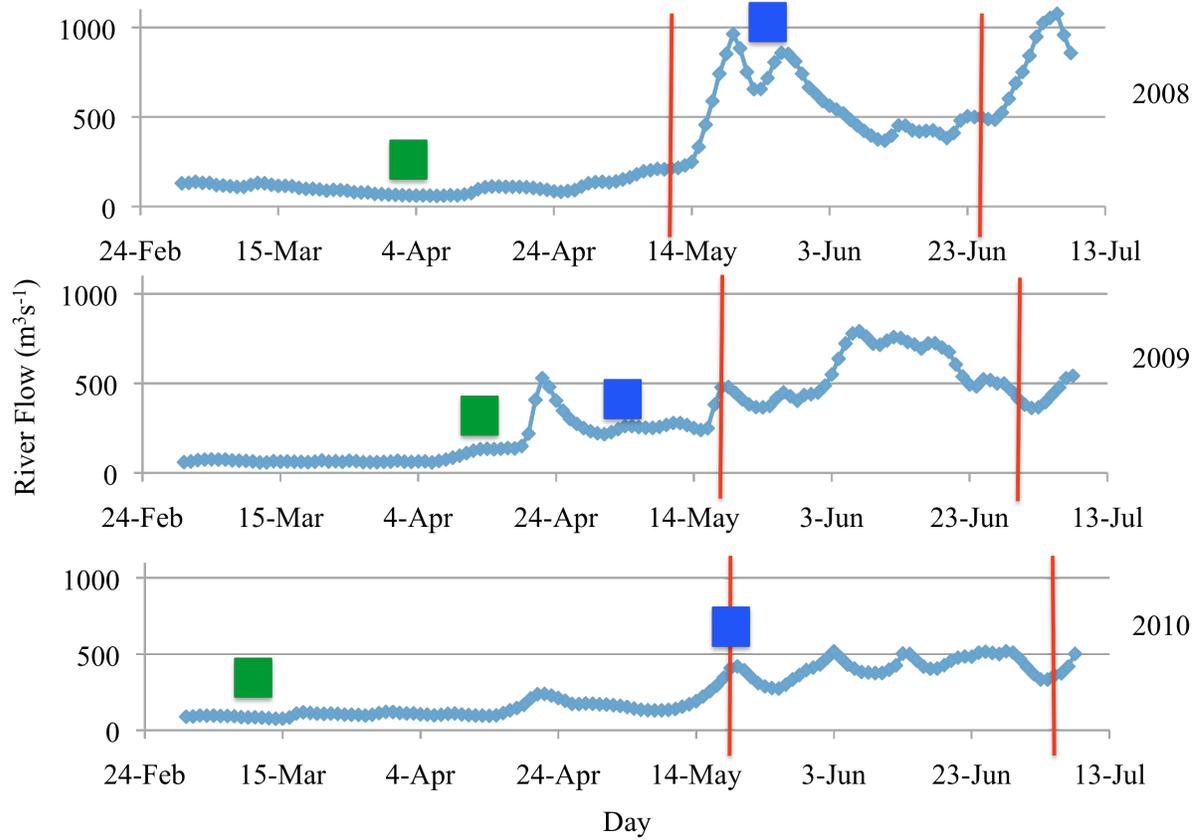


Figure 37: Daily river flow ($\text{m}^3 \text{s}^{-1}$) from March-July in 2008, 2009 and 2010. Green boxes indicate the initiation of the spring phytoplankton bloom. Blue boxes show the peak in zooplankton abundance (ind. m^{-3}) from 0-300 m and 0-10 m. Red lines indicate the presence of the smolts in the inlet during the sampling season.

The migration time of the smolts may vary on an inter-annual or intra-annual basis, depending on prey availability and environmental conditions. Previously, migration times in Rivers Inlet were qualitatively estimated to be 2 weeks (Buchanan 2006). Using travel rates from Wood et al. (1993), Peterman et al. (1994), and Welch et al. (2011), new estimates of migration times were determined to be between 7 and 21 days (1 – 3 weeks). Migration time was also calculated using potential growth rates derived from daily ration. Estimates taken from 24-hour stations conducted in 2008 and 2009 indicate that on average sockeye salmon smolts in Rivers Inlet consume 4.2-4.4% of body wet weight per day (E. A. Pakhomov unpublished data). While 2010 did not have a 24-hour station, the mean daytime gut fullness indices were not significantly different from the other two years (2008 = 2.62%; 2009 = 2.84%; 2010 = 2.48%). Therefore, one can assume the 2010 daily ration over 24-hours could be comparable to that of 2008 and 2009. Interestingly, 2010 had the lowest mean value, possibly indicating the availability of better quality prey items (e.g. higher energy, more caloric content), which could reduce the required daily ration. Assuming 2/3 of the daily ration goes to maintenance metabolism, than 1.43% WW/day can be allocated towards growth. With this amount of energy going towards growth, smolts in 2008, 2009, and 2010 would need to spend 19, 27 and 40 days, respectively, in the inlet to account for the change in the fish mass observed in this study. These values may not be accurate because they assume conditions such as prey availability, temperature, and advection rates are the same between years and that daily ration is constant over the entire season, but they do highlight the importance of the smolts' migration time through the inlet to their growth and condition.

