AN ABSTRACT OF THE THESIS OF

Angelica Munguia for the degree of Master of Science in Fisheries Science presented on September 11, 2019.

Title: Feeding Ecology and Food Web Linkages of Yearling Chinook Salmon (*Oncorhynchus tshawytscha*) Migrating Through the Lower Columbia River and Estuary.

Abstract approved:

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Jessica A. Miller

The Columbia River Basin historically supported abundant populations of Pacific salmon (*Oncorhynchus* spp.) but, largely due to anthropogenic influence, many populations are now listed as threatened or endangered under the U.S. Endangered Species Act. Habitat restoration efforts have been a critical component of salmon recovery plans. However, although the importance of shallow-water wetland habitats is well documented for sub-yearling Chinook Salmon (*O. tshawytscha*), or individuals that spend <1 yr. in freshwater before migrating to the ocean, their importance is less clear for yearling Chinook Salmon, or individuals that migrate more rapidly and at larger sizes after 1 yr. in freshwater. Therefore, we need a better understanding of the importance of wetland habitat for yearling Chinook Salmon. The overall goal for this thesis was to determine if yearling Chinook Salmon rely on wetland-derived prey during their ocean-ward migration and whether their foraging habits change as they migrate through the Lower Columbia River and Estuary (LCRE), which extends from the lowermost mainstem

dam (Bonneville) to the mouth of the estuary. Therefore, I examined stomach fullness (relative indicator of feeding success), diet composition, and stable isotope signatures ($\delta^{13}C$ & $\delta^{15}N$) of prey supporting migrating yearling Chinooks.

. Yearling Chinook were collected in April and May, 2016 and 2017, from three riverine sites and at the mouth of the estuary during peak yearling Chinook migration. Yearling Chinook collected in 2017 had greater stomach fullness and were in better condition than those collected in 2016. Additionally, mean condition and stomach fullness decreased as fish moved closer to the ocean. Yearling Chinook diet composition varied across sites and between years, but yearling Chinook consumed insects (primarily wetland-derived prey) more frequently in 2016, when dipterans occurred in 60-100% of the diets, than in 2017 (dipteran mean = 12%). In contrast, amphipods (benthic prey) were consumed more frequently in 2017, when they occurred in 85-100% of diets compared to 2016 (amphipod mean = 55%). $\delta^{13}C$ values of prey from 2016 diets were more reflective of the natural variation observed in prey collected in the field compared to 2017. These differences could be related to flow since 2017 was a higher flow year than 2016.

Based on biomass, benthic prey were identified as most important in yearling Chinook salmon diets, contributing 4x more than terrestrial prey taxa, which are primarily wetland-derived. However, based on energy density (kJ/g of fish meal), benthic and predominantly wetland-derived prey were equally important. Thus, the use of energy density to represent diet data provides an informative metric to evaluate wetland habitat subsidies, especially when some taxa have caloric values three times greater than others.

Feeding Ecology and Food Web Linkages of Yearling Chinook Salmon (*Oncorhynchus tshawytscha*) Migrating Through the Lower Columbia River and Estuary

by
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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.

Angelica Munguia, Author

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CONTRIBUTION OF AUTHORS

Dr. Jessica Miller was involved with the project development, design, analysis, and writing of Chapters 1, 2, and 3. Dr. Laurie Weitkamp was involved with project development, design, and data collection for Chapter 2. Dr. Tawnya Peterson provided additional data for analysis and inclusion in Chapter 2.

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Chapter 1 : General Introduction

Restoration ecology is a relatively recent field of study that has developed, in part, due to the declines in the population abundance of many taxa. U.S. Endangered Species Act (ESA) listings are often related to anthropogenic activities, which can result in habitat loss and associated declines in population size. Restoration has been defined as returning an impaired habitat back to its historical state, typically in relation to a reference site. How do we know if an area has been restored? There are many challenges associated with assessing habitat and restoration successes. Lack of baseline information or reference sites present a challenge because there are not appropriate standards for evaluation after restoration.

Identification of appropriate standards to measure restoration success is critical. Also, it is important to understand the time frame necessary to realize restoration benefits because a year to many years are often necessary to detect positive changes. Another challenge is the cost of restoration projects, which can require millions of dollars (US), and often include no funds for collection of baseline data or long-term monitoring. In these cases, it is extremely difficult to measure success. Learning from failures and successes of previous restoration projects is key since approaches that were effective in one system may not be appropriate in another system. Additionally, fragmentation of quality habitat

can result from numerous, small restoration actions within in large systems, which reduces connectivity of habitat and can perpetuate negative impacts to populations.

The high level of uncertainty associated with habitat restoration coupled with environmental variation have led to the consideration of other approaches and outcomes. The concept of novel ecosystems, which is defined by Hobbs et al. (2009) as “the development of ecosystems that differ in composition and/or function from present and past systems”, and is increasingly recognized as an almost inevitable consequence of changing species distributions and environmental alteration through climate and land use. In systems that have become extremely altered and can no longer be returned to their historical state, other approaches for restoration must be considered to improve habitat and support functions for various taxa.

In the Oregon and Washington, there have been many successful estuarine restoration projects focused around salmonid recovery, which begin to show positive changes in as little as a year. Many of these restoration projects involve removing levees, dams, or dykes in order to improve hydrological connection to the main stem (Shreffler et al. 1992; Simenstad and Thom 1996; Miller and Simenstad 1997). Some examples of successful restoration projects in the Pacific Northwest (PNW) include the Salmon River estuary and the Elwha River. The Salmon River estuary is a well-studied system that offered a unique opportunity to examine how dyke and levee removal affected marsh recovery over time and space. Ecosystem responses were observed with rebounding fish populations, shifts in prey resources, and returns of various salmon runs (Gray et al. 2002;

Bottom et al. 2005). From 2011-2014, the Elwha River dams were removed, which allowed for the formation of new estuarine habitat and restored access to historical salmon habitat. Within a few years, there were increases in salmonid populations and fish recolonized previously inaccessible areas of the river (Thornton et al. 2015; Shaffer et al. 2017). These successes highlight how species, including ESA-listed species such as Oregon Coast Coho, can show signs of recovery relatively soon after restoration.

There are many ESA-listed species with complex life histories that need a variety of habitats in order to complete their life cycle. For example, anadromous species, such as Pacific Salmon, rear in freshwater, spend most of their life in marine waters, and then return to freshwater to spawn. Early research on salmonids was primarily focused on their freshwater phase of life, even though anadromous fish migrated through estuarine habitats and would spend years in the ocean (Neave 1953; Bottom 1997). A shift in research occurred, around the 1970s, when researchers began to study estuarine habitats since little was known about how salmon used this transitional habitat. Since then, studies have been done on both life histories of Chinook salmon, sub-yearling Chinook (emigrate at < 1-year old) and yearling Chinook (emigrate at 1+-year old) although most of the focus has been on sub-yearling Chinook. Sub-yearling Chinook use shallow-water estuary habitat longer than yearling Chinooks, which tend to stay in the deeper waters and move quickly through the system (McCabe et al. 1983; Dawley et al. 1984).

There are particular challenges to evaluating habitat for migrating species due to their limited residence in certain habitats. This short-term residence is why it is critical to identify metrics that can be informative over relatively short periods of time. Measuring growth rates, for example, can be difficult when the time spent in a habitat is so short and there are no detectable differences in size. One method for studying fast moving species is by following a cohort where individuals that are similar in age are sampled as they migrate through a system, which can provide information on movement, growth, feeding habits, and survival along a continuum.

The Columbia River has been a focus for studying salmonid recovery due to population declines in ESA-listed species. Dredging, damming, diking, and both urban and agricultural development have all led to the loss of habitat (Quinn 2005). With over 70% of wetland habitat in the lower Columbia River estuary (LCRE) lost, many salmonid populations have been ESA-listed as endangered or threatened (Sherwood et al. 1990) (Brophy et al. 2019). Of the salmonids, Chinook or “King” Salmon has been the most studied in estuaries since they are believed to use this habitat the most (Dawley et al. 1984). Currently, five Chinook Salmon Evolutionarily Significant Units are ESA-listed with the Interior stocks being at the highest risk of extinction and they include Snake River Spring/Summer and Mid-Upper Columbia River Spring Chinook Salmon.

Study Objectives

The primary objective of this study was to evaluate the ecological benefits of habitat restoration actions in the LCRE for Interior spring Chinook Salmon by

characterizing their feeding habits in order to quantify their reliance on wetland-derived prey. Snake River Spring/Summer and Mid-Upper Columbia River Spring Chinook Salmon have some of the lowest survival to maturity in the Columbia basin (Miller et al. 2014). Information regarding estuarine use by yearling Chinook Salmon has been limited to the estuary and lower river (0-75 Rkm), because most of the research has focused on sub-yearling Chinooks throughout the LCRE (Dawley et al. 1984; Weitkamp et al. 2012; Weitkamp et al. 2015).

For this thesis, we designed a longitudinal study to assess habitat use and characterize feeding ecology of yearling Chinook by following cohorts through time and space as they migrated through the LCRE. Our project objectives were to (1) describe yearling Interior Columbia River Spring Chinook Salmon size and condition as they move through the LCRE; (2) characterize their feeding habits (diet composition and stomach fullness) during emigration (April-May) over two years (2016-2017); (3) determine the contribution of prey from distinct habitat groups in the yearling Chinook diets at four sites during emigration in order to quantify the relative dietary importance of wetland habitat and (4) identify nitrogen and carbon signatures of prey supporting their recent meals in order to characterize changes in carbon sources supporting Chinook Salmon prey across sites over two years (2016 – 2017).

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Chapter 2 : Food Habits of Interior Spring Chinook Salmon (*Oncorhynchus tshawytscha*) Migrating through the Lower Columbia River and Estuary (LCRE)

Introduction

Pacific salmon (*Oncorhynchus* spp.) are highly regarded for their ecological importance, cultural significance, and economic value (Quinn 2005). However, many Pacific salmon populations are in decline due to several factors, including hydropower systems, development, logging, diking, and land conversions, among others (Raymond 1979; Nehlsen et al. 1991; Bottom et al. 2005). To mitigate the negative impacts on Pacific salmon populations, some recovery programs have focused on estuarine and freshwater restoration. However, detecting biological and environmental benefits that result from habitat restoration is challenging, especially for fast moving and highly migratory species, such as yearling Chinook Salmon (*O. tshawytscha)*. Improved understanding of habitat use can aid evaluation of habitat restoration and is critical for science-based restoration planning and prioritization.

Restoration of estuaries can benefit juvenile salmonids by increasing available habitat and prey, which can result in higher growth and survival rates (Gray et al. 2002; Magnusson and Hilborn 2003; Cordell et al. 2011). Estuaries are areas of high productivity that provide nursery habitat for many commercially important fish and invertebrate species (Beck et al. 2001). The characterization of the ecological functions of wetlands along the transition from freshwater to marine waters could identify areas of energy dense prey for migrating salmonid species. An important consideration is that migrating juvenile salmon do not need to directly occupy marsh habitats in order to benefit

because tidally-influenced marshes can export invertebrate prey to main channel habitats (Simenstad and Cordell 2000; Ramirez 2008; Bottom et al. 2011). These wetland subsidies can contribute prey for migrating juvenile salmonids, thereby indirectly influencing their growth and survival.

In the lower Columbia River and estuary (LCRE), flow alterations and wetland habitat loss are factors hypothesized to be responsible for the decrease in macro-detrital input from localized wetland sources, which could negatively impact juvenile salmon (Bottom and Jones 1990; Sherwood et al. 1990; Shreffler et al. 1992; Maier and Simenstad 2009). A theorized organic carbon budget comparing pre-1870 to the present estuary indicates that there have been increases in exogenous phytoplankton and detritus but a decrease in wetland macro-detritus, which is known to support Pacific salmonids in the estuaries (Simenstad et al. 1990; Maier and Simenstad 2009). Wetland-derived prey (i.e. food sourced from vascular plants) are also known to be high energy density, which contribute to greater growth rates (Maier and Simenstad 2009). Terrestrial and emergent insect prey can have energy densities five times greater than planktonic and benthic prey (David 2014). Overall, systems with greater estuarine habitat area are associated with greater survival in juvenile sub-yearling Chinook Salmon, emphasizing the importance of this habitat (Magnusson and Hilborn 2003).

Chinook Salmon is an anadromous species and exhibits complex life histories that require multiple habitat types for survival and reproduction. In the Columbia River Basin, there are currently five Evolutionary Significant Units of Chinook salmon listed as either threatened or endangered under the Endangered Species Act: Lower Columbia River, Snake River spring and summer, Snake River fall, upper Columbia River spring, and

upper Willamette River (Ford 2015). Chinook Salmon in the Columbia River Basin display two types of juvenile migration patterns, yearling Chinook and sub-yearling Chinook. Yearling Chinook spend their first year of life in the river before migrating to the ocean while sub-yearling Chinook emigrate during their first year of life and are known to spend weeks to months in the estuary (Moran et al. 2012). Yearling Chinook Salmon tend to migrate through estuaries faster and earlier and spend more time in deep, main stem habitats than sub-yearling Chinooks (Raymond 1979; Dawley et al. 1984; Fresh et al. 2005; Harnish et al. 2012; Roegner et al. 2016).

Survival of juvenile Chinook Salmon during estuarine and early ocean residence, which is often cited as a “critical period,” can be highly variable by year, population and life history (Hjort 1914; Beamish and Mahnken 2001; Houde 2008). Prior research determined that size at capture and marine growth rates after 30 days of ocean residence were positively related to survival of Interior Columbia River spring Chinook Salmon (Tomaro et al. 2012; Miller et al. 2014). These Interior stocks (Mid & Upper Columbia Spring and Snake River Spring/Summer populations) also have some of the lowest survival to maturity rates (Miller et al. 2014). These low rates could be a result of the greater number of dams these fish need to pass as they emigrate, although alterations to spillways and turbines on dams have improved survival through the hydropower system (Trumbo et al. 2014) (Ferguson et al. 2007). However, little is known about yearling Chinook survival and habitat use through the LCRE, creating a knowledge gap regarding factors affecting growth, foraging, and migration through this system.

Examining the food web in order to identify habitat use by fast moving, highly migratory, yearling Chinook Salmon is challenging and requires a suite of tools that can

elucidate changes in feeding at various spatial and temporal scales. Traditional diet analysis provides a snapshot of the last meal, up to 24 hours, while stable isotope analysis of various tissues can provide information on its assimilated diet over time (Baldwin et al. 2008; Benkwitt et al. 2009; Heady and Moore 2013). Carbon stable isotope values are indicators of an organism's diet since dietary carbon becomes incorporated into the consumers tissue with relatively minimal fractionation. These values can help identify dominant carbon energy pathways in food webs. For estuarine studies, it is important to note that $\delta^{13}C$ become less negative as you move from freshwater to marine and terrestrial to aquatic habitats (Fry and Sherr 1989; Chaloner et al. 2002). An important thing to consider is that when using stable isotopes in food web studies, the variability within and between taxa can be high. This is likely due to seasonality and variation in the primary producers available to the prey. In a study conducted in the LCRE, results indicated considerable isotopic difference among and within groups of primary producers which is likely be due to the available dissolved inorganic carbon (Maier et al. 2011).

Muscle, liver tissues are commonly used for stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) in aquatic food web studies. This is because they integrate diet over weeks to several months, which would not be useful in our study since we know yearling Chinook Salmon can migrate from Bonneville Dam to the lower estuary in one to ten days (Carter et al. 2009). Other tissues, fin, blood plasma, and mucus, are not commonly used for in food web studies because it can be difficult to acquire enough material for analysis. However, these tissues have faster turnover rates, days to weeks, which makes them beneficial when investigating feeding habits of highly migratory fish moving through a gradient of freshwater to marine (Church et al. 2009; Heady and Moore 2013). Even though these

tissues can have a faster turnover rate, it is important to consider these yearling Chinook can have variable stable isotope signatures to start with since most are coming from hatchery where their feed may not be the same. This dissimilarity in stable isotope values for hatchery feed can make it difficult to interprate changes when there is not an appropriate baseline to compare to.

A more appropriate approach for food web studies of fast-moving fish is to analyze their stomach contents to examine $\delta^{13}C$ of their recent prey. A study conducted off the Pacific coast of Japan examined stable isotope ratios of gut contents to compare the feeding habitats of sea urchins in two distinct habitat types and found that although *Corallina* spp. were dominant in one habitat where urchins were collected, the urchins were selectively feeding on drifting *Sargassum* spp., even when scarce (Yatsuya and Nakahara 2004). These results highlight the value of examining individual taxa from recent meals to characterize changes in the carbon sources supporting salmon as they migrate in order to estimate wetland habitat use. We expect the lighter the $\delta^{13}C$ value, the greater likelihood the prey was dependent on freshwater vascular plants and other terrestrial plants found in wetlands.

The overall goal of this research is to evaluate the ecological benefits of habitat restoration actions for juvenile spring Chinook Salmon in the LCRE. My research focused on assessing short-term habitat use by Interior Columbia River Spring Chinook Salmon. My research objectives are to: 1) describe Interior Columbia River Spring Chinook Salmon size and condition as they move through the LCRE; 2) characterize their feeding habits (diet composition and stomach fullness) during emigration (April-May) over two years (2016-2017); 3) determine the contribution of prey from distinct habitat groups in

the yearling Chinook diets at four sites during migration in order to quantify the relative dietary importance of wetland habitats; and 4) identify nitrogen and carbon signatures of prey supporting their recent meals in order to characterize changes in carbon sources supporting Chinook Salmon across sites over two years (2016 – 2017).

