# AN ABSTRACT OF THE THESIS OF

Kailan F. Mackereth for the degree of Master of Science in Fisheries Science presented on March 15, 2016.

Title: Juvenile Coho Salmon (*Oncorhynchus kisutch*) Diet in Brackish and Freshwater Habitats in the Stream-estuary Ecotones of Coos Bay, Oregon.

Abstract approved: ______________________________________________________

Guillermo R. Giannico

Loss of lowland estuarine and freshwater off-channel habitats along the Pacific Northwest coast has contributed to the decline of salmonid populations. These habitats serve as nursery grounds for juvenile salmonids providing them with food, winter shelter, and a transition zone between freshwater and saltwater. Lowland areas have undergone anthropogenic alterations (e.g., installation of tide gates, construction of dikes, channelization) to increase the net area of land suitable for agriculture and development resulting in watershed fragmentation and reduction in the amount of habitats with high intrinsic potential to support populations of juvenile salmonids. Until recent years, sub-yearling coho salmon found in lowland riverine habitats and estuarine marshes were assumed to have been displaced from optimal upland reaches by competition and high water discharge. Recent studies have concluded that early estuarine migrant behavior is volitional and these fish return as 20-40% of the spawning population, but there are few studies that delve into the capacity of estuarine habitat to support early estuarine life history strategies in systems heavily altered by human practices. This study documented differences in diet and condition factor (K) between sub-yearling and yearling coho salmon foraging concurrently in brackish or freshwater lowland habitat of the upper estuarine intertidal zone. Fish stomach contents were sampled by means of gastric lavage in three coastal lowland creeks in Coos Bay on the southern Oregon coast. Prey found in the samples were sorted, counted, identified, and dried to obtain dry weight biomass. Condition factor (K) and total dry weight prey biomass of fishes were not different between brackish and freshwater habitat; however, non-metric multidimensional scaling indicated that prey composition was substantially different between habitat and age class. These findings suggest that early migrating sub-yearlings and yearling smolts diverge in their diets whether they occupy the same or different habitats in the stream to estuary transition zone. Insects were important prey within the diets of yearling and sub-yearling freshwater foragers and sub-yearling brackish water foragers while crustaceans were important in the diets of yearling brackish water foragers. Future research exploring prey abundance and availability in relation to prey selected by juvenile coho salmon would denote habitat foraging quality and habitat exploitation by early estuarine migrants. Expanding this research to contrast natural intertidal habitats with those regulated by tide gates would be beneficial towards understanding the impact different styles of tide gates have on biotic communities and hydrological attributes (e.g., flow, chemistry, temperature, tidal exchange). Identification of factors that influence habitat selection in the stream-estuary ecotone by alternative early life history strategies of juvenile coho salmon is essential towards enhancing genetic diversity thereby strengthening the resiliency of the population.

# Juvenile Coho Salmon (*Oncorhynchus kisutch*) Diet in Brackish and Freshwater Habitats in the Stream-estuary Ecotones of Coos Bay, Oregon

by
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APPROVED:

Major Professor, representing Fisheries Science

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Kailan F. Mackereth, Author

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## CHAPTER 1

## INTRODUCTION

Oregon Coast wild coho salmon (*Oncorhynchus kisutch*) populations, from the Necanicum River and south to the Sixes River, are listed under the Endangered Species Act (ESA) as a threatened evolutionarily significant unit (ESU) (Anlauf et al. 2009). Loss of estuarine and freshwater off-channel habitats is one of the many factors contributing to the decline of salmonid populations in the Pacific Northwest. It is estimated that in Oregon there has been a 68% loss of tidal marsh and swamp habitats (Good 2000). These habitats provide quality nursery grounds for juvenile salmonids to feed, overwinter and adjust their physiology to cope with salt water (Simenstad et al. 1982**,** Craig and Crowder 2000). Habitat scarcity in the coastal lowlands is attributed to the installation of tidal control structures (e.g., dikes, levees and tide-gates), dredging of main channels, and the simplification of tidal systems to increase the net area of land suitable for agriculture and other human activities (Kostow 1997, Good 2000, Ibañez et al. 2000). These alterations result in the simplification and fragmentation of what was once a dynamic system with high intrinsic potential to support populations of juvenile salmonids (Burnett et al. 2003). Despite the ubiquity of tidal control devices throughout coastal systems along the Oregon coast, salmonid populations persist. However, the indirect effects of these structures on certain salmonid life histories and overall population resilience are not clear. This study examined early-estuarine residency of juvenile coho salmon within altered coastal lowland creeks on the southern Oregon coast – a life history strategy that has been observed for several coastal coho salmon populations from Alaska to California, but still remains poorly understood (Merrell and Koski 1978, Greene et al. 2012, Rebenack et al. 2015).

In an unaltered state, the dynamic zone of confluence between freshwater and estuarine ecosystems is driven by disturbances in the form of tidal pulses and seasonal fluctuations in freshwater discharge that combine forces to redistribute nutrients and sediments through the complex, dendritic layout of marsh channels and floodplains (Odum et al. 1995, Resh et al. 1988, Day et al. 2000). These recurring processes promote the formation of microhabitats incorporating both terrestrial and aquatic nutrients under a vast range of abiotic conditions that support diverse communities (Valiela et al. 2000, Simenstad et al. 2000). Tidal and seasonal flooding provides juvenile salmonids with access to tidal channels, floodplains, and fringing emergent marshes; fish can benefit from increased in-situ macroinvertebrate biodiversity in off-channel habitats and increased transport of macroinvertebrate terrestrial and aquatic prey subsidies to the main-channel (Junk et al. 1989, Sommer et al. 2001, Roegner et al. 2010). Juvenile salmonid residents in lowland habitats have increased growth rates (Tschaplinski 1987, Gray et al. 2002, Jones et al. 2014, Craig et al. 2014), larger body sizes (Crone and Bond 1976, Levy and Northcote 1982, Tschaplinski 1987, Miller and Sadro 2003), and higher winter survival rates when compared with individuals in the same cohorts that remained in upstream freshwater habitats (Reimers 1973).

Until the turn of this century, anadromous coho salmon were thought to rear entirely in freshwater during the first year of life before migrating to the ocean in the spring of their second year (Merrell and Koski 1978**,** Sandercock 1991**,** Quinn 2005). The presence of sub-yearling coho salmon within the upper stream-estuary ecotone

(Merrell and Koski 1978**,** Miller and Sadro 2003), was considered involuntary, the result of displacement from upstream habitat by high stream discharge events or as a result of density dependent hierarchical competition (Chapman 1962, Chapman 1966, Sandercock 1991, Thorpe 1994). Little was known about the fate of these individuals, but the consensus among managers and many researchers was that these juveniles did not survive to contribute to the spawning population (Crone and Bond 1976**,** Simenstad et al. 1982, Sandercock 1991).

Based on a combination of mark-and-recapture methods, PIT-tag technology, and scale and otolith analyses, researchers have concluded that coho salmon fry not only migrate to upper estuarine habitats but also that these early migrants thrive in those habitats (Miller and Sadro 2003, Koski 2009, Bennett et al. 2015). Studies examining juvenile coho salmon early residency in estuaries have identified four possible life history strategies: 1) spring estuary entrance of newly emerged fry that reside in those habitats until the following spring, 2) fall estuary entrance of parr that reside there until the following spring, 3) “migrants” or “nomads” that enter estuarine habitats from spring through summer after emergence but return to freshwater habitats during the winter and migrate out the following spring as yearlings, and 4) freshwater residence during the first year of life followed by spring smolting outmigration as yearlings (Jones et al. 2014, Nordholm 2014). In each of the studies, returning adults most often were yearling spring outmigrants; however, both detected returning adults (from 20% to 41%) that had early estuarine migrant life histories (Jones et al. 2014, Nordholm 2014, Bennett et al. 2015). Bennett et al. (2015) determined that while juvenile coho salmon spring migrants (yearling) were 3 times more likely to return as adults, the fall and winter migrant (sub-yearling) strategy was 2.5 times more common. Volitional downstream migration of sub-yearling coho salmon has been attributed to individual innate behavior (Kahler et al. 2001), as a response to environmental cues (Giannico and Healey 1998, Roni et al. 2012, Jones et al. 2014), or as a way to escape areas of high competition (Quinn 2005).