Brett (1976) found that growth and survival of smolts was indirectly related to changes in environmental variables through alterations in migration pathways, distribution,

and metabolic function / energy allocation. He proposed that effects of these changes on the zooplankton community indirectly affected the salmon population through changes in the prey available and the energy provided to the smolts (Brett 1976). Farley Jr. and Trudel (2009) supported these findings with their model of the distribution of smolts during warmer and cooler years off the Bering Sea shelf. They found that a 20% change in temperature or prey density altered the distribution and subsequent growth of the sockeye smolts by 8-98% (Farley Jr. and Trudel 2009). In particular, changes in temperature will affect the metabolism and swimming speed of sockeye smolts (Brett 1967, Brett 1976). Sockeye smolts can tolerate temperatures between $\sim 5^{\circ}\text{C}$ and 24°C (Pauley 1989, Brett 1967). At the extremes of this range, smolts exhibit slower growth or cessation of growth, reduced swimming speeds, and, in the case of warmer waters, increased metabolic rate and inefficiency in food processing (Brett 1967). These physiological rates determine the effect of prey availability on the smolts' growth (Brett 1967). In Rivers Inlet, integrated and averaged 30 m temperatures at DFO2 were less than 10°C in all years for the entire sampling season. This is on the lower end of tolerated temperatures, and may slow the growth of smolts. However, integrated 5m temperatures showed higher values in 2010 than in 2009 and 2008, reaching $\sim 13^{\circ}\text{C}$ at some locations, very close to the 15°C optimum temperature for the swimming and growth of sockeye smolts (Brett 1967). While the smolts' metabolic activities function better in near optimal conditions, the zooplankton community composition may be suboptimal, as warmer waters tend to favor smaller zooplankton that may not be as beneficial to the smolts in terms of energy derived. The smolts may also have osmoregulatory problems, as the majority of the population migrates after a one-year residence in the nursery lake, which, due to its low productivity, produces smaller fry compared to other systems (McKinnell et al. 1998,

McKinnell et al. 2001). These smolts may consequentially be poorly adapted for the transition from freshwater to marine conditions. Monitoring Na^+/K^- activity in the gills would determine if the smolts osmoregulate properly and the affects this process has on their vitality (Hinch personal communication).

It has also been shown that smolts follow temperature, salinity and prey gradients that provide more optimal conditions for growth and survival (Healey 1980, Farley Jr. et al. 2005). This should not be dismissed as an effect on the smolts' migration time, distribution and growth in Rivers Inlet, and should be examined on a finer spatial scale within the vertical distribution range of the smolts. Since temperature, salinity and photoperiod remain relatively constant in Rivers Inlet between years, river flow rates coupled with spring productivity may account for the differences in the smolts' growth. The length of the smolts' estuarine migration could be related to the surface water residence time (volume of the freshet) in three ways: 1) rapid flow rates may advect the smolts out of the inlet, 2) the zooplankton community may be advected out of the inlet, reducing prey resources available to the smolts, to which they may respond by favoring a faster estuarine migration to reach potentially more profitable feeding grounds, or 3) a combination of these effects. Surface water (0-10 m) residence time averaged 7 days during high flow events and 15 days during low flow events (Hodal 2011). In 2008, river flow increased dramatically in mid-May and lasted for about 2 weeks. These high flow rates coincided with the first observed presence of smolts in the inlet, and decreased approximately halfway through their migration. The opposite trend occurred in 2009, with flow rates remaining relatively low until early June, when they increased rapidly, again approximately halfway through the smolts' migration. The change in river flow rates in 2008 and 2009 may cause a change in migration time

midway through the season, suggesting that different cohorts of outmigrating smolts from the same population face different conditions and hence different growth and survival patterns. In 2010, river flow rates were steady and low throughout the duration of the smolts' migration.