We hypothesized that yearling Chinook collected from sites with greater adjacent wetland habitat (Lower and Middle River) would have a greater proportion of energy density derived from terrestrial habitat prey in their diets and greater stomach fullness. We expected to see a gradient in carbon stable isotope values of prey collected from the stomach contents of yearling Chinook, with upriver sites having lighter $\delta^{13}C$ values (< -24‰) and heavier $\delta^{13}C$ values (> -20‰) at the estuary mouth.

Methods

Study Area and Field Collections

The field sampling was designed to follow annual cohorts of Interior Columbia River Spring Chinook Salmon through the Lower Columbia River and Estuary (LCRE) (Bottom et al. 2011; Simenstad et al. 2011). We define the LCRE as the river below the lowermost mainstem dam, Bonneville Dam, to the ocean. Fish collections were made at four sites, including three freshwater tidal sites and one brackish site: an Upper River site (UR) at ~210 Rkm (45° 33.4' N, 122° 13.7' W); a Middle River site (MR) at ~92 Rkm (46° 10.2' N, 123° 5.6' W); a Lower River site (LR) at ~61 Rkm (46° 13.3' N, 123° 25.9' W), and a site at the Estuary Mouth (EM) at ~13-17 Rkm (46° 13.6' N, 123° 56.0' W) (Figure 2.1).

Interior Columbia River yearling Chinook Salmon migrate to the ocean from April-June (Tomaro et al. 2012; Miller et al. 2014; Weitkamp et al. 2015). In 2016 and 2017,

fish were collected from April to June; however, yearling Chinook catches were low in June and were not used In 2016 and 2017, yearling Chinook Salmon were collected using a two-boat tow net at the upper three sites and a fine-mesh purse seine (10.6-m deep and 155-m long, with stretched mesh opening 1.7-cm; knotless bunt mesh 1.5-cm) in the estuary. A small tow net (2.9-m deep and 6-m wide mouth, with a total length of 13-m, 1 ¼" mesh near mouth and ½" in cod-end) was used in 2016 and April 2017. However, a larger tow net (3.6-m deep and 9.1-m wide mouth, with a total length of 16-m) with the same mesh size was used in May and June 2017. Switching to a larger tow net was done to improve capture rates of the Interior yearling Chinook Salmon. Duration of each tow net set was 10 min., with boats oriented against river flow at an average speed of 3.5 and 2.3 knots for the small and large tow nets, respectively. Tow net collections occurred during daylight hours. Collections using the purse seine were restricted to early morning low tides (for detailed methods see Weitkamp et al. 2012).

Juvenile salmonids were identified, measured (fork length, FL, mm), and placed on ice onboard after being anaesthetized with tricaine methanesulfonate (MS-222). Juvenile salmonids that were not needed for further analyses were allowed to recover and were released. At the end of each day, fish were further processed on shore. Caudal fin clips were preserved in 95% ethanol for genetic stock identification (GSI), coded wire tags (CWT) and Passive Integrated Transponder (PIT) tags were removed (if present), and fish were stored at -80°C. Frozen fish were then transported to National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center (NWFSC) Research Station in Newport, Oregon where the fish were re-measured (0.1 mm), weighed (0.01 g), and the stomach was removed and stored in a -20°C.

Surface Prey Drift

In order to provide a snapshot of the potential salmon prey drifting at the surface, a neuston net (500-µm mesh), with a General Oceanics flowmeter, was towed for 5-min during every fish collection trip at each of the four sites. Neuston samples were collected immediately prior to fish collection and preserved in 10% buffered formalin. In the laboratory, potential salmon prey were counted, weighed, and identified to lowest taxonomical level practicable using a stereoscope (Borror et al. 1989; Merritt and Cummins 1996). Subsamples were collected by using a Folsom plankton splitter along with a 1-mL Hensen-Stempel pipette (when needed). Data were extrapolated to organism number m^{-2} and biomass $mg \cdot m^{-2}$ based on counts and weights over the total area sampled using a flow meter.

Juvenile Chinook Salmon Analysis

Genetic stock identification (GSI) was determined using Single Nucleotide Polymorphisms (SNPs), which allow for automated, rapid genotyping (Schlötterer 2004; Campbell et al. 2015). A “Genotyping-in-Thousands by sequencing” (GT-seq) method that uses next-generation sequencing of multiplexed PCR products to generate genotypes from relatively small panels (50–500) of targeted single-nucleotide polymorphisms (SNPs) was used (Van Doornik et al. 2019). The focus of this study was on fish assigned to an Interior Columbia River Spring Chinook Salmon stocks, which includes Snake River Spring and Middle & Upper Columbia River Spring. The average

posterior probability of genetic assignment as Interior Columbia River Spring Chinook Salmon was high (mean = 0.926 +/- 0.124 SD). Yearling Chinook Salmon catch at all sites in both years was dominated by Interior Columbia River Spring Chinook Salmon stock (>74% of the total) (Table 2.1).

To evaluate condition of yearling Chinook Salmon as they moved through the LCRE, an index was estimated based on the residuals from a linear regression of log-transformed FL and mass (R^2=0.88). Fish condition index values by site and month were compared within and between years using Analysis of Variance (ANOVA) followed by Tukey's Honestly Significant Difference (HSD) for pair-wise comparisons to determine if fish condition differed among sites within each year and if there were any overall condition differences across the two different years.

Diet analysis

We examined the feeding habits of yearling Chinook Salmon by quantifying individual stomach fullness and diet composition. Stomach fullness was calculated based on Eq. 1.

$$\text{Fullness (\%)} = \frac{\text{stomach content weight (g)}}{\text{total fish weight (g)} - \text{stomach content weight (g)}}\ x\ 100 \qquad \text{(Eq. 1)}$$

Stomach fullness was compared by site and month within and across years using ANOVA and Tukey HSD tests. For each fish, prey were identified to lowest taxonomic

level, counted, and each prey taxon was blotted dry and weighed (0.00001g) (Borror et al. 1989; Merritt and Cummins 1996). In order to determine the amount of energy each taxon contributed to each meal, prey taxa were converted to energy density based on their mass and reported energy density values and then divided by the total wet weight of the stomach contents (David 2014). This approach yielded a value of kilojoules (kJ) of each taxon per gram of a fish's meal, which allowed for comparisons across sites and between months within each year. A fish's "meal" refers to the everything extracted from the stomach, i.e., the entire contents.

To evaluate the contribution of terrestrial habitat production to juvenile Chinook Salmon diets, the identified prey taxa were assigned to categories based on the habitats needed to complete their respective life cycle. This approach resulted in seven categories, including (1) "holo-terrestrial taxa" whose entire life cycle occurs in terrestrial habitats; (2) "mero-terrestrial taxa" that rely on terrestrial habitats for only part of their life cycle; (3) "pelagic taxa" that inhabit the water column; (4) "benthic taxa" that remain on the bottom or in sediment for their life cycle; (5) "unidentified insect" with unknown life cycle; and (6) "unidentified other", which included non-insect general taxa with unknown life cycles such as Nematoda, unidentified crustacean parts, and fish; and (7) "other", which included unidentified material (Borror et al. 1989; Merritt and Cummins 1996). These categories were used to better quantify the importance of wetland-derived prey in the diets of migrating yearling Chinook Salmon. Finally, the overall wet weight of the stomach contents, the mean energy density per fish (kJ) and the mean energy density per gram of fish meal (kJ/g) from each habitat prey group were compared to determine the relative value of using prey energy density as a metric.

We characterized the diet of Interior Columbia River spring Chinook Salmon and identified which taxa contributed the greatest energy to diets across years. Taxa were categorized into four levels based on varying taxonomical resolutions; Level 1 taxa = subphylum Crustacea and Class Insecta, and Other; Level II taxa = mostly Orders; Level III = a mix of mostly family and life stage; Habitat group = habitats required to complete life cycle (Table A2). For overall diet summaries, prey items were separated into sixteen groups (a subset of Level III taxa; Table A2) : Diptera, Coleoptera, Hemiptera, Hymenoptera, Ephemeroptera, Lepidoptera, Trichoptera, Plecoptera, Odonata, other insects, Arachnida (mites and spiders), Amphipods (gammarids and unidentified amphipods), other crustaceans (Isopoda, Cladocera, Copepoda, Cirripedia, crab larvae, and Mysida), Bivalvia (clams), other (fish larvae, fish eggs, Nematoda, plastic, and plant material), and unidentified material. For the NMS analyses, nine Level II prey taxa were that were present in >10% of the overall diets were included: Amphipoda, Bivalvia, Diptera, Hemiptera, Hymenoptera, Odonata, other Crustacea, other insects, and unidentified material. Finally, the previous nine categories used in NMS along with the following rarer taxa groups: Arachnida, Coleoptera, Ephemeroptera, and other (fish and Nematoda) were included in MRPP and ISA analyses since they were rare and could possibly serve as indicator species.

First, in order to look at similarities among prey items between years (2016 and 2017), individual fish meal energy density (kJ/ g per taxon) data were analyzed using Nonmetric Multidimensional Scaling (NMS) (McCune et al. 2002). NMS is an ordination technique commonly used by ecologists to identify patterns among sample units, in our case individual fish diets, by plotting each fish diet as a point and is an iterative process.

Departure from monotonicity is measured as stress and is typically interpreted as the lower the stress (<20), the more accurately the differences in the original matrix are represented (Kruskal 1964; McCune et al. 2002). Relative Sørensen distance measure was used to create all of the distance matrices (McCune and Mefford 2015) because it standardizes by sample unit totals to focus on proportions rather than abundances. The ordinations were run with the following parameters: 1) random starting coordinates, 2) 200 runs for both the real and Monte Carlo test, 3) and up to 500 iterations were allowed for a stability criterion <0.0000001. Our secondary matrix included biological and physical factors which we hypothesized were related to the diet of yearling Chinook. Pearson's correlation analysis was then used to evaluate the correlation between NMS ordination axes and these biological and physical factors: fish length, fish weight, condition factor, stomach fullness, stomach wet weight, river flow below Bonneville Dam (kcfs), and river temperature at Bonneville Dam. The axes account for a portion of the variation in the dataset and these correlations tell you what biological or physical factor is correlated with that variation, i.e., positive or negative relationships and potentially important factors regulating the diet variation. Flow and temperature were averaged for each site to include the sampling date and three days prior, overall a four-day average. Correlation significance levels were adjusted for multiple comparisons using the Bonferroni correction.

We evaluated the differences in fish diet energy among sites and between years using the nonparametric Multi-Response Permutation Procedure (MRPP) which tests for differences among two or more groups. This analysis was completed for all diets and then separately for 2016 and 2017. Lastly, Indicator Species Analysis (ISA) was used to

evaluate differences in species composition among sites and between years when MRPP identified distinct groups (Dufrêne and Legendre 1997). As part of the ISA, a randomization test is run 4,999 times to test the hypothesis that the Indicator Value (IV) for a given species is no larger than expected by chance. IV is calculated by taking the frequency of taxa abundance in a group and the fidelity of that taxa to a group, the higher the IV the more likely it is an indicator for a specific group (Dufrêne and Legendre 1997; McCune et al. 2002).

Stable Isotope Analysis of Prey

Stable isotope composition of common prey from the stomachs of yearling Chinooks was determined in order to characterize the food sources supporting yearling Chinooks as they emigrate. The stable isotope analysis of common prey taxa found in the stomach contents provides information on the $\delta^{13}C$ and $\delta^{15}N$. This allows for comparisons to the natural variation we see in similar taxa collected in adjacent wetlands.

Prey taxa collected from salmon stomachs were dried at ~60°C after being identified, counted, and weighed (Levin and Currin 2012). Taxon-specific prey samples were analyzed at Oregon State University's College of Earth, Ocean, and Atmospheric Sciences' Stable Isotope Laboratory. Dried prey tissue samples were ground into a fine powder (if > 3 mg) or processed whole (< 3 mg) and 1.0 ± 0.5 mg of sample was placed into a tin capsule. Prepared samples and international standards (USGS40, SIL Sucrose, and IAEA-N2) were combusted at >1000 °C using a Carlo Erba NA1500 elemental analyzer connected to a Thermo DeltaPlus isotope ratio mass spectrometer (IRMS). Stable isotopes values were expressed in the delta notation using Eq. 2:

$$\delta^{13}C \text{ and } \delta^{15}N\ (‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

where *R* is $^{13}C:^{12}C$ or $^{15}N:^{14}N$. This method had an accuracy of ±0.1‰ for carbon and ±0.2‰ for nitrogen. Samples with C:N ratios >3.5 were lipid-corrected in order to adjust $^{13}C:^{12}C$ for tissues with high lipid content (Post et al. 2007). Diet prey samples were separated into taxa specific groups of most commonly consumed prey, which included: Diptera, *Americorophium* sp., Ephemeroptera, Hymenoptera, Odonata, and *Ramellogammarus* sp. Stable isotope values for two dominant yearling Chinook prey taxa, amphipoda and diptera, that were collected in the LCRE wetlands were summarized to provide an indication of the natural variation in carbon stable isotope ratios (Peterson, unpublished data; Anderson 2006). The compiled wetland field data encompass potential yearling Chinook prey taxa that were collected from wetlands throughout the LCRE, from below Bonneville Dam (Franz Lake) to the estuary (Ilwaco, WA) to. Only carbon stable isotope values for Diptera (Chironomidae) and amphipods (*Americorophium* sp.) collected during peak yearling Chinook outmigration (March – June) were used in summaries.

Results

Relative Size and Condition Factor

We collected 560 yearling Chinook Salmon from six genetic stock groups during the study period, of which 417 were genetically identified as Interior Columbia River spring

Chinook Salmon (Table 2.1). Average size of yearling Chinooks was 140 mm FL and 23.9 g in 2016 and 143 mm FL and 27.5 g in 2017 (Figure 2.2, Table 2.2). For 2016, size increased as fish approached the ocean. However, fish size was not formally compared across sites because there could be size bias due to the different net types used to collect fish. Yearling Chinook Salmon condition index was greater in 2017 (mean ranged from 0.01 to 0.10) than in 2016 (-0.07 to 1.3) (ANOVA and Tukey HSD, $p < 0.001$) and, on average, fish were in better condition in April than in May both years (Table 2.2). Additionally, during April for both years, fish condition decreased as fish moved downriver (Figure 2.3). It is important to note that the weight of the stomach contents was not a confounding factor for calculating condition index since the results from the regression did not change even when the weight of the stomach contents were removed.

Surface Prey Drift

Across the 2-year sampling period, the potential salmon prey collected using the neuston net included 17 taxonomic groups (Figure 2.5 - 2.6, Table 2.3). Dipteran taxa were collected at all sites during both years, contributing 7-93% (2016) and 18-75% (2017) of the total number of organisms collected. Amphipoda were present across all months in 2016, except for the upper river site in June. In 2017, Amphipoda were also present across all sites and months, except for the lower river site in June. Amphipoda made up a greater proportion of taxa collected in April of both years, while Dipterans were found in greater abundance in May and June of both years.

Stomach Fullness

Of the 417 Interior Columbia River spring Chinook Salmon, 229 were subsampled for stomach content analyses. On average, stomach fullness (% of total body weight) ranged from 0.50 to 1.11% in 2016 and 0.8 to 1.58% in 2017 (Table 2.2). As seen with condition factor, average stomach fullness decreased as fish moved closer to the ocean. Values were pooled across months for each year because there was no effect of month on stomach fullness. In 2016 all fish collected above the estuary were significantly fuller than those collected at the estuary mouth (Figure 2.6; ANOVA and Tukey HSD, $p < 0.05$). In 2017 only fish collected at the upper river site were significantly fuller than those collected in the middle, lower, and estuary sites (ANOVA and Tukey HSD, $p < 0.05$). There was a negative correlation between fish FL and stomach fullness ($r = -0.26$, $P < 0.001$). Fish collected in 2017 had significantly fuller stomachs than those collected in 2016 (2016: 0.87 and 2017:1.16; t-test, $p < 0.001$).

Diet Composition

Diets of Interior yearling Chinook Salmon collected from the LCRE contained prey from 22 taxonomic groups including 43 insect and other invertebrate categories that include life stage. Yearling Chinook Salmon diets varied across sites and between years, potentially reflecting differences in flow and prey available (Figure 2.7, Table 2.4). Similar to the neuston, Diptera (primarily mero- and holo-terrestrial taxa) and Amphipoda (benthic taxa) were present in diets across all sites and in both years. Dipterans occurred in 64-97% of the diets, whereas amphipods occurred in 77-100% of the diets with the greatest frequency of occurrence in the middle and lower river sites (Table 2.4).