As efforts to restore tidal floodplain habitat have been completed within the upper estuary, juvenile salmonids have been shown to occupy off-channel habitats as tidal processes and accessibility is restored (Bottom et al. 2005, Roegner et al. 2010). This indicates that the initial loss of these habitats may have masked the presence and viability of alternative life history strategies, especially concerning early-migrant juvenile coho salmon. As a result, there is increased interest in determining the role of the upper estuary in supporting early migrant life history strategies of juvenile coho salmon. This study examined how two age classes, migrant sub-yearling residents and yearling smolt outmigrants, utilized freshwater and brackish water habitat within the spring by looking at diet within the upper estuarine ecotone of coastal lowland streams altered by land development infrastructure (i.e., tide-gates, berms and dikes). Growth of juvenile salmonids is an important determinant of survival and their diet, in terms of prey abundance and acquisition of prey by the fish, provides the energy needed for growth (Quinn 2005). My first objective was to determine the relative condition of the fish standardized by using Fulton’s Condition Factor (K) in freshwater and brackish water habitat and between yearling and sub-yearling age classes. This condition factor is a useful proxy of obtaining relative condition at a particular moment in time and, because it is based on weight in relation to fork length, it has been used to quantify differences in habitat exploitation related to diet and is indicative of smolting (Rodgers et al. 1987, Miller and Sadro 2003). My second objective was to determine whether there is a difference in total biomass of prey in the diets of juvenile coho salmon between foraging habitats and age classes. The final objective was to determine differences in diet composition between habitats and between age classes under the hypotheses that prey availability is influenced by water salinity and that prey selection is influenced by fish size and behavior (Chapman 1966, Williams and Williams 1998). This study describes juvenile coho diet in tide gated intertidal habitat adding to existing studies of juvenile coho diet in upland riverine reaches (Nielsen 1992), intertidal sloughs and marshes (Miller and Simenstad 1997, Roegner et al. 2010), ocean near-shore habitat (Brodeur 1991, Brodeur 2011), and floodplains (Bellmore et al. 2013). Understanding the role of the upper estuary to early estuarine migrant juvenile coho salmon will aid in the preservation of this novel life history strategy.

# CHAPTER 2

# METHODS

## *Site Description*

This study was carried out from April 15 through July 2, 2014 in Palouse, Larson, and Willanch Creeks, which drain into Coos Bay on the southern coast of Oregon. Larson and Palouse Creeks flow into Haynes Inlet on the northern portion of the bay while Willanch Creek is situated approximately 7 km south and it drains into Willanch Slough, which in turn connects directly to Coos Bay (Fig. 1). The coastal lowlands of these three creeks have been altered by deforestation, urbanization, and agriculture since they were settled in the late 1800s (Weybright 2011, Nordholm 2014). Dredging, diking, and channel changes to reduce tidal flooding and convert tideland for agricultural use have simplified the channel networks of each creek (Coos Watershed Association 2006). Riparian vegetation in the lowlands is dominated by *Phalaris arundinacea* (reed canary grass), but where the dikes have degraded and brackish water intrudes, *Carex obnupta* (slough sedge) and *C. lyngbyei* (Lyngbye's sedge) are present. Other riparian species include: *Alnus rubra* (red alder), *Salix lucida* (Pacific willow), and *Pseudotsuga menzeisii* (Douglas fir). Despite the changes, all creeks support wild populations of salmonids, including: coho salmon, Chinook salmon (*Oncorhynchus tshawytscha*), cutthroat trout (*O. clarkii*) and steelhead (*O. mykiss*) as well as hatchery reared Chinook salmon.

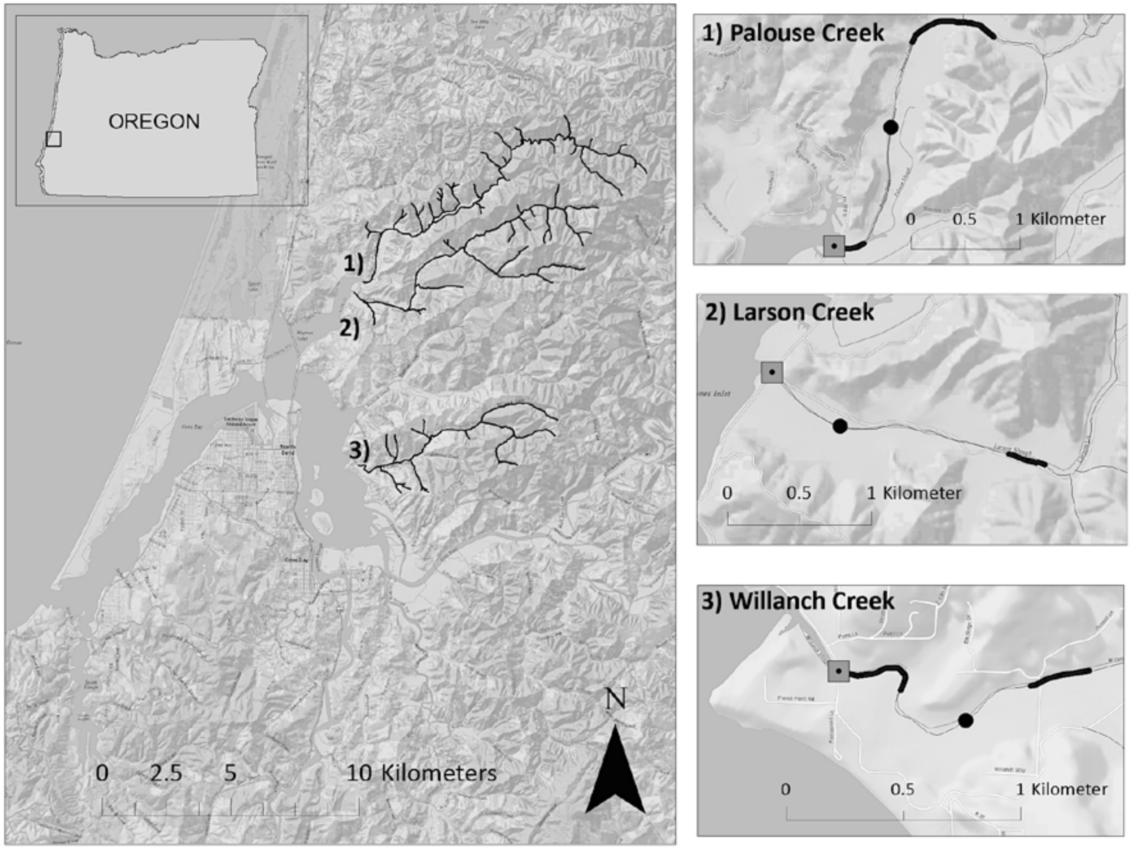

Figure 1. Study creeks of Coos Bay Estuary. The square on the inset map depicts the location of Coos Bay on the Oregon coast. Three side maps depict the sampling habitats for each creek. Symbol ▣ represents the location of the tide gate. Symbol ● represents the head of saltwater intrusion. Sampling habitat is depicted by the thick line where the brackish habitat is that closest to the tide gate and freshwater habitat is farthest from the tide gate. Brackish habitat for Larson Creek is represented by the tide gate icon.

### *Fish and Lavage Sampling*

Each creek is regulated with a tide gate at the mouths of Palouse and Larson Creeks where they empty into Haynes Inlet and 0.35 km up Willanch Slough from Coos Bay. These structures decreased the magnitude and duration of upstream intrusion of saline water in the lower stream reach during flood tides albeit to different extents due to the design and functionality of the tide gate. Due to significant scour around the Palouse tide gate box, the head of saltwater intrusion extended roughly 1.4 km upstream seasonally capable of reaching salinity levels in excess of 20 ppt at high tide. The tide gate at Larson Creek was better at regulating upstream tidal flow. However, when bayside water levels exceeded those upstream of the tide gate, saline waters penetrated the seal around the doors and salinity levels approached 23 ppt within 0.01 km upstream of the tide gate. Beyond this point, salinity drops abruptly and the creek becomes freshwater dominated. Willanch Creek was regulated by a muted tide gate system that allowed for prolonged mixing of intertidal water upstream of the tide gate. The extent of saltwater intrusion on Willanch Creek was roughly 1 km upstream reaching salinities of up to 20 ppt.

Fish were collected upstream of the tide gates within the historic head of tide, or the stream-estuary ecotone, in each of the three creeks and in the bay downstream of the tide gates. The bay of Haynes Inlet was counted as one sampling site because both Larson and Palouse Creeks drain into this area. The stream-estuary ecotone upstream of the tide gates was divided into two sampling habitats: brackish water and freshwater. Habitat selection was chosen to standardize the chemical conditions under which fish were sampled across the three creeks and within stipulations established by the private landowners upon whose property the sampling took place. Tidally influenced freshwater habitats had salinities below 0.5 ppt at high and low tide, whereas tidal brackish habitats upstream of tide gates were characterized by the presence of a salt wedge. During winter and spring floods, salinity concentrations and the upstream extent of salt intrusion in each creek declined. Prior to fish collection, transects were set across the channel to determine the distribution and characteristics of the brackish water wedge, especially when sampling followed a rain event. Salinity and temperature were measured with a handheld reader (YSI 30 Handheld Salinity, Conductivity, & Temperature System, Yellow Springs, Ohio) at the water's surface, at mid-depth and above the substrate approximately 0.5 meter from each channel margin and in the thalweg of the channel. In the brackish habitat, the average range of the salinity across the three creeks ranged from 14.2 ± 5.8 ppt at 2 cm above maximum depth to 2.3 ± 2.7 ppt 2 cm below the surface (Table 1). To monitor the tidal cycle, additional salinity and temperature data loggers suspended from a float approximately 1 m below the water surface upstream of the tide gate were set to record measurements every 15 minutes from May 5 through July 4 (Star-Oddi DST CT, Reykjavik, Iceland) (Table 1). Sampling in brackish habitats was suspended following precipitation events until salinity concentrations stabilized at 3 ppt or greater at mid-depth in the thalweg.