Despite the match in timing between the migration of the smolts and peak zooplankton abundance, the 2008 smolts grew the slowest of the three years. Since the smolts migrated during a period of high river discharge, they could have been advected out of the inlet more quickly and consequentially at a smaller size and in poorer condition. Depending on the direction of the river flow, this could also be the reason behind the higher proportion of smolts exiting via the main channel as opposed to the Darby Channel, especially in the early seining surveys, when river flow rates were the highest (Figure 37). Therefore, despite a match of peak zooplankton densities overlapping with the timing of the smolts' outmigration in 2008, the high river flow rates likely created conditions of shorter migration (or residence) times of the smolts. In 2009, the low river flow rates at the beginning of the season would not have advected the smolts out of the inlet as quickly as in 2008, allowing them to forage and grow to a larger size before the onset of the freshet. This would present as faster growth rates when compared to 2008; however, the mismatch in timing of summer productivity and the smolts' migration was likely the cause of reduced fish growth and condition in 2009 compared to 2010. In 2010, the bloom began earlier in the season, but freshwater discharge at any point was lower than in previous years and remained steadily low throughout the duration of the smolts' migration. This suggested a higher surface residence time of the freshwater layer, or alternatively, that the smolts had more control over their migration than in previous years. Surface concentrations of zooplankton were higher than in

2008, despite lower total concentrations, indicative of surface water and zooplankton retention. The smolts grew significantly larger during their estuarine migration, possibly due to their increased ability to exploit available prey resources. Therefore, the faster growth in 2010 may simply be a reflection of their longer migration (residence) time, allowing the smolts to exit the inlet at a significantly larger size and higher condition factor. This longer duration in the inlet may be crucial to the smolts' survival, allowing them to attain the critical size that would later be beneficial to their survival through predator avoidance and maintenance of metabolic function in winter (Beamish and Mahnken 2001).

In conclusion, the migration time and growth of the smolts appeared to be related to river flow rates coinciding with their outmigration. Ainsworth et al. (2011) hypothesized that the rate of river influx controlled the timing and intensity of spring production, and consequentially the amount of prey available to the outmigrating smolts. To estimate survival, they divided the number of adult returns by the abundance of pre-smolt juveniles (Ainsworth et al. 2011). When regressed against river discharge rates, they found a weak negative relationship, in which discharge rates in March and April explained up to 40% of the variation in marine survival index (Ainsworth et al. 2011). Although their conclusion contradicts the findings in this study, they examined the entire marine life history of the sockeye, during which survival is influenced by a variety of factors, and found a relationship with discharge rates occurring prior to their marine entry period. This study focused specifically on the early marine life phase and freshwater influx from May-June, directly coinciding with the smolts' outmigration through the estuary. Results indicate that the smolts' fitness may be lower in years when river flow advects them out of the inlet before they can grow substantially and improve their condition index, increasing their risk of

mortality. The zooplankton prey community may also be advected out of the inlet, affecting the duration of spring productivity and reducing the foraging base available to the smolts. In years of optimal conditions, such as in 2010, the smolts may linger in the inlet for longer periods of time, exploiting resources and growing to a critical size in order to gain a survival advantage during their first marine winter. Therefore, future studies should further investigate how long-term changes in the initiation of periods of high river flow affect the survival of sockeye smolts during their outmigration through the estuary.

4.2 Outlook

Future work should include a focus on the physiological aspects of smoltification, and feeding (e.g. mouth gape, encounter rate, and speed) to gain a more comprehensive view of the feeding ecology of sockeye smolts. Studies of prey preferences and feeding ecology in relationship to optimal and opportunistic foraging behaviors, and the development of spatially explicit bioenergetics models should also be considered. These studies could be supplemented by genetic analyses, to see if the structure of the population has changed over time with fishing or climate effects. Changes in genetic history would affect the adaptability and plasticity of a stock to variations in the environment, subsequently affecting growth and survival. In light of stable isotope analyses, genetic analyses would also be prudent in determining the stock composition of Rivers Inlet (unpublished data).

Tracking techniques to determine the migration time of the smolts through the inlet would benefit the study of growth rates during their period of estuarine migration. If migration timing is indeed faster than predicted in this study, then the expansion of the study area to include the entire continental shelf area, namely the Queen Charlotte Sound, would be

beneficial to understanding how zooplankton communities and physical influences outside the inlet affect feeding regimes and growth. Competition with and predation on the population of sockeye smolts would provide a more comprehensive understanding on the trophic dynamics within Rivers Inlet. Climate change and subsequent changes in the environment, in particular a shift in the timing of initiation of high river flow, will have effects on the ability of the smolts to adapt to the marine phase, and studying the pertinence of the physical and biological aspects, as well as anthropogenic influences, of this phase to their survival will become a necessary tool in the pressing future.

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Appendices

Appendix A Total number of sets performed in 2008, by location and survey. Sites are divided into distance from the head of the inlet: Lower Inlet (35.46-41.87 km), Mid-Inlet (23.98-30.11 km) and Upper Inlet (0-13.64 km).

