Juvenile Chinook salmon (*Oncorhynchus tshawytscha)* life history diversity and growth variability in a large freshwater tidal estuary

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Abstract

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For many fish and wildlife species, a mosaic of available habitats is required to complete their life cycle, and is considered necessary to ensure population stability and persistence. Particularly for young animals, nursery habitats provide opportunities for rapid growth and high survival during this vulnerable life stage. My thesis focuses on juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and their use of estuarine wetlands as nursery habitat. Estuaries are highly productive systems representing a mosaic of habitats connecting rivers to the sea, and freshwater tidal estuaries provide abundant prey communities, shade, refuge from predation and transitional habitat for the osmoregulatory changes experienced by anadromous fishes. I will be discussing the freshwater tidal wetland habitat use of juvenile Chinook salmon in the Columbia River estuary, which are listed under the Endangered Species Act. I used otolith microstructural growth estimates and prey consumption to measure rearing habitat quality. This sampling effort was designed to target as much genetic diversity as possible, and individual assignment to regional stocks of origin was used to describe the diversity of juvenile Chinook salmon groups inhabiting the estuary. Diversity is important for resilience, and in salmon biocomplexity within fish stocks has been shown to ensure collective productivity despite environmental change. However much

of the research which links diversity to resilience in salmon has focused on the adult portion of the life cycle and many resource management policies oversimplify juvenile life history diversity. When this oversimplification of juvenile life history diversity is applied to salmon conservation it may be ignoring critical indicators for stability. Therefore in addition to genetic diversity I also explore methods for better defining juvenile life history diversity and its application in salmon management, such as permitting requirements, habitat restoration, hydropower practices and hatchery management.

This study addresses how juvenile salmon growth changes among a range of wetland habitats in the freshwater tidal portion of the Columbia River estuary and how growth variation describes and contributes to life history diversity. To do this, I incorporated otolith microstructure, individual assignment to regional stock of origin, GIS habitat mapping and diet composition, in three habitats (mainstem river, tributary confluence and backwater channel) along ~130 km of the upper estuary. For my first chapter I employed a generalized linear model (GLM) to test three hypotheses: juvenile Chinook growth was best explained by (1) temporal factors, (2) habitat use, or (3) demographic characteristics, such as stock of origin or the timing of seaward migration. I found that variation in growth was best explained by habitat type and an interaction between fork length and month of capture. Juvenile Chinook salmon grew faster in backwater channel habitat and later in the summer. I also found that mid-summer and late summer/fall subyearlings had the highest estuarine growth rates. When compared to other studies in the basin these juvenile Chinook grew on average 0.23, 0.11-0.43 mm/d in the freshwater tidal estuary, similar to estimates in the brackish estuary, but ~4 times slower than those in the plume and upstream reservoirs. However, survival studies from the system elucidated a possible tradeoff between growth and survival in the Columbia River basin. These findings present a unique example of the complexity in understanding the influences of the many processes that generate variation in growth rate for juvenile anadromous fish inhabiting estuaries.

In my second chapter, I used otolith microstructure and growth trends produced in a dynamic factor analysis (DFA, a multivariate time series method only recently being used in fisheries) to identify the life history variation in juvenile Chinook salmon caught in the Columbia River estuary over a two-year period (2010-2012). I used genetic assignment to stock of origin and capture location and date with growth trajectories, as a proxy for habitat transitions, to reconstruct life history types. DFA estimated four to five growth trends were present in juvenile Chinook salmon caught in the Columbia River estuary, diversity currently being simplified in many management practices. Regional stocks and habitats did not display divergent growth histories, but the marked hatchery fish did ordinate very similarly in the trend loadings from the DFA analysis, suggesting that hatchery fish may not experience the same breadth of growth variability as wild fish. I was not able to quantify juvenile life history diversity, and juvenile Chinook life history diversity remains difficult to catalog and integrate into species conservation and habitat restoration for resource management. However, by expanding our understanding of how juvenile Chinook salmon experience their freshwater rearing environment we improve our capacity to conserve and manage salmon populations. The findings from my thesis provide the necessary information for a restoration framework to link habitat features with salmon management goals, such as juvenile growth, wild and genetic origin and life history diversity.

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Preface

A central issue in ecology and conservation is understanding how populations respond to altered environments; an issue that has become increasingly important in view of the potentially irreversible and cascading effects of accelerated climate change. Rapid changes associated with anthropogenic impacts, such as climate change and biodiversity loss are already having large effects on regional population dynamics and species extinctions. Population diversity has emerged as an important mechanism for resilience in changing environments (Luck et al. 2003). The diversity-stability hypothesis suggests that species diversity stabilizes a community and can buffer the impact of perturbations. However, little is known about how to manage species and their requisite habitats in ways that promote the necessary population diversity for resilience to effectively mitigate the impacts of rapid environmental change. To answer these resource management questions, it is critical to better understand how diversity is expressed across landscapes and among populations. The aim of this study is to provide information for incorporating variability in habitat use and quality into a restoration framework. I investigate juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth, habitat use and genetic and life history diversity in the freshwater tidal reaches of the Columbia River estuary. Chinook salmon are an ideal model system because they are reproductively isolated when spawning due to high fidelity to their natal habitats (Quinn 2005), exhibit a wide range of life history characteristics and genetic variation within single watersheds (Waples et al. 2001), and have been suggested to be the most estuarine dependent of the salmon species (Healey 1982). Due to extensive hydropower, irrigation and other development, less than 50% of the historically available basin area within the Columbia River watershed is currently available rearing habitat for juvenile Chinook salmon. This extensive rearing habitat loss in Columbia River basin's streams and rivers may make estuarine nursery habitat restoration particularly important. In addition to contributing to the management of an Endangered Species Act (ESA) listed and culturally important natural resource, this study attempts to provide the information necessary to integrate the management of resilience into salmon habitat restoration design.

Habitat complexity is necessary for species survival, the support of varied life stages and local adaptation (Forman and Godron 1981; Forman 1986; Hilborn et al. 2003). Human induced declines in habitat and species diversity have raised concerns about the effects of diversity loss on ecosystem processes (Vitousek et al. 1997, Sala et al. 2000). The existence and maintenance of metapopulations (e.g., regionally variable and genetically distinct sub-stocks) relies upon conserving habitat complexity (Hilborn et al. 2003; Olsen et al. 2008). These metapopulations contribute to overall species resilience and productivity; therefore species resilience is largely dependent on the maintenance of all the diverse life history types and the range of geographic locations inhabited by each metapopulation (Hilborn et al. 2003; Schindler et al. 2010).

When applying these principles to Pacific salmon (*Oncorhynchus* spp.), population diversity loss and with it decreased adaptive potential for responses to environmental change, in concert with declines in available habitat, could greatly degrade species resilience. Several studies analyzing forty years of Bristol Bay sockeye (*O. nerka*) catches emphasize the significance of the biocomplexity of fish stocks in ensuring collective population productivity despite major environmental change (Hilborn et al. 2003; Moore et al. 2010; Schindler et al. 2010). Schindler *et al.* (2010) used this information to measure the portfolio effects of the asynchrony within Bristol Bay sockeye populations and their life history diversity. A portfolio analysis is the examination of the bio-folio concept, in which genes, species and ecosystems make use of the trends observed in the formation of portfolios, where returns are additive, while risks diversify. This suggests species conservation can be approached analogously to managing an investment portfolio; biological variation will hedge catastrophic losses in productivity and improve long-term stability of a system (Figge 2004). These Alaskan sockeye salmon studies present watershed-scale habitat complexity as an important driver of population diversity, and suggest that some aspects of population diversity are dependent upon the maintenance of a mosaic of habitats (Walsworth et al. 2014). However, these studies do not describe a threshold of habitat complexity necessary to insure the maintenance of biological variation and resilience in salmon populations, which is desirable for designing and implementing salmon conservation of less pristine systems.

Anthropogenic impacts may have disrupted contributions to population resilience provided by habitat complexity in many systems. In the contiguous western United States, Pacific salmon and steelhead are excluded from nearly 45% of the area historically available to anadromous salmonids (McClure et al. 2008). Additionally, more than half of all Pacific salmon evolutionary significant units (ESUs) are listed as threatened or endangered under the Endangered Species Act (ESA) (Good 2005). The major causes for the degraded state of Pacific salmon in the western United States are habitat loss and damage, overfishing and negative interactions with non-native and hatchery-origin fish (Nehlsen et al. 1991). Since the early 1990s, managers have focused the remediation of declining salmon stocks on habitat restoration, rehabilitating ecosystem function (e.g., modification of hydropower passage facilities), harvest management and decreased reliance on hatchery production. Targeted habitat restoration could potentially recover ecosystem functions by reducing habitat fragmentation and promoting connectivity, increasing habitat complexity and with it the adaptive capacity for Pacific salmon.

A great deal of salmon recovery theory has focused on identifying limiting factors and bottlenecks to rehabilitation, targeting a range of alternative recovery conditions, taking a landscape perspective and prioritizing approaches (Palmer 2009; Simenstad and Cordell 2000). However, many salmon habitat restoration projects have concentrated on opportunistic removal of barriers to increase connectivity to historically available habitats (Tanner et al. 2002; Bottom et al. 2005; Roegner et al. 2010). These projects reduce habitat fragmentation and bottlenecks to recovery, but many are limited primarily by scale and the ability to match ecological prioritization with practical goals and land allocation. Although the realities of implementation are an inevitable constraint, restoration projects must be designed at the appropriate scale and include sufficient planning to address their management goals (Simenstad et al. 2006). Specifically because habitat loss is a multifaceted stress, restoration planning should consider organismal responses to habitat quality, incorporating performance metrics such as prey consumption and growth. Growth has been shown to be an important indicator for habitat quality and a measure of fitness consequences to individuals (Sogard 1994; Hayes et al. 1996; Beck et al. 2001). For Chinook salmon, the rate of juvenile growth in the estuary and coastal ocean can be an important indicator for survival (Pearcy 1992; Magnusson and Hilborn 2003; Duffy and Beauchamp 2011).

Few studies incorporate a landscape scale evaluation of habitat performance, and genetic and life history diversity that can be integrated into restoration design. Therefore, a targeted and research based approach to building a restoration framework focused on landscape scale juvenile Chinook diversity and habitat quality across a range of estuarine wetland habitats could advance salmon management. My aim is to provide the necessary information to populate such a restoration framework for the Columbia River estuary. In this study, I focused on estuarine growth and growth variation histories as indicators of juvenile Chinook salmon rearing habitat quality and the expression of diversity in the Columbia River freshwater tidal estuary. Using otolith microstructure analyses to estimate recent estuarine growth rates, I examined the effect of genetic origin, size, timing and habitat occurrence on individual juvenile Chinook salmon entering and migrating through the tidal freshwater reaches of the Columbia River estuary. I also investigated the juvenile life history diversity expressed among individuals by integrating (1) growth trajectories, as a proxy for habitat transitions (2) time, and (3) demographics or origin. Resilience occurs on a timescale impractical for a graduate study, but I hope to provide critical information for incorporating habitat complexity and habitat quality into the planning of future restoration actions.

<u>Study species</u>: Pacific salmon are an ideal model system, because they are reproductively isolated when spawning due to high fidelity to their natal habitats (Quinn 2005), and also exhibit a wide range of life history characteristics and genetic variation within single metapopulations (Waples et al. 2001, Hilborn et al. 2003). Additionally, Pacific salmon are culturally, economically and historically significant to the Pacific Northwest. Pacific salmon are considered a flagship animal for environmental conservation in the northern Pacific Rim. Many communities have a sense of pride and responsibility for the prosperity of salmon populations. Timothy Egan, a Pacific Northwest correspondent for the New York Times wrote that, "the Pacific Northwest is any place a salmon can get to"(Egan 2012). In the United States many Pacific salmon populations are also protected by national law, and subject to Native American and First Nation treaties. These iconic species have caused decades of contentions between the United States, Canada, Japan and Russia, resulting in years of debate and several treaties and

agreements. Not only do these fish have the respect and admiration of most people sharing their landscape, but they are also commercially, recreationally, historically and legally embedded in Northern Pacific communities.

Like all six species of Pacific salmon that inhabit the Columbia River, Chinook salmon externally fertilize their eggs in freshwater gravel nests, which hatch and develop into alevin, and rear as juveniles in the ocean, estuary, or stream. Eventually they migrate to the ocean as smolts and after a time at sea a series of physiological processes lead them to migrate back to the freshwater system from which they emerged, and spawn (Quinn 2005). The size, age and habitat in which these life phases are completed are specific to each life history type and species of Pacific salmon. This diversity is particularly important for the conservation and evolutionary legacy of each species of Pacific salmon. To protect this population diversity, in 1991 NOAA Fisheries established the protection of Evolutionary Significant Units (ESU) as well as species under the Endangered Species Act (Good 2005). One example of these divergent characteristics, which promotes species and population diversity, is juvenile migration timing. Two studies examining Chinook salmon in small Pacific Northwest streams detected three life history strategies within one species and adult run-type alone. The life history strategies were attributed to juvenile rearing habitat and the timing of movement among habitats (Carl and Healey 1984; Bottom et al. 2005). For the purpose of this study, in my first chapter I will not be explicitly defining life history diversity. I will be testing the relative importance of several demographic descriptors of juvenile Chinook diversity, such as genetic stock of origin and an interaction between size and timing of capture in the estuary. An interaction between size and timing is meant to mimic the standard National Oceanic and Atmospheric Administration's permitting protocol (Healey 1983; Dawley 1986). My second chapter attempts to explain the variability in life history trends using temporal variation in growth from examinations of otolith microstructure transects, age, time and a number of explanatory variables.

Several studies have examined the diversity of Pacific salmon across their range using genetic markers and phenotypic variation. Waples *et al.* (2001) used ecology, life history strategy and biochemical genetics to characterize population diversity in seven species of Pacific salmon. Their study suggested that genetic data alone provides information about the strength and duration of reproductive isolation among salmon populations, but that life history characteristics are necessary to contextualize these data with fitness consequences and responsive traits. Furthermore, Chinook salmon had the largest level of diversity of all seven anadromous salmonid species native to the Pacific Northwest (Waples et al. 2001). However much of this diversity has been and is being lost. Gustafson *et al.* (2007) estimated that 29% of the nearly 1,400 historical populations of Pacific salmon have been extirpated from the Pacific Northwest and California since European contact. He identified Chinook as one of the species with significantly higher proportional population losses, partly due to the obstruction of Chinook populations from three major historically occupied ecological regions (Gustafson et al. 2007). Furthermore, based on the analysis of 100 Chinook populations from California to British Columbia, Waples *et al*. (2004) found that 62% of Chinook salmon hierarchical gene diversity is explained by differences among major geographic and ecological descriptors. Declines in available habitat may have led to a synchronization of the remaining accessible habitat and decreases in biocomplexity, which in turn degraded population diversity and species resilience. Moore *et al*. (2010) suggested that Snake River spring/summer Chinook (a Columbia River basin stock listed as endangered on ESA) are subject to more impacted and possibly homogenized habitats (due to structures which reduce the disturbance regime, such as dams), and that this synchronization of the salmon stock decreased the portfolio performance, and may have compromised their productivity. They concluded that explicit consideration and protection of population diversity and the varied habitats upon which they depend is a requirement of the management of spatially structured species such as Pacific salmon (Moore et al. 2010). These studies illuminate the importance of habitat complexity for the preservation of population diversity for salmon species and therein the sustainability and resilience of a wild, commercially valuable resource. My study strives to incorporate resilience in habitat restoration design by explicitly targeting diversity and habitat complexity.