To increase the likelihood that fish diets represented the habitat within which each individual had been foraging, brackish water fish were sampled within the range of saltwater intrusion, but as near to the tide gates as possible where salinity concentrations were the greatest and most stable (Figure 1). Brackish samples were collected within 0.32 km of the tide-gate in Palouse Creek, 0.01 km on Larson Creek, and 0.38 km on Willanch Creek. Freshwater samples were collected 0.8 km, 1.0 km, and 0.15 km upstream from the saltwater wedge limit in Palouse Creek, Larson Creek and Willanch Creek respectively (Figure 1). Sampling in brackish water and bayside habitats were conducted during high tide to ensure maximum salinity concentrations while freshwater habitats were sampled at low tide to improve access to sampling locations.

Table 1. Salinity and temperature (mean ± standard deviation) in brackish water habitat. Parenthetic numbers indicate the number of measurements recorded at that location from April 15 to July 2, 2014. Star-Oddi loggers recorded data from May 4 to July 4, 2014.

| Site | | Willanch | Palouse | Larson |
|---|---|---|---|---|
| Maximum Depth (m) | | 1.1 ± 0.2 (9) | 1.2 ± 0.5 (8) | 3.1 ± 1.3 (7) |
| [1]Salinity (ppt) | Surface | 2.2 ± 2.9 (10) | 2.5 ± 2.5 (8) | 2.2 ± 2.8 (7) |
| | Mid-depth | 8.5 ± 7.8 (10) | 7.9 ± 5.3 (8) | 7.5 ± 4.7 (3) |
| | Bottom | 14.8 ± 5.5 (10) | 13.2 ± 6.3 (8) | 14.5 ± 6.0 (6) |
| [1]Temperature (°C) | Surface | 13.5 ± 2.4 (10) | 17.5 ± 2.1 (8) | 18.5 ± 2.5 (7) |
| | Mid-depth | 14.6 ± 2.9 (10) | 17.0 ± 1.7 (8) | 16.1 ± 2.0 (3) |
| | Bottom | 15.3 ± 2.2 (10) | 17.5 ± 1.5 (8) | 18.6 ± 2.9 (6) |
| [2]Salinity (ppt) | Mean ± SD | 8.9 ± 6.4 | 8.9 ± 6.3 | - |
| | Range | 0.5 - 20.2 | 1.0 - 24.6 | - |
| [2]Temperature (°C) | Mean ± SD | 16.8 ± 3.0 | 18.0 ± 2.0 | - |
| | Range | 9.5 - 24.3 | 11.0 - 23.4 | - |

[1] Reach measurements recorded with a YSI handheld reader

[2] Salinity Measurements were taken using Star-Oddi temperature and salinity loggers in the tide gate reservoir. Logger readings were inaccurate at Larson Creek due to placement within the tide gate.

Yearling and sub-yearling juvenile coho salmon were sampled with beach- and stick-seine nets every day between April 15 and July 2, 2014. I planned to sample both habitats (brackish and freshwater) in each one of the three study creeks on a rotating basis until 25 fish per age class and habitat were captured in each creek. However, the sampling rotation sequence had to be altered in many occasions in response to highly variable hydrological conditions. Fish sampling was interrupted for the day whenever water temperatures exceeded 20 ºC.

In a previous study completed in Coos Bay, coho salmon smolts were observed to range from 62 to 158 mm fork length (FL) with an average FL of 106 mm (Bass 2010). An additional study using otolith microchemistry to determine fork length at estuarine entrance indicated that fish with a minimum of 70 mm FL were smolt (Nordholm 2014). For the purpose of this study, juvenile coho salmon with ≥ 90 mm FL were classified as yearling smolts (brood year 2012) and all smaller individuals were considered estuarine sub-yearling migrants (brood year 2013). Captured fish were anesthetized with buffered MS-222 (tricaine methanesulfonate) solution, weighed to the nearest 0.1 g, and FL measured to the nearest 1 mm.

Gastric lavage was performed on all individuals ≥ 65 mm FL (Hyslop 1980). A catheter connected to a bottle of water was inserted orally into the gastric cavity and used to gently flush the stomach. Flushing continued until no more prey items were observed and the stomach area felt depleted. Contents were collected in a basin and poured through a standard coffee filter. The sample was preserved in 95% ethanol for laboratory analysis. Sampled fish were fin clipped on the lower lobe of the caudal fin to identify recaptured fish. If a site was resampled within a period of three days, clipped fish did not undergo gastric lavage.

### *Diet Processing*

Gut contents were sorted, identified to the lowest possible taxonomic category, and counted. For the purpose of obtaining dry weight biomass, items were assigned to one of the following prey sample groups: crustaceans, insects, and “other” organisms. “Insects” consisted of both aquatic and terrestrial insects. The “other” group consisted of pieces that could not be linked to a specific prey taxa, prey items that were too digested to be properly identified, and those that did not fit into the other two categories (e.g., arachnids, Collembola, annelids). For each fish, prey sample groups were placed in individual aluminum tins and dried in a precision convection oven at 60 °C for 24 hours to obtain dry weight biomass (0.1 mg). To obtain a stable weight samples were allowed to cool in a desiccator for a minimum of 12 hours prior to weighing.

### *Statistical Analysis*

To test for differences in prey biomass consumed by sample habitat and age class, a linear mixed model, incorporating the creek of origin as a random effect, was applied using R package “nlme” (Pinheiro et al. 2014). Larger fish are capable of eating more prey than small fish so prey biomass consumed was standardized by dividing the total dry weight prey biomass consumed by fish fork length (g dw/mm). The data were then log-transformed to improve the normality of the distribution.

To standardize the physical condition of the fish, Fulton’s Condition Factor (K) was determined using the following equation (Rodgers et al. 1987, Miller and Sadro 2003, Ebersole et al. 2009):

$$K = \left[\frac{\text{weight (g)}}{\text{FL}^3\ \text{(mm)}}\right] 10^5$$

Lower K values represent fish that are long and lean and decreases in K can be indicative of smolting yearlings (Rodgers et al. 1987). Although K has been shown to vary across spatial and temporal scales and is less reliable when sample sizes are small (Gray 2005, Lang et al. 2006), it is a useful proxy to represent the relative condition of juvenile salmonids at a specific moment in time. Differences in fish condition between sample habitats and age classes were also examined using a linear mixed model with creeks included as a random effect.

Non-metric multidimensional scaling (NMS) fitted with Sørensen (Bray-Curtis) distance measurement was used to explore patterns in diet composition among juvenile coho salmon. Multi-response permutation procedure (MRPP) was applied to make pair-wise comparisons determining the degree of dissimilarity in diets of fish against the foraging habitat and age class. For the ordination, the frequency of prey in the diet was increased by a factor of 1 and log-transformed to account for the high degree of variation within the samples. The percent numerical composition was used to emphasize differences in prey composition among fish diets.

Importance of prey sample groups were ranked by numerical composition, frequency of occurrence, and gravimetric contribution using an Index of Relative Importance (IRI) to standardize diet analysis (Pinkas et al. 1971, Hyslop 1980):

$$IRI = (\%N + \%G)\ \%F$$

where %N is the numerical composition, %G is the gravimetric composition, and %F is the frequency of occurrence of each prey group.

# CHAPTER 3

## RESULTS

Juvenile coho were captured at each of the sampling sites; however, capture rates in the bay were extremely low yielding 9 yearlings (4 from Haynes Inlet and 5 from Willanch) and no sub-yearlings (Fig. 2). As a result, bay fish were excluded from the subsequent analyses. Coho salmon fry, some as small as 30 mm FL, were caught with migrating smolts both in brackish and fresh water habitats of the intertidal zone. Periods of high discharge at the end of April combined with narrow channels in Willanch Creek severely reduced fish capture of yearlings despite multiple sampling attempts. To maintain a balanced study design in keeping with the limits set by Willanch Creek, final sample sizes for analyses were reduced using a random selection process from 20 to 7 fish per location and age class for a total of 84 fish (Table 2). Samples for a habitat and age class were grouped across the creeks for analysis resulting in four groups of 21 fish each in the analysis.