Year	2008	Date	29-Apr	11-May	28-May	10-Jun	25-Jun	
		Survey No.	1	2	3	4	5	Total per survey
Site	Upper Inlet (Distance from head: 0-13.64 km)	Wannock	1	1	1	1	1	5
		Kilbella	1	1	1	1	1	5
		Scandinavia	1	1	1	1	1	5
		McPhee	1	1	1	1	1	5
		Ralph	1	1	1	1	1	5
	Mid-Inlet (Distance from head: 23.98-30.11 km)	Dawson's Shore	1	1	1	7	1	11
		Dawson's Open	1	1	1	1	1	5
		Geetla	1	1	1	1	1	5
	Lower Inlet (Distance from head: 35.46-41.87 km)	Mouth	1	1	1	1	1	5
		Bosquet Open	1	1	1	1	1	5
		Bosquet Shore	1	1	1	1	1	5
		Dimsey Shore	1	1	1	1	1	5
		Dimsey Open	1	1	1	1	1	5
		Total	13	13	13	19	13	71

Appendix B Total number of sets performed in 2009, by location and survey. Sites are divided into distance from the head of the inlet: Lower Inlet (35.46-41.87 km), Mid-Inlet (23.98-30.11 km) and Upper Inlet (0-13.64 km). Grey boxes indicate that no set was performed at that time.

Year	2009	Date	1-May	17-May	31-May	15-Jun	29-Jun	
		Survey No.	1	2	3	4	5	Total per survey
Site	Upper Inlet (Distance from head: 0-13.64 km)	Wannock		1	1	1		3
		Kilbella	1	1	1	1	1	5
		Scandinavia	1	1	1	1	1	5
		McPhee	1	1	1		1	4
		Ralph	1	1	1	1	1	5
	Mid-Inlet (Distance from head: 23.98-30.11 km)	Dawson's Shore		1	5	1	1	8
		Dawson's Open	1	1	2	1	1	6
		Geetla	1	1	1	1	1	5
	Lower Inlet (Distance from head: 35.46-41.87 km)	Mouth	1	1	1		1	4
		Bosquet Open	1	1	1	1	1	5
		Bosquet Shore	1	1	1	1	1	5
		Dimsey Shore	1	1	2	1	1	6
		Dimsey Open	1	1	1	1	1	5
		Total		11	13	19	11	12

Appendix C Total number of sets performed in 2010, by location and survey. Sites are divided into distance from the head of the inlet: Lower Inlet (35.46-41.87 km), Mid-Inlet (23.98-30.11 km) and Upper Inlet (0-13.64 km). Grey boxes indicate that no set was performed at that time.

Year	2010	Date	6-May	19-May	4-Jun	19-Jun	27-Jun	5-Jul	
		Survey No.	1	2	3	4	5	6	Total per survey
Site	Upper Inlet (Distance from head: 0-13.64 km)	Wannock	1	2	1		1	1	6
		Kilbella	1	1	1		1	1	5
		Scandinavia	1	1	1		1	1	5
		McPhee	1	1	1		1	1	5
		Ralph	1	1	1		1	1	5
	Mid-Inlet (Distance from head: 23.98-30.11 km)	Dawson's Shore	1	1	1	1	1	1	6
		Dawson's Open	1	1	1	1	1	1	6
		Geetla	1		1		2	1	5
	Lower Inlet (Distance from head: 35.46-41.87 km)	Mouth	1		1		1	1	4
		Bosquet Open	1	1	1		1	1	5
		Bosquet Shore	1	1	1		1	1	5
		Dimsey Shore	1		1		1	1	4
		Dimsey Open	1		1		1	1	4
		Total	13	10	13	2	14	13	65

Appendix D Sockeye smolts caught in 2008, showing catch per survey at each seining location, total per survey, and total per site. Sites are divided into distance from the head of the inlet: Lower Inlet (35.46-41.87 km), Mid-Inlet (23.98-30.11 km) and Upper Inlet (0-13.64 km).

Year	2008	Date	29-Apr	11-May	28-May	10-Jun	25-Jun		
		Survey No.	1	2	3	4	5	Total per survey	
Site	Upper Inlet (Distance from head: 0-13.64 km)	Wannock	0	1	3	0	0	4	
		Kilbella	0	0	527	0	0	527	
		Scandinavia	0	0	7	0	13	20	
		McPhee	0	0	1	33	0	34	
		Ralph	0	0	119	1	39	159	
	Mid-Inlet (Distance from head: 23.98-30.11 km)	Dawson's Shore	0	0	44	180	5	229	
		Dawson's Open	0	0	3	1068	7	1078	
		Geetla	0	0	8	194	171	373	
	Lower Inlet (Distance from head: 35.46-41.87 km)	Mouth	0	0	0	80	4	84	
		Bosquet Open	0	0	6	30	5	41	
		Bosquet Shore	0	0	3	138	10	151	
		Dimsey Shore	0	0	2	441	3	446	
		Dimsey Open	0	0	0	97	142	239	
		Total	0	1	723	2262	399	3385	
			No. of sets per survey	13	13	13	19	13	71
			CPUE	0	0.08	55.62	119.05	30.69	47.68

Appendix E Sockeye smolts caught in 2009, showing catch per survey at each seining location, total per survey, and total per site. Sites are divided into distance from the head of the inlet: Lower Inlet (35.46-41.87 km), Mid-Inlet (23.98-30.11 km) and Upper Inlet (0-13.64 km). Grey boxes indicate that no set was performed at that location.