This study focuses on Columbia River Chinook salmon, some of which are listed on the Endangered Species Act. Chinook salmon in the Columbia River have extensive, moderate and short freshwater migrations (1500 km to 300 km), high and moderate altitude (500-2000 m) spawning and rearing, ocean maturing and stream maturing populations, and northern and southern ocean migration (Waples et al. 2001). Of the eight Chinook ESUs that inhabit the Columbia River Basin, one is endangered and four are threatened under the Endangered Species Act (Good 2005). Natural production of Columbia River salmon has not returned to more than 12% of historic levels (Bottom et al. 2005), despite the investment of nearly $170 million annually on hatchery releases and the reestablishment of more natural habitat processes (Naiman et al. 2012). Therefore, a comprehensive understanding of the relationships between Chinook salmon and their diverse estuarine habitat requirements is needed to improve habitat restoration efforts, especially in those systems obstructed by human interference and inhabited by dwindling salmon populations.

Estuarine wetlands are important nursery habitat for juvenile Chinook salmon (Healey 1982; Simenstad et al. 1982). Within freshwater tidal wetlands, riparian wetlands are characterized by high insect production and offer shade and are particularly important for anadromous species, which require transitional habitat during their osmoregulatory shift into the marine environment (Simenstad et al. 1982; Thorpe 1994). In one study, 90% of returning spawners of fall Chinook consisted of a life history type with an extended juvenile estuary-rearing period (Reimers 1971). Studies have also shown high growth and survival of steelhead (*O. mykiss*) juveniles rearing in small central Californian intermittent estuaries (Bond et al. 2008, Hayes et al. 2008). In addition, estuaries may provide a critical contribution to salmon habitat complexity as the mosaic of habitats connecting watersheds to the sea. Carl and Healey (1984) described three life history types of Chinook salmon, which represent genetically distinct subpopulations adapted for juvenile rearing in the ocean, estuary and river. Each juvenile rearing habitat supported a separate metapopulation and aggregate biocomplexity. This has also been shown through habitat restoration; by the expression of a previously depressed juvenile life history type with the removal of dykes and the restoration of historic tidal marsh habitat for fry and fingerling Chinook (Bottom et al. 2005). The reestablishment of previously unavailable estuarine habitat expanded life history variation. These studies elucidate the relationship between juvenile rearing habitat complexity and life history diversity. Therefore, estuaries contribute to life history variation and growth among out-migrating juveniles as well as the productivity and resilience of the adult population. My study strives to further elucidating the role of estuaries and juvenile estuarine rearing life history types, by explicitly targeting diversity and landscape scale habitat complexity.

Objectives: My study is part of a collaborative Columbia River estuary project, which aims to determine the estuary's contribution to the spatial structure and life history diversity of Columbia

River Chinook salmon stocks, and provide evidence for the benefits of estuarine rearing through a preference for detrital food webs, increased foraging success and growth. The Columbia River estuary project addresses Reasonable and Prudent Alternatives (RPAs) of the Biological Opinion for the Operation of the Federal Columbia River Power System (Bottom et al. 2012). The goals of my research were to investigate the variability within juvenile Chinook life history types and estuarine growth rates in the freshwater tidal Columbia River estuary. These data can be integrated into a restoration planning framework through mapping and simulation techniques. Below I have outlined my specific hypotheses, developed into two discrete chapters:

1. Identify the factors affecting juvenile Chinook growth variability in a large freshwater tidal estuary
    a. Juvenile Chinook estuarine growth rate will vary over space, time and juvenile Chinook demographics, such as genetic stock of origin
    b. These patterns in juvenile Chinook salmon estuarine growth rate can be described by the possible mechanisms measured in this study, such as diet composition, and estuarine temperature and discharge.
2. Test the use of dynamic factor analysis to estimate common trends in juvenile Chinook salmon growth variability: describing the freshwater experience
    a. The dynamic factor analysis (on juvenile Chinook salmon daily growth estimates) will describe more than two trends, confirming that the use of two life history types (e.g., subyearling and yearling) integrates over substantially more ecologically relevant diversity.
    b. Regional stocks, habitat of capture, marked hatchery origin and estuarine residence (methods from Neilson et al. 1985) will display divergent growth

histories, illuminating the relationship between the variability in growth and the distribution and demographics of juvenile Chinook salmon captured in the Columbia River estuary.

Chapter I: Factors affecting juvenile Chinook (*Oncorhynchus tshawytscha*) growth variation in a large freshwater tidal estuary

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Estuarine rearing habitat has been shown to enhance within watershed biocomplexity and support growth and survival for juvenile salmon (Oncorhynchus sp.). However, less is known about how growth varies across different types of wetland habitats and what explains this variability in growth. We examined juvenile fish growth over a range of wetland habitats in the freshwater tidal Columbia River estuary. We focused on the estuarine habitat use of Columbia River Chinook salmon (*Oncorhynchus tshawytscha*), which are listed under the Endangered Species Act. We employed a generalized linear model (GLM) to test three hypotheses: (1) juvenile Chinook growth was best explained by temporal factors, (2) juvenile Chinook habitat use was the most important driver of estuarine growth rate, and (3) demographic characteristics, such as stock of origin or the timing of seaward migration best explain juvenile Chinook salmon growth rate. This study examined juvenile Chinook estuarine growth rate, incorporating otolith microstructure, individual assignment to stock of origin, GIS habitat mapping and diet composition in three habitats (mainstem river, tributary confluence and backwater channel) along ~130 km of the upper estuary. When compared to other studies in the basin these juvenile Chinook grew on average 0.23, 0.11-0.43 mm/d in the freshwater tidal estuary, similar to estimates in the brackish estuary, but ~4 times slower than those in the plume and upstream reservoirs. However, survival studies from the system elucidated a possible tradeoff between growth and survival in the Columbia River basin. We found that variation in growth was best explained by habitat type and an interaction between fork length and month of capture. Juvenile Chinook salmon grew faster in backwater channel habitat and later in the summer. We also found that mid-summer and late summer/fall subyearlings had the highest estuarine growth rates. These findings present a unique example of the complexity of understanding the influences of the many processes that generate variation in growth rate for juvenile anadromous fish inhabiting estuaries.

Introduction:

Estuaries are important nursery habitat for juvenile anadromous fishes, providing energetically rich foraging grounds and refuge from predation (Beck et al. 2001). Many marine and anadromous fish life cycles rely upon the maintenance of a mosaic of wetland habitats from the low salt marsh to tidal freshwater for rearing habitat (Healey 1982; Simenstad et al. 1982;

Gunderson et al. 1990). Within freshwater tidal wetlands, riparian wetlands provide abundant insects communities, shade, refuge from predation, and are particularly important for anadromous species, which require transitional habitat during their osmoregulatory shift into the marine environment (Simenstad et al. 1982; Thorpe 1994). In this study, we focus on juvenile Chinook salmon (*Oncorhynchus tshawytscha*), which use estuaries for rearing and migration (Quinn 2005), and have been suggested to be the most estuarine dependent of the salmon species (*Oncorhynchus sp.*) (Healey 1982). We evaluated juvenile Chinook salmon estuarine rearing with growth rate estimates from otolith microstructural analysis. Our study addressed the relative contributions of a range of temporal, environmental and demographic factors affecting juvenile Chinook salmon estuarine growth rate. We employed a generalized linear model (GLM) to test three hypothesis: (1) juvenile Chinook growth was best explained by temporal factors (e.g., month and year in the estuary), (2) juvenile Chinook habitat use was the most important driver of estuarine growth rate, and (3) demographic characteristics, such as stock of origin or the timing of seaward migration best explained juvenile Chinook salmon growth rate.

Juvenile salmon estuarine rearing habitat has been linked to growth and survival as well as biocomplexity (Bottom et al. 2005). Chinook salmon may complete their life cycles through a variety of pathways, and temporal and spatial patterns of estuary rearing and migration vary within and among populations (Reimers 1971; Simenstad et al. 1982; Levings et al. 1986). These alternate pathways or life history types are generally defined by the size, timing (month or season) and duration spent in riverine, estuarine or marine environments. In estuaries, juvenile Chinook salmon can rear or migrate as fry, mid-summer subyearlings, late summer or fall subyearlings and yearlings (Reimers 1971; Healey 1991). Juvenile Chinook salmon also spend some time rearing in rivers and the coastal ocean; therefore estuaries provide habitat complexity within the juvenile rearing landscape (Healey et al. 1980, Carl and Healey et al. 1984, Bottom et al. 2005b). Habitat complexity has been shown to promote population diversity and resilience in salmon through what has been described as a “portfolio effect” (Hilborn et al. 2003; Schindler et al. 2010). Thus, estuarine habitat is not only an important nursery habitat, but influences the expression of diversity and therefore provides insight into the stability of salmon populations.

Despite their importance to juvenile Chinook salmon survival (Magnusson and Hilborn 2003), adult salmon returns (Reimers 1971), and within-watershed biocomplexity (Bottom et al. 2005), much of the coastal and estuarine habitat in the United States has been lost or degraded by development activity. Estuaries have been converted into farmland, cities, ports and marinas, and incur hydrological impacts from upriver development, and in some cases may no longer function as effective nursery habitat for young fish (Maier and Simenstad 2009). This history of estuarine development presents a critical concern as many estuarine rearing and anadromous fish species have been listed under the Endangered Species Act (ESA) (Good 2005). One example of a developed estuary, which provides habitat to declining Chinook salmon populations, is the Columbia River estuary; in which five of eight Chinook salmon Evolutionary Significant Units (ESU) are listed under ESA (Nehlsen et al. 1991). Development of the Columbia River basin and estuary has extensively altered juvenile fish habitat. Local and landscape scale development has noticeably reduced rearing habitat availability (Kukulka and Jay 2003) and altered the food base of much of the estuarine community (Sherwood et al. 1990). Upland logging and agriculture, shoreline armoring, over-water structures, removal of large wood, and channel deepening and widening has progressively channelized and detached the estuary from its floodplain (Bottom et al. 2005). Between 1870 and 1980, approximately 65% of lower estuary was diked or filled (Thomas 1983). Today, up to 75% of the tidal riparian vegetation is estimated to have been lost estuary-wide (Marcoe et al. 2013). Additionally, 23 mainstem and hundreds of tributary dams regulate the flow of the Columbia River, and without providing for fish passage have reduced spawning and rearing habitat to 45% of the historically available basin area (NRC 1996). The installment of hydropower and irrigation diversion dams have had a significant impact on the timing and magnitude of the river discharge; reducing spring freshets and freshwater inputs to the estuary and effecting estuarine circulation patterns, as well as altering the natural disturbance regime that structured historic juvenile salmon habitat in the estuary (Simenstad et al. 1992).

The decline in available habitat throughout the Columbia River estuary has paralleled the diminution in Columbia River Chinook salmon populations (Nehlsen et al. 1991), and it has been suggested that the estuary's current state is that of reduced salmon-rearing capacity (Bottom et al. 2005). Natural production of Columbia River salmon has not returned to more than 12% of historic levels (Bottom et al. 2005), despite the investment of nearly $170 million annually on hatchery releases and the reestablishment of more natural habitat processes (Naiman et al. 2012). A comprehensive understanding of how the quality or availability of estuarine habitat influences the fitness of juvenile Chinook salmon is needed, especially for heavily modified systems inhabited by dwindling salmon populations. We are not aware of any studies that compare juvenile Chinook growth across a range of freshwater tidal habitats. Additionally, there is little published data from the freshwater tidal reaches of estuaries on divergent growth from different regional stocks of origin, year-round and at a range of sizes. This study examined juvenile Chinook growth in a range of anthropogenically-impacted sites to address how growth opportunities in the remaining estuarine rearing habitat are distributed over space, time and among individuals.

We examined juvenile Chinook growth and diet composition in the Columbia River estuary. To assess factors that affect variability in the estuarine growth rates of juvenile Chinook salmon occupying different estuarine wetland and migratory habitats. Specifically because habitat loss is a multifaceted stress we focus on sublethal effects, such as growth and prey consumption. Growth has been shown to be an important indicator for habitat quality and a measure of fitness consequences to individuals (Sogard 1994; Hayes et al. 1996). Our study tested how well temporal, environmental and demographic explanatory variables at two scales of relevance describe juvenile Chinook salmon estuarine growth rate. Our explanatory variables included (1) short-term estuarine-specific variables, such as month of capture (and its associated temperature), habitat type, hydrogeomorphic estuarine reach, diet composition and consumption rate; and (2) predetermined or permanent variables, such as stock of origin (identified using genetic assignment (Teel et al. 2014)) and timing of outmigration or estuarine residence (an interaction between fish size and month of capture in the estuary). We used these explanatory variables to describe the variability in estuarine growth rate and incorporated the diet analysis as a link between growth rate estimates and the estuarine food-web. This study presents and unique example of the complexity in understanding the seasonal, environmental, and demographic drivers responsible for variations in the estuarine growth rates of juvenile anadromous fish. Additionally, by targeting habitat specific growth rate this study can be used to inform strategic habitat restoration and fisheries management.

Methods:

Study system

The Columbia River estuary is dominated by a strong river flow and tidal currents that connect a 660,480 km^2 drainage basin to the sea. The estuary extends approximately 233 river kilometers inland from the Pacific Ocean with more than three quarters of this length tidal freshwater (Simenstad et al. 1990). The Columbia River has undergone significant modifications in its more recent history. The estuary contains three major ports in Astoria and Portland, Oregon and Longview, Washington (Simenstad et al. 1990). Changes to the Columbia River estuary have decreased the wetland and shoreline area, physical variability, estuary surface area and tidal prism, vertical mixing, tidal mixing and sedimentation, as well as increased flushing time and residence time for detritus and nutrients (Sherwood et al.1990). These changes in the organization and productivity of autotrophic organisms could propagate through the food-web (Maier and Simenstad 2009) and impact rearing habitat quality for juvenile Pacific salmon.