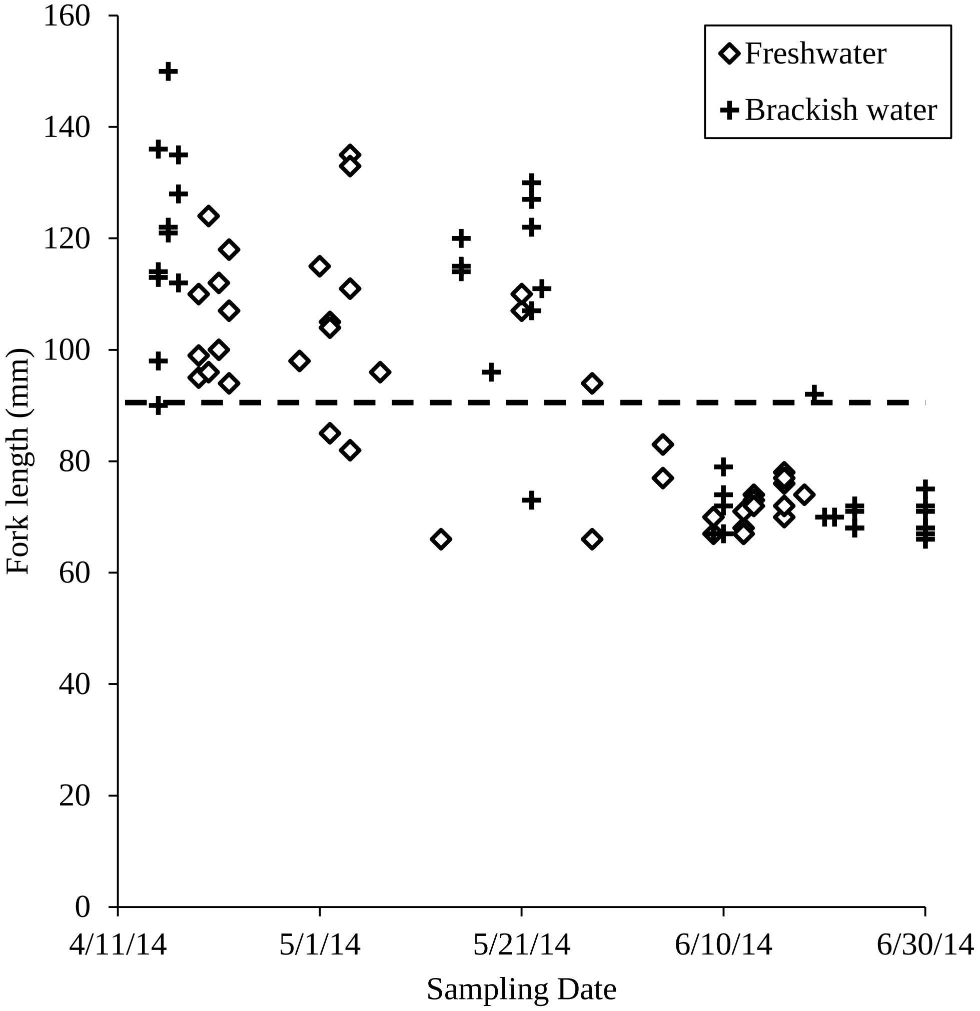

Figure 2. Juvenile coho salmon fork length (FL) distribution during sampling period. The dashed line identifies the 90 mm FL mark where FL 90 mm and greater were considered yearlings. Fish less than 90 mm FL were considered sub-yearlings. Yearlings were sampled a month earlier than most sub-yearlings.

Table 2. Juvenile coho salmon fork lengths and weights by age class and habitat type. Measurements listed by creek system and habitat. Numbers in parentheses correspond to number of fish sampled.

| | | Mean ± S.D. | | | | |
|---|---|---|---|---|---|---|
| Habitat | Sampling Period | Fork Length (mm) | Weight (g) | Age Class | Fork Length (mm) | Weight (g) |
| Brackish water | 4/15/14 - 6/30/14 | 93.5 ± 26.0 (42) | 11.7 ± 8.9 | Yearling (21) | 116.8 ± 15.2 | 18.8 ± 7.4 |
| | | | | Sub-yearling (21) | 70.1 ± 3.3 | 4.6 ± 0.8 |
| Freshwater | 4/19/14 - 6/18/14 | 90.6 ± 19.7 (42) | 9.9 ± 6.1 | Yearling (21) | 107.8 ± 12.1 | 14.7 ± 5.1 |
| | | | | Sub-yearling (21) | 73.5 ± 5.9 | 5.0 ± 1.2 |

| System | **Freshwater** | | | **Brackish water** | | |
|---|---|---|---|---|---|---|
| | Age Class | Fork Length (mm) | Weight (g) | Age Class | Fork Length (mm) | Weight (g) |
| Larson Creek | Yearling (7) | 105.1 ± 10.6 | 13.5 ± 4.3 | Yearling (7) | 122.9 ± 18.2 | 21.2 ± 9.2 |
| | Sub-yearling (7) | 69.4 ± 5.3 | 4.2 ± 1.2 | Sub-yearling (7) | 69.6 ± 3.2 | 4.5 ± 0.5 |
| Willanch Creek | Yearling (7) | 112.3 ± 16.2 | 17.0 ± 7.0 | Yearling (7) | 108.3 ± 15.4 | 15.0 ± 7.2 |
| | Sub-yearling (7) | 74.3 ± 6.2 | 5.3 ± 1.5 | Sub-yearling (7) | 69.6 ± 1.6 | 4.2 ± 0.3 |
| Palouse Creek | Yearling (7) | 105.9 ± 8.6 | 13.7 ± 3.2 | Yearling (7) | 119.3 ± 8.0 | 20.3 ± 4.7 |
| | Sub-yearling (7) | 76.9 ± 4.1 | 5.5 ± 0.8 | Sub-yearling (7) | 71.3 ± 4.6 | 5.2 ± 1.1 |

An ANOVA generated from the linear mixed model analyzing the difference in fish condition between habitats indicated that there was no difference in Fulton's Condition Factor (K) between brackish and freshwater foraging fish ($F_{1, 80} = 2.18$, p-value = 0.1437). The mean K for freshwater foragers was 1.19 (95%CI: 1.14, 1.24) g/mm$^3$ and 1.23 g/mm$^3$ for brackish foragers (Fig. 3a). There was a difference in K between the age classes of fish where the mean K of yearlings was 1.13 g/mm$^3$ (95%CI: 1.10, 1.17) and sub-yearlings was 1.29 g/mm$^3$ (95%CI: 1.24, 1.33) ($F_{1, 80} = 55.87$, p-value << 0.0001) (Fig. 3b).

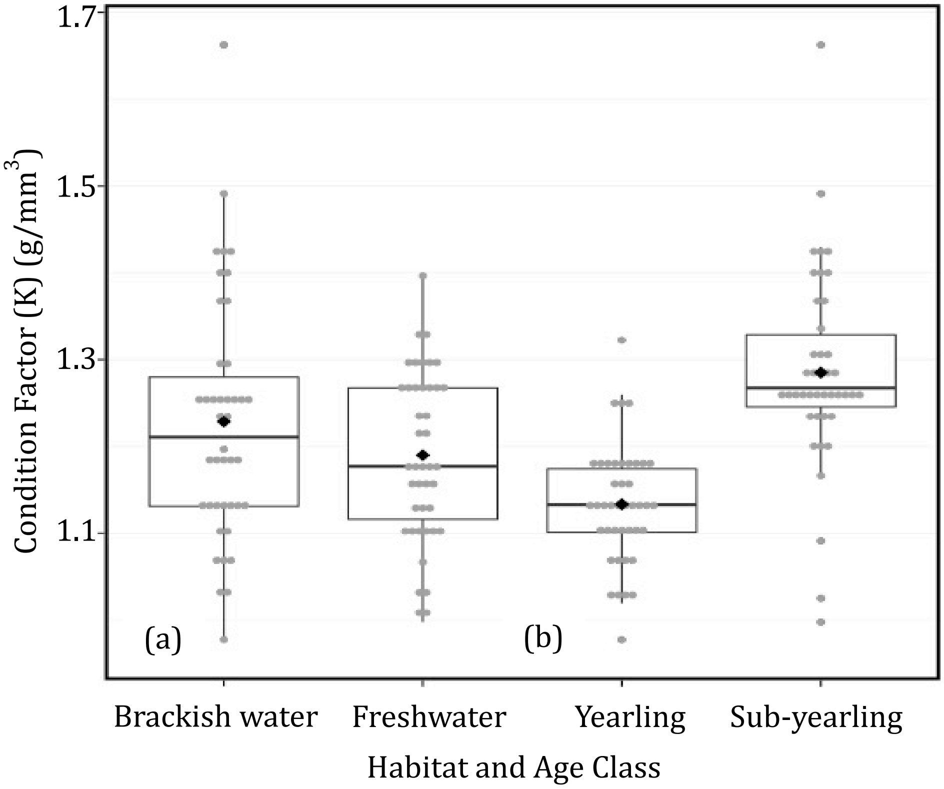

Figure 3. Juvenile coho salmon condition factor (K) by (a) habitat and (b) age class. Black diamond is the group mean, black line is the median, and gray dots are the distribution.

An ANOVA generated from the linear mixed model comparing the log of the dry weight of prey biomass between fish foraging in either a brackish or freshwater habitat indicated that there was no difference in the mean dry weight of prey biomass of the log transformed data between the diets of juvenile coho salmon foraging in either habitat ($F_{1, 80} = 2.36$, p-value = 0.1285). On a log transformed scale, brackish water fish consumed a mean of -9.197 g dw of prey per mm FL (95%CI: -9.625, -8.768) while freshwater foraging fish consumed a mean of -9.547 g dw of prey per mm FL (95%CI: -10.001, -9.093) (Fig. 4a). Comparison of prey biomass between yearling and sub-yearling fish was statistically different ($F_{1, 80} = 21.87$, p-value << 0.0001). On a log transformed scale, yearling fish consumed a mean of -8.892 g dw of prey per mm FL (95%CI: -9.309, -8.475) while sub-yearling fish consumed a mean of -9.851 g dw of prey per mm FL (95%CI: -10.259, -9.443) (Fig. 4b).