Year	2009	Date	1-May	17-May	31-May	15-Jun	29-Jun		
		Survey No.	1	2	3	4	5	Total per survey	
Site	Upper Inlet (Distance from head: 0-13.64 km)	Wannock		0	454	16		470	
		Kilbella	0	0	14	1	10	25	
		Scandinavia	0	19	0	0	16	35	
		McPhee	0	0	84		27	111	
		Ralph	0	1	0	1	2	4	
	Mid-Inlet (Distance from head: 23.98-30.11 km)	Dawson's Shore		0	0	1	48	49	
		Dawson's Open	0	0	21	109	14	144	
		Geetla	0	0	0	0	0	0	
	Lower Inlet (Distance from head: 35.46-41.87 km)	Mouth	0	0	0		18	18	
		Bosquet Open	0	0	2	30	23	55	
		Bosquet Shore	0	0	1	296	0	297	
		Dimsey Shore	0	0	3	46	0	49	
		Dimsey Open	0	0	1	5	0	6	
		Total	0	20	580	505	158	1263	
			No. of sets per survey	11	13	19	11	12	66
			CPUE	0	1.54	30.53	45.91	13.17	19.14

Appendix F Sockeye smolts caught in 2010, showing catch per survey at each seining location, total per survey, and total per site. Sites are divided into distance from the head of the inlet: Lower Inlet (35.46-41.87 km), Mid-Inlet (23.98-30.11 km) and Upper Inlet (0-13.64 km). Grey boxes indicate that no set was performed at that location.

Year	2010	Date	6-May	19-May	4-Jun	19-Jun	27-Jun	5-Jul		
		Survey No.	1	2	3	4	5	6	Total per survey	
Site	Upper Inlet (Distance from head: 0-13.64 km)	Wannock	0	48	0		0	0	48	
		Kilbella	0	365	0		0	1	366	
		Scandinavia	0	0	0		1	57	58	
		McPhee	0	2	0		3	0	5	
		Ralph	0	0	0		2	37	39	
	Mid-Inlet (Distance from head: 23.98-30.11 km)	Dawson's Shore	0	3	820	0	13	0	836	
		Dawson's Open	0	65	36	15	5	4	125	
		Geetla	0		0		0	17	17	
	Lower Inlet (Distance from head: 35.46-41.87 km)	Mouth	0		0		15	0	15	
		Bosquet Open	0	0	4		39	15	58	
		Bosquet Shore	0	0	31		64	0	95	
		Dimsey Shore	0		9		15	12	36	
		Dimsey Open	0		0		0	15	15	
		Total	0	483	900	15	157	158	1713	
			No. of sets per survey	13	10	13	2	14	13	65
			CPUE	0	48.3	69.23	7.5	11.21	12.15	26.35

Appendix G Average prey length, dry weight (DW; mg), wet weight (WW; mg), and DW:WW conversion factors, by species (when possible) and taxon. References refer to the literature source of the DW and DW:WW conversion factors.

Category	Species	Length (mm)	DW (mg)	WW (mg)	DW:WW	References
Amphipoda		1.64	0.57	2.73	0.21	Ricciardi and Bourget (1998)
	<i>Calliopu</i> spp.	2.35	1.32	5.09	0.26	Brey (2001)
	Gammaridea	2.04	0.51	1.89	0.27	Brey (2001)
	<i>Primno</i> spp.	2.30	0.26	1.23	0.21	Brey (2001)
	<i>Themisto pacifica</i>	1.40	0.20	1.14	0.18	Brey (2001)
Bivalve Veliger		0.38	0.00045	0.00253	0.18	Brey (2001)
Cirripedia		0.79	0.23	1.00	0.23	Brey (2001)
Cladocera		1.09	0.01	0.05	0.17	Brey (2001)
Copepoda		3.06	0.58	2.77	0.21	Brey (2001)
	<i>Calanus marshallae</i>	2.80	0.92	4.61	0.20	Brey (2001)
	<i>Calanus pacificus</i>	2.07	0.67	3.53	0.19	Brey (2001)
	<i>Calanus</i> spp.	1.32	0.53	2.63	0.20	Brey (2001)
	<i>Metridia pacifica</i>	1.78	0.80	4.22	0.19	Brey (2001)
	<i>Neocalanus plumchrus</i>	3.26	0.50	2.80	0.18	Brey (2001)
	<i>Pseudocalanus</i> spp.	0.94	0.01	0.02	0.36	Brey (2001)
Crustacea		1.87	0.34	1.48	0.23	Cauffopé and Heymans (2005)
	Euphausiidae	2.90	0.04	0.26	0.15	Brey (2001)
	Isopoda	1.13	0.02	0.08	0.23	Ricciardi and Bourget (1998)
	<i>Thysanoessa</i> spp.	16.30	0.97	30.69	0.23	Brey (2001)
Decapoda		2.13	1.03	3.82	0.27	Brey (2001)
	Crab larvae	2.83	0.97	3.34	0.29	Brey (2001)
	Shrimp larvae	2.60	1.09	4.37	0.25	Brey (2001)