Salmon collection

Our sampling was embedded in a larger collaborative study design, from which the samples presented here are a sub-sample (Bottom et al. 2012). Sites were chosen to depict a range of environments in which both landscape scale influences (reaches) and as much stock and life history diversity as feasible could be captured (habitat types) specifically for a genetic survey, which is described in Teel *et al.* 2014. Sites were stratified among six freshwater tidal Level 3-Hydrogeomorphic Reaches (Fig. 1: C-H) defined by the Columbia River Estuary Ecosystem Classification (Simenstad et al. 2011). We sampled three habitat types within each reach: mainstem channel, backwater channel and confluence. A total of eighteen sampling sites were sampled every-other month for two years (March 2010-March 2012). In all tables and figures, each site was coded by the sampling design, with the first letter representing the reach and the second letter representing the habitat type (Appendix). For more specific sampling location information, see Teel *et al*. 2014 (Appendix). Beach seine sampling for juvenile salmon occurred down the full extent of each beach with a 38-meter beach seine (1 cm mesh size), with a one-meter by one and a half-meter central bag (1/3 cm mesh size), which samples the top three meters of the water column. During flooding periods when beach seining was impractical, we used a 9-meter pole seine. Given the propensity for small size classes to favor shallow water habitats (Bottom et al. 2012), this sampling design and method targeted subyearling Chinook salmon. All fish caught were identified and counted. Up to 100 juvenile Chinook salmon were weighed and measured to the nearest millimeter (fork length). Fish were also scanned for coded wire tags (CWT), passive integrated transponder (PIT) tags and other markings (such as the removal of the adipose fin) to identify hatchery origin and other experimentally tagged groups. Tissue samples were obtained from the caudal fin for genetic analysis of up to 30 juvenile Chinook salmon, and preserved in nondenatured ethanol (Bottom et al. 2012). Additionally, temperature loggers were deployed at sampling sites (Fig. 1). Discharge and additional temperature data were obtained from U.S. Geological Society measurements at Beaver Terminal, gauge number 14246900 (USGS 2011, 2012 ,2013).

Genetic assignment of fish to stock of origin

Individual assignment estimates to stock of origin are reported in Teel *et al*. (2014), and used in this study as a variable in the generalized linear model. Genomic DNA was isolated from fin tissue samples using Wizard genomic DNA purification kits (Promega Corp.). The isolated genomic DNA was used in polymerase chain reactions (PCRs) to amplify 13 microsatellite loci, which have been standardized among several West Coast genetics laboratories (Seeb et al. 2007).

GeneScan and Genotyper software programs (Applied Biosystems) were used to identify the size and number of alleles detected at each locus. The likelihood model described by Rannala and Mountain (1997), and employed by the genetic stock identification program ONCOR (Kalinowski et al. 2007), was used to estimate the stock origin of each individual. Population baselines correspond to a previously compiled multilaboratory standardized Chinook salmon genetic database (Teel et al. 2009, Johnson et al. 2010, Appendix). Fish were individually assigned to eleven regional stocks (Teel et al. 2014). Nine regional stocks were identified as within basin (Table 1, Fig. 1), and fish originating from the two out of basin groups were not used in the otolith analysis (e.g., Rogue River and coastal populations). We chose to exclude out of basin stocks because they represented a small proportion of the juvenile Chinook salmon caught in this study, and it is unknown if they were the offspring of strays or juveniles migrating into the estuary from the marine environment.

In addition, we used the GSI program ONCOR with the likelihood model of Rannala and Mountain (1997) to compute the posterior probability of stock membership of each individual fish (Mantel et al. 2005). To ensure overall stock assignment accuracy in the data used for the generalized linear model, we excluded juveniles with relative assignment probabilities < 0.80, N=665 (82% of the individual assignments determined from the total genetics survey).

Otolith microstructure

A subset of samples (N=665) was examined to estimate daily age and growth rate. This subsample was an opportunistic collection of several Columbia River estuary project objectives and therefore is not uniformly balanced over space or time (Appendix). Individual fish age and growth were estimated by the microstructure features of each right sagittae otolith, viewed at adjacent transverse sections by two readers; left sagittae otoliths were used when the right was unavailable. Each otolith was mounted in Crystalbond resin, ground with fine grain sandpaper (1500 grit) and polished with MasterPrep® Polishing Solution (Buehler, 0.05 µ) on both sides, alternating with microscopic inspection. Otoliths were photographed with a compound microscope (10x and 40x) and digital (Olympus B071) camera. Otolith increments were counted and measured along 90° transects from the post-rostrum primordial in the dorsal direction (Titus et al. 2004). For each transect, daily increment measurements originated at the exogenous feeding check (Marshall and Parker 1982) and extended to the otolith edge. Daily otolith rings were measured and enumerated with the program ImageJ (Abramoff et al. 2004) and a customized otolith and tree ring macro from the plugin ObjectJ (Developed by Vischer and Nastase, University of Amsterdam). Estuarine growth was estimated by the mean increment width of the 14 days prior to capture (Miller et al. 2013). Mean increment width was used to estimate estuarine growth in order to incorporate growth variation and decrease the influence of edge effects. Additionally, we established the necessary assumptions for examining growth with otolith microstructure of a good fit between otolith size and fish size ($R^2 = 0.95$) (Campana and Neilson 1985).

For comparisons with other juvenile Chinook growth studies throughout the Columbia River basin we converted growth from mean otolith increment widths per day to millimeters of fork length per day, using the proportional method (Francis 1990). The proportional method incorporates both the linear relationship between otolith size and fish size and an adjustment to avoid bias. We used a linear relationship between otolith transect length (equal to approximately half the otolith width) to fork length ($R^2 = 0.91$) to proportionally convert growth measured in increment width to fork length in millimeters. We considered the proportional method appropriate because no interactions between fish length and any covariate (i.e. stock of origin or date and site of capture) added 2% or more to the R-squared value, and the estimates of known fork length and the predicted fork length at capture were 99% accurate on average.

Diet analysis

A subset of the samples examined for otolith microstructure were also examined for diet composition and relative consumption rate (N=130). These samples were taken exclusively from reaches D and H and only mainstem channel and backwater channel habitat types (Fig. 1), but include samples from all applicable size ranges, stock groups and time periods (Table 1). These sites were chosen because they had the most balanced samples of size ranges, stock groups and time periods given the budget and time constraints for sample processing. Fish diet samples were obtained by direct removal of intact stomach and placed in 10% buffered formalin. The stomach contents were then removed, sorted to lowest taxonomic level possible given the digestive state, and enumerated and weighed. Relative consumption rate was calculated as a ratio of the stomach contents weight to the predator weight (Terry 1977). A total of 86 prey taxa were identified from these samples. Therefore, for simplification the taxa groups were binned into five groups denoting the habitat within which the prey would most likely have been consumed: benthic/epibenthic, emergent, planktonic and terrestrial (Merritt and Cummins 1996; Light 2007; Thorp and Covich 2009). The fifth taxa group, nondescript, was all prey matter that was too digested to be categorized by habitat. In addition to percent numerical and gravimetric contribution and frequency of occurrence, we assessed the contribution of each prey item group with the Index of Relative Importance (Pinkas et al. 1971). We also reported the total and percent digested matter, which represents the weight of prey items, which were too digested to be categorized into taxa groups.

Statistical analysis:

The quality of the growth rate data was assessed following the methods reported in Zuur *et al.* (2010). Our response variable was estuarine growth rate, and the main effects were habitat type, reach, month of capture, fork length, year, and stock of origin. No outliers were detected, however heterogeneity of variance was present for variables with particularly uneven sample sizes (i.e. month and reach; Appendix). The variance inflation factor was less than three for all covariates, and so collinearity was not accounted for. Not all interactions could be considered to avoid instances in which no data were collected (e.g., the otolith subset did not include juvenile Chinook salmon collected at all sites, reach:habitat type, for all months). Therefore only interactions of interest were included. The presence of a dependence structure was not detected for estuarine growth rate, however month of capture and fork length were not independent.

To discern the relative importance of the seasonal, environmental and demographic factors that contribute to the variation in estuarine growth rate, a generalized linear model (GLM, Dobson 1945) with log link was applied using the program R (R Development Core Team 2011). Our response variable, estuarine growth rate was normally distributed, but not zero or negative due to only positive growth rings being detectable by otolith microstructural methods. Therefore, for all models we used GLMs with a log link, which accounted for the normal truncated distribution. The main effects operated on two time-scales: (1) short-term, estuarine or capture specific (i.e. habitat type, reach, month of capture, fork length, and year) and long-term or predetermined (i.e. stock of origin). Due to small sample sizes in the winter months November, January and March were summarized as “Winter” for both the model and figures. One interaction between length and month of capture was used to incorporate the dependence between these explanatory variables, and describe the size and timing in which each fish may have been using the estuary as rearing or migratory habitat. Main effects and interactions were included as explanatory variables in the GLM using a hypothesis testing procedure, and all possible interactions were not included to minimize complexity.

We tested three central hypotheses to assess what factors affect the variation in juvenile Chinook salmon estuarine growth rate. Our null model considered only seasonal variation (e.g., month and year) affecting growth rate. Our two contending alternative hypotheses tested that either environmental factors (e.g., reach and habitat) or individual fish characteristics (e.g., fork length, an interaction between month and fork length and stock of origin) dictated the variation in growth. In all, twelve candidate models were tested: the null model, full model, environmental factors only, demographic factors only, and eight alternative models, four of which combined both environmental and demographic factors and four of which included the effect of only one environmental or demographic factor. The models were compared using Akaike Information Criterion with a correction for small sample sizes (AICc) for model performance (Burnham and Anderson 2002), using the package MuMIn (Barton 2013). The model with the lowest AICc value was considered the best representation of the data. Akaike weight was also calculated to give the overall weight of evidence for each model, this weight was used to test the degree of support or explanatory variable importance for the three different processes (seasonal, environmental and demographic) that were tested to generate variation in growth rate (Burnham and Anderson 2002).

Results:

Growth variability

Of the 665 otoliths dissected approximately 5% (34) were lost due to processing errors and 23 otoliths were determined to be vatritic, and therefore unusable. Consequently 608 otoliths were used to examine estuarine growth rate. Variability in juvenile Chinook growth rate was best explained by both environment and individual fish characteristics. The GLM model with the lowest AICc score included habitat of capture, fork length, month of capture, year and an interaction between length and month (Table 2, $R^2 = 0.13$). The AICc values indicated that model one in Table 2 was the best representation of the data, however a delta AIC of 4.5 implies only marginal evidence for habitat. The Akaike weight, which measures the degree of support for explanatory variables shows this more clearly with only ~9% improvement in model with the addition of habitat, as well as little support for reach, but strong support for length and length by month interaction.

The significance of the regression coefficients of the best model are reported in figure 2. Categorical variable coefficients are expressed relative to one of the categories, and the significant effect of each explanatory variable is explained by comparing each category relative to another. There are four significant comparisons within the categorical main effects (Fig. 2). The regression coefficients from the best model show that (1) fish grew faster in 2010 than 2011, (2) fish grew slower in May than July, (3) fish grew faster in September than July, and (4) mainstem habitat has a lower growth rate than backwater channel habitat (Fig. 2).

Fork length and an interaction between length and month were consistent in all of the top three ranked GLM models, and strongly supported by Akaike weight. However the interaction term between fork length and month of capture, presents a complex relationship with estuarine growth (Fig 5). Comparing estuarine growth rate at different lengths was difficult because some of the largest individuals were only present in the fall and winter periods, and similarly small sizes were only present in spring and summer, therefore intermediate sizes are compared to small and large size classes only. Interestingly, stock of origin was not included in any of the top models, the model with all fish characteristics was ranked 5th out of 12 (Table 2).

The null model, which included month and year, was not the most parsimonious description of the variation in estuarine growth rate (given the delta AIC in Table 2). However, growth did vary among years and months. Juvenile Chinook grew faster in the estuary in 2010 (0.00187 mm/day ± 0.0003) than 2011 (0.00177 mm/day ± 0.0003), and this pattern was most apparent by the substantially slower growth in May 2011 (0.00167 mm/day ± 0.0004) than May 2010 (0.00182 mm/day ± 0.0002) (Fig. 3). Estuarine growth was markedly higher on average in July (0.00191 mm/day ± 0.0003) and September (0.00194 mm/day ± 0.004) than in May (0.00173 mm/day ± 0.0003) (Fig. 3). Juvenile Chinook growth also varied across habitat types, however reaches, which represented landscape scale environmental differences were not included in any of the highest ranked models (Table 2). Among the habitat types juvenile Chinook grew more on average in back channel habitats (0.00185 mm/day ± 0.0003) than mainstem channel habitats (0.00178 mm/day ± 0.0003), while confluence habitats (0.00184 mm/day ± 0.0004) exhibited an intermediate growth rate on average (Fig. 4). The model including reach and habitat type was not distinguishable from the full model.

Diet Composition of juvenile Chinook salmon

Of the 130 diet samples dissected one was improperly stored and was not processed for prey weight and identification. We focused our subsample of diet analyses on differences that related directly to the growth rate results. The most distinct differences in diet composition samples of juvenile Chinook salmon were the relative importance of the planktonic and emergent prey groups between years and habitats. As the results related to temporal differences in growth rate we found that individuals captured in May 2011 had less planktonic prey and more heavily digested (nondescript) prey in stomachs than in May 2010 (Fig 6). The Index of Relative Importance and percentages of emergent prey was lower in July 2011 than July 2010 (Fig 6). The volumetric percentage of planktonic prey decreased from May to July to September (Fig 7). Fish captured in September had not fed on planktonic prey and seemed to rely more heavily on emergent and terrestrial prey (Fig 7). The percent total digested material, prey digested to the point at which the taxa could not be identified, was five times higher in May 2011 than May 2010 (Table 3).

Fish diet analysis from the mainstem channel habitats had more planktonic prey and those caught in backwater channel habitats had more emergent prey items numerically, by weight and Index of Relative Importance (Fig 8). Relative consumption rate (Fig. 9) did not reveal any distinguishable patterns that could be tied to the relationship between fork length and month with the estuarine growth rate results.

Discussion:

The variability in juvenile Chinook salmon estuarine growth rate was best explained by habitat type, fish size and an interaction between fish size and month of capture. The GLM model with the lowest AICc score included habitat of capture, fork length, month of capture, year and an interaction between length and month. Our study addressed the relative contributions of a range of temporal, environmental and demographic factors affecting juvenile Chinook salmon estuarine growth rate, however no one group of factors best represented these data. Both short-term estuarine-specific explanatory variables and predetermined or permanent explanatory variables were included in the model that best explained the variability in estuarine growth. Our first hypothesis, in which juvenile Chinook growth was best explained by temporal factors was ranked 6th. Temporal factors did not overwhelmingly contribute to the variability in estuarine growth, but there were trends in the average estuarine growth rate across months and years. In our second hypothesis juvenile Chinook salmon habitat use was predicted as the most important driver of the variability in estuarine growth rate, however only habitat type was included in the most representative model, and the Akaike weight implied only marginal evidence for habitat. Our third hypothesis was ranked 5th, and the interaction between size and timing of capture was strongly supported as a characteristic best explaining juvenile Chinook salmon estuarine growth rate. The relationship between juvenile Chinook salmon estuarine growth rate and the interaction between fork length and month was complex, but mid-sized juveniles captured in the estuary in the mid to late summer grew the fastest. Additionally, there is no statistical difference between mean estuarine growth rates by stock of origin. However our ability to discern the relative importance of the various seasonal, environmental and individual fish demographic factors that contribute to the variation in juvenile Chinook salmon estuarine growth rate was limited by our low explanatory power in this study.