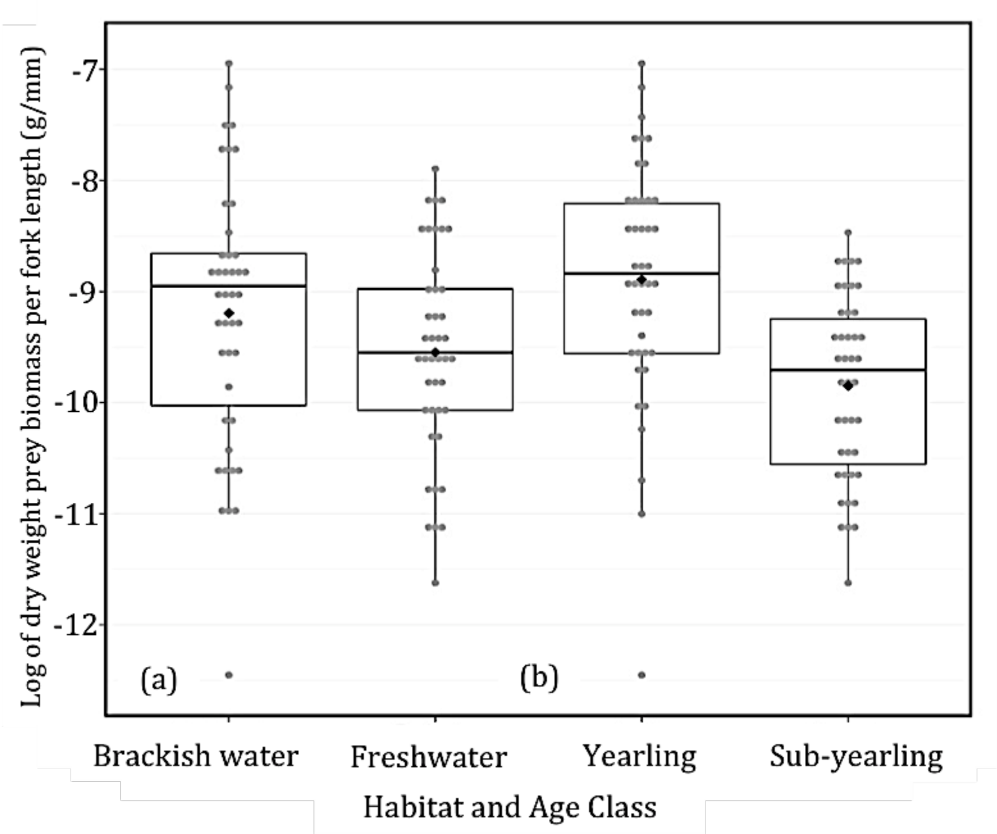

Figure 4. Log of dry weight prey biomass to fork length ratio (g/mm) by (a) habitat and (b) age class. Black diamond is the group mean, black line is the median, and gray dots are the distribution.

NMDS analysis illustrated that differences in prey composition for each fish were best represented with a 3-D model, which explained 85.8% of the total variation among fish diet with 56.1% of the variation explained by axis 1 and 15.6% by axis 2 ($A = 0.3116$, $p << 0.0001$) (Fig. 5 and Fig. 6). Axis 1 illustrates the separation of diet by habitat where freshwater foragers were clustered at the axes junction due to the abundance of chironomids (larvae, pupae, and adult), other diptera (larvae, pupae, and adult), and mayflies within the diet samples (Fig. 5). The diet of brackish water fish spread towards the right side of the figure due to the presence of *Americorophium* spp. and Cumacea spp. making these diets distinct from that of freshwater fish (Fig. 5). Spread along NMS axis 2 is attributed to the presence of prey organisms that occur either infrequently throughout the fish diets or in low abundance such as terrestrial hemipterans (e.g., aphids, leaf-hoppers) and thysanopterans (thrips).

The results of MRPP test based on the NMDS ordination comparing diet composition between habitats and age classes, as depicted in Figure 5, determined that diet composition was more similar within groups (e.g., freshwater yearlings, brackish water sub-yearlings) than among groups. The difference indicated by the MRPP results was seen in the brackish water foragers as yearling diets spread to the far right of the figure while sub-yearling diets fell throughout the middle of the figure. Differences in composition of yearling and sub-yearling freshwater diets were less apparent in the NMDS plot (Fig. 5). The results of an additional MRPP test based on the NMDS ordination show that the overall diets of fish within Willanch and Larson Creeks were not significantly different in prey composition (Willanch vs. Larson: A-statistic = 0.002; $p$ = 0.349); however, they differed significantly from those of fish in Palouse Creek, which isn’t apparent in Figure 6 (Larson vs. Palouse: A-statistic = 0.030; $p$ = 0.0227, Willanch vs. Palouse: A-statistic = 0.047; $p$ = 0.003).

Differences in diet composition between the foraging habitats and age classes as indicated by the results of the MRPP analysis is best represented by the percent abundance of individual prey items present within the diets. In brackish water diets, crustaceans represented 76.6% of the total diet in yearlings and 25.6% in sub-yearlings (Fig. 7). In yearlings, amphipods make up 55.1% of the diet with *Americorophium* spp. representing 82.2% of the amphipods. Yearlings also consumed Cumacea spp. (15.3%) and the isopod *Gnorimosphaeroma oregonensis* (4.0%). In sub-yearlings, 21.4% of crustaceans were Cumacea spp. while amphipods represent 65.7% of total crustaceans with 91.0% of amphipods being *Americorophium* spp. Additional crustaceans consumed across the foraging groups in lower abundances and frequencies were Copepods, Cladocerans, Ostracods, and Mysids. Crustaceans compose a mere 0.91% of the diets of freshwater yearlings and 1.0% of freshwater sub-yearling (Fig. 7). Freshwater yearlings consume predominantly amphipods, albeit none from the family Corophiidae, and sub-yearlings select zooplankton and mysid shrimp**.**

Aquatic insects were important to the diets of each foraging group, specifically diptera from the family Chironomidae (Fig. 7). In sub-yearling diets, chironomids were the most numerically common prey organism (57.0% brackish and 71.8% freshwater), but brackish foragers consumed predominantly adults (91.2% of total chironomids consumed) while freshwater sub-yearlings relied on all three life history stages resulting in 31.6%, 16.7%, and 51.7% of the total amount of chironomids consumed being larvae, pupae, or adults respectively (Fig. 7). Yearling coho ate lower amounts of chironomids (16.7% brackish and 30.8% freshwater), but their diets demonstrated similar preferences for certain developmental stages; 80.1% of chironomids consumed by brackish water yearlings were adults while freshwater yearlings ate 41.8% larvae and 51.6% adults. Diets of yearling freshwater foraging coho salmon also contained a large abundance (21.6%) of EPTs (Ephemeropteran nymphs and adults; Plecopteran nymphs; and Trichopteran larvae, pupae, and adults) and aquatic Dipteran larvae and pupae (19.0%) represented by families Chironomidae, Ceratopogonidae, Simulidae, Tipulidae, and Empididae, which resulted in the separation of this foraging group from sub-yearling freshwater foragers (Fig. 7).

Each foraging group also consumed terrestrial insects, which contributed to the finer differences in diet composition between the foraging groups. Yearling brackish water foragers consumed a meager amount of terrestrial insects (1.0**%**), which were mainly represented by Diptera and Hemiptera (Fig. 7). The terrestrial insect contribution in yearling freshwater foragers (9.75%) was represented by species within Diptera, Coleoptera, Psyllidae, and Hymenoptera (85.7% of total terrestrial insects). The diets of sub-yearling brackish water foragers consisted of 14.6% terrestrial insects with the majority represented by Diptera (66.8%), Hymenoptera (8%), and Hemiptera (18.7%), specifically aphids (5.2%) and leaf-hoppers (7.3%). While sub-yearling freshwater foragers had the greatest species diversity in the terrestrial insect contribution (16.3%) over the other foraging groups, overall, they ate a large amount of Diptera (50.7%), Hymenoptera (6.6%) and Hemiptera (32.6%) where the Hemiptera composition consisted mainly of aphids (29.1%).

The final component of each of the diets that contributed to differences in composition were prey organisms that occurred either infrequently throughout the diets within a habitat, were present in low numerical abundance, or were difficult to identify due to digestion. This “other” category was rare within the diets of yearling brackish water foragers consisting of Gastropods (4.6% of total diet), specifically *Potamopyrgus antipodarum*, which also appeared in the diets of freshwater yearling fish in very low abundance (Fig. 7). The most numerically abundant organism within the “other” category were Collembola, which appeared in every foraging habitat and age class; however, the majority of Collembola (58.7%) were consumed by one yearling fish in freshwater (Fig. 7). Yearling freshwater foragers also selected unidentified eggs (Fig. 7).