Category	Species	Length (mm)	DW (mg)	WW (mg)	DW:WW	References
Fish		9.58	8.10	34.23	0.24	Brey (2001)
	Clupeiformes	13.52	18.26	70.22	0.26	Brey (2001)
	Gadiformes	6.61	2.30	11.50	0.20	Brey (2001)
	Perciformes	14.28	3.75	14.99	0.25	Brey (2001)
Other	Chaetognatha	14.94	0.67	6.75	0.10	Brey (2001)
	Gastropoda	0.90	0.08	0.42	0.20	Brey (2001)
	Insecta	1.85	0.40	1.80	0.22	Brey (2001)
	Polychaeta	2.23	0.02	0.08	0.20	Ricciardi and Bourget (1998)
	Siphonophora	4.62	0.44	8.87	0.05	Brey (2001)

Appendix H Frequency of occurrence (Freq.), relative abundance (Abund.), and relative biomass (Bio.) contributions of each prey species (spp.) or taxon to the diet composition of sockeye salmon smolts for each sampling year (2008, 2009, and 2010).

Taxon	2008			2009			2010			2008-2010		
	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)
<i>Calliopus</i> spp.	3.86	0.35	0.56	0.00	0.00	0.00	0.00	0.00	0.00	1.80	0.06	0.29
<i>Cyphocaris</i> spp.	0.48	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.01
Gammaridea	1.45	0.07	0.04	0.81	0.01	0.03	1.77	0.03	0.08	1.35	0.02	0.05
Hyperiididae	2.90	0.20	0.02	0.00	0.00	0.00	4.42	0.34	0.20	2.48	0.16	0.06
<i>Primno</i> spp.	3.38	0.89	0.35	0.00	0.00	0.00	0.88	0.03	0.05	1.80	0.15	0.19
<i>Themisto pacifica</i>	26.09	6.81	2.47	15.32	0.41	0.93	21.24	3.09	5.86	21.85	2.48	2.93
Chaetognatha	3.38	0.61	1.31	5.65	0.08	1.02	0.88	0.01	0.10	3.38	0.13	0.94
Cladocera	0.00	0.00	0.00	38.71	61.11	5.48	53.98	38.79	2.95	24.55	42.67	2.02
Copepoda	9.66	3.51	3.10	29.03	4.16	22.67	23.89	1.77	8.17	18.69	3.13	8.99
<i>Calanus marshallae</i>	7.73	6.36	9.34	8.87	1.04	9.45	8.85	2.13	16.32	8.33	2.31	11.06
<i>Calanus pacificus</i>	0.48	0.17	0.20	2.42	0.05	0.32	1.77	0.02	0.10	1.35	0.06	0.20
<i>Calanus</i> spp.	1.45	0.07	0.05	1.61	0.11	0.56	4.42	0.24	1.05	2.25	0.15	0.42
<i>Metridia pacifica</i>	4.83	6.29	8.47	4.84	0.25	2.10	1.77	0.02	0.12	4.05	1.12	4.93
<i>Neocalanus plumchrus</i>	2.90	0.28	0.25	12.10	0.52	2.87	4.42	0.35	1.61	5.86	0.41	1.21
<i>Pseudocalanus</i> spp.	0.97	0.91	0.01	0.00	0.00	0.00	0.88	0.05	0.00	0.68	0.17	0.00
Crustacea	22.22	10.65	5.03	9.68	1.49	4.34	21.24	2.69	6.63	18.47	3.41	5.26
Cirripedia	18.84	28.72	9.12	45.16	15.53	30.44	45.13	22.68	37.64	32.88	20.42	21.13
Isopoda	4.35	0.37	0.01	1.61	0.02	0.00	0.00	0.00	0.00	2.48	0.07	0.01
Tanaidacea	5.80	1.84	1.52	4.03	0.10	0.51	5.31	0.07	0.31	5.18	0.37	0.98
Siphonophora	0.00	0.00	0.00	0.00	0.00	0.00	3.54	0.04	0.65	0.90	0.02	0.16
Decapoda	1.45	0.11	0.13	2.42	0.08	0.63	12.39	0.30	1.92	4.50	0.17	0.68
Crab larvae	14.98	5.34	5.69	14.52	0.23	1.51	15.04	0.23	1.28	14.86	1.04	3.62
Euphausiacea calyptopis	0.00	0.00	0.00	6.45	4.83	2.45	2.65	0.12	0.05	2.48	2.22	0.59
Euphausiacea furcilia	0.00	0.00	0.00	5.65	0.47	0.24	1.77	0.06	0.03	2.03	0.24	0.06
Euphausiidae	1.45	0.43	0.04	10.48	0.35	0.18	0.00	0.00	0.00	3.60	0.23	0.06
Shrimp larvae	0.48	0.02	0.03	0.81	0.04	0.33	9.73	0.59	4.32	2.93	0.25	1.14