Finally, we quantified the importance of wetland habitats to yearling Chinook diets using the habitat groups. The holo-terrestrial habitat group contributed a greater proportion of the energy density (ED) to fish diets in 2016 (2016 = 27%, 2017 = 8%) while the benthic habitat group contributed more energy density per fish's meal in 2017 (2016 = 27%, 2017 = 69%) (Figure 2.8). Although 2017 fish had greater stomach fullness, total energy density per gram of meal was also significantly lower in 2017 compared to 2016 (2016: 2.05 and 2017:1.43; ANOVA and Tukey HSD; $p < 0.005$; Figure 2.8, Table 2.5). Based only on the wet weight of prey, the benthic habitat group contributed more to the diet in both years compared to the holo-terrestrial group (Figure 2.9). However, the contribution of the holo-terrestrial group increases in value by over 200% when based on mean energy density while the benthic habitat group shows no change (Figure 2.9).

The NMS ordination for diets of both years combined yielded a three-dimensional solution with a fair final stress of 11.95 (Monte Carlo $p < 0.05$). The ordination explained a total of 92.4% of the variation in diet community structure (Figure 2.10, Table 2.6). Axis 1 represented 50.2% of the variation and was positively associated with amphipods and negatively associated with other insects (Table 2.6). Axis 2 represented 22.4% of the variation and was positively associated with dipteran taxa. The results from the MRPP analysis of the 13 taxa groups for both years indicated that the species composition differed between the two years (MRPP, A = 0.08; $p < 0.001$), the two months (MRPP, A = 0.01; $p < 0.005$), and across sites (MRPP, A = 0.04, p , 0.001). Based on the ISA, Amphipoda and Ephemeroptera were an indicator of 2017 diets (ISA, $P<0.004$; Table 2.7), while Hemiptera and other insects were indicators of 2016 diets. Ephemeroptera was an indicator taxon for April in both years.

When each year was evaluated independently, the NMS solution for 2016 diets also yielded a three-dimensional solution with a fair final stress 13.22 (Monte Carlo $p < 0.05$). The ordination explained 86.4% of the variation in diet community structure (Figure 2.11, Table 2.6). Axis 1 accounted for 23.6% of the variation and was negatively associated with amphipod taxa. Axis 2 accounted for 39.0% of the variation and was positively associated with dipteran taxa, but negatively associated with Hymenoptera and other crustacean taxa (Table 2.6). In 2016, yearling Chinook diet composition varied significantly across sites but not months (MRPP; $A = 0.05$; $p < 0.001$). Pairwise comparisons indicated that the upper river site diets were distinct from fish diets from all other site diets ($p < 0.001$). Based on the ISA, the upper river site diets were most associated with Hemiptera taxa (Table 2.7, $p < 0.005$).

Finally, the NMS for 2017 data yielded a two-dimensional solution with a final stress of 14.39 (Monte Carlo $p < 0.05$). The ordination accounted for 93.1% of the variation in diets (Figure 2.11, Table 2.1). Axis 1 represented 78.3% of the variation and was positively associated with other insects, Hymenoptera, and Diptera taxa. Axis 2 represented 14.8% of the variation and was negatively associated with Odonata taxa but was not positively associated with any taxa. In 2017, yearling Chinook diets were significantly different across months and sites (MRPP, $A= 0.05$; $p < 0.001$; MRPP, $A = 0.06$, $p < 0.001$). In April diets, the other Insecta were indicators while Amphipoda were indicators for May diets. For 2017, pairwise comparisons indicated that diets at the lower river site were distinct from all other sites and diets from the estuary mouth and middle river sites differed from each other ($p < 0.01$). Based on the ISA, diets from the lower river

site were associated with Ephemeroptera (Table 2.7, $p < 0.001$) and the upper river site diets were associated with Amphipoda (Table 2.7, $p < 0.001$).

Diet and Wetland Taxa Stable Isotopes

Stable isotope values of common prey items collected from yearling Chinook diets varied across sites and years. In 2016 yearling Chinook diets, $\delta^{13}C$ values of *Americorophium* ranged from -26.0‰ to -18.9‰ with a mean of -22.3‰, and values increased towards the ocean. Dipteran $\delta^{13}C$ followed a similar trend with values ranging from -24.9‰ to -18.9‰ with a mean of -21.3‰ (Figure 2.12). In 2017 $\delta^{13}C$ values were lower and less variable. *Americorophium* ranged from -28.0‰ to -24.1‰ and Diptera ranged from -25.0‰ to -20.5‰, with no increase in values towards the ocean (Figure 2.12). Similar trends were seen in other insect taxa collected from yearling Chinook diets (Hymenoptera, Ephemeroptera, Odonata, and *Ramellogammarus*) (Figure 2.13). Overall, stable isotope values of various prey taxa collected from 2016 yearling Chinook stomach contents had greater $\delta^{13}C$ values and more variable than 2017 prey taxa (2016 = 21.6‰, CV = 12.1%; 2017 = -24.8‰, CV = 6.9%).

The $\delta^{13}C$ values of potential yearling Chinook prey taxa collected in the wetlands along the LCRE follow a trend of higher $\delta^{13}C$ values closer to the ocean (Figure 2.15). The $\delta^{13}C$ for wetland collected *Americorophium* sp. ranged from -28.1‰ to -17.6‰ and -32.2‰ to -20.4‰ for Diptera. When $\delta^{13}C$ values of prey from stomach contents of yearling Chinook are compared to the mean of field invertebrates, 2016 stomach content prey were more reflective of the natural variation seen in the wetlands compared to 2017

stomach content prey. This difference could be associated with flow since 2017 was a higher flow year than 2016 (Figure 2.15).

Discussion

This study advances our understanding of the feeding ecology of Interior yearling Chinook Salmon migrating through the lower Columbia River estuary using diet and stable isotope analyses. Previous studies of Chinook feeding habits in the LCRE focused on sub-yearling Chinooks because this life stage typically reside for extended periods in estuaries and occupy shallow water habitats, directly accessing wetlands. However, there is little information on how yearling Chinooks benefit from wetlands. By sampling yearling Chinooks during peak emigration throughout the LCRE, we examined spatial and temporal patterns in feeding in order to quantify the benefits yearling Chinooks obtain from adjacent wetlands. Even though yearling Chinooks tend to stay in deeper waters and are not directly accessing wetlands, we demonstrated that yearling Chinook were consuming high energy prey likely from adjacent wetlands, which can act as a subsidy for fish traveling in the mainstem. This information is critical to future management and habitat restoration efforts given how little is known about yearling Chinooks because they move rapidly through the system and are often assumed to not feed extensively as they travel through the LCRE.

By grouping prey taxa into categories based on how reliant they are on either aquatic or terrestrial habitat, we directly quantified the importance of wetland-derived prey for yearling Chinooks. We found that holo-terrestrial habitat group contributed more energy density to fish diets in 2016 while the benthic habitat group contributed more

energy density per meal in 2017. Over 75% of the high-energy prey identified in yearling Chinook diets in this study have been previously documented in LCRE wetlands (Gray et al. 2002; David 2014). (Lott 2004; Ramirez 2008).

The use of energy density to analyze diet data provides a metric that could better characterize wetland benefits. Diet studies typically use count, mass, and frequency of occurrence or a combination of all three (Index of Relative Importance, IRI) to describe feeding ecology (Pinkas 1971; Miller and Simenstad 1997; Baker et al. 2014). As seen in in our study, when we examined wet weight alone, benthic prey were identified as most important (Figure 2.9). However, when for holo-terrestrial prey that have caloric values 3 times greater than strictly benthic taxa, their relative importance increased by over 200% (for both years combined) based on mean energy density (Figure 2.9). Thus, it is important to consider energy density when evaluating habitat contributions to food web support (David 2014). We further compared the mean energy density consumed per fish across years to see if fish were still consuming similar amounts of kJ even though they were feeding primarily on two different taxa in 2016 compared 2017. The results remained similar to that of energy density per kJ of fish meal.

Considering energy density of prey is also important because it can impact yearling Chinook's foraging behaviors. For example, the need to forage, which is influenced by prey abundance and energy density, affects an individual's level of risk to predation and mortality. This type of risk-taking behavior has been studied extensively, and organisms in habitats with low prey abundance experience greater mortality than individuals in habitats with high prey abundance (Anholt and Werner 1995; Biro et al. 2003). In the

LCRE, there may be similar foraging and risk trade-offs associated with prey energy density as they move through the mainstem.

In our study, many of the terrestrial insects that yearling Chinooks consumed had a greater energy density than amphipods (Table A2). In 2017 we saw that stomach fullness was greater than 2016, but the stomachs were full of amphipods. Therefore, it is plausible that fish in 2017 had to consume greater amounts of benthic prey, which have relatively low energy content, to meet their metabolic needs. In contrast, fish collected in 2016 consumed over 2.4x more energy-rich taxa, but fish were less full. This finding highlights a potential foraging tradeoff that fish may be experiencing in the river. It is important to note that fish condition also followed a similar trend where in 2017 fish were in better condition that in 2016. We considered that the weight of the stomach contents could affect these results, since fish were more full in 2017 than 2016, but even when stomach contents were subtracted from the fish weight the same trend held true.

Yearling Chinook diet composition has been examined within the Bonneville reservoir and along the LCRE, and *Americorophium* spp. were important prey (IRI 40-97%) across April and May (Bottom and Jones 1990; Dawley et al. 1984; Muir and Emmett 1988; Muir 1996). Although our study is not directly comparable to these previous studies because we did not identify important prey using IRI, our results for energy density of meal indicate that similar benthic taxa contributed 27% in 2016 and 48% in 2017 to yearling Chinook diets in the LCRE (Figure 2.9). In contrast, terrestrial insects contributed 48% in 2016 and 19% in 2017 to the meal energy density of yearling Chinook diets. The importance of insects in the diets of yearling Chinooks as they emigrate was observed across all sites and years.

Yearling Chinooks diets in 2016 had greater variability and they fed on many terrestrial taxa, while yearling Chinooks in 2017 had less variable diets and primarily consumed benthic taxa. *Americorophium* and Dipterans were the most common prey item found in yearling Chinook diets we sampled, but we also observed other terrestrial taxa, including Hymenopteran and Hemipteran prey, which contributed up to 6 times more energy to 2016 diets compared to 2017 diets. In April 2016 and 2017, during lower flows, insects made up a 47% and 25%, respectively, of the total energy density in diets of fish collected at the UR site (Table 2.2). Although neuston data provides only a snapshot of the prey available, 2016 samples had over 10 times more terrestrial taxa biomass than 2017 samples. The terrestrial biomass also nearly doubled as flows declined in June and July of 2016. We speculate that flow had an important role in availability of insects throughout the LCRE. The high flow may reduce the residence time of insects in the system and ultimately make them less available to Chinook salmon, as we saw in the low neuston biomass in 2017 (Figure 2.5).

Stable isotope values of diet prey items were compared to potential prey collected in the wetlands in order to examine trends to the long-term natural variation along the LCRE. The $\delta^{13}C$ values of both *Americorophium* and other invertebrate taxa from 2016 Chinook diets were more similar to the mean $\delta^{13}C$ of samples collected in nearby wetlands. Whereas in 2017, mean $\delta^{13}C$ values of both amphipods and insects collected from stomach contents were less variable throughout the LCRE, and they did not reflect the trend of increasing $\delta^{13}C$ values towards the ocean that was observed in invertebrates collected in wetlands. One explanation for this trend is that the lower flows in 2016 allowed for greater retention and concentration of neustonic prey that are exported from nearby

wetlands compared to 2017 when prey could have been transported through the river more quickly. In general, the lower flows in 2016 could affect the primary producers available to terrestrial and benthic prey. With lower flows, the prey would reflect the carbon sources from where it was consumed from. Due to the relatively small sample sizes from both wetland and diet prey, we cannot make a definitive conclusion but note that the clear difference between 2016 and 2017 prey $\delta^{13}C$ values are consistent with observed variation in flow. Not only did we see variation in $\delta^{13}C$ values across years, but in 2016 we were able to detect greater site variation for $\delta^{13}C$ values. These changes in $\delta^{13}C$ values provides evidence that yearling Chinooks are feeding differentially as they move through the system since changes in $\delta^{13}C$ values likely reflect changes in carbon sources (Maier and Simenstad 2009; Maier et al. 2011) We did not see a similar level of variation in 2017, and $\delta^{13}C$ values appeared more terrestrial/riverine. We also know that values can vary greatly even within a single wetland and in areas that are tidally influenced (Maier et al. 2011; Howe and Simenstad 2015).

The differences in feeding habits that we observed between years and across sites were likely affected by flow and temperature. Relatively low flows and higher temperatures in 2016 likely increased the number of insects hatching which were then exported from adjacent wetlands and aggregated in slower waters. In contrast the higher flows seen in 2017 could explain the number of amphipods in the water column. Studies on *Americorophium* densities, diel patterns, and life history have been conducted in the Bonneville reservoir and in the lower estuary (Davis and Holton 1976; Muir 1990). Muir (1990) concluded that *A. salmonis* densities were positively correlated with flow and sediment particles. The relationship between *Americorophium* and flow could explain why

we saw more amphipods in the diets of yearling Chinook in 2017. Since flow was relatively high in 2017 and fish likely moved more quickly through the system, this could explain the differences in stomach fullness as well. Fish in 2017 had fuller stomach compared to 2016 fish. Overall, across both years, fish in April were less full than those collected in May. During these times of higher than average flow, we see fish with fuller stomachs which suggests there may be a positive relationship with these environmental factors. Other approaches, such as PIT tagging and otolith chemical and structural analyses, can provide additional information on individuals residence times and their potential effects on condition and stomach fullness.

These results support the conclusion that yearling Chinook salmon migrating through the LCRE benefit from adjacent wetlands, which provide an energy rich prey subsidy. Although yearling Chinooks do not directly access shallow water wetlands, we found wetland-derived prey in their diets across both years. Fish in 2016 had an overall greater proportional contribution of terrestrial insects to their diet which was supported by the neuston data, which also had greater biomass of wetland-derived potential prey in 2016. These findings were also reflected in the stable isotope values of both diet and potential prey. $\delta^{13}C$ values in 2016 were more similar to the observations of invertebrates collected from wetlands, which suggests potential spatial differences in carbon sources supporting yearling Chinook salmon as they emigrate through the LCRE.

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Figure 2.1 Map showing the general locations where Interior Columbia River Spring Chinook Salmon and neuston samples were collected in 2016 and 2017. Site abbreviations are: EM – Estuary Mouth, LR – Lower River, MR – Middle River, and UR – Up River. Estuary mouth was the only site where a purse seine was used to collect juvenile Chinook Salmon.

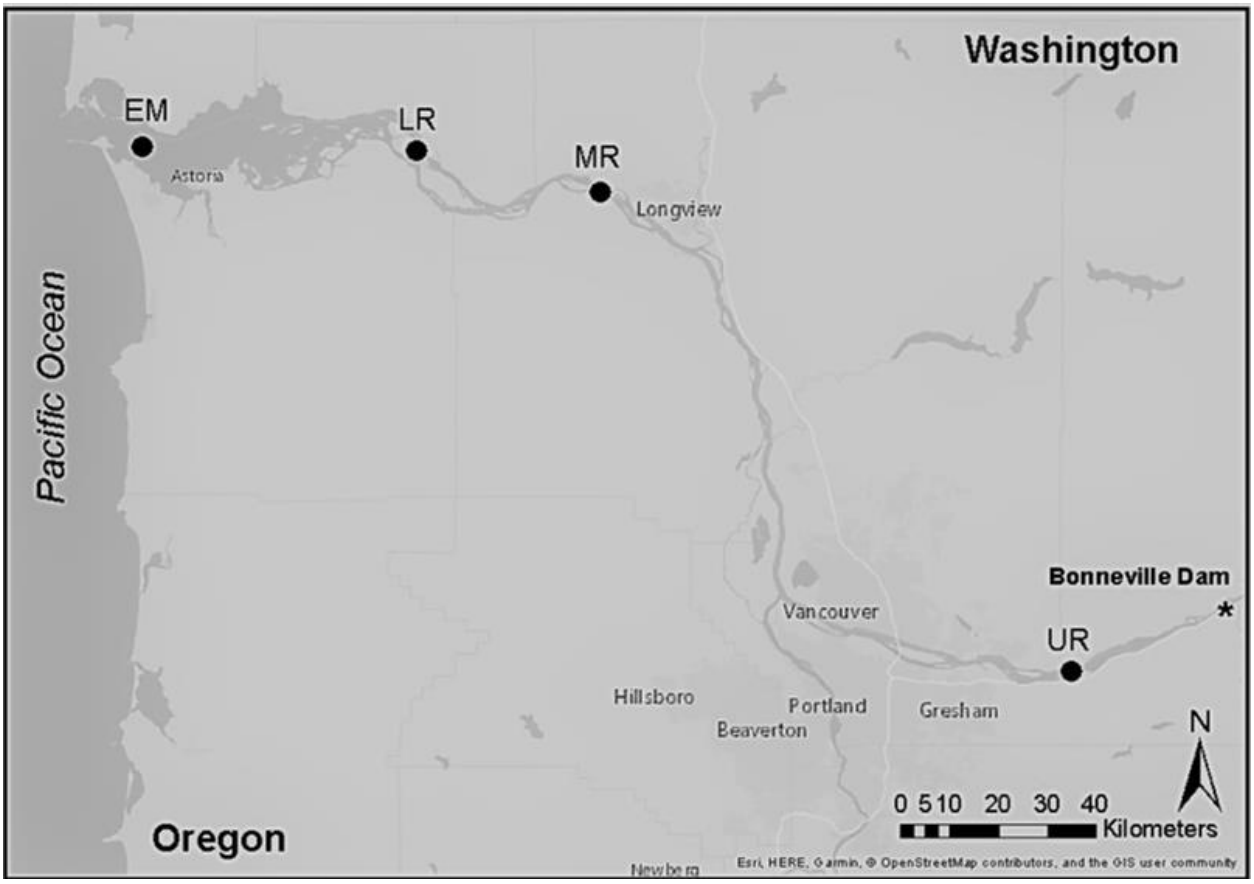

Figure 2.2 Plots of average (±SE) fork length and weight of Interior Columbia River Spring Chinook Salmon collected in the Lower Columbia River and Estuary for 2016 (top graphs) and 2017 (bottom graphs). UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth.