One of the strongest indicators for the variability in estuarine growth rate in our study was fork length and the interaction between fork length and month, as the only parameter consistent in all the top three ranked models. Fork length and month of estuarine residence or out-migration are both characteristics of life history type for juvenile Chinook salmon. The diversity of life history characteristics can be very complex (Bradford and Taylor 1997; Volk et al. 2010; Rice et al. 2011), and in our study month of capture and fork length are not independent. The size and timing in the estuary is an indication of one juvenile life history transition (Healey 1983; Dawley 1986). However, the individuals sampled more likely represent a broad continuum of juvenile life history types of fish migrating and rearing in the estuary. Because this study focused on most recent growth and there is no established (otolith microchemistry) chemical signature for entry into the freshwater tidal, we are limited in our ability to describe the true variation in the system. One of the most comprehensive examinations of juvenile Chinook estuarine life history variation found two estuarine rearing life history types: mid-summer and late summer/fall subyearlings (Reimers 1971). In this study, we also found the highest growth in these two sizes and months, suggesting that mid-summer and late summer/fall subyearlings may be rearing in the estuary. Additionally, the Reimers (1971) study also found that juvenile Chinook salmon entering the estuary in early summer and remained for a period of improved growth in the estuary represented ~90% of the returning spawners, despite representing a disproportionally small fraction of the total juvenile out-migrants. We have no knowledge of the residency time of these juvenile salmon in the estuary; however the possible presence of these juvenile estuarine life history type and improved growth suggests there may be a similar range of life history types from the Reimers (1971) study present in the Columbia River estuary. There is evidence that life history variation in Columbia River Chinook salmon has been constrained and homogenized (Bottom et al. 2004; Burke 2004). However, it is unclear if the current state of juvenile Chinook salmon growth is limited by the decline of life history diversity or if poor growth performance is one factor constraining life history expression.

Additionally, genetic stock of origin was not an important driver in the variability of estuarine growth rate. Divergent stock performance may be homogenized by the history of hatchery practices throughout the western United States. Historically hatcheries promoted fish transportation programs and transplanted non-native or extra-regional salmon eggs (Naish et al.

2008), which may have diluted the growth rate differences between genetic groups. Additionally, approximately 80% of the juvenile Chinook salmon in the Columbia River basin are hatchery origin (Ferguson 2010; Dey 2012; Zabel 2013), and many hatcheries produce the same juvenile salmon phenotype. To counter act species declines and ameliorate rearing habitat loss, hatcheries target fast growth and large sized juveniles. Although growth has been shown to be an important indicator for juvenile salmon survival (Scheuerell and Williams 2005; Zabel et al. 2006, Duffy and Beauchamp 2011), there is no one optimum phenotype. Large, hatchery-produced fish may have limited interaction with the shallow-water rearing environment (Roegner et al. 2010; Weitkamp et al. 2012) sampled in this study and experience similar estuarine growth rates among genetic groups. However it is also possible that the resolution of our genetic classification and power of our assignments were limited by our genetic assignment techniques and mixture proportions.

The null model (temporal factors exclusively) was not identified as the most representative of the variability in juvenile Chinook estuarine growth, but the average estuarine growth rate differed between months and years. This may be due to differences between Columbia River estuary temperature and discharge between the months and years in this study. In the Columbia River basin and many other regulated rivers, the spring freshet has been dampened by dams, regulating water storage in reservoirs. However, the peak discharge in 2011 was very similar to estimates of mean historic river flows before the impacts of modern infrastructure (Sherwood et al. 1990), and much higher than the peak discharge in 2010 (Fig. 1). Many studies have suggested that high water years or periods of flooding, especially floodplain inundation, create better habitat for rearing and migratory fish. These studies cite higher biotic diversity (Junk et al. 1989), increased production (Halyk and Balon 1983; Gladden and Smock

1990; Bayley 1991), increased available habitat (Junk et al. 1989; Sommer et al. 2001), and inputs of terrestrial material into the aquatic food web (Winemiller and Jepsen 1998; Sommer et al. 2001). However in our study, the high discharge year and spring freshet time period did not coincide with increased juvenile Chinook salmon growth. Furthermore, there was no detectable increase in growth in the months following the freshet. In comparison to 2010, 2011 was a year of slower average estuarine growth rate, and the slower growth in 2011 was most prominent in May 2011. It may be that shoreline diking and armoring in the Columbia River estuary is so pervasive that high river discharge periods have limited flooding capability. If flooding habitats were not available for juvenile Chinook salmon we would expect them to only benefit from increased connectivity during migration (Bennett and Moyle 1996). In the context of slower average estuarine growth rate in May 2011, May 2011 diet samples had fewer planktonic prey than those collected in May 2010. The increased water discharge may have dispersed the prey, decreasing foraging opportunity for these fish. We also found that the percent digested material in fish captured in May 2011 was five times higher than fish captured in May 2010, suggesting that the May 2011 fish may not have been eating continuously. Restoration efforts, such as the removal of tide gates and dikes in the Columbia River estuary has increased ecosystem connectivity and reduced habitat fragmentation for the benefit of Chinook salmon (Roegner et al. 2010). However, we see no positive impacts on juvenile Chinook salmon growth from flooding events at the broader freshwater tidal estuary scale.

We also found that both mean juvenile Chinook growth rate and mean daily water temperature increased from May to July to September, in both years (Fig. 10 and 3). Moderate to high water temperatures are thought to be a bioenergetic limitation for juvenile Chinook salmon, and temperatures above 19 C are associated with shallow wetland habitat exclusion in the lower estuary (Bottom et al. 2011). Therefore, stressful temperature months in the estuary corresponded to high growth months. Studies have found that growth may be more limited by prey availability and quality than by temperature (Beauchamp et al. 2009). The monthly comparisons between diet composition results show a transition away from planktonic prey and an increased reliance on emergent and terrestrial prey from May to September; however there are pulses of high caloric prey in some diets in July when a subset of juvenile Chinook fed on small stickleback (*Gasterosteus aculeatus*). There is no clear relationship between the diet composition results and mean estuarine growth rates by month; however we do see a clear pattern of increased growth rate through the spring and summer for juvenile Chinook salmon. Regulating summer temperatures to prevent habitat exclusion in the estuary may be an important factor in improved juvenile salmon growth and production.

Another factor tested for its relative contribution to the variability in juvenile Chinook growth rate was habitat. We found that backwater channel sites had approximately 4% higher growth on average than mainstem channel sites. The primary difference between mainstem channel and backwater channel sites is that mainstem channel sites are situated along armored shorelines in the dredged and often diked and heavily used shipping channel. The backwater channel sites, usually in a secondary or tertiary channel on the back side of an island are potentially less anthropogenically impacted sites, and may have better growth opportunity for many reasons. A study by Hansen *et al*. (2012) found that backwater channel habitat use by juvenile Chinook salmon mitigated for energy declines incurred during migration in the Columbia River freshwater tidal estuary, suggesting that these fish were foraging at a greater rate than fish in the mainstem channel. Our relative consumption rates showed no clear pattern with habitat type, wherein feeding intensity seemed to be more closely related to fish size (as smaller fish inherently have a larger ratio of stomach weight to fish weight). This may be due to small samples sizes, or our limited knowledge of residency times in the capture habitat type. These high growth habitats may provide higher prey availability by way of connectivity to more productive wetland detritus-based food-webs (Healey 1982; Limm and Marchetti 2009; Maier and Simenstad 2009). The diet composition analysis showed that back channel sites had higher percentages of emergent prey items and mainstem channel sites had higher percentages of planktonic prey items. This pattern may be due to a loss of connectivity to wetland habitats for juvenile Chinook salmon in the more channelized mainstem river shipping canal. However other differences between backwater channel and mainstem channel sites, such as the amount of shelter from high river flows and the complexity of habitat may also be affecting the difference in estuarine growth rates between habitats. This study adds to the evidence for the quality of off-mainstem channel habitat for juvenile Chinook health while on their seaward migration. However habitat was only marginally supported by the GLM analysis and we have limited knowledge of habitat-specific residency times and sampled only three of many possible habitat types in the estuary.

Finally, two other studies have estimated growth rates from other regions in the Columbia River estuary. The growth rate estimates from the brackish estuary (0.4, 0.11 to 0.67 mm/day) are slightly higher (Campbell 2010), but within the range of what we have found in the freshwater tidal estuary (0.23, 0.11-0.43 mm/day). However, growth estimates from the plume (1.04 ± 0.51 mm/day, natural origin and 1.01 ± 0.44, mm/day hatchery origin)) and coast near the mouth of the Columbia River are much higher than what we found in this study (Claiborne et al. 2013). These high growth rates in the plume are also seen in reservoirs above dams in two of the major tributaries of the Columbia River, the Snake River (between1.0 ± 0.355 mm/day and1.3 ± 0.225 mm/day; Connor et al. 2011), and Willamette River (0.96 mm/day, reservoir and 0.38 mm/day, river; Friesen et al. 2013). The reservoir growth study conducted on the Middle Fork Willamette River and Middle Fork Willamette River reservoirs (Lookout point, Dexter and Hills Creek) found that fish had much high growth in the reservoir, but five times lower survival (Friesen et al. 2013). Another study from the Columbia River basin measured the survival of juvenile Chinook salmon from the upper basin in the Snake and Yakima Rivers through the hydropower system, the estuary, plume and coastal ocean. Rechisky *et al.* (2012) found that the highest survival was in the estuary and lowest survival was seen in the plume. These studies suggest that there may be a tradeoff between growth and survival in the Columbia River basin. The tradeoff between growth and survival is a common theme, when high growth environments are also high risk environments (Werner and Gilliam 1984). Perhaps these studies in context with one another are additional evidence for the importance of maintaining a mosaic of rearing and migratory habitats for juvenile salmon; providing a range of growth opportunities and risks.

Differences among juvenile Chinook salmon growth rate have been attributed to climactic and seasonal changes (Reimers 1973, Macfarlane et al. 2005, Miller et al. 2013), habitat use (Kjelson et al. 1982; Neilson 1985; Limm and Marchetti 2009; Volk et al. 2010), and origin and life history characteristics (Levings et al.1986; Burke 2004; Claiborne et al. 2013) throughout the eastern Pacific. However, very few studies have examined juvenile Chinook salmon estuarine growth over a range of genetic origins, sizes, seasons, years and freshwater tidal habitats to assess the many factors that may be influencing growth rate. Our results show that juvenile Chinook growth variability in the Columbia River estuary is influenced by many variables. Unfortunately the covariates measured in this study explain little of the variability in growth. There are likely more processes acting on juvenile Chinook estuarine growth, and habitat descriptors may need to be associated with more specific habitat features linked closely to food-webs (Naiman et al. 2012), and reliable habitat-specific residence times. It is also possible that there is little environmental and demographic specific variation in growth rate, or that the randomness of biological studies overshadowed detectable results with the sample sizes used in this study. Moller and Jennions (2002) found that depending on the exact analysis the mean amount of variance explained in a range of ecologic and evolutionary published studies was 2.51-5.42%. Irrespective of our low coefficient of determination, the novelty of this comprehensive and landscape scale study sheds light on how juvenile Chinook salmon experience a large freshwater tidal system during a crucial life stage. Growth is an evaluation of habitat performance, and by incorporating the range of Chinook salmon's genetic stocks of origin and measurable life history characteristics we have an expansive view of rearing habitat use, which can be used to inform wetland and fisheries conservation and management.

Juvenile Chinook growth in the estuary and coastal ocean can be an important indicator of survival (Pearcy 1992; Duffy and Beauchamp 2011) and is of critical concern to Chinook salmon management. Our GLM analysis has described which estuarine-specific and permanent factors were the most relevant contributors to the variation in juvenile Chinook salmon growth rate in the freshwater tidal Columbia River estuary. These results yielded two specific recommendations, which can be applied to strategic rearing habitat restoration: (1) improve or maintain habitat connectivity; and (2) maintaining a mosaic of rearing and migratory habitats may be an important factor for juvenile Chinook salmon growth. Our examinations of mean growth rate and diet composition among months and years showed no positive impacts on juvenile Chinook growth from flooding events at the broader freshwater tidal estuary scale. Therefore, restoration practitioners may consider a continued focus on habitat connectivity and removing barriers to flooding. Additionally higher temperature months were also faster growth months and maintaining habitat connectively throughout the hydropower system could also prevent habitat exclusion in summer months. We found that fish captured in backwater channel sites grew faster than fish in mainstem channel sites. Therefore, improved connectivity between backwater channel and mainstem channel sites may also improve growth opportunities for juvenile Chinook salmon while on their seaward migration.

Although the realities of implementation are an inevitable constraint, restoration projects should also consider promoting habitat complexity. A mosaic of rearing and migratory habitats may provide juvenile Chinook salmon with a range of growth opportunities and risks. Our comparisons between growth and survival studies throughout the Columbia River basin showed that no one region may provide the best alternatives for juvenile Chinook salmon. Opportunities for both growth and refuge throughout these environmental gradients could balance the tradeoffs and challenges presented to juvenile Chinook salmon while out-migrating. The relationship between juvenile Chinook salmon estuarine growth rate and size and timing within the estuary was complex. Without residency times or an indication of estuarine entrance it is unclear if the current state of juvenile Chinook salmon growth in the freshwater tidal Columbia River estuary is limited by the decline of life history diversity or if poor growth performance is one factor constraining life history expression. However, the strength of this relationship may be additional evidence for the importance of promoting a diversity of out-migration timing and juvenile rearing habitat use in salmon conservation and management. Additionally, genetic stock of origin was not an important driver in the variability of estuarine growth rate. The Endangered Species Act manages Chinook salmon within genetically distinguishable Evolutionarily Significant Units, but if these groups do not apply to fitness consequences we many need to manage diversity differently. For example, instead of mandated releases of water from the hydropower system during the currently recognized out-migratory season in the spring months, we may need to incorporate water management policies which recognize the use of the estuary by a broad range of out-migration timing and tidal habitat use for all ESUs. By managing the system for mechanisms for diversity, such as a more natural disturbance regime and habitat complexity, we may be able to increase the expression of genetic and life history diversity so important for species resilience. This comprehensive and landscape scale study presents relevant suggestions for estuarine habitat restoration and elucidates the many factors affecting the variability in juvenile Chinook salmon growth in a large freshwater tidal system during a critical life stage for salmon conservation and management.

Tables/Figures:

Table 1: A list of the stock of origin abbreviations, their source tributaries within the Columbia River basin and return timing of their stock of origin.