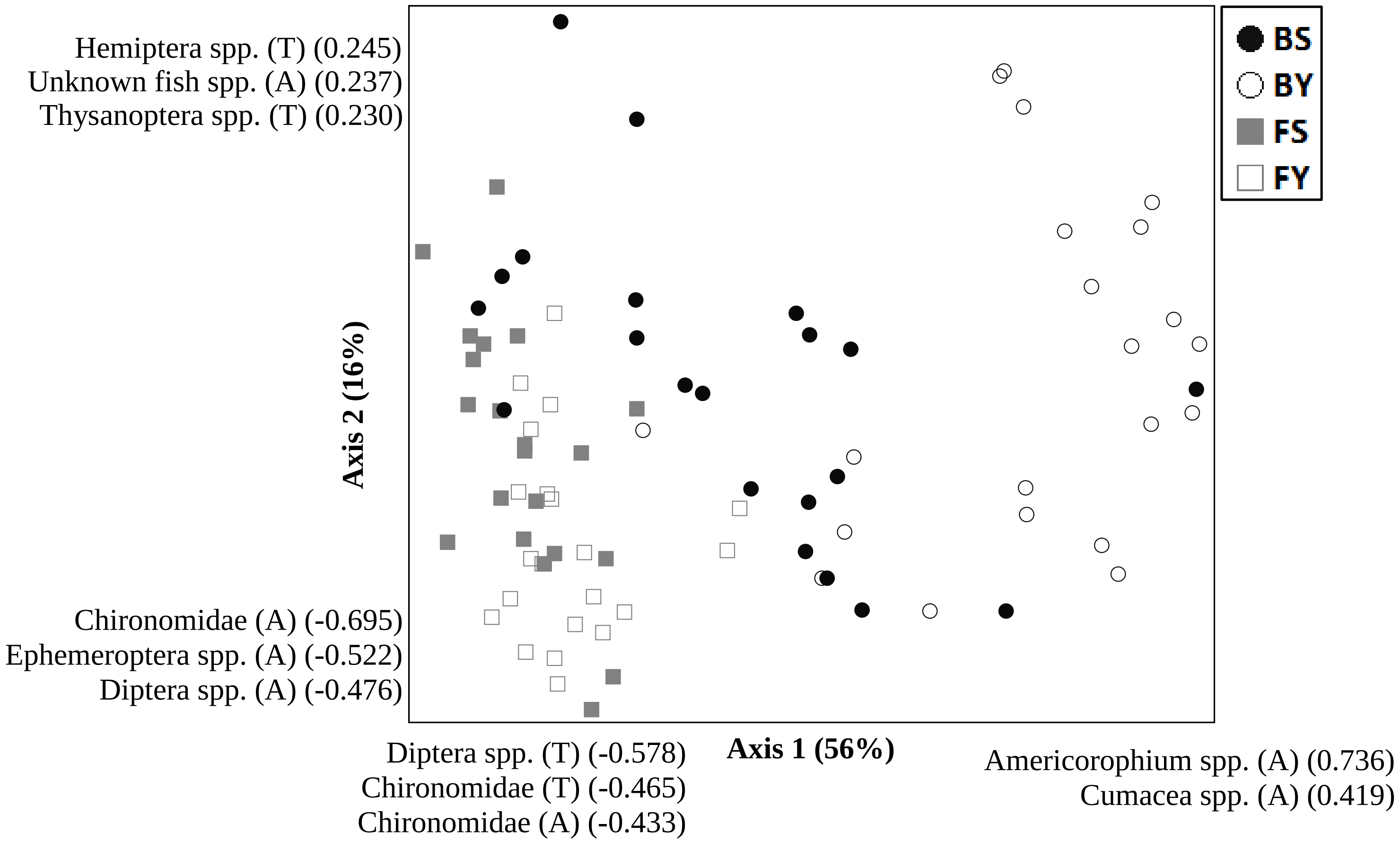

Figure 5. Nonmetric multidimensional scaling (NMDS) ordination plot of juvenile coho salmon diet for each age class (-S = sub-yearling, -Y = yearling) and habitat (B- = brackish, F- = freshwater). Parenthetic numbers with axis titles are the percent variation ($R^2$) explained by the axis. Parenthetic numbers with prey are the correlation coefficients. Parenthetic letters indicate whether the prey was terrestrial or aquatic. For Chironomidae spp., the "T" represents the adult phase and "A" represents the pupae and larval phase.

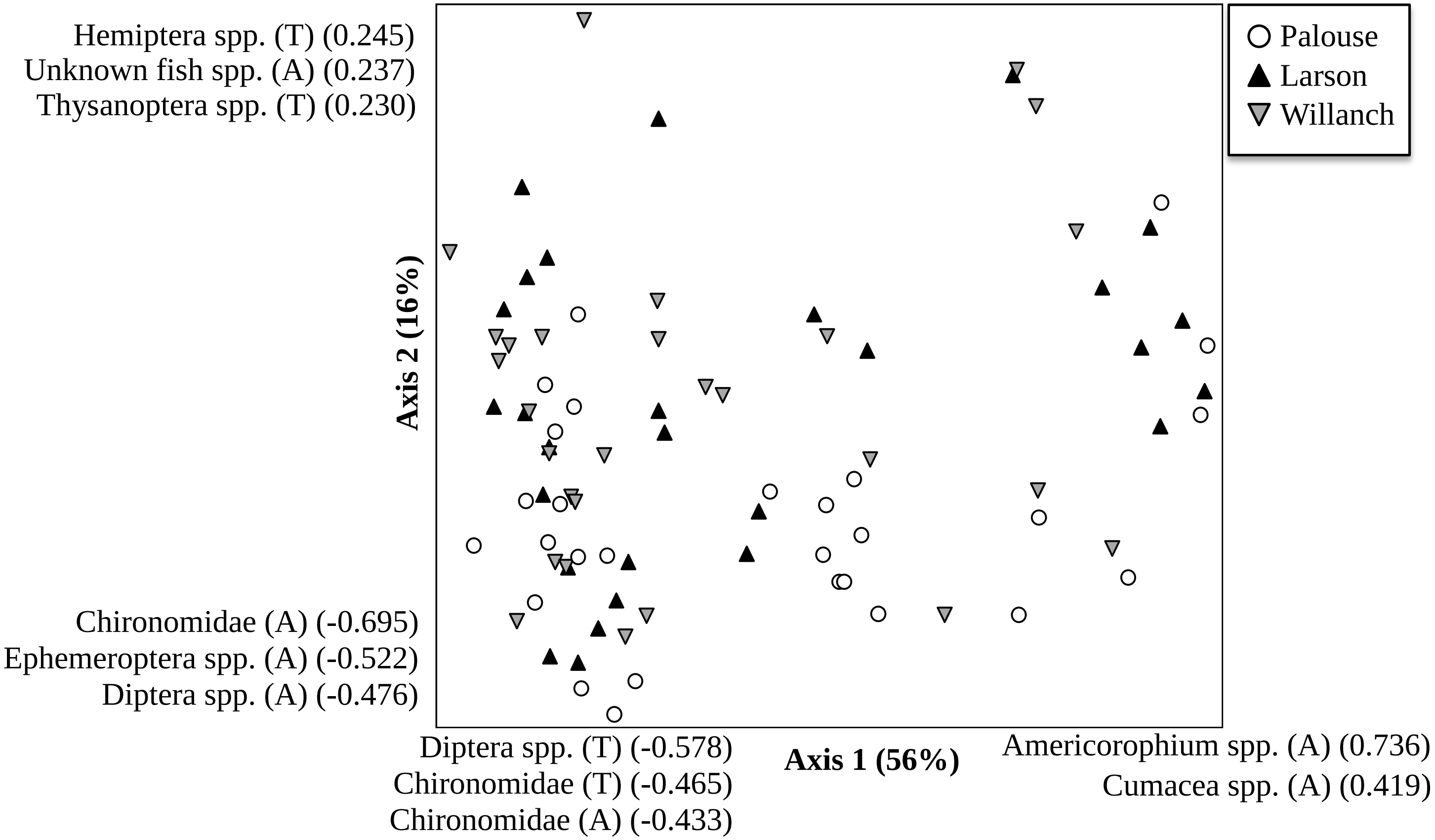

Figure 6. Nonmetric multidimensional scaling (NMDS) ordination plot of juvenile coho salmon diet for each creek. Parenthetic numbers with axis titles are the percent variation ($R^2$) explained by the axis. Parenthetic numbers with prey are the correlation coefficients. Parenthetic letters indicate whether the prey was terrestrial or aquatic. For Chironomidae spp., the “T” represents the adult phase and “A” represents the pupae and larval phase.