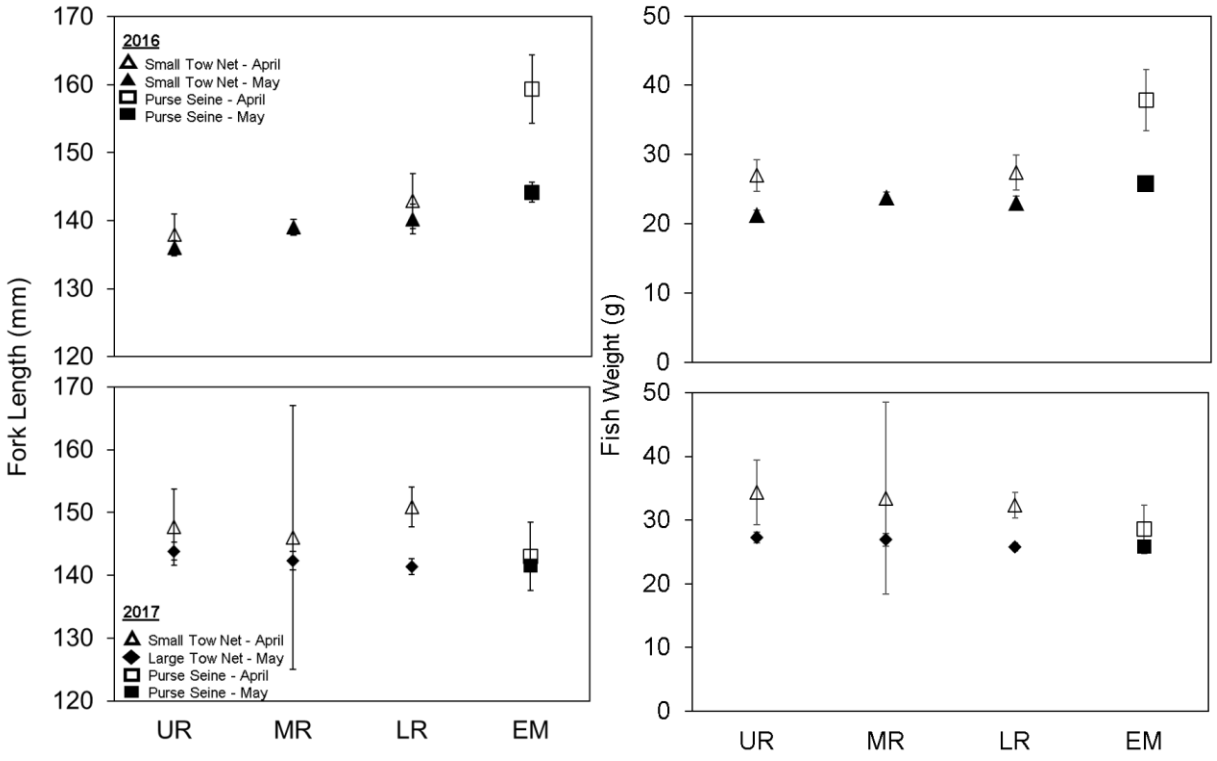

Figure 2.3 Average (±SE) index of condition of Interior Columbia River Spring Chinook Salmon collected in the Lower Columbia River and Estuary in April and May of 2016 and 2017. UR = Upper River, MR = Middle River, LR=Lower River, and EM=Estuary Mouth. Sample sizes per site are included in lower portion of the graph.

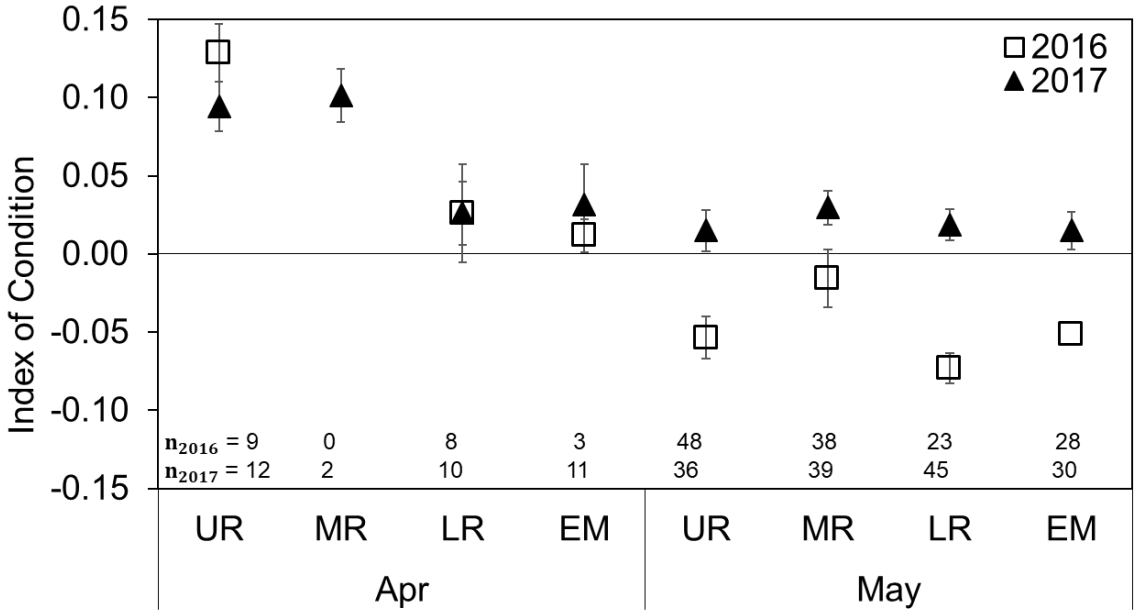

Figure 2.4 Total number of organisms per square meter collected in the neuston at four sites in the Lower Columbia River and Estuary in 2016 and 2017. April and May were combined for each sampling site. UR = Upper River, MR = Middle River, LR=Lower River, and EM=Estuary Mouth in 2016 and 2017. Shades of green indicate insect orders.

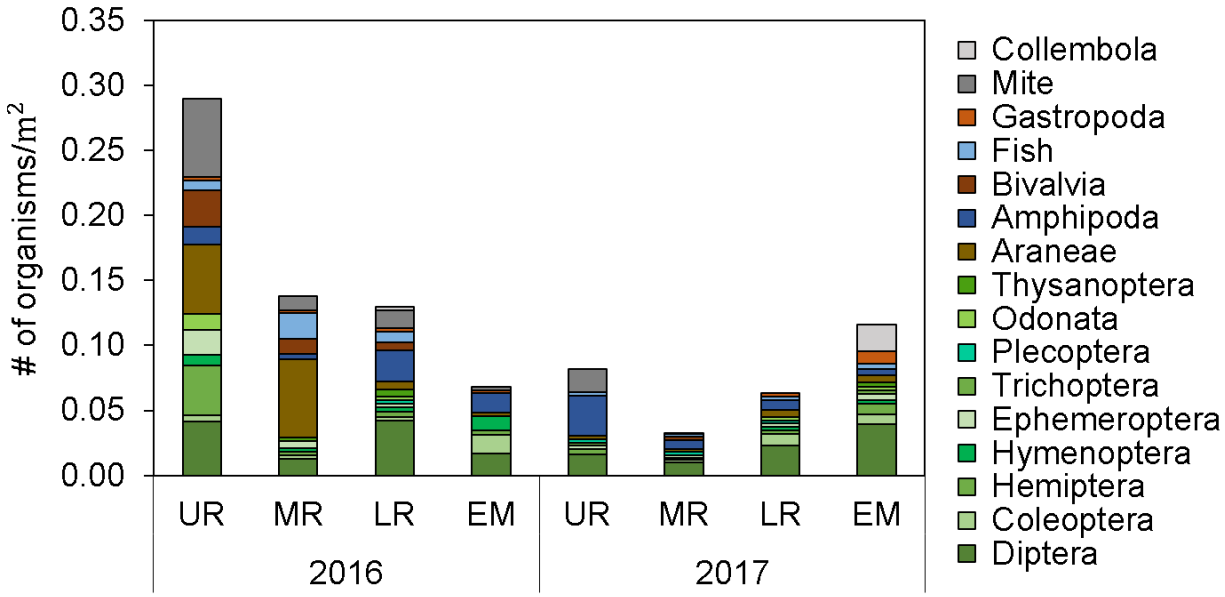

Figure 2.5 Top: Biomass of all taxa (excluding bivalves) and Bottom: Biomass of bivalves. Calculated per square meter collected in the neuston at four sites in the Lower Columbia River and Estuary in 2016 and 2017. Bottom: Biomass of bivalves per square meter collected in April and May were combined for each sampling site. UR = Upper River, MR = Middle River, LR=Lower River, and EM=Estuary Mouth in 2016 and 2017. Shades of green indicate insect orders.

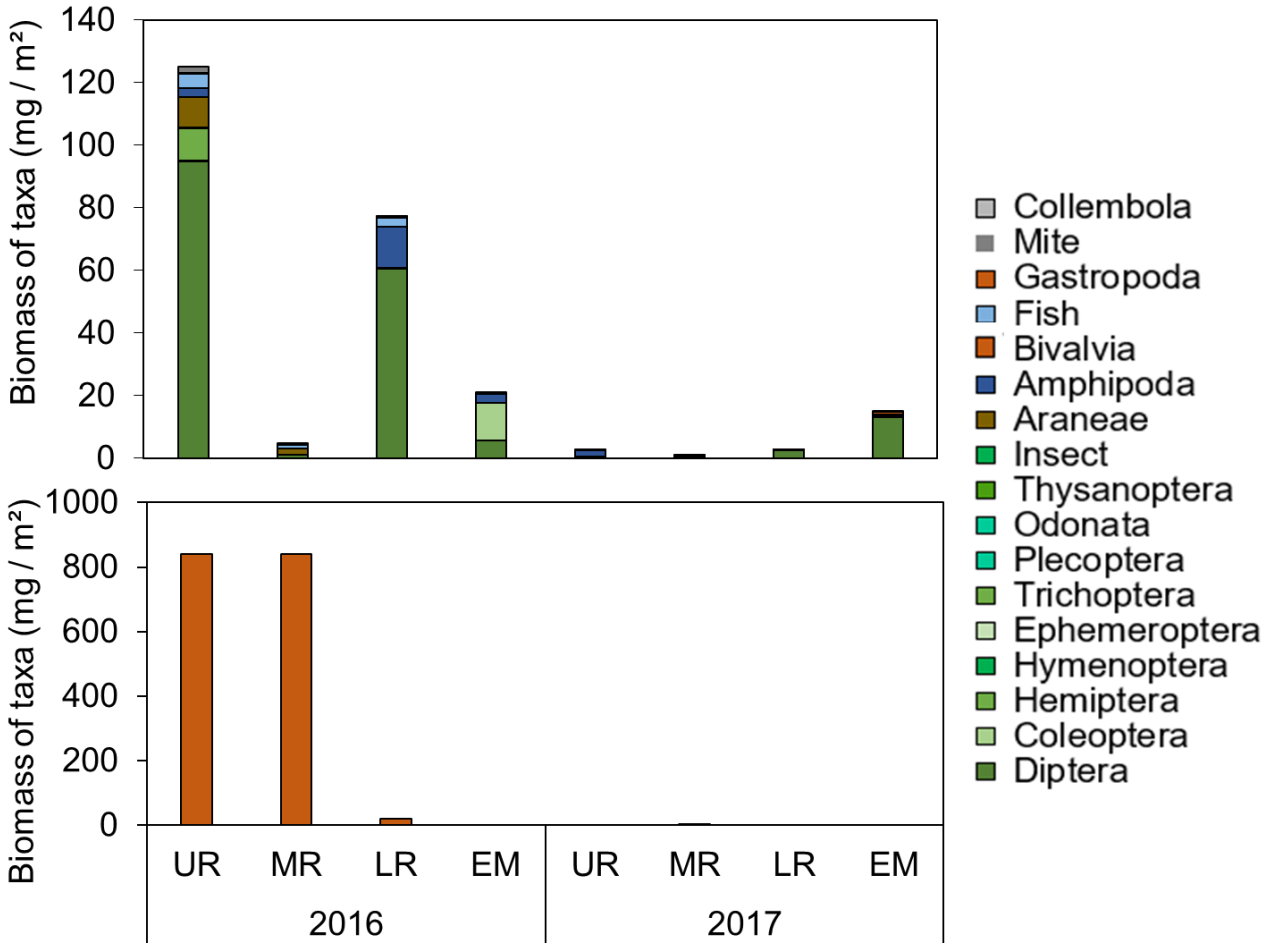

Figure 2.6 Average (±SE) stomach fullness (as a % of body weight) of Interior Columbia River Spring Chinook Salmon collected in the Lower Columbia River and Estuary in April and May 2016 and 2017. UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth.

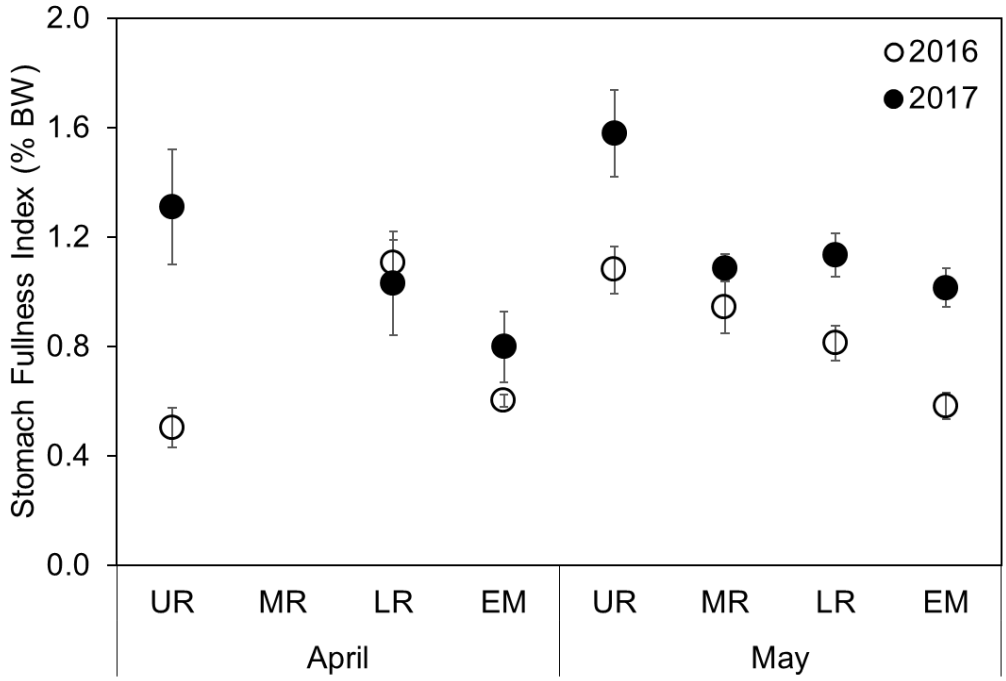

Figure 2.7 Interior Columbia River Spring Chinook Salmon diet composition represented as mean energy density (kJ/g) for the prey groups across sites and months in 2016 and 2017. Insect orders represented by shades of green. UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth

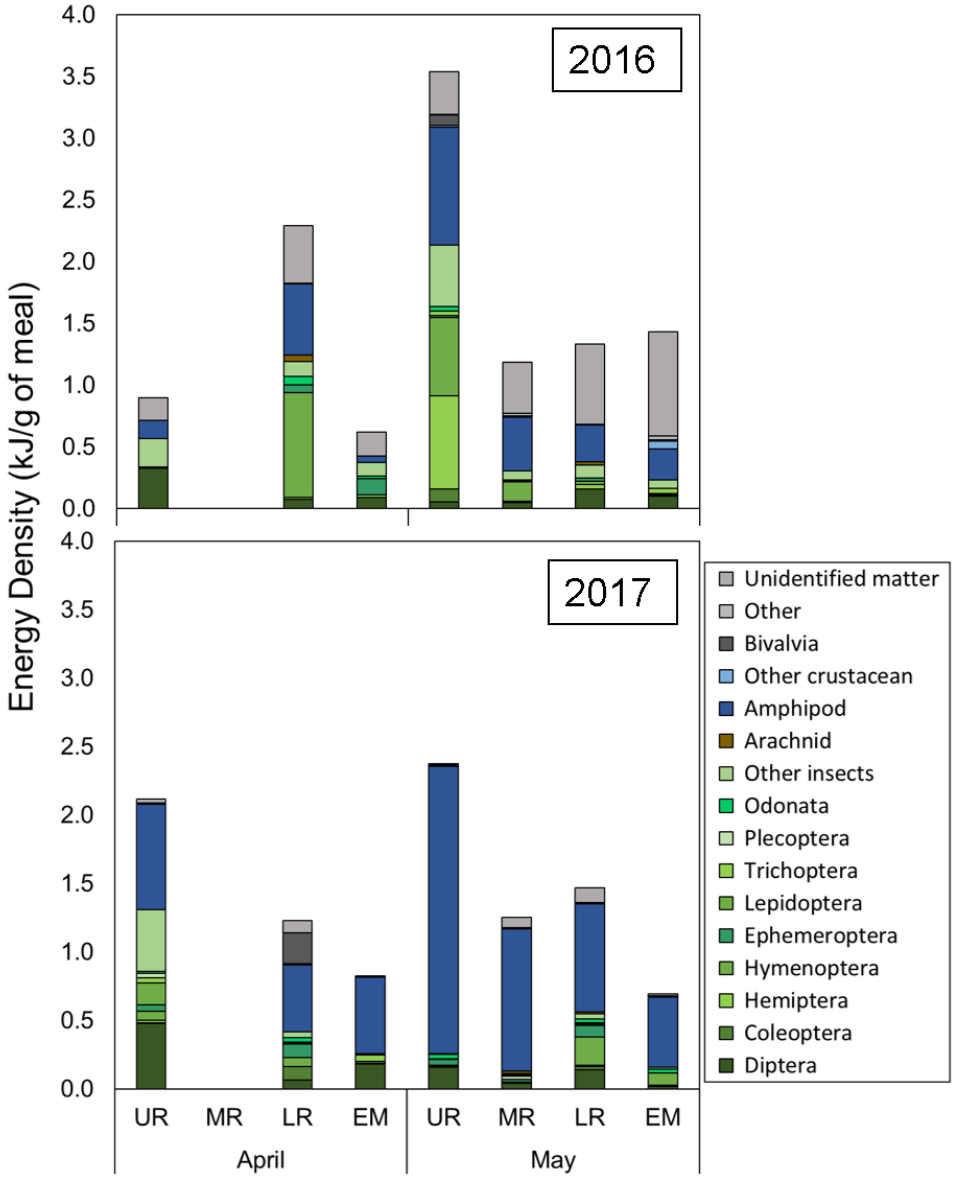

Figure 2.8 Comparison of annual mean energy density (kJ/g) for the prey habitat groups of Interior Columbia River Spring Chinook Salmon stock diets. Insect groups represented by shades of green.

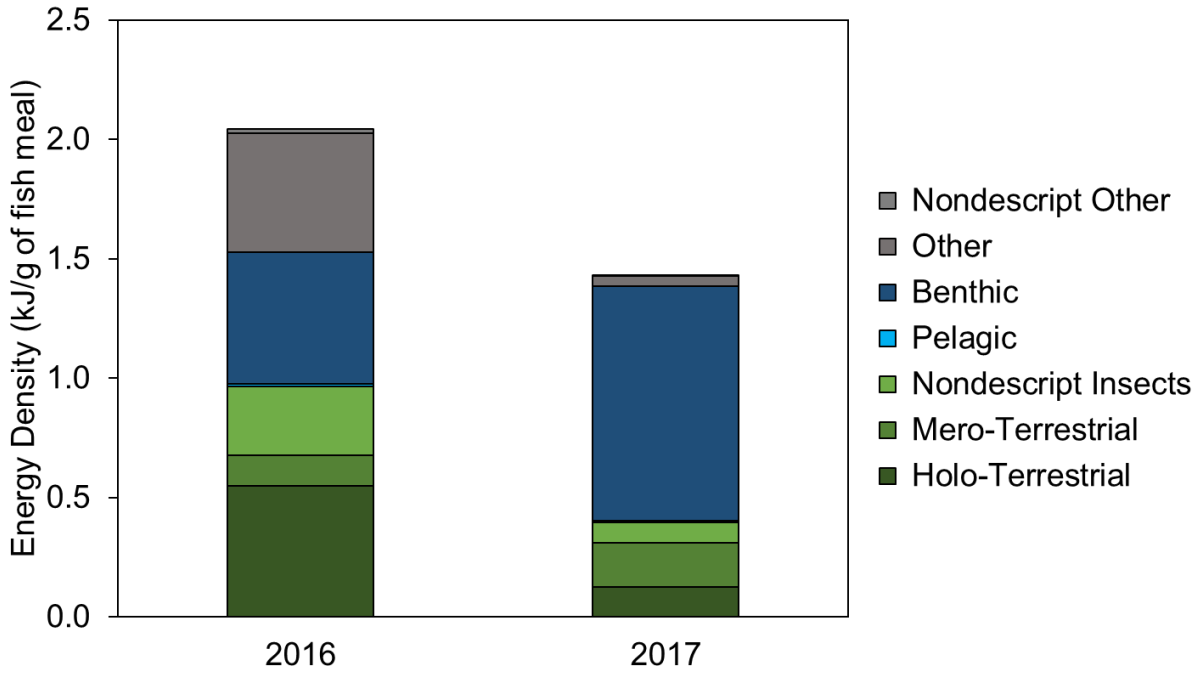

Figure 2.9 Comparison of mean taxa wet weight (g) – dark grey, mean total energy density per fish (kJ) – blue- and mean energy density per gram of meal – green- for the prey habitat groups of Interior Columbia River Spring Chinook Salmon diets. Top graph: 2016. Bottom graph: 2017

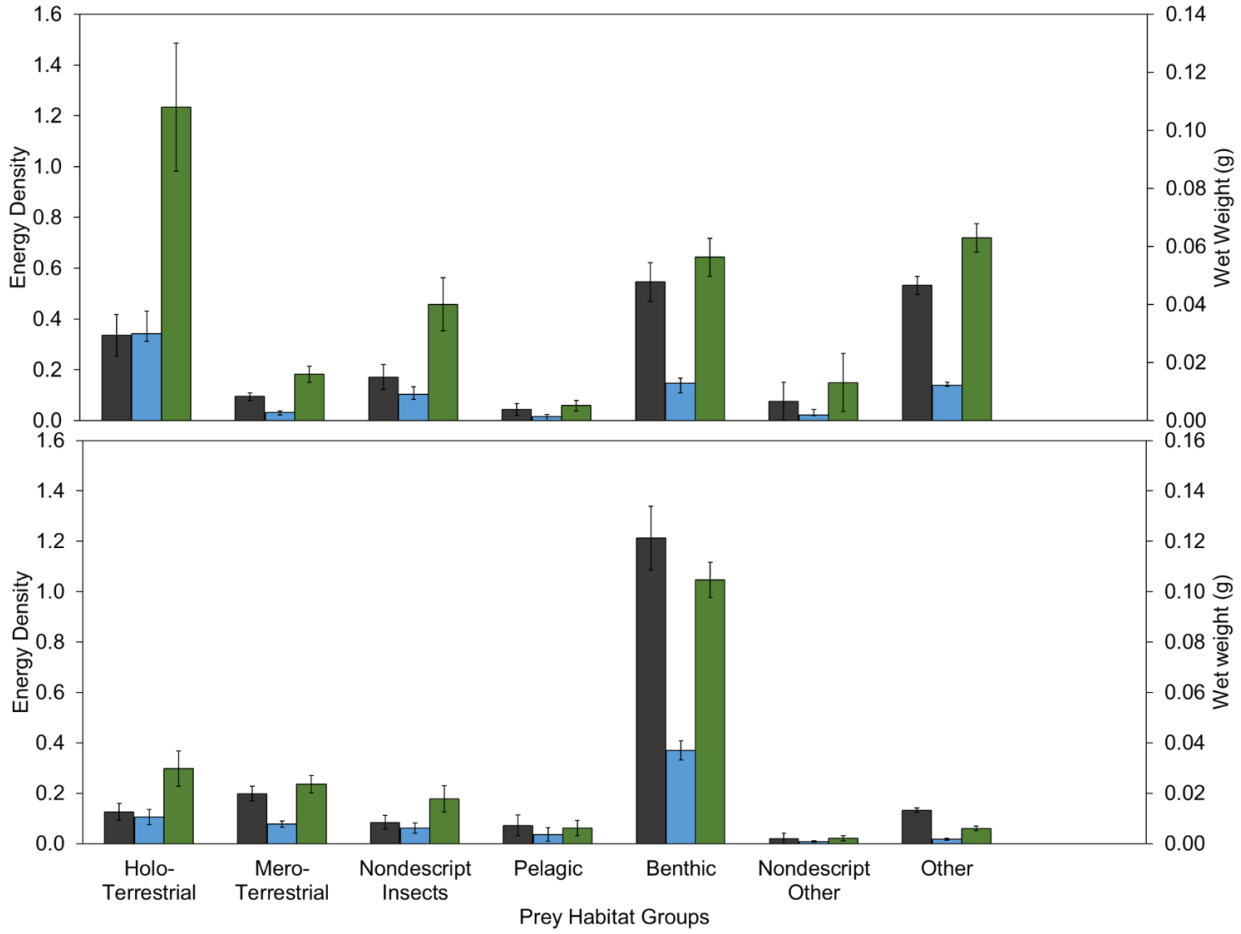

Figure 2.10 Nonmetric multidimensional scaling analysis of 230 Interior Columbia River Spring Chinook Salmon diets. Each point represents the energy density per gram of a fish's meal collected at four sites from April and May of 2016 and 2017. Taxa that were correlated with each axis were included along each axis.

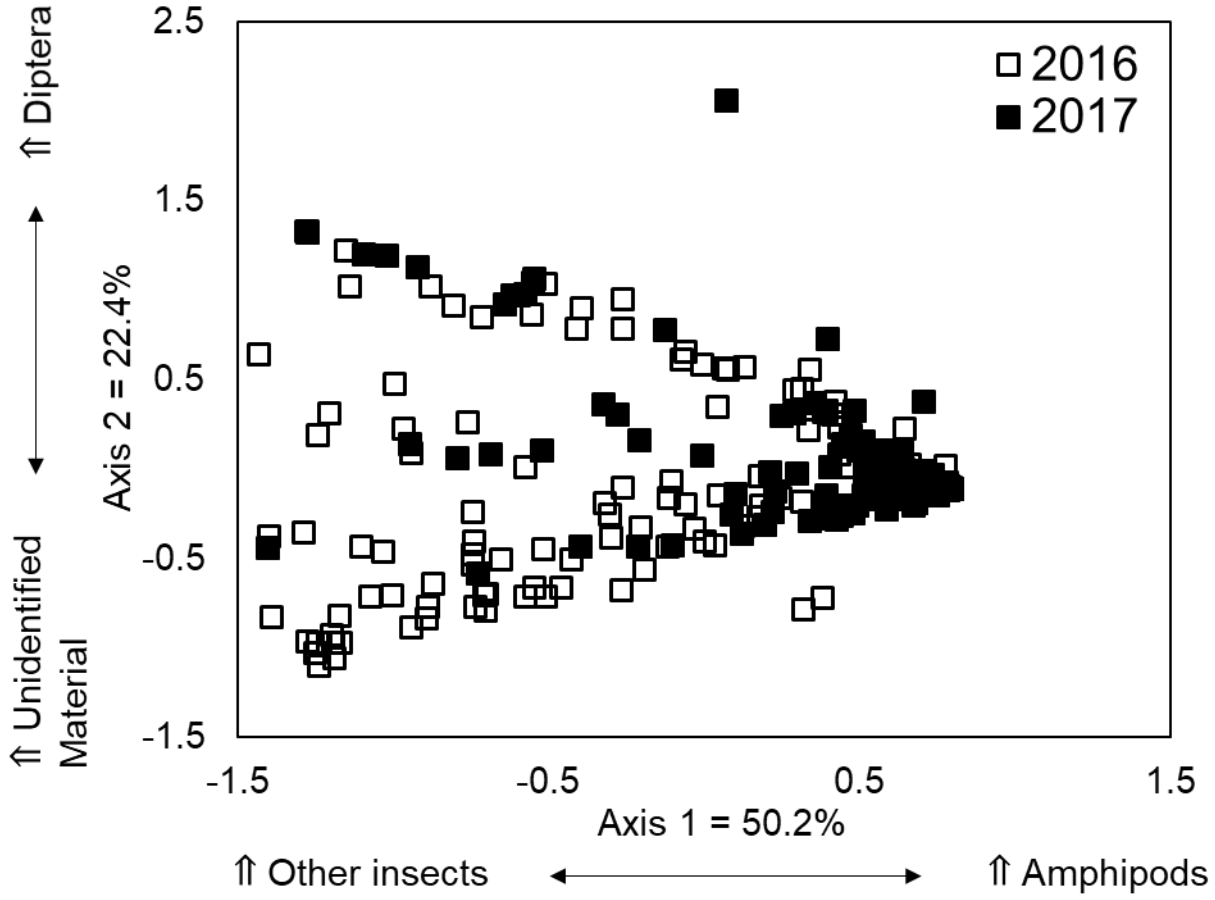

Figure 2.11 Nonmetric multidimensional scaling analysis of Interior Columbia River Spring Chinook Salmons diets for 2016 (top) and 2017 (bottom). Each point represents the total energy density per gram of a fish's meal collected per site in April and May. Symbols are based on groupings by site: Upper River (UR) = grey circle, Middle River (MR) = orange diamond, Lower River (LR) = green square, and Estuary Mouth (EM) = blue triangle. Taxa that were correlated with each axis were included along each axis. Plots show elliptical hulls for each year by site.

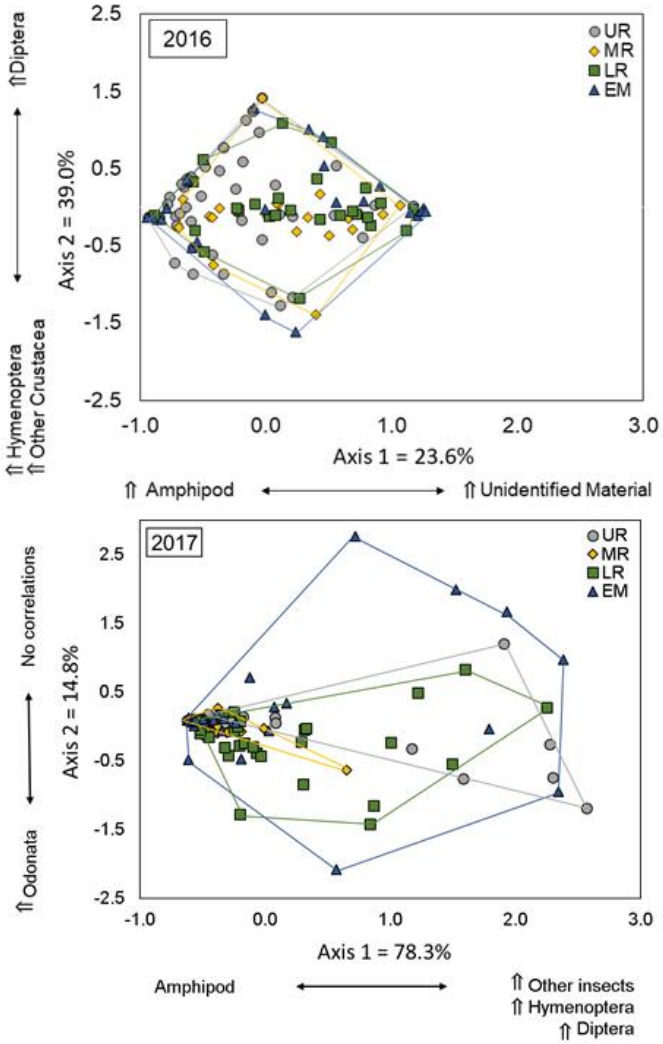

Figure 2.12 Carbon stable isotope ratios for *Americorophium* and diptera collected in yearling Chinook Salmon diets. **A.** *Americorophium* 2016. **B.** *Americorophium* in 2017 **C.** Diptera in 2016 **D.** Diptera in 2017