Abbreviation	Source Tributary(s)	Adult Return Timing
Desch_F	Deschutes River	fall
MCR&UCR_Sp	Mid and Upper Columbia River Region	spring
SCG_F	Spring Creek	fall
Snake_F	Sanke River	fall
Snake_Sp	Sanke River	spring
UCR_Su/F	Upper Columbia River	summer or fall
WC_F	West Cascade Range	fall
WC_Sp	West Cascade Range	spring
WR_Sp	Willamette River	spring

Table 2: A summary of the AICc ranking and Akaike weights of each GLM tested in this study, the models are ranked by most representative (1) to least representative (12) of the growth rate data. Each column is a dependent variable in the GLM describing the variability in juvenile Chinook salmon estuarine growth rate, and an X denotes the inclusion of each variable. For example, the full model is 10th and null model is 6th.

Rank	**Year**	**Month**	**Habitat**	**Reach**	**Genetic Group**	**Length**	**Length: Month interaction**	**Δ AIC**	**AICc wt**
1	X	X	X			X	X	0	0.893
2	X	X				X	X	4.50	0.094
3	X	X		X		X	X	10.50	0.005
4	X	X	X					11.23	0.003
5	X	X			X	X	X	11.60	0.003
6	X	X						12.61	0.002
7	X	X	X		X			14.57	0.001
8	X	X			X			15.91	0
9	X	X	X	X				20.80	0
10	X	X	X	X	X	X	X	21.15	0
11	X	X		X				21.23	0
12	X	X		X	X			21.53	0

Table 3: The total (g) and percent digested matter in stomach samples among years and months. Digested matter represents the stomach contents that were too digested to be identified to taxa.

Group	Total Digested Matter	% Digested Matter
March 2010	0.004	0.13
May 2010	0.04	0.08
July 2010	0.143	0.27
May 2011	0.203	0.4
July 2011	0.139	0.18
September 2011	0.112	0.36

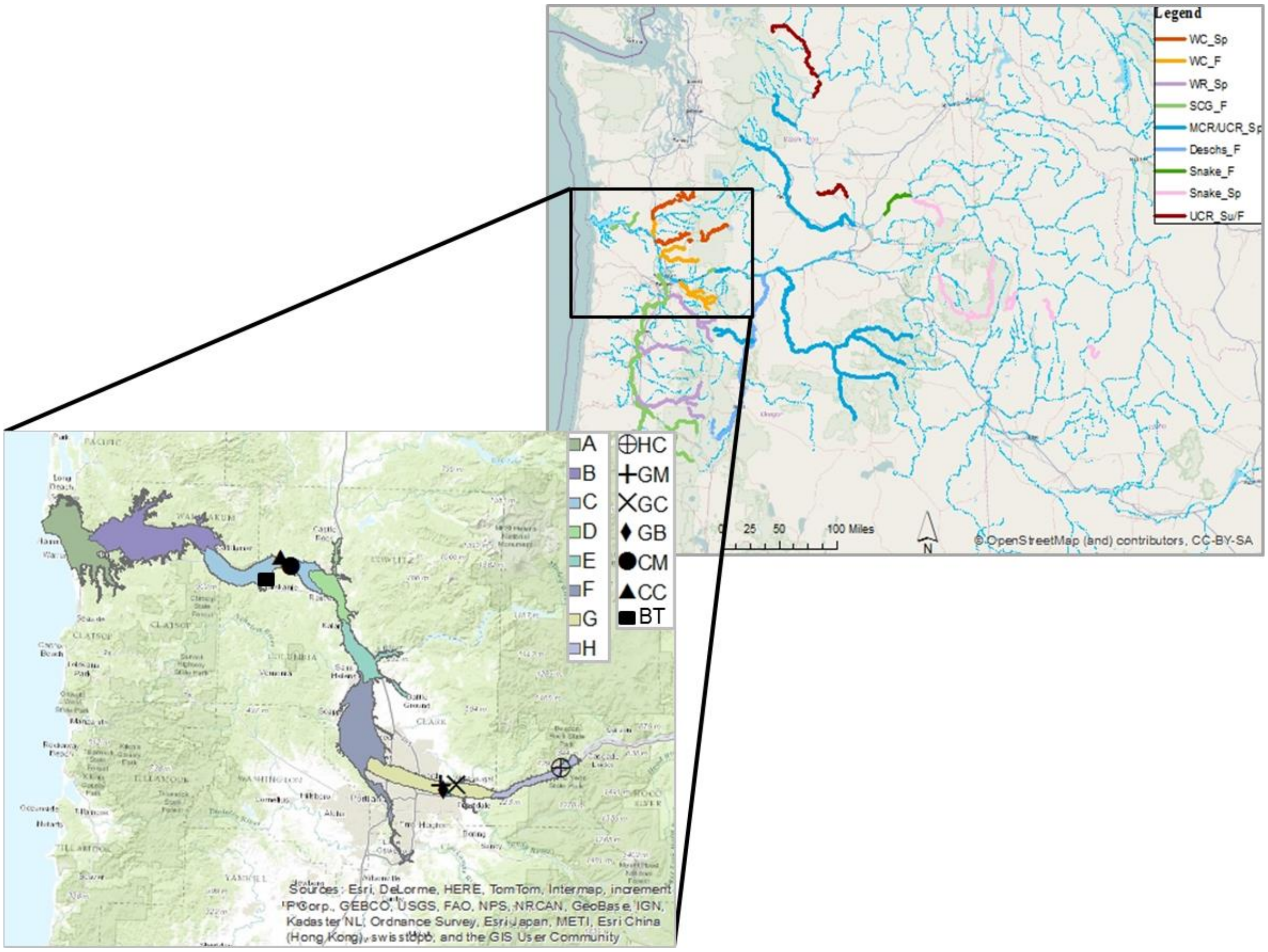


Figure 1: Columbia River basin and Chinook salmon populations used as baseline data for genetic stock identification analysis in this study (adapted from Teel et al. 2014). Inset: Estuarine reaches from the Columbia River Estuary Ecosystem Classification (adapted from Simenstad et al. 2011) (including temperature logger locations; BT dotes the USGS site at Beaver Terminal).

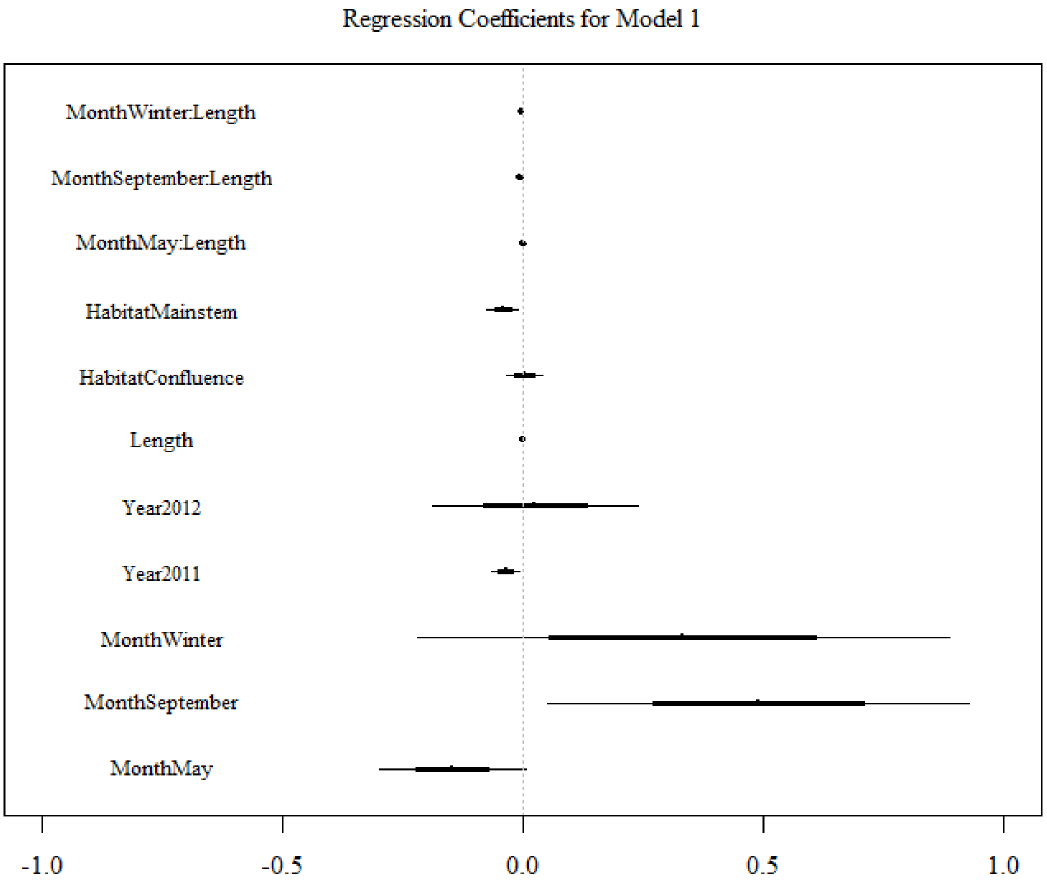


Figure 2: The significance of the regression coefficients of the best model represented as the regression coefficients and plus or minus two standard errors with categorical coefficients expressed relative to one of the categories.

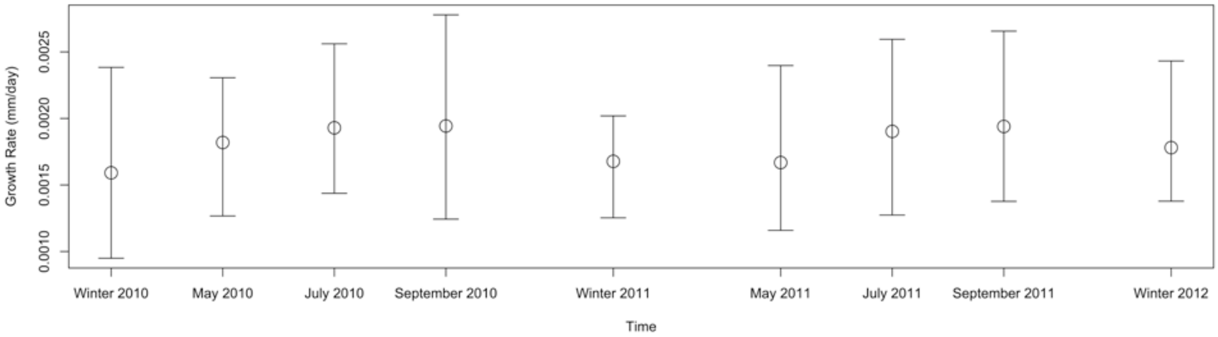


Figure 3: Means and 95% confidence intervals of estuarine growth rate (mm/day) over time.

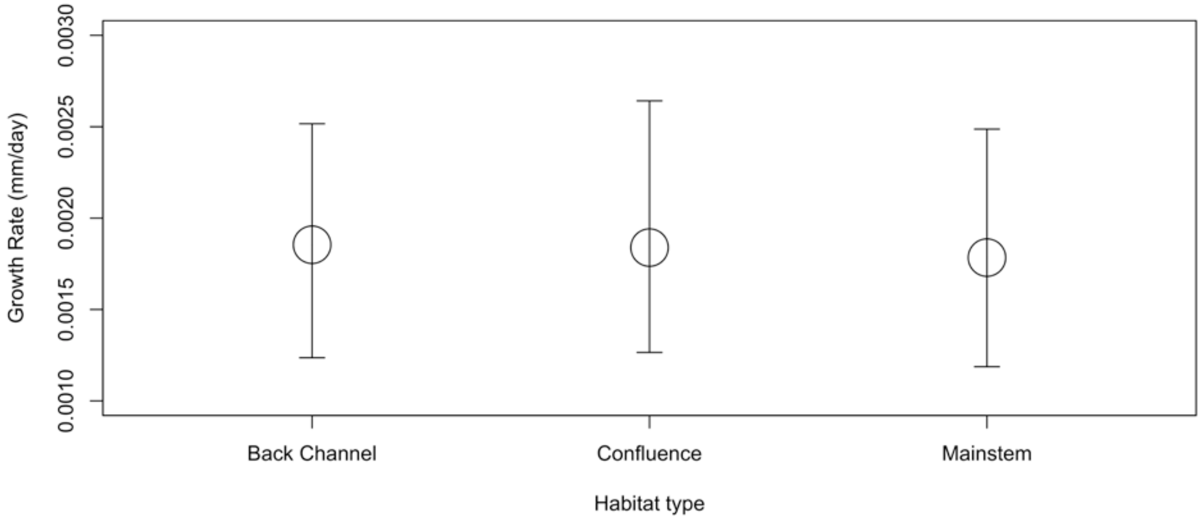


Figure 4: Average estuarine growth rate (mm/day) and 95% confidence intervals for each habitat type, summarized over all months and years.

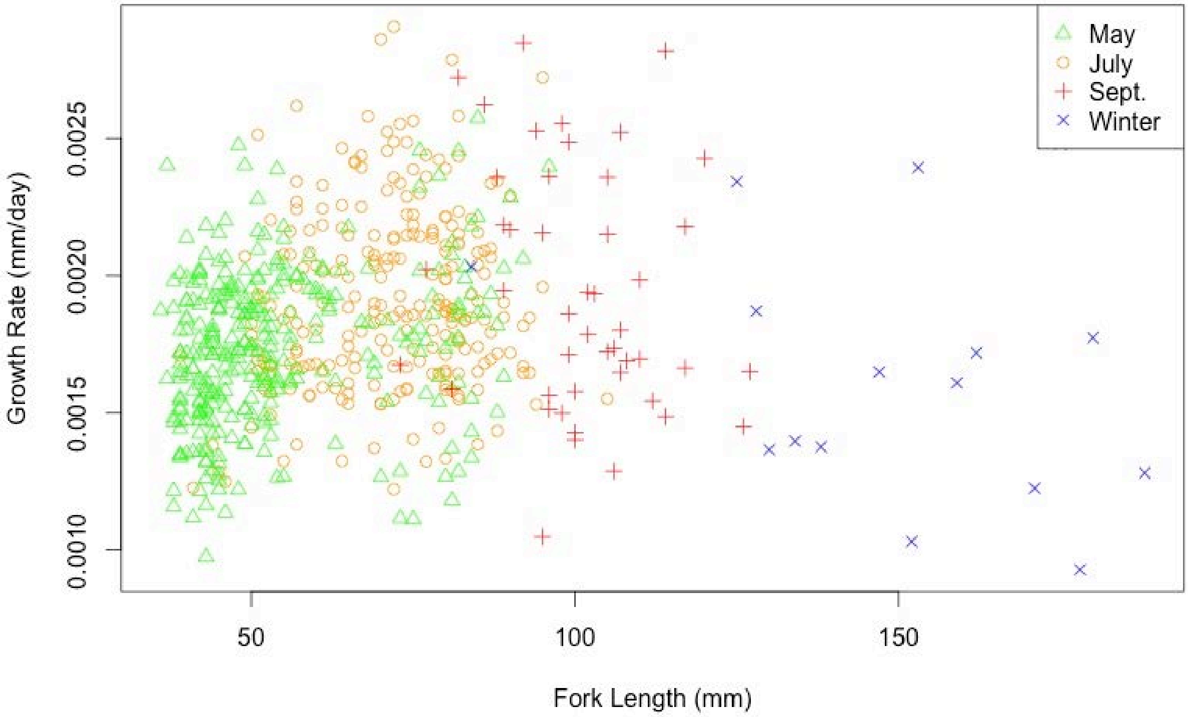


Figure 5: Estuarine growth rate estimates (mm/day) and fork length (mm) at capture by month to represent the relationship between estuarine growth and life history type.