Taxon	2008			2009			2010			2008-2010		
	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)
<i>Thysanoessa</i> spp.	0.48	0.07	0.13	0.00	0.00	0.00	0.88	0.04	0.38	0.45	0.02	0.16
Insecta	18.84	0.98	0.56	41.94	0.77	2.75	16.81	0.25	0.74	24.77	0.60	1.13
Bivalve veliger	2.42	1.43	0.00	34.68	7.65	0.04	37.17	22.01	0.09	20.27	12.26	0.03
Gastropoda	1.45	0.11	0.01	4.03	0.04	0.03	0.88	0.01	0.01	2.03	0.04	0.02
Pteropoda	9.18	10.91	1.45	4.84	0.08	0.07	9.73	3.08	2.13	8.11	2.98	1.29
Pisces	28.99	1.93	21.07	7.26	0.12	8.26	3.54	0.04	2.02	16.44	0.38	13.39
Clupeiformes	5.31	0.61	13.60	0.00	0.00	0.00	0.00	0.00	0.00	2.48	0.10	7.06
Gadiformes	0.48	0.17	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.03	0.33
Perciformes	14.01	1.61	7.67	0.81	0.02	0.45	2.65	0.04	1.11	7.43	0.28	4.36
Polychaeta	0.48	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00

Appendix I Frequency of occurrence (Freq.), relative abundance (Abund.), and relative biomass (Bio.) contributions of each zooplankton species (spp.) or taxon found in the water column (0-300 m) to the community composition for each sampling year (2008, 2009, and 2010).

Taxon	2008			2009			2010			2008-2010		
	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)
Amphipoda	95.83	0.20	4.86	95.83	0.13	9.24	100.00	0.22	6.12	96.67	0.18	5.88
Bryozoa	37.50	0.09	0.00	54.17	0.66	0.03	33.33	0.30	0.00	43.33	0.33	0.01
Chaetognatha	87.50	0.16	1.65	91.67	0.11	3.26	91.67	0.27	3.18	90.00	0.17	2.30
Podonidae spp.	25.00	0.11	0.01	70.83	1.61	0.25	83.33	1.08	0.07	55.00	0.84	0.06
Copepoda	175.00	14.68	0.05	158.33	26.62	0.25	200.00	16.64	0.06	173.33	19.27	0.08
<i>Acartia longiremis</i>	354.17	5.72	0.24	445.83	6.37	0.87	550.00	4.77	0.23	430.00	5.74	0.34
Aetideidae spp.	66.67	0.21	0.31	70.83	0.17	0.77	91.67	0.28	0.48	73.33	0.21	0.43
Calanidae spp.	133.33	1.66	0.08	137.50	0.62	0.33	75.00	0.08	0.02	123.33	0.96	0.10
<i>Calanus marshallae</i>	225.00	1.12	1.94	287.50	1.33	7.50	308.33	0.67	1.34	266.67	1.10	2.67
<i>Calanus pacificus</i>	104.17	0.10	0.17	41.67	0.02	0.10	108.33	0.06	0.10	80.00	0.06	0.14
<i>Candacia</i> spp.	20.83	0.04	0.11	33.33	0.01	0.07	75.00	0.09	0.32	36.67	0.04	0.16
<i>Corycaeus anglicus</i>	12.50	0.00	0.00	0.00	0.00	0.00	16.67	0.01	0.00	8.33	0.00	0.00
<i>Eucalanus bungii</i>	283.33	0.75	1.74	254.17	1.15	4.13	266.67	0.19	0.55	268.33	0.77	1.82
<i>Heterorhabdus tanneri</i>	33.33	0.04	0.07	58.33	0.07	0.40	75.00	0.09	0.19	51.67	0.06	0.16
<i>Metridia okhotensis</i>	162.50	0.48	1.56	154.17	0.30	3.58	183.33	0.40	2.06	163.33	0.40	2.01
<i>Metridia pacifica</i>	587.50	6.82	4.05	633.33	6.60	10.56	666.67	6.49	3.64	621.67	6.67	4.98
<i>Microcalanus pusillus</i>	362.50	5.09	0.11	350.00	3.24	0.22	391.67	3.28	0.09	363.33	4.05	0.12
<i>Microsetella</i> spp.	58.33	0.09	0.00	50.00	0.31	0.01	66.67	0.34	0.01	56.67	0.22	0.00
<i>Neocalanus cristatus</i>	4.17	0.00	0.00	20.83	0.01	0.23	8.33	0.00	0.09	11.67	0.00	0.06
<i>Neocalanus plumchrus</i>	95.83	0.23	1.32	162.50	0.33	4.64	108.33	0.11	0.73	125.00	0.24	1.70
<i>Oithona</i> spp.	100.00	11.47	0.19	100.00	15.94	0.78	100.00	19.10	0.36	100.00	14.68	0.33
<i>Oncaea borealis</i>	100.00	4.29	0.05	95.83	4.82	0.18	83.33	2.06	0.03	95.00	3.99	0.07
<i>Paracalanus</i> spp.	8.33	0.02	0.00	12.50	0.01	0.00	33.33	0.09	0.00	15.00	0.03	0.00
<i>Paraeuchaeta elongata</i>	262.50	0.11	0.68	337.50	0.20	2.16	450.00	0.24	1.37	330.00	0.17	1.09