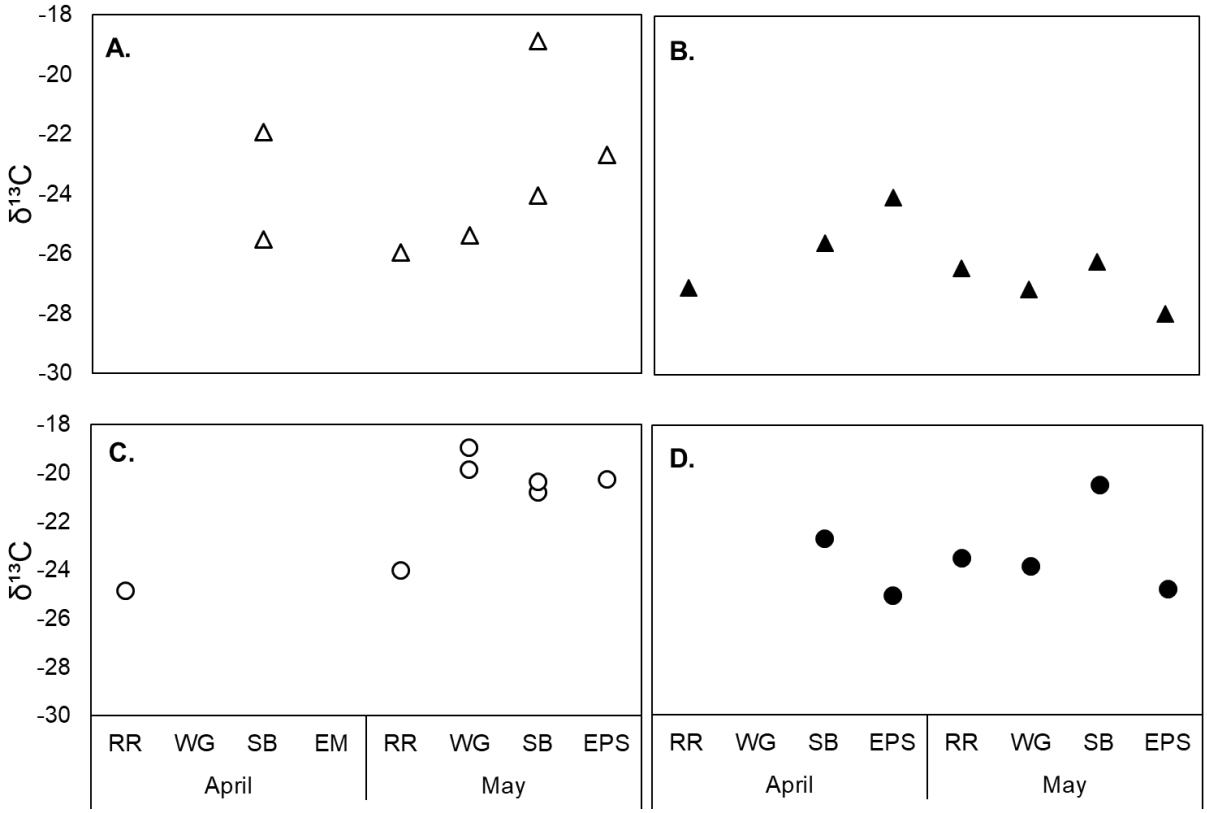

Figure 2.13 Carbon stable isotope ratios for prey collected in diets of yearling Chinook Salmon. **A.** Mayfly **B.** Hymenoptera **C.** Odonata **D.** *Ramellogammarus spp*. (Open squares = 2016, Filled squares = 2017)

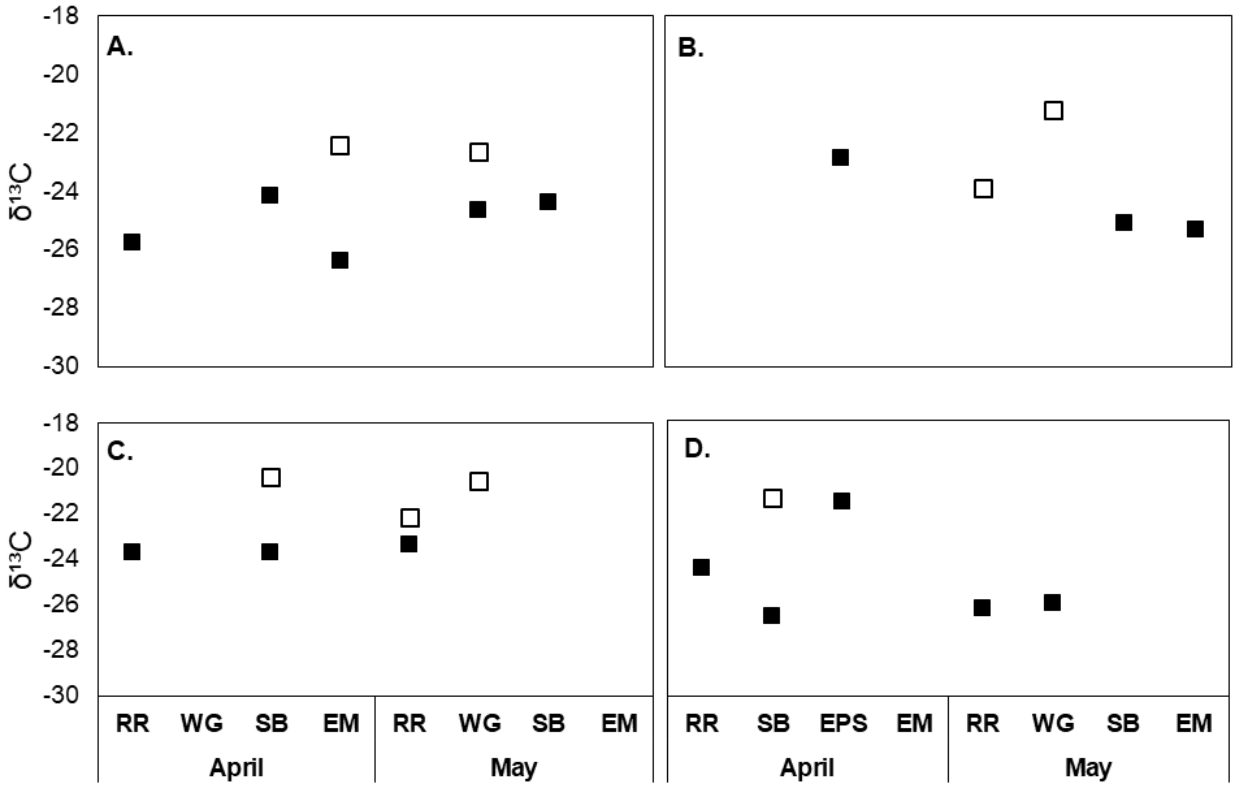

Figure 2.14 Mean (±SE) carbon stable isotope ratios for amphipods and diptera collected in the LCRE wetlands during peak yearling Chinook outmigration (March – May). Data includes invertebrates collected in 2005, 2011, 2012, 2013, 2014, 2015, and 2016. Locations are in river kilometers. Triangles = Diptera and Squares= Amphipoda

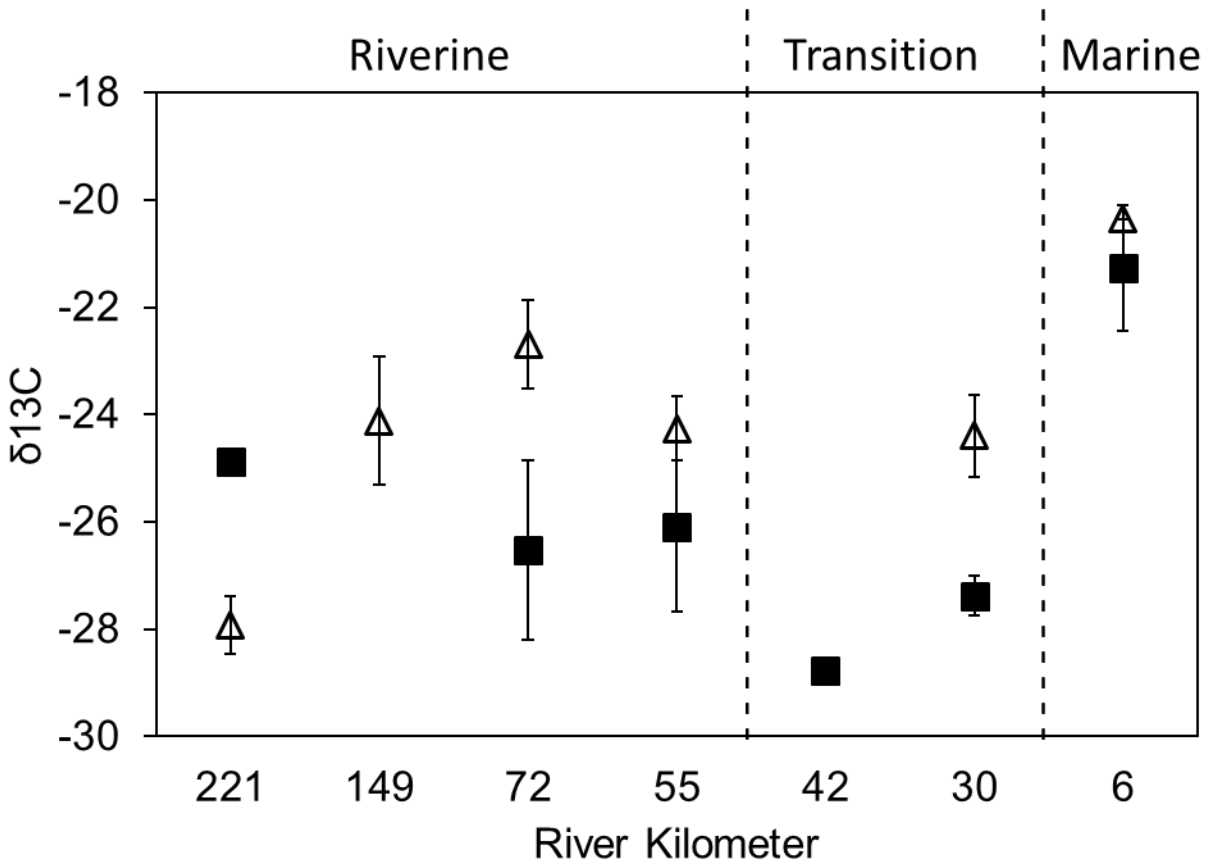

Figure 2.15 Outflow data from Bonneville forebay during peak yearling Chinook outmigration (March – May) during two year sampling period. 10 year average flow included. Shaded blue areas indicate time periods when fish sampling occurred for both 2016 and 2017(Courtesy of U.S. Army Corps of Engineers, NWD)

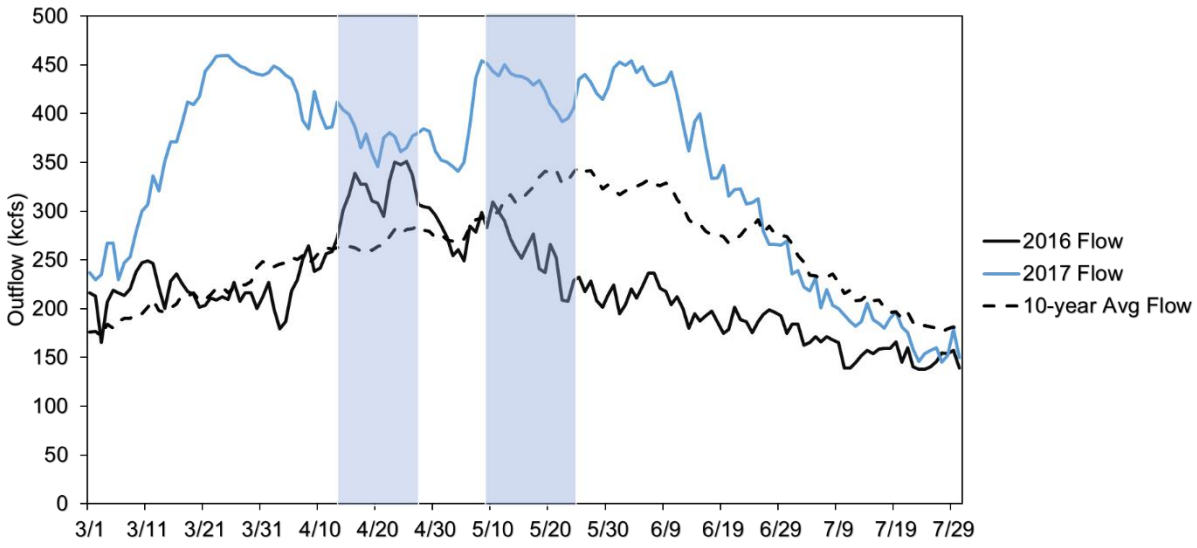

Figure 2.16 Total amount of wetland acres available at each site (includes 20 rkm above each fish collection point for each site).

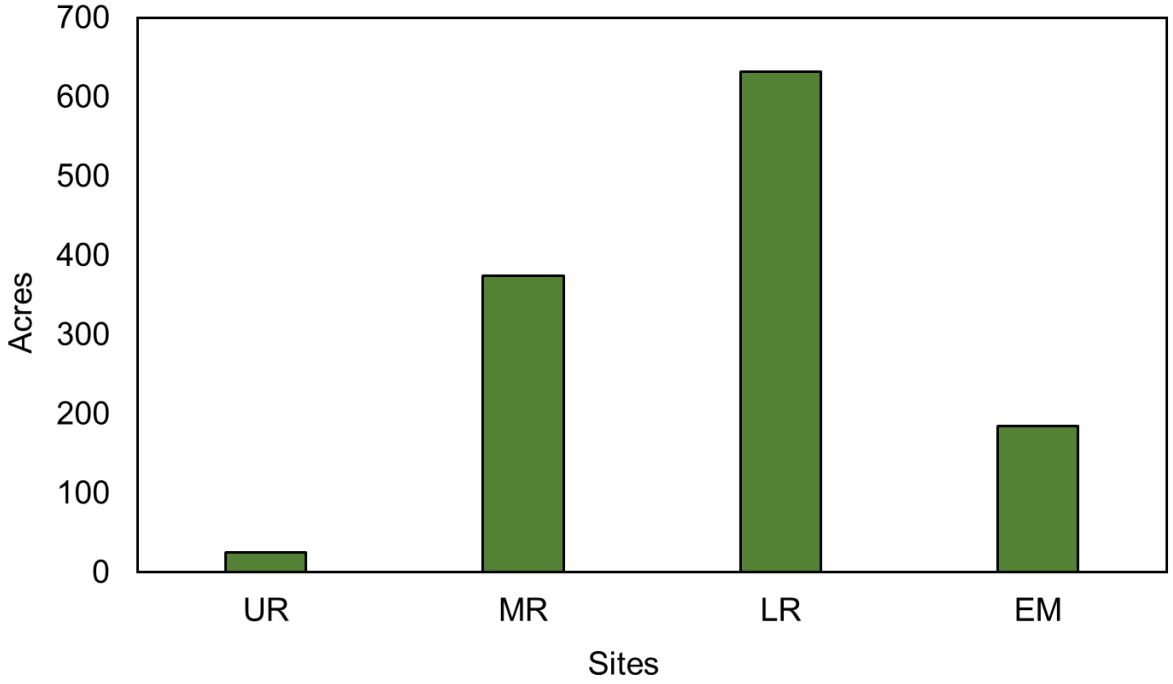

Table 2.1 Genetic stock composition of yearling Chinook Salmon collected during 2016 and 2017 across all sites. Stocks are abbreviated IS = Interior Columbia River Spring; SF = Snake River Fall; UCR = Upper Columbia River Summer/Fall; WF = West Cascade Fall; WS = Willamette River Spring). UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth.

Year	Month	Site	IS	SF	UCR	WS	Total Chinook
2016	**April**	UR	16	2	2	0	20
		MR	0	0	0	1	1
		LR	15	1	1	3	20
		EM	7	9	7	11	34
	May	UR	60	0	14	0	74
		MR	42	0	2	0	44
		LR	28	0	9	0	37
		EM	33	0	7	0	40
		2016 Total	**201**	**12**	**42**	**15**	**270**
2017	**April**	UR	18	11	3	0	32
		MR	4	0	1	0	5
		LR	13	4	2	2	21
		EM	13	3	2	9	27
	May	UR	37	0	8	0	45
		MR	44	0	8	0	52
		LR	52	1	9	0	62
		EM	33	0	11	1	45
		2017 Total	**214**	**19**	**44**	**12**	**289**

Table 2.2 Number of Interior Columbia River spring Chinook Salmon collected and diets processed in 2016 and 2017. Average (±SE) length (mm), weight (g), condition index, stomach fullness (%BW), outflow (1000^3/s), and water temperature (°C). UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth.

Year	Month	Site	Fish (n=)	Diets (n=)	Fork Length (mm)	Fish Weight (g)	Condition Index	Stomach Fullness (%BW)	Outflow (kcfs)	Temperature (°C)
2016	**Apr**	UR	9	8	138.0 (2.98)	27.0 (2.25)	0.13(0.02)	0.5(0.07)	287(13.18)	11.1(0.06)
		MR	0	0	-	-	-	-	-	-
		LR	8	8	142.9 (4.05)	27.4 (2.55)	0.03(0.02)	1.11(0.08)	311(7.52)	12.0(0.1)
		EM	3	3	159.3 (5.04)	37.8 (4.42)	0.01(0.03)	0.6(0.02)	326(5.81)	11.5(0.14)
	May	UR	48	37	136.0 (1.12)	21.3 (0.66)	-0.05(0.01)	1.08(0.09)	296(5.66)	14.1(0.19)
		MR	38	20	139.0 (1.20)	23.8 (0.80)	-0.02(0.01)	0.94(0.1)	289(7.76)	14.3(0.25)
		LR	22	18	140.1 (2.31)	22.8 (1.03)	-0.07(0.02)	0.81(0.06)	259(7.71)	14.8(0.1)
		EM	28	23	144.2 (1.48)	25.7 (0.88)	-0.05(0.01)	0.58(0.05)	255(9.58)	15.0(0.09)
2017	**Apr**	UR	13	11	146.5 (5.70)	34.4 (5.08)	0.09(0.02)	1.31(0.21)	362(6.95)	9.1(0.09)
		MR	2	0	146.0 (21.0)	33.4 (15.11)	0.1(0.02)	-	371(4.62)	10.1(0.07)
		LR	10	9	150.9 (3.17)	32.3 (2.03)	0.03(0.02)	1.03(0.19)	366(8.53)	9.7(0.28)
		EM	11	11	143.0 (5.46)	28.5 (3.79)	0.03(0.03)	0.8(0.13)	370(4.05)	10.0(0.07)
	May	UR	36	20	143.8 (1.42)	27.3 (0.84)	0.01(0.01)	1.58(0.16)	436(2.12)	12.2(0.19)
		MR	39	19	142.3 (1.48)	26.9 (1.01)	0.03(0.01)	1.09(0.05)	434(1.86)	12.1(0.15)
		LR	45	20	141.4 (1.22)	25.8 (0.65)	0.02(0.01)	1.13(0.08)	409(5.78)	12.9(0.2)
		EM	30	22	141.5 (1.04)	25.8 (0.72)	0.01(0.01)	1.01(0.07)	407(9.98)	13.3(0.07)

Table 2.3 Proportion of total per site for the neustonic for taxa collected in 2016 and 2017 and separated by month. UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth.