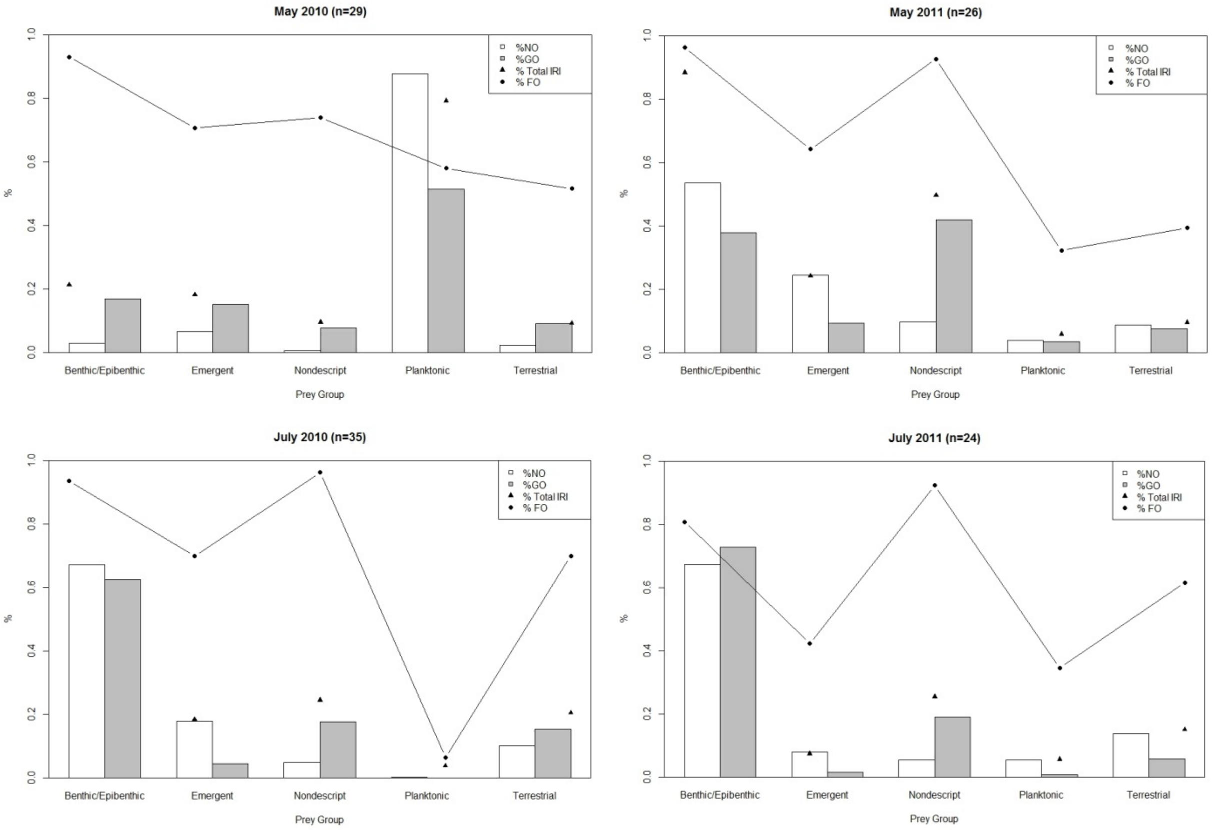


Figure 6: Percent of numerical and gravimetric composition, frequency of occurrence and Index of Relative Importance of taxa categories in individual diets for 2010 and 2011, May and July.

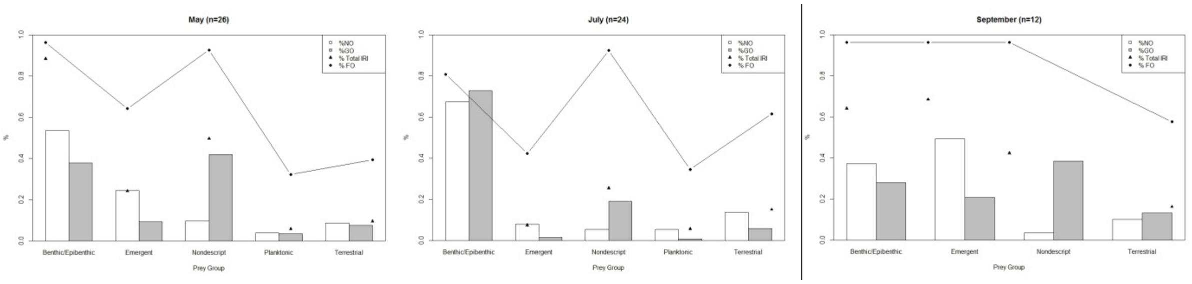


Figure 7: Percent of numerical and gravimetric composition, frequency of occurrence and Index of Relative Importance of taxa categories in individual diets for each month.

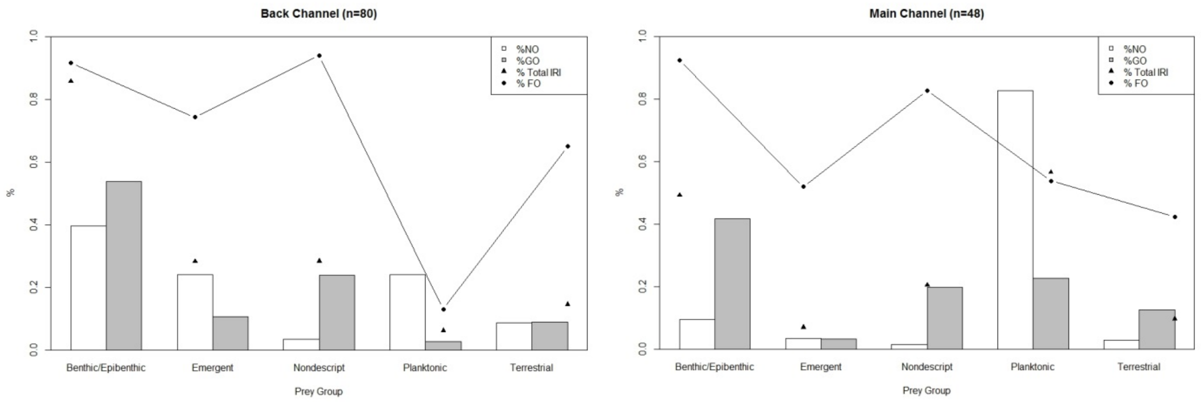


Figure 8: Percent of numerical and gravimetric composition, frequency of occurrence and Index of Relative Importance of taxa categories in individual diets for each habitat type (Back water Channel and Mainstem Channel).

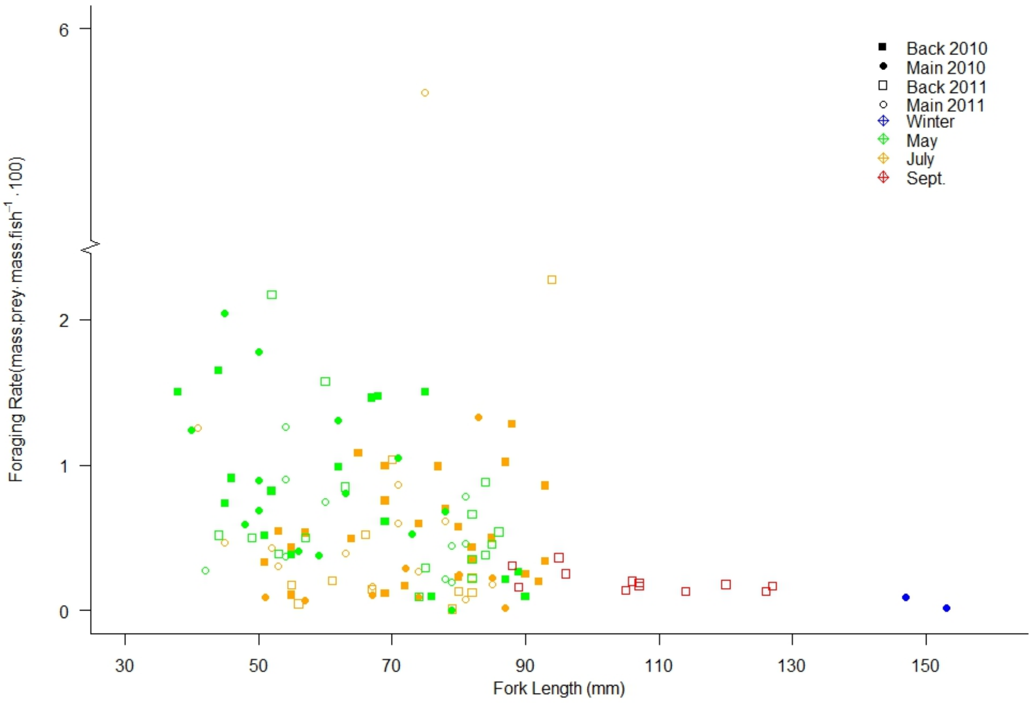


Figure 9: Relative consumption rate (mass of prey/mass of fish x 100) from a subset of diet samples (N=129) plotted by fish fork length (mm). Square symbols denote backwater channel habitat and circles represent mainstem channel habitat. Solid symbols denote year 2010 and open symbols represent year 2011. Each color represents the month of capture for each fish sample.

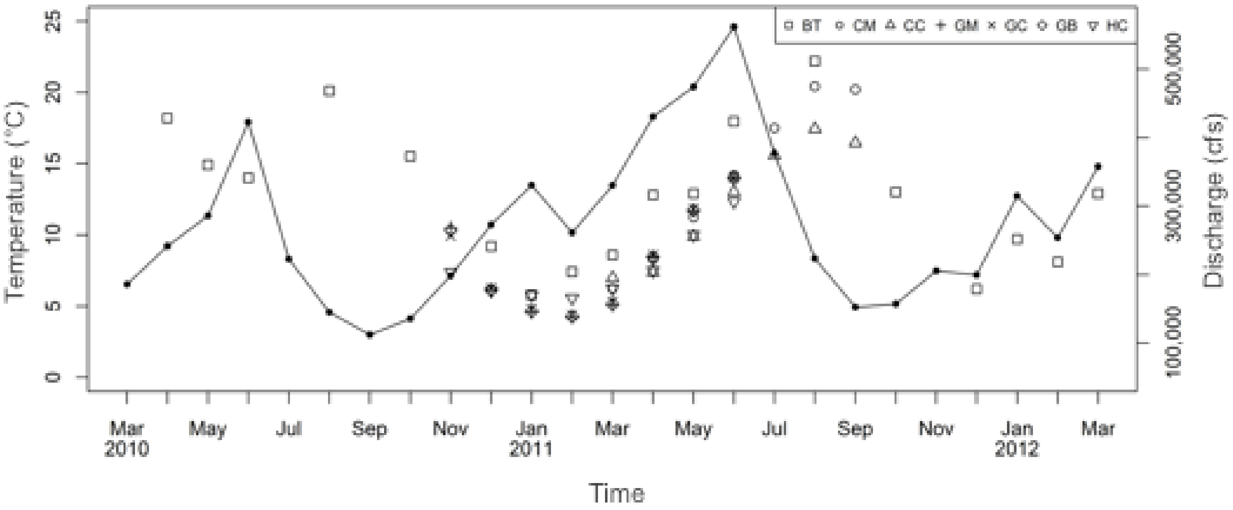
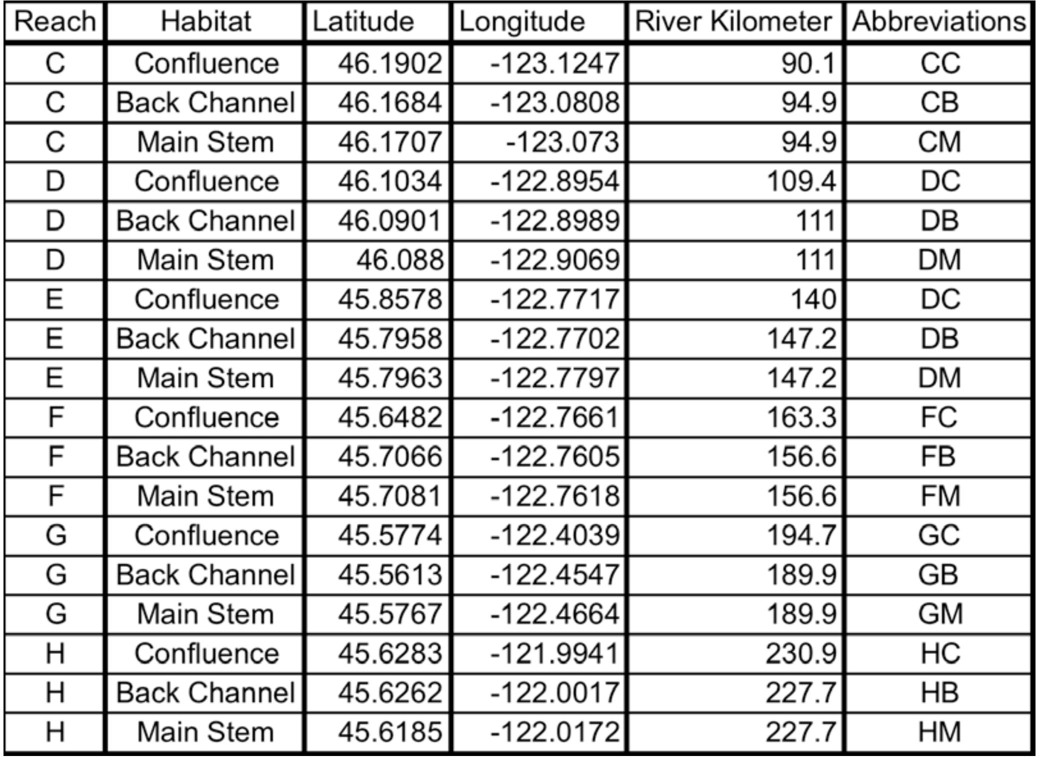


Figure 10: Mean monthly Columbia River estuary discharge and mean monthly Columbia River estuary temperature over the sampling period. Each temperature point symbol is a different location. BT denotes the USGS gauge at Beaver Terminal and all other symbols are temperature loggers recovered at sampling sites.