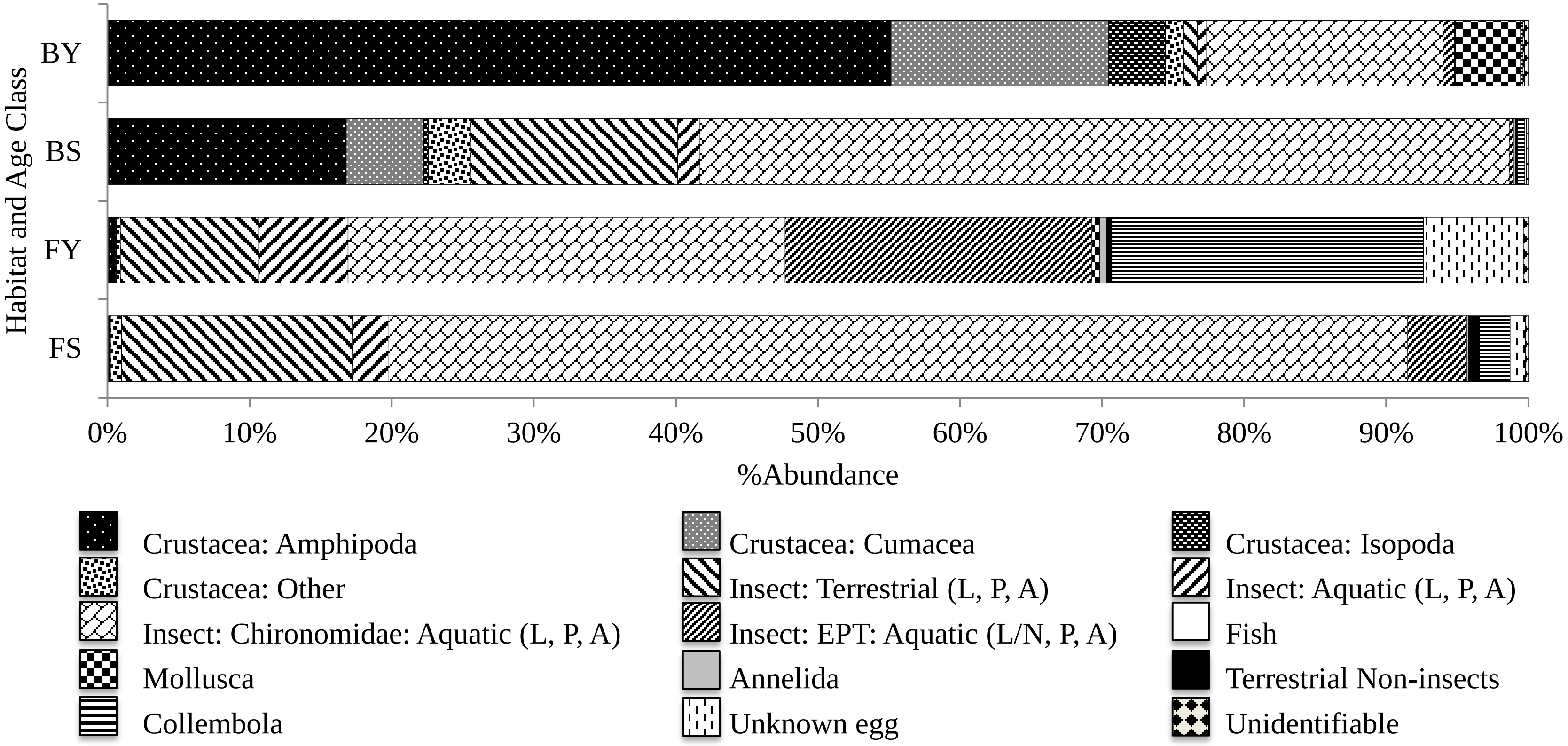

Figure 7. Percent prey abundance in diets of freshwater and brackish habitats and age classes (Bx = brackish water, Fx = freshwater, xY = yearling, xS = sub-yearling). Parenthetic letters refer to the prey developmental stages where L = larvae, N = Nymph, P = pupae, A = adult. "EPT" represents the Ephemeropterans, Plecopterans, and Trichopterans.

For the results of the IRI, the prey were split into the three dominant prey groupings determined by looking at the percent abundance: crustaceans, insects (aquatic and terrestrial), and "other" organisms that appeared either infrequently throughout the diets, were present in low numbers, or were unidentifiable due to digestion. Crustaceans were the most important dietary item within the diets of yearling brackish water foragers appearing in 100% of the diets and were significant both in numeric contribution and gravimetric contribution to the overall diet for an IRI of 84.6% (Table 3). Although crustaceans were also important in the diets of sub-yearling brackish foragers (32.8% IRI), the contribution of insects had the greatest IRI of 62.2%. For freshwater foraging coho salmon, insects were the most important prey items representing 60.1% IRI in yearlings and 83.1% IRI in sub-yearlings (Table 3). Yearling diets also had a significant portion of IRI attributed to the presence of "other" prey items (39.3% IRI), which could be attributed to the presence of large amounts of collembola and eggs (Fig. 7).

In all four foraging groups, the gravimetric contribution (%GC) of crustaceans always exceeds that of the numerical contribution (%NC). This held true within the freshwater foraging coho salmon despite consumption of a very small amount of crustaceans (yearlings = 13 and sub-yearlings = 14) in comparison to brackish water foragers (yearlings = 1,414 and sub-yearlings = 510). The inverse was observed regarding the insect contribution where the numeric contribution was greater than the gravimetric contribution. The relationship between %NC and %GC related to the contribution of "other" prey items to the diets of juvenile coho salmon imply that at low numerical abundance, these prey items have the potential to contribute substantially to the gravimetric contribution as observed in the diets of brackish water foragers (Table 3).

Table 3. Components of Index of Relative Importance (%IRI) for the prey sample groups found in diets of yearling and sub-yearling coho salmon foraging in brackish or freshwater habitat. %NC is the percent numerical contribution. %GC is the percent gravimetric contribution. %FO is the percent frequency of occurrence.

| Habitat and Age Class | Sample Type | %NC | %GC | %FO | %IRI |
|---|---|---|---|---|---|
| **Brackish water** | | | | | |
| Yearling: | Crustacean | 75.7 | 82.5 | 100.0 | 84.6 |
| | Insect | 19.1 | 4.8 | 66.7 | 8.5 |
| | Other | 5.2 | 12.7 | 71.4 | 6.9 |
| Sub-yearling: | Crustacean | 25.6 | 45.5 | 85.7 | 32.8 |
| | Insect | 73.4 | 42.3 | 100.0 | 62.2 |
| | Other | 1.1 | 12.2 | 71.4 | 5.1 |
| **Freshwater** | | | | | |
| Yearling: | Crustacean | 0.9 | 2.9 | 33.3 | 0.6 |
| | Insect | 68.4 | 50.3 | 100.0 | 60.1 |
| | Other | 30.7 | 46.8 | 100.0 | 39.3 |
| Sub-yearling: | Crustacean | 1.0 | 2.2 | 33.3 | 0.6 |
| | Insect | 94.7 | 68.5 | 100.0 | 83.1 |
| | Other | 4.4 | 29.3 | 95.2 | 16.3 |

# CHAPTER 4

## DISCUSSION

The results of this study indicate that juvenile coho salmon diet differs in composition with age (sub-yearlings vs. yearlings) and between the brackish and freshwater habitats of tide-gated streams in Coos Bay. Moreover, the total biomass of prey consumed and the relative body condition of fish, as indicated by Fulton's Condition Factor (K), were not different between brackish and freshwater habitats, but differed between yearling and sub-yearling fish. These findings suggest that early migrating sub-yearlings and yearling smolts diverge in their diets whether they occupy the same or different habitats in the stream to estuary transition zone. This difference in foraging preferences among juvenile coho salmon of different age classes and life histories underlines the importance of the rich mosaic of diverse habitats that characterize upper estuarine ecotones. The enhancement and maintenance of such transitional ecosystems is dependent on the unimpeded connectivity between both streams and estuaries, a key feature that is negatively affected by dikes, tide gates and other coastal infrastructure.

The most noticeable difference in juvenile coho salmon diet composition was the shift from aquatic insects in freshwater, specifically EPTs (i.e., mayflies, caddisflies and stoneflies), to crustaceans, specifically amphipods, in brackish waters. The downstream movement of yearling smolts could account for this transition in diet composition as they move from stream into estuarine habitats. In the case of sub-yearling fish, however, diets were more similar between fresh and brackish waters than it was the case for yearling individuals. One possible reason for that is the highly mobile behavior that Weybright (2011) observed among coho salmon fry in the tidally influenced reaches of these creeks, which would allow them relatively equal access through the day to both freshwater and brackish prey. If fish are not moving back and forth between both habitats, then another possible explanation for the presence of freshwater prey in the stomachs of fish captured in brackish waters could be the partial tolerance to salinity that some insects have (Lancaster and Downes 2013). Most brackish water diet samples containing high proportions of EPTs for both sub-yearlings and yearlings were from Willanch Creek. This creek has a muted-tide gate at its mouth, which allows for the less restricted intertidal exchange among all three study streams. At low tide, Willanch Creek experienced the highest freshwater discharge into the estuary and did not retain a brackish water lens above the tide gate; the unidirectional downstream currents that its tide gate allowed during ebb tides were likely to carry more freshwater invertebrates into the upper estuary than may have been possible in the other two creeks.

Crustaceans of the genus Americorophium spp. were not present in the diets of any sub-yearling or yearling fish captured in freshwater. In brackish waters, *Americorophium salmonis* and *A. spinicorne,* were the dominant prey item in yearling fish but the second most common prey item in sub-yearlings. These epibenthic crustaceans constitute important prey for juvenile salmonids in the intertidal zones of the Pacific Northwest and are often caught by the fish as they crawl over the substrate in search of mates (Bottom and Jones 1990, Levings et al. 1991, Howe et al. 2014). *Americorophium* spp. are tolerant of a wide range of salinity concentrations, feed on detritus and require the sandy-mud substrates of intertidal depositional habitats to dig the U-shaped tubes they live in (Higley et al. 1984).