2016

	April				May				June			
Order	UR	MR	LR	EM	UR	MR	LR	EM	UR	MR	LR	EM
Diptera	0.27	0.09	0.09	0.26	0.07	0.24	0.60	0.44	0.51	0.09	0.93	0.33
Coleoptera	0.02		0.02	0.26	0.03	0.05	0.05				0.02	0.06
Hemiptera			0.04	0.06	0.19	0.05	0.05	0.11		0.03		
Hymenoptera			0.02	0.25	0.04	0.05					0.03	
Ephemeroptera	0.11		0.02			0.10				0.06		
Trichoptera												
Plecoptera			0.02									
Odonata			0.02		0.04							
Thysanoptera			0.04							0.03		
Insect	0.02				0.01			0.11				
Araneae					0.43		0.10	0.11	0.10	0.66		0.06
Amphipoda	0.03	0.04	0.56	0.13	0.08	0.10	0.10	0.11		0.03	0.02	0.56
Bivalvia	0.18				0.11	0.37	0.10		0.39	0.06		
Fish	0.05	0.70	0.05		0.02	0.05				0.03		
Gastropoda			0.02					0.11		0.03		
Mite	0.34	0.17	0.09	0.04								
Collembola			0.02									

2017

	April				May				June			
Order	UR	MR	LR	EM	UR	MR	LR	EM	UR	MR	LR	EM
Diptera	0.18	0.23	0.43	0.68	0.75	0.49	0.55	0.19	0.37	0.46	0.44	0.54
Coleoptera				0.03		0.04	0.11	0.13				0.15
Hemiptera			0.12	0.15		0.04	0.03	0.05	0.08			0.15
Hymenoptera				0.03			0.03	0.03			0.19	
Ephemeroptera	0.03	0.14		0.05			0.03	0.03		0.11		
Trichoptera								0.03	0.06			
Plecoptera	0.03	0.14					0.03					
Odonata							0.03	0.03				
Thysanoptera				0.03								
Insect							0.03	0.03				
Araneae					0.08	0.04	0.09	0.07		0.11	0.19	
Amphipoda	0.72	0.35	0.34	0.03	0.17	0.28	0.08	0.05	0.11	0.22		0.15
Bivalvia						0.08						
Fish	0.03	0.14		0.03		0.04				0.11	0.19	
Gastropoda			0.12					0.13				
Mite									0.38			
Collembola								0.23				

Table 2.4 Frequency of occurrence of prey taxa for 230 Interior Columbia River spring Chinook Salmon collected in April and May of 2016 and 2017. UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth

	2016				2017			
Taxa	**UR**	**MR**	**LR**	**EM**	**UR**	**MR**	**LR**	**EM**
Amphipod	84	90	92	77	94	100	100	85
Arachnid	7	5	23	4	19	11	10	0
Bivalvia	13	0	4	4	3	0	21	0
Coleoptera	22	15	8	4	6	5	21	6
Diptera	73	80	85	65	88	84	97	64
Ephemeroptera	9	25	35	4	53	42	83	12
Hemiptera	58	5	23	4	31	5	14	3
Hymenoptera	24	35	35	4	19	0	38	21
Lepidoptera	0	0	0	0	3	0	3	0
Odonata	11	10	12	4	31	16	21	3
Other	9	35	23	35	19	16	3	12
Other crustacea	9	10	0	27	9	5	10	15
Other insects	60	55	42	23	50	21	31	33
Plecoptera	0	0	4	0	19	5	17	3
Trichoptera	4	0	0	4	9	0	10	3
Unidentifed material	20	80	81	50	9	63	62	3

Table 2.5 Average (±SE) energy (kJ/g) of meal for prey taxa and prey habitat groups based on 230 Interior Columbia River spring Chinook Salmon collected in April and May of 2016 and 2017. UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth.

	2016				2017			
	UR	MR	LR	EM	UR	MR	LR	EM
Taxa								
Diptera	0.10(0.03)	0.05(0.01)	0.13(0.06)	0.10(0.06)	0.28(0.09)	0.04(0.01)	0.12(0.03)	0.07(0.03)
Coleoptera	0.09(0.04)	0.01(0.01)		0.01(0.01)		0.01(0.01)	0.05(0.03)	0.01(0.01)
Hemiptera	0.62(0.20)		0.03(0.01)		0.02(0.01)		0.01	
Hymenoptera	0.52(0.20)	0.15(0.07)	0.28(0.24)	0.01(0.01)	0.03(0.01)		0.17(0.08)	0.06(0.03)
Ephemeroptera	0.01(0.01)	0.01(0.01)	0.04(0.01)	0.02(0.02)	0.04(0.02)	0.01(0.01)	0.09(0.02)	0.01
Lepidoptera					0.06(0.06)			
Trichoptera	0.03(0.02)			0.04(0.04)	0.01(0.01)		0.01	0.02(0.02)
Plecoptera					0.02(0.01)	0.02(0.02)	0.01	
Odonata	0.03(0.02)		0.02(0.01)		0.02(0.01)	0.01	0.03(0.01)	0.02(0.02)
Other insects	0.45(0.16)	0.07(0.03)	0.11(0.04)	0.07(0.04)	0.17(0.09)	0.01(0.01)	0.04(0.02)	0.01
Arachnid			0.03(0.02)			0.02(0.01)	0.01(0.01)	
Amphipod	0.81(0.14)	0.41(0.08)	0.39(0.07)	0.23(0.06)	1.60(0.16)	0.99(0.09)	0.70(0.06)	0.53(0.1)
Other crustacean	0.01(0.01)	0.01(0.01)		0.06(0.03)				
Bivalvia	0.07(0.04)			0.01(0.01)			0.07(0.06)	
Other		0.02(0.01)		0.02(0.02)	0.01(0.01)			
Unidentified material	0.32(0.15)	0.40(0.09)	0.59(0.1)	0.77(0.25)		0.07(0.02)	0.10(0.02)	0.01(0.01)
Habitat groups								
Holo-Terrestrial	1.15(0.3)	0.17(0.09)	0.34(0.33)	0.01(0.02)	0.16(0.11)	0.02(0.03)	0.21(0.1)	0.07(0.05)
Mero-Terrestrial	0.16(0.05)	0.05(0.01)	0.11(0.02)	0.15(0.09)	0.32(0.07)	0.09(0.02)	0.21(0.04)	0.09(0.06)
Nondescript Insects	0.55(0.19)	0.09(0.03)	0.20(0.08)	0.09(0.05)	0.17(0.12)	0.02(0.02)	0.09(0.04)	0.03(0.01)
Pelagic	0.01(0.03)	0.02(0.01)		0.01(0.01)	0.01(0.04)	0.01(0.01)	<0.01	<0.01
Benthic	0.88(0.15)	0.43(0.08)	0.39(0.07)	0.24(0.07)	1.61(0.15)	1.04(0.07)	0.77(0.07)	0.53(0.1)
Other	0.32(0.21)	0.42(0.09)	0.59(0.1)	0.77(0.27)		0.08(0.02)	0.10(0.02)	0.01(0.01)
Nondescript Other	<0.01	0.01(0.02)		0.07(0.05)				

Table 2.6 Pearson's correlation coefficients for Axis 1, 2, and 3 scores from the Nonmetric Multidimensional Scaling ordinations of 230 Interior Columbia River spring Chinook Salmon diets. Correlations include values for the axis scores and taxa included in ordination ("Taxa") and for the axis scores and relevant biological and physical factors. Significance values were adjusted for multiple comparisons and those that were significant are in bold ($p < 0.004$; both years $|r| > 0.206$; 2016 and 2017 $|r| > 0.288$)

	Both years			**2016**			**2017**	
	Axis 1	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**
Taxa								
Amphipod	**0.537**	-0.013	0.071	**-0.429**	-0.106	-0.043	**-0.515**	0.058
Bivalvia	-0.057	-0.044	**0.206**	-0.091	-0.184	0.016	0.263	0.027
Diptera	-0.170	**0.321**	**-0.325**	0.065	**0.387**	0.230	**0.434**	0.167
Hemiptera	-0.165	0.192	**0.301**	0.002	-0.020	**-0.489**	0.227	0.092
Hymenoptera	-0.183	-0.172	**0.517**	0.052	**-0.465**	**-0.384**	**0.432**	0.100
Odonata	0.033	0.017	0.063	-0.087	0.012	-0.005	0.067	**-0.295**
Other crustacea	0.020	-0.034	-0.201	-0.064	**-0.357**	0.118	-0.050	0.052
Other insect	**-0.233**	**0.347**	0.134	-0.100	0.254	**-0.361**	**0.451**	-0.149
Unidentified material	**-0.512**	**-0.474**	-0.194	**0.699**	-0.027	0.151	0.071	-0.217
Biological and Physical Factors								
Fish FL	0.027	-0.204	0.003	0.224	-0.081	0.184	-0.038	**-0.293**
Fish Wt	0.027	-0.119	-0.004	0.217	-0.015	0.192	0.085	**-0.314**
Condition Index	-0.060	-0.203	0.026	0.096	-0.181	-0.021	**-0.294**	0.034
Stomach Fullness	0.189	-0.051	**0.211**	-0.038	**-0.308**	-0.267	-0.059	0.093
Wet weight stomach	0.201	-0.109	0.199	0.075	**-0.318**	-0.176	-0.025	-0.033
Flow (kcfs)	**0.522**	0.081	0.071	-0.231	0.100	**-0.300**	**-0.446**	0.059
Mean Temp °C	**-0.224**	**-0.277**	0.078	0.041	-0.192	-0.032	**-0.344**	0.062

Table 2.7 Results from the indicator species analysis (ISA) with values for taxa from diets of 230 Interior Columbia River spring Chinook Salmon. P-values were adjusted for multiple comparisons (Bonferroni)

Both years				**2016**			**2017**		
Taxa	IV	Randomized Indicator Value	p *	IV	Rand Mean	p *	IV	Rand mean	p *
Amphipod	60.9	47.5	0.0002	36.9	28.2	0.0216	39.3	27.7	0.0002
Arachnid	5.6	7	0.76	20.1	7.7	0.0098	6.6	8.4	0.5971
Bivalvia	4	5.1	0.7137	11.1	6.4	0.0968	19.4	7.2	0.0052
Coleoptera	9.5	8.5	0.2723	18.4	9.9	0.0436	15.1	8	0.0534
Diptera	47.5	44.8	0.2378	29.3	30	0.4823	47.5	31.9	0.0148
Ephemeroptera	31.8	18.7	0.0004	16.6	9.8	0.0542	47.3	19.5	0.0002
Hemiptera	28.3	14.6	0.0004	54.8	15.2	0.0002	21	8.8	0.0084
Hymenoptera	19.4	14.7	0.0704	13.2	13.1	0.4097	25.1	12.2	0.0128
Odonata	9.8	9.1	0.3053	5.6	7.4	0.6653	10.1	10.6	0.4553
Other	14.1	12.1	0.2116	17.7	14.3	0.2184	10.7	10.2	0.3893
Other crustacea	9.3	7.8	0.2044	18.7	8	0.013	3.2	7.8	0.992
Other insect	35.8	26.7	0.0168	37.1	21.5	0.0124	33.9	20	0.0232
Unidentified	46.4	24	0.0002	22.8	19.7	0.1918	33.2	13.6	0.0006

Table 2.8 Mean carbon stable isotope ratios (± SE) for amphipods and insects collected either in Interior Columbia River Spring Chinook Salmon diets or wetland at a given river kilometer in the Lower Columbia River and Estuary. **A.** Diet samples were summarized for the 2016-2017 sampling season. **B.** Wetland samples are an overall mean of prey collected in March, April, May, and June across 9 years (2004-05, 2011-17).

A.

	Amphipod		**Insect**	
RKM	**2016**	**2017**	**2016**	**2017**
210	-26.3	-25.92(0.4)	-23.63(0.37)	-24.1(0.57)
92	-25.38	-26.58(0.56)	-20.86(0.78)	-24.24(0.41)
61	-21.01(1.64)	-26.13(0.28)	-20.16(0.37)	-23.34(0.44)
13	-22.69	-24.54(1.85)	-20.32(1.22)	-25.39(0.36)

B.

RKM	Amphipod	Dipteran
221	-24.87	-27.92(0.54)
149	–	-24.11(1.20)
72	-26.53(1.66)	-22.69(0.82)
55	-26.08(1.59)	-24.25(0.61)
42	-28.76	–
30	-27.37(0.36)	-24.4(0.76)
6	-21.26(1.17)	-20.36

Chapter 3 : Conclusion

The results from this study indicate that Interior spring Chinook Salmon actively feed as they move through the LCRE. More importantly, yearling Chinooks are feeding on a variety of high-energy, wetland-derived insects. There were differences in stomach fullness, condition, and diet composition along the river and estuarine gradient, but the biggest difference was observed between years. In 2016, when flows, on average, were 86% of the long-term mean (based on 10 years of data), wetland-produced insects contributed to 47% of yearling Chinook diet's energy density. In contrast, in 2017, when flows were an average of 34% greater than the long-term mean, and yearling Chinooks fed almost exclusively on benthic amphipods (69% of energy density in diet). This provides some evidence that during periods when flows are below 300 kcfs, neustonic yearling Chinook prey is more available to yearling Chinook salmon. When flows are greater than 300 kcfs, neustonic prey may be less available, potentially due to reduced abundance or accumulation, therefore not be as accessible to yearling Chinooks. The neuston data also supports this idea since there was the biomass of neustonic taxa was consistently more abundant in 2016 compared to 2017.

While this study only encompassed two years of sampling, the results of this thesis provided new information of feeding habits of Interior spring Chinook yearling Chinooks and changes in carbon sources of prey items supporting yearling Chinooks as they migrate. Flow is an important factor in the LCRE, especially since it can be used to manage fisheries for increased survival over dams. Currently Columbia River flow is lower than historical values and the spring freshet is substantially reduced. However, we need

to understand how restoration and management can coexist with urbanization and the hydrosystem in this altered system to support native species such as Chinook salmon. With climate change and growing human populations, it is important that we apply adaptive management to our efforts in the recovery of salmon and wetlands in order to maintain ecosystem processes.

APPENDICES

Appendix A:

Supplemental material for Chapter 2:

Table A1 Diet composition of taxa broken down by %number (N), %wet weight (W) (g), and % energy density (ED) (kJ/g of fish meal) for across all sites for 2016 and 2017. Months were combined.

	2016												2017											
	UR			MR			LR			EM			UR			MR			LR			EM		
Taxa	%N	%W	%ED	%N	%W	%ED	%N	%W	%ED	%N	%W	%ED	%N	%W	%ED	%N	%W	%ED	%N	%W	%ED	%N	%W	%ED
Diptera	14	3	3	28	4	4	46	9	8	66	7	8	34	10	12	12	3	4	34	8	8	29	5	10
Coleoptera	1	2	3	2	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	3	0	0	1
Hemiptera	45	10	20	1	0	0	3	1	2	2	0	0	1	0	1	0	0	0	1	0	0	0	0	0
Hymenoptera	2	8	17	4	4	13	4	12	17	1	0	1	1	0	1	0	0	0	2	5	12	1	3	8
Ephemeroptera	0	0	0	3	1	1	4	2	2	0	1	1	2	1	2	2	1	1	6	6	6	1	1	1
Lepidoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0
Trichoptera	0	1	1	0	0	0	0	0	0	1	2	3	0	0	1	0	0	0	0	0	1	0	1	2
Plecoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	1	1	1	0	0	0
Odonata	1	1	1	1	1	0	2	2	1	1	0	0	1	1	1	1	1	1	1	2	2	0	2	3
Other insects	1	11	15	5	3	6	4	4	7	0	3	5	0	3	7	1	1	1	0	2	3	0	0	1
Arachnid	1	0	0	1	0	0	3	1	2	1	0	0	0	0	0	1	1	1	1	0	1	0	0	0
Amphipod	35	46	26	54	46	36	34	31	24	23	17	17	60	81	70	82	86	83	48	54	50	65	86	72
Other crustacea	0	1	0	1	1	1	0	0	0	3	5	4	0	1	0	0	0	0	5	1	0	2	0	0
Bivalvia	0	4	2	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	12	5	0	0	0
Other	0	0	0	1	1	2	1	0	0	2	1	2	0	1	1	1	0	0	1	0	0	1	0	1
Unid matter	0	13	10	0	40	35	0	39	37	0	63	58	0	0	0	0	6	6	0	7	7	0	1	1

Table A2 Energy density and functional habitat group for all juvenile salmon prey found in diets of Snake River spring/summer Chinook Salmon.