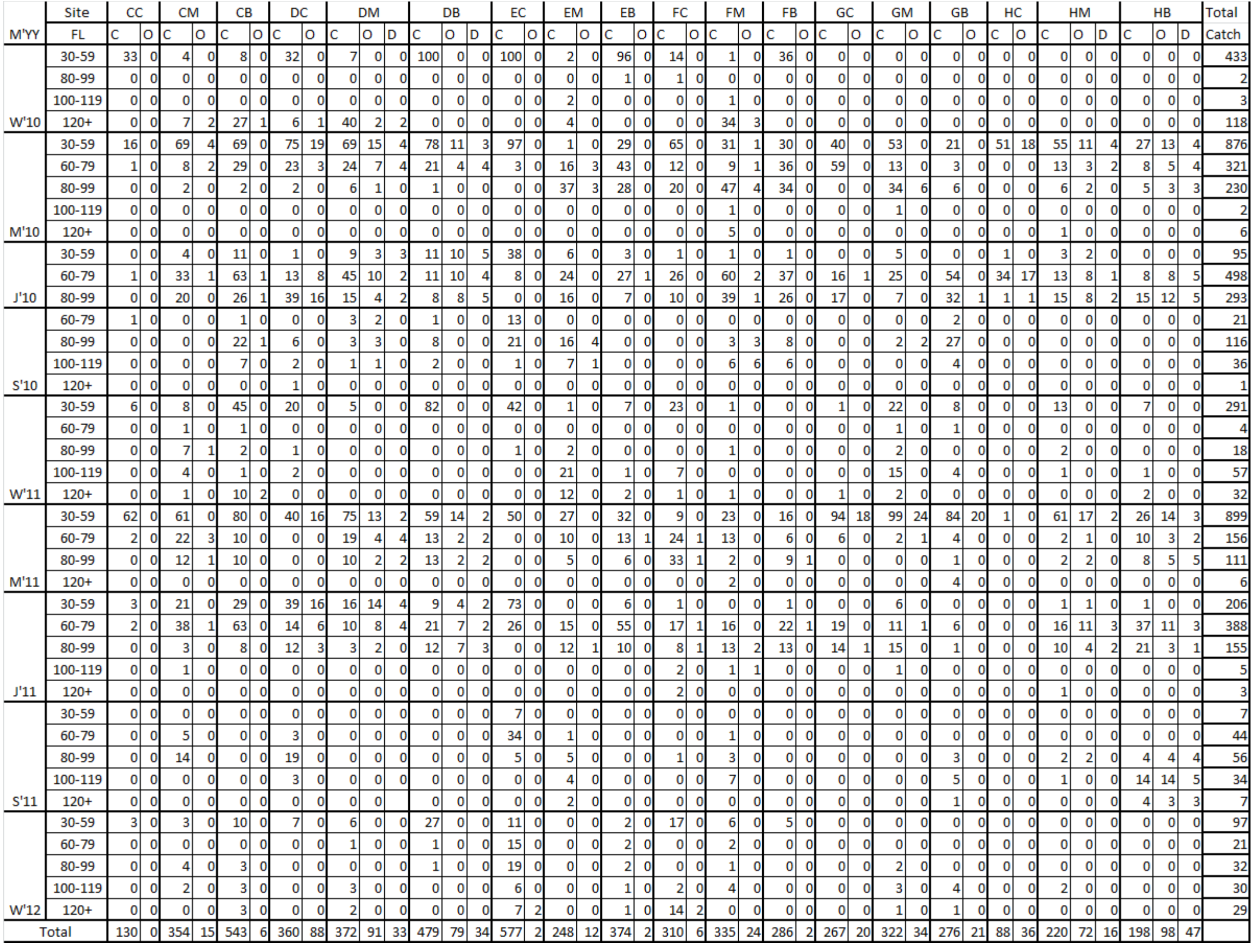
Appendix:

All sampling locations listed by reach, habitat type and site abbreviation.



Reach	Habitat	Latitude	Longitude	River Kilometer	Abbreviations
C	Confluence	46.1902	-123.1247	90.1	CC
C	Back Channel	46.1684	-123.0808	94.9	CB
C	Main Stem	46.1707	-123.073	94.9	CM
D	Confluence	46.1034	-122.8954	109.4	DC
D	Back Channel	46.0901	-122.8989	111	DB
D	Main Stem	46.088	-122.9069	111	DM
E	Confluence	45.8578	-122.7717	140	DC
E	Back Channel	45.7958	-122.7702	147.2	DB
E	Main Stem	45.7963	-122.7797	147.2	DM
F	Confluence	45.6482	-122.7661	163.3	FC
F	Back Channel	45.7066	-122.7605	156.6	FB
F	Main Stem	45.7081	-122.7618	156.6	FM
G	Confluence	45.5774	-122.4039	194.7	GC
G	Back Channel	45.5613	-122.4547	189.9	GB
G	Main Stem	45.5767	-122.4664	189.9	GM
H	Confluence	45.6283	-121.9941	230.9	HC
H	Back Channel	45.6262	-122.0017	227.7	HB
H	Main Stem	45.6185	-122.0172	227.7	HM

Summary of the number of fish sampled by month, year and size class. For the total catch, otolith samples and stomach contents analysis.



	Site	CC		CM		CB		DC		DM			DB			EC		EM		EB		FC		FM		FB		GC		GM		GB		HC		HM			HB			Total
M'YY	FL	C	O	C	O	C	O	C	O	C	O	D	C	O	D	C	O	C	O	C	O	C	O	C	O	C	O	C	O	C	O	C	O	C	O	C	O	D	C	O	D	Catch
W'10	30-59	33	0	4	0	8	0	32	0	7	0	0	100	0	0	100	0	2	0	96	0	14	0	1	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	433
	80-99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	100-119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
	120+	0	0	7	2	27	1	6	1	40	2	2	0	0	0	0	0	4	0	0	0	0	0	34	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	118
M'10	30-59	16	0	69	4	69	0	75	19	69	15	4	78	11	3	97	0	1	0	29	0	65	0	31	1	30	0	40	0	53	0	21	0	51	18	55	11	4	27	13	4	876
	60-79	1	0	8	2	29	0	23	3	24	7	4	21	4	4	3	0	16	3	43	0	12	0	9	1	36	0	59	0	13	0	3	0	0	0	13	3	2	8	5	4	321
	80-99	0	0	2	0	2	0	2	0	6	1	0	1	0	0	0	0	37	3	28	0	20	0	47	4	34	0	0	0	34	6	6	0	0	0	6	2	0	5	3	3	230
	100-119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
	120+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6
J'10	30-59	0	0	4	0	11	0	1	0	9	3	3	11	10	5	38	0	6	0	3	0	1	0	1	0	1	0	0	0	5	0	0	0	1	0	3	2	0	0	0	0	95
	60-79	1	0	33	1	63	1	13	8	45	10	2	11	10	4	8	0	24	0	27	1	26	0	60	2	37	0	16	1	25	0	54	0	34	17	13	8	1	8	8	5	498
	80-99	0	0	20	0	26	1	39	16	15	4	2	8	8	5	0	0	16	0	7	0	10	0	39	1	26	0	17	0	7	0	32	1	1	1	15	8	2	15	12	5	293
S'10	60-79	1	0	0	0	1	0	0	0	3	2	0	1	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	21
	80-99	0	0	0	0	22	1	6	0	3	3	0	8	0	0	21	0	16	4	0	0	0	0	3	3	8	0	0	0	2	2	27	0	0	0	0	0	0	0	0	0	116
	100-119	0	0	0	0	7	0	2	0	1	1	0	2	0	0	1	0	7	1	0	0	0	0	6	6	6	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	36
	120+	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
W'11	30-59	6	0	8	0	45	0	20	0	5	0	0	82	0	0	42	0	1	0	7	0	23	0	1	0	0	0	1	0	22	0	8	0	0	0	13	0	0	7	0	0	291
	60-79	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	4
	80-99	0	0	7	1	2	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	18
	100-119	0	0	4	0	1	0	2	0	0	0	0	0	0	0	0	0	21	0	1	0	7	0	0	0	0	0	0	0	15	0	4	0	0	0	1	0	0	1	0	0	57
	120+	0	0	1	0	10	2	0	0	0	0	0	0	0	0	0	0	12	0	2	0	1	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0	2	0	0	32
M'11	30-59	62	0	61	0	80	0	40	16	75	13	2	59	14	2	50	0	27	0	32	0	9	0	23	0	16	0	94	18	99	24	84	20	1	0	61	17	2	26	14	3	899
	60-79	2	0	22	3	10	0	0	0	19	4	4	13	2	2	0	0	10	0	13	1	24	1	13	0	6	0	6	0	2	1	4	0	0	0	2	1	0	10	3	2	156
	80-99	0	0	12	1	10	0	0	0	10	2	2	13	2	2	0	0	5	0	6	0	33	1	2	0	9	1	0	0	0	0	1	0	0	0	2	2	0	8	5	5	111
	120+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	6
J'11	30-59	3	0	21	0	29	0	39	16	16	14	4	9	4	2	73	0	0	0	6	0	1	0	0	0	1	0	0	0	6	0	0	0	0	0	1	1	0	1	0	0	206
	60-79	2	0	38	1	63	0	14	6	10	8	4	21	7	2	26	0	15	0	55	0	17	1	16	0	22	1	19	0	11	1	6	0	0	0	16	11	3	37	11	3	388
	80-99	0	0	3	0	8	0	12	3	3	2	0	12	7	3	0	0	12	1	10	0	8	1	13	2	13	0	14	1	15	0	1	0	0	0	10	4	2	21	3	1	155
	100-119	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5
	120+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
S'11	30-59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
	60-79	0	0	5	0	0	0	3	0	0	0	0	0	0	0	34	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
	80-99	0	0	14	0	0	0	19	0	0	0	0	0	0	0	5	0	5	0	0	0	1	0	3	0	0	0	0	0	0	0	3	0	0	0	2	2	0	4	4	4	56
	100-119	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	7	0	0	0	0	0	0	0	5	0	0	0	1	0	0	14	14	5	34
	120+	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	4	3	3	7
W'12	30-59	3	0	3	0	10	0	7	0	6	0	0	27	0	0	11	0	0	0	2	0	17	0	6	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	97
	60-79	0	0	0	0	0	0	0	0	1	0	0	1	0	0	15	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21
	80-99	0	0	4	0	3	0	0	0	0	0	0	1	0	0	19	0	0	0	2	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	32
	100-119	0	0	2	0	3	0	0	0	3	0	0	0	0	0	6	0	0	0	1	0	2	0	4	0	0	0	0	0	3	0	4	0	0	0	2	0	0	0	0	0	30
	120+	0	0	0	0	3	0	0	0	2	0	0	0	0	0	7	2	0	0	1	0	14	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	29
Total		130	0	354	15	543	6	360	88	372	91	33	479	79	34	577	2	248	12	374	2	310	6	335	24	286	2	267	20	322	34	276	21	88	36	220	72	16	198	98	47	

Chinook salmon baseline data used for genetic stock analysis in this study (adapted from Teel *et al.* 2014).

Genetic stock	Source populations
West Cascade fall	Cowlitz Hatchery
	Lewis Hatchery
	Sandy River
West Cascade spring	Cowlitz Hatchery
	Kalama Hatchery
	Lewis Hatchery
Willamette River spring	North Fork Clackamas River
	North Santiam Hatchery
	North Santiam River
	McKenzie Hatchery
	McKenzie River
Spring Creek group fall	Spring Creek Hatchery
	Big Creek Hatchery
	Elochoman River
	Willamette River
Deschutes River fall	Lower Deschutes River
	Upper Deschutes River
Upper Columbia River summer/fall	Hanford Reach
	Methow River
	Wells Hatchery
	Wenatchee River
Snake River fall	Lyons Ferry Hatchery
Mid and Upper Columbia River spri	John Day River
	Upper Yakima River
	Warm Springs Hatchery
	Wenatchee River
	Wenatchee Hatchery
Snake River spring/summer	Imnaha River
	Minam River
	Rapid River Hatchery
	Secech River
	Tucannon River
	Tucannon Hatchery
	Newsome Creek
	West Fork Yankee Creek

Chapter II: The use of dynamic factor analysis to estimate common trends in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth variability: describing the freshwater experience

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Life history variation in Pacific salmon (*Oncorhynchus spp*.) has been attributed to biocomplexity and supports species resilience; an acute management concern in view of the effects of climate change on natural resources. Yet juvenile life history variation is difficult to characterize through conventional sampling. In this study we used otolith microstructure and growth trends produced in a dynamic factor analysis (DFA) to describe the life history variation in juvenile Chinook salmon caught in the Columbia River estuary over a two year period (2010-2012). Otoliths are fish ear stones through which structural and chemical analysis can be used to document the age, growth and major migratory movements of individuals over their life-time. However over 75% of the Columbia River estuary is freshwater tidal and to date there is no known chemical signature for estuarine entrance. Therefore we used genetic assignment of fish to stock of origin and capture location and date with growth trajectories, as a proxy for habitat transitions, to reconstruct life history types. Dynamic factor analysis estimated that four to five growth trends are present in juvenile Chinook salmon caught in the Columbia River estuary, more diversity than is currently being accounted for in many management practices. Regional stocks and habitats did not display divergent growth histories, but the marked hatchery fish did ordinate very similarly in the trend loadings from the DFA analysis, suggesting that hatchery fish may not express the same breadth of growth variability as wild fish. We were not able to quantify juvenile life history diversity, and juvenile Chinook life history diversity remains difficult to catalog and integrate into species conservation and habitat restoration for resource management. However, by expanding our understanding of how juvenile Chinook salmon experience their freshwater rearing environment we improve our capacity to conserve and manage salmon populations.

Introduction:

Diversity is essential for the stable productivity of wild ecosystems and provides insurance against the uncertainty of future environmental change (Tilman 1996; Lehman and Tilman 2000). The diversity-stability hypothesis suggests that species diversity stabilizes a community and can buffer the impact of perturbations. In Pacific salmon (*Oncorhynchus spp*.), population diversity is an important mechanism for resilience. Several studies analyzing forty years of Alaskan sockeye (*O. nerka*) catches emphasize the significance of the biocomplexity of fish stocks in ensuring collective population productivity despite major environmental change (Hilborn 2003, Schindler 2010). In these studies resilience is dependent on the maintenance of all the diverse life history types and geographic locations that comprise the stock (Hilborn 2003). However much of the research that ties salmon diversity to resilience has focused on the adult portion of the life cycle.