Although aquatic midges were important in the diet of all four fish groups, the freshwater diet samples contained midge larvae, pupae and adults in relatively similar numbers, whereas mostly adult midges were present in brackish water samples. Chironomids, non-biting small midges, are often preyed upon as emerging or newly emerged adults due to their limited mobility at that time and increased visibility to fish when at the air-surface interface (Lott 2004, Ramirez 2008). While some aquatic midges are very tolerant to saline conditions and can be found in estuarine habitats, the fact that midges in brackish water fish diets were almost exclusively represented by adult specimens suggest that this developmental stage was the one more readily available to fish in this environment. Aquatic and terrestrial Diptera, in particular Chironomids, have been consistently reported in other studies as important components of juvenile salmonid diets (Tschaplinski 1987, Levings et al. 1991, Shreffler et al. 1992, Miller and Simenstad 1997, Sommer et al. 2001, Gray 2005, Roegner et al. 2010, Cordell et al. 2011). Chironomids are found worldwide and their larvae occupy a diverse array of aquatic habitats including intertidal environments and hydric soils. Although their life histories are quite variable, Chironomids are available to fish as larvae, pupae and adults throughout spring and summer (Ferrington et al. 2008).

The observed differences in juvenile coho salmon diet could be attributed to both the ontogenetic development of the young fish and their shifts between various nursery habitats, which support different invertebrate communities that change in composition over space and through time (Power and Dietrich 2002, Hodgson et al. 2011). Juvenile coho salmon adopt different foraging strategies based on their hierarchical positions relative to that of other members of their cohort, and these strategies shift over time as fish grow in size and also in response to temporal changes in invertebrate abundance (Nielsen 1992). As riparian vegetation communities mature and change with the seasons so do their insect communities and the abundance and composition of the resulting terrestrial infall available to fish (Mason and Macdonald 1982, Edwards and Huryn 1996, Kawaguchi and Nakano 2001). Despite the fact that the sampling dates of yearling and sub-yearling coho salmon in my study overlapped, most yearling smolts were sampled from early to mid-spring while the majority of sub-yearling individuals were sampled nearly 1.5 to 2 months later. Over this six to eight week period, I observed a slight increase in the abundance of terrestrial insects in the diets of sub-yearling coho salmon, independently of habitat, when compared to their older counterparts. This difference could be attributed to a decline over time in the abundance of the EPT taxa and the amphipods that sub-yearling individuals relied heavily on in freshwater and brackish water respectively. Although most of the terrestrial invertebrate input in either habitat consisted of true flies, sub-yearling coho salmon in freshwater ate large numbers of aphids and had a more diverse diet than any of the other three fish groups. In brackish waters, juvenile coho salmon of both age classes also consumed aphids but to a lesser degree than sub-yearlings in freshwater; their diets included higher proportions of other hemipterans and leaf-hoppers.

In this study, I observed a significant difference in fish body condition between coho salmon of both age classes. Thus, yearlings had significantly lower K values than sub-yearlings, which may be explained by the relatively rapid elongation of the caudal peduncle during the smolting process (Rodgers et al. 1987, Winans and Nishioka 1987). As juvenile salmonids grow, they undergo morphological changes that result in: a) body elongation, which improves swimming efficiency and maneuverability (Glova and McInerney 1977); b) gape size and inter-gill raker space expansion, which facilitates the consumption of larger prey (Eggers 1977, Wańkowski 1979); and c) visual acuity increase, which enhances prey detection and acquisition (Dunbrack and Dill 1983, Li et al. 1985). Dissimilarities in diet caused by changes in behavior and/or growth reduce intraspecific competition through resource partitioning (Keast 1985). Although juvenile salmonids are visual and opportunistic foragers, their distribution and habitat selection varies with fish size, with smaller individuals occupying channel margins and other areas of reduced water velocity and larger fish selecting deeper and faster flowing waters (Chapman 1966, Healey 1982, Nielsen 1992, Quinn 2005, Eaton 2010). In this study, such spatial distribution may explain why sub-yearling foragers consumed more prey associated with the air-water interface (emerging aquatic invertebrates or terrestrial infall), whereas the diet of yearlings was characterized by types of prey that are available as drift in the water column or on the epibenthos.

According to theories on optimal foraging, it is in an organism's best interest to either select the largest prey available, change diet preferences in response to availability or pursue easy-to-acquire prey to maximize the energy intake needed for growth and survival (Eggers 1977, Stephens et al. 2007). While the quantity of prey available to juvenile fish is important, bioenergetics models indicate that the quality of prey is a better determinant of potential growth and to increase energy return a fish should select for the largest available prey (Gray 2005, Roegner et al. 2010, Wipfli and Baxter 2010). Energy attributed to insects, especially terrestrial insects which typically have less water content, is estimated to be nearly double that of crustaceans in kJ per gram of dry weight (Gray 2005). For example, Gray (2005) determined that insects such as adult Chironomids contribute 25.56 kJ/g dw per individual while crustaceans, like *Americorophium* spp., contribute 13.42 kJ/g dw each. In my study, when the total dry weight biomass of a prey type (e.g., crustaceans, aquatic insects, terrestrial insects) is divided by the number of organisms within the group, the mean dry weight biomass of a crustacean consumed by sub-yearling fish was 1.3 - 1.5 times that for the average insect (terrestrial and aquatic combined) in either habitat. Based on Gray's (2005) findings and my estimated mean dry weight biomass, there is an energetic advantage for sub-yearling coho salmon to select insects over crustaceans because the former may provide almost twice as much energy per gram of dry weight than the latter. In the case of yearling fish, the ratio of mean dry weight biomass of crustaceans in their stomach samples was 2.1 - 2.2 times that of insects. This means that yearlings need to consume twice as much crustacean as insect biomass to get the same benefits in terms of energy. These assumptions do not take into account the energy needed for catabolism and metabolism, the inclusion of which would be necessary to gain a full understanding of how prey nutritional value ends up influencing fish diet and growth (Diana 2004). The use of existing length to dry mass regressions to determine prey weight would result in a more accurate estimate of energetic contribution as it considers the actual weight of the prey prior to digestion (Benke et al. 1999). Unfortunately, funding limitations prevented me from collecting drift, terrestrial infall and benthic invertebrate data to determine actual prey availability. These data would have been critical to the understanding of fish prey preferences and assessing the foraging quality of freshwater and brackish water habitats in this study.

Given the regulated nature of the three study creeks, it is likely that their tide gates, which are different in design and operation, shaped the nearby invertebrate communities in contrasting ways. In general, tide gates interfere with the normal circulation of water in the tidally influenced reaches of coastal creeks. They induce changes to the chemical, biological, and physical parameters of the ecosystem while physically becoming a barrier to the movement and distribution of salmonids and other aquatic organisms (Giannico and Souder 2004). The results of the MRPP tests of the NMDS ordinations revealed differences in fish diet composition in relation to both age class and habitat type, some of which could be attributed to the effects of tide gates on hydrological conditions. For example, the muted tide gate in Willanch Creek was the one that allowed for the most natural daily tidal exchange between both its sides, and its fish diet samples were the only ones that contained the isopod *Gnorimosphaeroma oregonensis* as well as harpacticoid copepods in high numbers while lack any invasive New Zealand mud snails, *Potamopyrgus antipodarum,* in the particular case of yearlings from brackish waters. By contrast, the restricted tidal exchange allowed by the side-hinged tide gate in Larson Creek may be in part responsible for the lack of cumaceans found in the diet samples of yearling fish captured in the limited brackish water habitat that developed upstream from the tide gate.

The results of my study provide insight into sub-yearling and yearling coho salmon diets in main-channel habitats of the stream-estuary ecotone in tide-gated coastal creeks. I observed that there was great variability in diet composition in juvenile coho salmon between creeks, habitats, and age classes over a short time frame of 2.5 months and in close spatial proximity to one another. Other studies have demonstrated that dynamic estuarine conditions, often exacerbated by anthropogenic alterations, result in spatial and temporal differences in estuarine residence patterns and densities of juvenile salmonids and other aquatic organisms (Crone and Bond 1976, Craig and Crowder 2000, Healey 1982, Gray 2005). Identifying ecosystem mechanisms that influence the distribution and residence of juvenile salmonids in intertidal habitat is imperative as projections for climate change predict that coastal lowland areas will undergo vast transformations due to sea levels rise, further affecting coastal structure and resident biological communities (Flitcroft and Giannico 2013). Future research examining not only the diets of juvenile coho salmon foraging in intertidal habitats, but also seasonal transitions in prey availability (e.g., drift, terrestrial infall, benthic) and prey abundance would provide information on the foraging quality of those habitats and their exploitation by early-migrating juvenile salmonids. In addition, expanding the focus of this research to include natural intertidal habitats contrasted with those that are regulated by tide gates would help us better understand the impact that different types of tide gates have on biotic communities and hydrological conditions (e.g., flow, chemistry, temperature, tidal exchange) where coastal streams meet their estuaries. Efforts to maintain connectivity and enhance habitat diversity in the stream-estuary ecotone is important towards sustaining multiple life history strategies of juvenile coho salmon, thereby strengthening the genetic diversity and resiliency of their populations (Bottom et al. 2009, Healey 2009).

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