Level I	Level II	Level III, stage	Habitat group	Energy density (kJ g-1 wm)	Source	Source taxa and notes
Insecta						
	Coleoptera	Cantharidae, adult	Holo-Terrestrial	7.94	Gray 2005	Cantharidae adult
		Coccinellidae, adult	Holo-Terrestrial	7.97	Gray 2005	Coleoptera adult
		Coleoptera, adult	Nondescript Insects	7.97	Gray 2005	Coleoptera adult
		Coleoptera, larvae	Nondescript Insects	2.41	Gray 2005	Coleoptera larva
		Dytiscid, larvae	Mero-Terrestrial	2.41	Gray 2005	Coleoptera larva
		Elmidae, larvae	Mero-Terrestrial	2.41	Gray 2005	Coleoptera larva
		Staphylinidae, adult	Holo-Terrestrial	7.97	Gray 2005	Coleoptera adult
	Diptera	Bibionidae, adult	Holo-Terrestrial	8.81	Brodmann and Reyer 1999	Bibionidae
		Cecidomyiidae, adult	Holo-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Cecidomyiidae, pupae	Holo-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Ceratopogonidae, adult	Mero-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Ceratopogonidae, larvae	Mero-Terrestrial	2.58	Gray 2005	Diptera larva
		Ceratopogonidae, pupae	Mero-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Chironomidae, adult	Mero-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Chironomidae, larvae	Mero-Terrestrial	2.58	Gray 2005	Diptera larva
		Chironomidae, pupae	Mero-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Diptera, adult	Nondescript Insects	8.92	Gray 2005	Other Diptera

Table A2	Continued					
Level I	**Level II**	**Level III, stage**	**Habitat group**	**Energy density (kJ g-1 wm)**	**Source**	**Source taxa and notes**
		Diptera, larvae	Nondescript Insects	2.58	Gray 2005	Diptera larva
		Diptera, pupae	Nondescript Insects	8.92	Gray 2005	Other Diptera
		Empididae, adult	Mero-Terrestrial	8.99	Brodmann and Reyer 1999	Empididae
		Ephydridae, adult	Mero-Terrestrial	8.92	Gray 2005	Other Diptera
		Mycetophilidae, adult	Holo-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Nematocera	Nondescript Insects	3.83	Gray 2005	Chironomidae adult
		Nematocera, adult	Nondescript Insects	3.83	Gray 2005	Chironomidae adult
		Nematocera, egg	Nondescript Insects	3.83	Gray 2005	Diptera larva
		Nematocera, larvae	Nondescript Insects	3.83	Gray 2005	Diptera larva
		Nematocera, pupae	Nondescript Insects	3.83	Gray 2005	Chironomidae adult
		Phoridae, adult	Mero-Terrestrial	8.92	Gray 2005	Other Diptera
		Psychodidae, adult	Holo-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Sciaridae, adult	Holo-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Simuliidae, adult	Mero-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Simuliidae, larvae	Mero-Terrestrial	2.58	Gray 2005	Diptera larva
		Simuliidae, pupae	Mero-Terrestrial	3.83	Gray 2005	Chironomidae adult
		Sphaeroceridae, adult	Holo-Terrestrial	8.92	Gray 2005	Other Diptera
		Tipulidae, adult	Mero-Terrestrial	7.95	Brodmann and Reyer 1999	Tipulidae
	Ephemeroptera	Ephemeroptera, adult	Mero-Terrestrial	3.66	Pizzul et al. 2009	Ephemeroptera

Table A2	Continued					
Level I	**Level II**	**Level III, stage**	**Habitat group**	**Energy density (kJ g-1 wm)**	**Source**	**Source taxa and notes**
		Ephemeroptera, nymph	Mero-Terrestrial	3.66	Pizzul et al. 2009	Ephemeroptera
		Baetidae, nymph	Mero-Terrestrial	3.66	Pizzul et al. 2009	Ephemeroptera
		Ephemerellidae, nymph	Mero-Terrestrial	3.66	Pizzul et al. 2009	Ephemeroptera
		Heptageniidae, nymph	Mero-Terrestrial	3.66	Pizzul et al. 2009	Ephemeroptera
		Hexaginidae, nymph	Mero-Terrestrial	3.66	Pizzul et al. 2009	Ephemeroptera
	Hemiptera	Hemiptera, nymph	Holo-Terrestrial	10.93	Gray 2005	Hemiptera (adult and immature)
		Aphididae, adult	Holo-Terrestrial	10.93	Gray 2005	Hemiptera (adult and immature)
		Aphididae, nymph	Holo-Terrestrial	10.93	Gray 2005	Hemiptera (adult and immature)
		Cicadellidae, adult	Holo-Terrestrial	10.93	Gray 2005	Hemiptera (adult and immature)
		Corixidae, adult	Mero-Terrestrial	10.93	Gray 2005	Hemiptera (adult and immature)
		Psyllidae, adult	Holo-Terrestrial	10.93	Gray 2005	Hemiptera (adult and immature)
		Tingidae, adult	Holo-Terrestrial	10.93	Gray 2005	Hemiptera (adult and immature)
	Hymenoptera	Hymenoptera, adult	Holo-Terrestrial	12.67	Gray 2005	Hymenoptera
		Apidae, adult	Holo-Terrestrial	12.67	Gray 2005	Hymenoptera
		Chalcid, adult	Holo-Terrestrial	12.67	Gray 2005	Hymenoptera
		Eurytomidae, adult	Holo-Terrestrial	12.67	Gray 2005	Hymenoptera
		Formicidae, adult	Holo-Terrestrial	5.69	Brodmann and Reyer 1999	Formicidae
		Ichneumonidae, adult	Holo-Terrestrial	12.67	Gray 2005	Hymenoptera
	Other Insect	Insecta	Nondescript Insects	7.41	Bieber 2005	Other Insecta

Table A2	Continued					
Level I	**Level II**	**Level III, stage**	**Habitat group**	**Energy density (kJ g-1 wm)**	**Source**	**Source taxa and notes**
		Insecta, adult	Nondescript Insects	7.41	Bieber 2005	Other Insecta
		Insecta, egg	Nondescript Insects	7.41	Bieber 2005	Other Insecta
		Insecta, larvae	Nondescript Insects	7.41	Bieber 2005	Other Insecta
		Insecta, nymph	Nondescript Insects	7.41	Bieber 2005	Other Insecta
		Insecta, pupae	Nondescript Insects	7.41	Bieber 2005	Other Insecta
		Lepidoptera, adult	Holo-Terrestrial	8.5	Gray 2005	Lepidoptera (Adult and larval)
		Perlodidae, nymph	Mero-Terrestrial	4.13	Pizzul et al. 2009	Plecoptera
		Petrophila, larvae	Mero-Terrestrial	8.5	Gray 2005	Lepidoptera (Adult and larval)
		Plecoptera, nymph	Mero-Terrestrial	4.13	Pizzul et al. 2009	Plecoptera
		Thysanoptera, adult	Holo-Terrestrial	7.43	Bieber 2005	Other Insecta
		Trichoptera, adult	Mero-Terrestrial	7.76	Gray 2005	Trichoptera adult
		Trichoptera, larvae	Mero-Terrestrial	5.81	Gray 2005	Trichoptera (larval, emergent)
	Odonata	Anisoptera, nymph	Mero-Terrestrial	4.13	Author's estimate	
		Coenagrionidae, nymph	Mero-Terrestrial	4.13	Author's estimate	
		Gomphiidae, nymph	Mero-Terrestrial	4.13	Author's estimate	
Other Arthropoda						
	Arachnid	Acari	Mero-Terrestrial	5.32	Gray 2005	Araneae
		Aranaea	Holo-Terrestrial	5.32	Gray 2005	Araneae

Level I	Level II	Level III, stage	Habitat group	Energy density (kJ g-1 wm)	Source	Source taxa and notes
Crustacea						
	Amphipod	Americorophium	Benthic	3.07	Cordell et al. 2011; Gray 2005	Mean of values from both studies
		Americorophium salmonis	Benthic	3.07	Cordell et al. 2011; Gray 2005	Mean of values from both studies
		Americorophium spinicornis	Benthic	3.07	Cordell et al. 2011; Gray 2005	Mean of values from both studies
		Amphipoda	Benthic	2.97	Cordell et al. 2011; Gray 2005	Mean of values from both studies
		Gammaridea	Benthic	2.97	Cordell et al. 2011; Gray 2005	Mean of values from both studies
		Ramellogammarus oregonsis	Benthic	2.97	Author's estimate	
	Other Crustacea	Asellidae	Benthic	2.96	Cordell et al. 2011; Gray 2005	Mean of values from both studies
		Chydorid	Benthic	1.37	Higgs et al. 1995	Cladocera. Mean of 189 values
		Cirripedia	Pelagic	2.16	Lucas et al. 1979	Cirripedia cypris
		Crab Megalope	Pelagic	3.36	Higgs et al. 1995	Crab zoea
		Crustacean parts	Nondescript other	3.37	Bieber 2005	Other Crustacea
		Cyclopoid	Pelagic	4.62	Higgs et al. 1995	Copepoda. Mean of 8 values
		Daphnia	Pelagic	1.37	Higgs et al. 1995	Cladocera. Mean of 189 values
		Mysida	Pelagic	3.55	Gray 2005	Mysida
		Simocephalus	Pelagic	1.37	Higgs et al. 1995	Cladocera. Mean of 189 values
Other						
Table A2	**Continued**					

Level I	Level II	Level III, stage	Habitat group	Energy density (kJ g-1 wm)	Source	Source taxa and notes
	Bivalvia	Bivalvia	Benthic	3.57	Ciancio et al. 2007	Mean of 3 values
	Other	Fish, egg	Nondescript other	6.83	Higgs et al. 1995	Mean of 20 values
		Fish, larvae	Pelagic	6.83	Higgs et al. 1995	Mean of 20 values
		Nematoda	Nondescript other	3	Author's estimate	
		Plastic		0	Author's estimate	
		Plant Material		0	Author's estimate	Plant material
	Unidentified Material	Digested material	Other	3.37	Author's estimate	

Table A3 Frequency of occurrence of prey taxa level III, stage for 230 Interior Columbia River spring Chinook Salmon collected in April and May of 2016 and 2017. UR=Upper River, MR=Middle River, LR=Lower River, and EM=Estuary Mouth.

	2016				2017			
	UR	**MR**	**LR**	**EM**	**UR**	**MR**	**LR**	**EM**
n=	45	20	26	26	32	19	29	33
Taxa								
Bibionidae, adult	0	0	0	0	6	0	0	0
Cecidomyiidae, adult	0	0	12	0	13	5	17	6
Cecidomyiidae, pupae	0	0	0	0	0	0	3	0
Ceratopogonidae, adult	0	0	8	0	0	0	0	0
Ceratopogonidae, larvae	0	0	8	8	0	5	3	0
Ceratopogonidae, pupae	0	0	4	0	3	0	0	0
Chironomidae, adult	42	25	38	35	53	26	48	27
Chironomidae, larvae	11	15	54	8	31	53	52	9
Chironomidae, pupae	20	35	19	12	41	26	31	6
Diptera, adult	0	0	8	0	6	5	3	9
Diptera, larvae	0	0	0	0	3	0	3	3
Diptera, pupae	0	0	0	0	0	5	10	9
Empididae, adult	0	0	0	0	3	0	0	0
Ephydridae, adult	0	0	4	0	6	0	0	6
Mycetophilidae, adult	0	0	0	0	9	5	7	0
Nematocera	7	5	4	0	0	0	7	0
Nematocera, adult	9	15	19	8	0	0	3	15
Nematocera, egg	0	5	4	0	0	0	0	0
Nematocera, larvae	7	5	4	8	0	0	0	0
Nematocera, pupae	11	15	19	8	0	0	0	0

Table A3 Continued

	2016				2017			
	UR	**MR**	**LR**	**EM**	**UR**	**MR**	**LR**	**EM**
Phoridae, adult	0	0	0	0	6	0	0	0
Psychodidae, adult	0	0	4	0	13	0	3	9
Sciaridae, adult	0	0	0	0	28	0	28	6
Simuliidae, adult	0	0	0	0	34	11	0	0
Simuliidae, larvae	0	5	0	0	13	0	3	0
Simuliidae, pupae	0	5	0	0	13	21	7	0
Sphaeroceridae, adult	0	0	0	0	0	0	3	0
Tipulidae, adult	0	0	0	0	3	0	0	0
Cantharidae, adult	0	0	0	0	0	0	3	0
Coccinellidae, adult	2	10	0	0	0	0	0	0
Coleoptera, adult	18	5	0	4	6	5	14	6
Coleoptera, larvae	0	0	4	0	0	0	0	0
Dytiscid, larvae	0	0	4	0	0	0	0	0
Elmidae, larvae	0	5	0	0	0	0	0	0
Staphylinidae, adult	2	0	0	0	0	0	3	0
Aphididae, adult	58	0	23	4	25	5	14	3
Aphididae, nymph	0	0	0	0	3	0	0	0
Cicadellidae, adult	2	0	0	0	0	0	0	0
Corixidae, adult	0	0	0	0	3	0	0	0
Hemiptera, nymph	4	0	0	0	0	0	0	0
Psyllidae, adult	0	0	4	0	13	0	0	0
Tingidae, adult	0	5	0	0	0	0	0	0
Apidae, adult	0	0	0	0	0	0	10	0

Table A3 Continued

	2016				2017			
	UR	**MR**	**LR**	**EM**	**UR**	**MR**	**LR**	**EM**
Chalcid, adult	0	0	0	0	6	0	0	0
Eurytomidae, adult	0	0	0	0	0	0	3	0
Formicidae, adult	0	5	8	0	9	0	10	12
Hymenoptera, adult	27	35	31	4	3	0	14	9
Ichneumonidae, adult	0	0	0	0	3	0	0	0
Baetidae, nymph	0	5	0	0	13	0	7	0
Ephemerellidae, nymph	0	5	0	0	0	5	10	0
Ephemeroptera, adult	0	0	0	0	3	0	3	0
Ephemeroptera, nymph	7	5	27	4	28	26	55	6
Heptageniidae, nymph	2	10	8	0	9	11	10	3
Hexaginidae, nymph	0	0	0	0	0	0	0	3
Lepidoptera, adult	0	0	0	0	3	0	0	0
Petrophila, larvae	0	0	0	0	0	0	3	0
Trichoptera, adult	0	0	0	0	6	0	7	3
Trichoptera, larvae	4	0	0	4	3	0	3	0
Perlodidae, nymph	0	0	0	0	6	5	0	0
Plecoptera, nymph	0	0	4	0	13	0	17	3
Anisoptera, nymph	0	5	0	0	0	0	3	0
Coenagrionidae, nymph	11	5	12	4	31	16	14	0
Gomphiidae, nymph	0	0	0	0	0	0	3	3
Insecta	42	40	31	23	47	21	21	30
Insecta, adult	16	10	23	0	6	0	3	6
Insecta, egg	2	5	0	0	0	0	0	0

Table A3 Continued

	2016				2017			
	UR	**MR**	**LR**	**EM**	**UR**	**MR**	**LR**	**EM**
Insecta, larvae	0	5	0	0	6	5	7	0
Insecta, nymph	4	0	0	0	0	0	0	0
Insecta, pupae	2	5	0	0	3	0	0	0
Thysanoptera, adult	0	0	4	0	0	0	0	0
Acari	0	0	0	4	9	0	3	0
Aranaea	7	5	23	0	9	11	7	0
Americorophium	69	15	31	54	0	5	0	0
Americorophium salmonis	2	35	31	0	72	100	90	30
Americorophium spinicornis	4	70	58	0	91	95	97	70
Amphipod	13	35	15	23	3	11	14	12
Gammaridae	9	20	27	4	31	21	7	0
Ramellogammarus oregonsis	33	30	27	8	97	79	76	24
Cirripedia	2	0	0	8	0	0	0	3
Chydorid	0	0	0	0	0	0	0	3
Daphnia	0	0	0	8	3	0	7	3
Simocephalus	0	0	0	0	0	0	3	3
Cyclopoid	0	0	0	0	0	0	0	3
Asellidae	0	0	0	0	3	0	0	0
Mysida	4	0	0	0	0	0	0	0
Crab Megalope	0	0	0	0	0	5	0	0
Crustacean parts	4	10	0	12	3	0	0	3
Bivalve	13	0	4	4	3	0	21	0
Fish, egg	0	0	0	0	0	0	3	0

Table A3 Continued

	2016				2017			
	UR	**MR**	**LR**	**EM**	**UR**	**MR**	**LR**	**EM**
Fish, larvae	0	0	0	0	3	0	0	0
Fish parts	7	25	15	27	3	5	0	3
Nematoda	2	10	8	12	13	11	3	9
Digested material	20	85	96	54	9	63	66	3

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