Taxon	2008			2009			2010			2008-2010		
	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)	Freq. (%)	Abund. (%)	Bio. (%)
<i>Pseudocalanus</i> spp.	545.83	19.08	1.60	604.17	10.73	3.22	433.33	11.39	1.22	546.67	14.50	1.76
<i>Scolecithricella minor</i>	45.83	0.12	0.01	70.83	0.24	0.05	58.33	0.12	0.01	58.33	0.17	0.02
Cirripedia spp.	120.83	0.93	1.80	141.67	1.14	2.10	166.67	1.20	0.92	138.33	1.06	1.62
Epicarid spp. larvae	25.00	0.03	0.08	62.50	0.04	0.28	91.67	0.05	0.14	53.33	0.04	0.13
<i>Neomysis raya</i>	0.00	0.00	0.00	8.33	0.00	0.02	8.33	0.00	0.00	5.00	0.00	0.00
Ostracoda spp.	91.67	1.12	1.18	83.33	2.12	6.61	83.33	3.96	4.80	86.67	2.08	2.97
<i>Beroe</i> spp.	12.50	0.00	0.01	16.67	0.00	0.02	8.33	0.00	0.00	13.33	0.00	0.01
Anomura spp. zoea	58.33	0.05	0.04	45.83	0.05	0.10	41.67	0.01	0.01	50.00	0.04	0.04
Brachyura spp. zoea	66.67	0.03	0.08	37.50	0.01	0.08	41.67	0.01	0.02	50.00	0.02	0.06
Caridae spp. zoea	58.33	0.01	0.01	50.00	0.02	0.03	66.67	0.01	0.01	56.67	0.01	0.01
Euphausiid spp.	275.00	1.43	2.37	437.50	6.67	3.84	350.00	3.92	6.34	355.00	3.79	3.62
<i>Pasiphaea pacifica</i>	20.83	0.00	0.02	33.33	0.00	0.03	16.67	0.00	0.00	25.00	0.00	0.02
<i>Sergestes</i> spp.	12.50	0.00	0.00	0.00	0.00	0.00	8.33	0.00	0.00	6.67	0.00	0.00
Medusae	37.50	0.01	0.23	50.00	0.02	1.13	58.33	0.02	0.44	46.67	0.02	0.42
Bivalvia spp. veligers	83.33	5.08	0.03	83.33	5.12	0.10	91.67	8.14	0.06	85.00	5.76	0.05
<i>Clione limacina</i>	41.67	0.00	0.12	4.17	0.00	0.05	41.67	0.02	1.04	26.67	0.01	0.34
<i>Limacina helicina</i>	100.00	18.14	70.83	91.67	1.58	18.12	100.00	13.08	58.29	96.67	11.27	59.21
Pisces	58.33	0.06	0.12	62.50	0.01	0.17	25.00	0.00	0.00	53.33	0.03	0.10
Polychaeta	91.67	0.15	1.59	95.83	0.24	7.30	100.00	0.20	2.33	95.00	0.19	2.69
Siphonophora	58.33	0.03	0.42	83.33	0.07	3.19	100.00	0.13	2.31	76.67	0.07	1.35
Larvacea spp.	75.00	0.25	0.27	95.83	1.30	4.01	66.67	0.85	1.01	81.67	0.75	1.05