Pacific salmon are anadromous species and may complete their life cycles through a variety of alternate pathways. Pacific salmon externally fertilize their eggs in freshwater gravel nests, which hatch and develop into alevin, and rear as juveniles in the ocean, estuary, or stream. Eventually they migrate to the ocean as smolts and after a time at sea a series of physiological processes lead them to migrate back to the freshwater system from which they emerged, spawn and die (Quinn 2005). The size, age and habitat in which these life phases are completed are specific to each life history type and species of Pacific salmon. Juvenile life history types include different temporal and spatial patterns of habitat use, and are generally defined by their size relative to the age of migration or location of their rearing habitat in their natal watershed. A central dogma in salmon ecology and management is constraining juvenile life history diversity to an ocean type and stream type juvenile, denoting if they out-migrate to the ocean in their first year of life (Healey 1983; Dawley 1986). However, this is only one habitat transition and one age. This ocean type and stream type dichotomy is an over simplification of juvenile life history rearing and out-migration, that has been described in few systems (Reimers 1973; Bottom et al. 2005; Anderson 2006). For example, Reimers 1973 described five juvenile life history types in the Sixes River, two of which exhibited extended estuarine rearing. By oversimplifying our descriptions of juvenile salmon life history diversity we may be ignoring critical indicators for stability in salmon conservation and management. Understanding how juvenile salmon life history variants contribute to resilience through the diversity-stability hypothesis will facilitate salmon conservation and management.

A central goal in salmon conservation is to understand how populations respond to altered environments (Nehlson 1991; Simenstad 2000; Palmer 2009). This issue has become increasingly important considering the potentially irreversible and cascading effects of climate change (Batin et al. 2007). Rapid environmental changes associated with anthropogenic impacts, such as climate change and habitat loss are already having large effects on regional population dynamics and species extinctions. More than half of all Pacific salmon evolutionary significant units (ESUs) are listed as threatened or endangered under the Endangered Species Act (ESA) (Good 2005). The loss and degradation of freshwater habitat is one of the principal factors driving species declines in North America (Wilcove et al. 1998; Kerr and Deguise 2004; Jorgensen et al. 2009). For example, Chinook salmon (*Oncorhynchus tshawytscha*) have been extirpated from ~40% of its historical freshwater range in the contiguous United Sates (Gustafson et al. 2007), partly due to the loss and degradation of habitat (Nehlsen et al. 1991). Therefore much of the juvenile Chinook life history diversity could already be lost in altered systems.

Wild juvenile salmon life history diversity, especially freshwater estuary entrance and residency can be difficult to describe, and juvenile salmon life history diversity is not often integrated into resilience studies (Thorsen et al. 2014). This may be due to the difficulty in tracking the migration of wild juvenile salmon and detecting their entrance into freshwater tidal estuaries. Most tags used to track juvenile salmon movements and habitat use are too large to be used with the smallest size classes of juveniles (e.g., fry < 60mm FL), limiting the breadth of life history types that can be studied. The otolith chemical markers (e.g., Sr and Ca) most widely used to indicate fish entry into salt water are not limited by fish size, but provide no information about salmon rearing histories in the freshwater tidal reaches of estuaries (Bath et al. 2000). It is important for habitat restoration and conservation efforts to know if juvenile salmon use fluvial or freshwater tidal wetlands. For example, the Columbia River estuary is over 75% freshwater tidal wetlands (Simenstad et al. 2011), and the freshwater basin (660,480 km^2) is an impractically large area of rearing habitat for salmon conservation and habitat restoration to target. In this study we use otolith microstructure, to reconstruct the growth history of individual fish with daily growth rings, similar to the methods of dendrochronology (Campana and Neilson 1985).

The daily increments were examined for patterns in habitat transition similar to those found by Neilson et al. (1985), who found a clear distinction within daily otolith increment widths between juveniles rearing in estuarine and freshwater environments (Neilson 1985). Although there is the possibility of some error in the subjective nature of otolith microstructure aging methods, many of these errors are inversely related to one-another (Campana 1985). Additionally, it has been suggested that aging fish with otolith microstructure by days lowers the risk of inaccuracies because of minor units of determination and determination is only accurate for the first year of life, implying that the clarity of daily growth increments is most accurate in younger fish (Campana 1985).

The aim of this study was to identify statistical evidence of life history diversity within freshwater habitat for juvenile Chinook salmon. More specifically, we evaluated the use of dynamic factor analysis (DFA; Zuur et al. 2003) to estimate common growth trends obtained from otolith microstructural analysis. Growth is a common metric for juvenile fish habitat quality (Sogard 1992: Able 1999; Meng et al. 2000; Necaise et al. 2005), and varies between different types of nursery habitats for juvenile fish (Kjelson et al. 1982; Neilson et al. 1985; Gunderson et al. 1990). Distinct changes in growth have been used to describe habitat changes in juvenile Chinook salmon (Neilson et al. 1985; Campana 1990). We used DFA to estimate predictable growth patterns and the effects of any explanatory variables as a proxy for life history type. We used genetic assignment of fish to stock of origin and capture location and date in the freshwater tidal to reconstruct the possible life history types and tested how those life history descriptors related to the trends produced in the DFA analysis. We also compared the results of DFA to other life history diversity description and demographic techniques, such as genetic regional stock of origin, the ocean-type/stream-type classification used by many fisheries managers and estuarine residence (methods from Neilson et al. 1985). To the best of our knowledge DFA has never been used to describe juvenile Chinook microstructural growth trends or as a method for identifying life history diversity in juvenile Chinook salmon. Our aim is to expand our understanding of how juvenile Chinook salmon experience their freshwater rearing environment and the effects of possible environmental covariates. In doing so, we will improve our capacity to inform efforts to conserve diversity and manage salmon populations for resilience.

Methods:

Study System

The Columbia River basin extends into seven US states and one Canadian province; by volume it is the fourth largest river in the United States. The Columbia River has undergone significant modifications in its recent history. Twenty-three mainstem and hundreds of tributary dams regulate the flow of the Columbia River. Dams without fish passage facilities have reduced access to spawning and rearing habitats, effectively eliminating 55% of the basin area historically available to salmon (NRC 1996). The installation of hydropower and irrigation diversion dams has had a significant impact on the timing and magnitude of the river discharge. For example, river regulation has reduced spring freshets and freshwater inputs to the estuary and effected estuarine circulation patterns (Simenstad 1992). Anthropogenic development of the Columbia River basin and estuary has extensively altered juvenile fish habitat. Diking, filling and other development in the estuary has noticeably reduced available rearing habitat (Kukulka and Jay 2003) and altered the food base of much of the estuarine community (Sherwood 1990). Upland logging and agriculture, shoreline armoring, over-water structures, removal of large wood, and channel deepening and widening has progressively channelized and detached the estuary from its floodplain (Bottom 2005). Today, estuary-wide loss of tidal riparian vegetation is estimated at 68% of the herbaceous tidal wetlands and 75% of forested tidal wetlands (Marcoe 2013). The reduction in wetland habitats in the Columbia River estuary has produced an 82% decline in emergent plant production and a 15% loss in benthic macroalgae production; a combined production loss of 51,675 metric tons of organic carbon per year (Sherwood et al. 1990). Cumulative development throughout the watershed has simplified Chinook salmon rearing habitat. These reductions may be an important factor in the apparent reduction in juvenile life history variation in Columbia River Chinook salmon (Burke 2004).

Juvenile Chinook Sample Collection

The samples used for this analysis were obtained from an estuary-wide survey to determine Chinook salmon genetic stock composition and distribution (Bottom et al. 2012; Teel et al. 2014). Sites were chosen to characterize a range of environments in which both landscape scale influences (reaches) and as much stock and life history diversity as feasible could be captured (habitat types) specifically for a genetic survey, which is described in Teel *et al.* 2014. Sites were stratified among six freshwater tidal Level 3-Hydrogeomorphic Reaches (Fig. 1: C-H) defined by the Columbia River Estuary Ecosystem Classification (Simenstad et al. 2011). We sampled three habitat types within each reach: mainstem channel, backwater channel and confluence. A total of eighteen sampling sites were sampled every-other month for two years (March 2010-March 2012). In all tables and figures, each site was coded by the sampling design, with the first letter representing the reach and the second letter representing the habitat type (Appendix). For more specific sampling location information, see Teel *et al*. 2014 (Appendix). Beach seine sampling for juvenile salmon occurred down the full extent of each beach with a 38-meter beach seine (1 cm mesh size), with a one-meter by one and a half-meter central bag (1/3 cm mesh size), which samples the top three meters of the water column. During flooding periods when beach seining was impractical, we used a 9-meter pole seine. Because small size classes of Chinook tend to favor shallow water habitats (Bottom et al. 2012), this sampling design and method primarily targeted subyearling Chinook salmon. All fish caught were identified to the species level and counted. Up to 100 juvenile Chinook salmon were weighed and measured to the nearest millimeter (fork length). Fish were also scanned for coded wire tags (CWT), passive integrated transponder (PIT) tags and other markings (such as the removal of the adipose fin) to identify hatchery origin and other experimentally tagged groups. For each sampling event, tissue samples were obtained from the caudal fin for genetic analysis of up to 30 juvenile Chinook salmon, and preserved in nondenatured ethanol (Bottom et al. 2012).

Genetic assignment of fish to stock of origin

Individual assignment estimates to stock of origin are reported in Teel et al. (2014), and used in this study as a demographic descriptor. Chinook salmon genotypes were determined using methods previously described in a Columbia River estuary study (Teel et al. 2009). Genomic DNA was isolated from fin tissue samples using Wizard genomic DNA purification kits (Promega Corp.). The isolated genomic DNA was used in polymerase chain reactions (PCRs) to amplify 13 microsatellite loci, which have been standardized among several West Coast genetics laboratories (Seeb et al. 2007). GeneScan and Genotyper software programs (Applied Biosystems) were used to identify the size and number of alleles detected at each locus. The likelihood model described by Rannala and Mountain (1997), and employed by the genetic stock identification program ONCOR (Kalinowski et al. 2007), was used to estimate the stock origin of each individual. Population baselines correspond to a previously compiled multilaboratory standardized Chinook salmon genetic database (Teel et al. 2009, Johnson et al. 2010, Appendix). Fish were individually assigned to eleven regional stocks (Teel et al. 2014). Nine regional stocks were identified as within basin (Table 1, Fig. 1), and fish originating from the two out of basin groups were not used in the otolith analysis (e.g., Rogue River and coastal populations). We chose to exclude out of basin stocks because they represented a small proportion of the juvenile Chinook salmon caught in this study, and it is unknown if they were the offspring of strays or juveniles migrating into the estuary from the marine environment.

In addition, we used the GSI program ONCOR with the likelihood model of Rannala and Mountain (1997) to compute the posterior probability of stock membership of each individual fish (Mantel et al. 2005). To ensure overall stock assignment accuracy in the data used for the DFA, we excluded juveniles with relative assignment probabilities < 0.80 (82% of the individual assignments determined from the total catch).

Growth Time Series

Daily incremental growth was estimated for a subset of lethal samples (N=665). These fish were opportunistically collected during several Columbia River estuary projects and therefore are not consistent over space or time (see Table 1 in previous chapter). Daily incremental growth was estimated by measuring the microstructure features of each right sagittae otolith, viewed at adjacent transverse sections by two readers. The left sagittae otolith was used when the right was unavailable. Each otolith was mounted in Crystalbond resin, ground with fine grain sandpaper (1500 grit) and polished with MasterPrep® Polishing Solution (Buehler, 0.05 micron) on both sides. Otoliths were photographed with a compound microscope (10x and 40x) and digital (Olympus B071) camera. Otolith increments were counted and measured along 90° transects from the post-rostrum primordial in the dorsal direction (Titus et al. 2004). For each transect, daily increment measurements originated at the exogenous feeding check (Marshall and Parker 1982) and extended to the otolith edge. Daily otolith rings were measured and enumerated with ImageJ (Abramoff et al. 2004, Rasband 2012) and a customized otolith and tree ring macro from the plugin ObjectJ (Developed by Vischer and Nastase, University of Amsterdam). Of the 665 otoliths dissected approximately 5% (34) were lost due to damage during processing and 23 otoliths were determined to be vatritic, and therefore unusable. A reader confidence (1-5) was recorded for every otolith age estimate and only the highest rated samples (N=524) were used for further analysis. To use otolith growth as a proxy for juvenile Chinook salmon growth there must be a strong relationship between fish size and otolith size (Campana and Neilson 1985). These data meet this necessary assumption with an R^2 value of 0.95 when using otolith width to predict fork length. Growth time series were defined as the width of daily otolith increments from emergence (exogenous feeding check) to capture in the estuary (otolith edge).

Dynamic Factor Analysis

We used dynamic factor analysis (DFA) to model shared temporal trends in the daily growth increments among all fish, which allowed us to simplify the temporal variability in growth and observe the common trends. DFA is a multivariate time series method that seeks to explain the variance in *n* time series with a linear combination of *m* hidden random where $n >> m$ (Zuur et al. 2003). The DFA model can be written as:

$$\mathbf{x}_t = \mathbf{x}_{t\text{-}1} + \mathbf{w}_t$$

$$\mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{v}_t$$

The *n* x1 vector of observations at time *t*, ($\mathbf{y}_t$) relate to the *m* x 1 vector of latent trends at time t, ($\mathbf{x}_t$) via the *n* x *m* matrix of factor loadings (**Z**). The vectors, where w_t and v_t are multivariate normal distribution with mean vectors 0 and variance-covariance matrices **Q** and **R**, respectively (Holmes et al. 2014). We used a diagonal observation error variance-covariance matrix (**B**) with different observation variance but no covariance among time series. We assumed that otolith reader observation error would be equal for all fish, as the reader was blind to the identity of each otolith sample. The daily juvenile Chinook salmon growth time series were grouped by capture month and year, totaling six capture groups: May 2010, July 2010, September 2010, May 2011, July 2011 and September 2011.

We compared model fits based on one to five common trends for each of the capture groups. We chose five as the maximum number of trends because that was the number of juvenile Chinook salmon life history types described by Reimers 1971. We fit the models in R (R Development Core Team 2011) using the package MARSS (Holmes et al. 2014). Support for each model was evaluated using Akaike information criterion, corrected for smalls sample sizes (AICc; Burnham and Anderson 2002).

Estuary Residence

We inferred estuarine residence times based on changes in otolith increment patterns that may coincide with the transition from fluvial to tidal environments. Specifically, estuarine residence was identified when the average ring width from the previous twenty rings increases by 25% over the following ten rings (Neilson et al. 1985). These methods, developed by Neilson *et al.* (1985) distinguish the juvenile Chinook salmon growth transition between freshwater residence and estuarine residence. We automated this process to identify this pattern for each individual's microstructural growth estimates in program R (R Development Core Team 2011). When we applied the methods from Neilson *et al.* (1985), the methods immediately excluded approximated 12% of the data set with the required 30 ring minimum. Therefore we dropped the requirements to a previous ten rings increasing by 25% over the following five rings. Moving forward we will call this revised method a growth check, because we have no evidence to validate whether salmon growth increases after entry into the Columbia River estuary.

Results:

Seasonal and stock distribution

The genetic analysis and capture data (adapted from Teel *et al.* 2014) showed that juvenile Chinook salmon are present in the estuary throughout the year and exhibited a consistent temporal pattern in genetic stock composition (Fig 2). In general, five genetic reporting groups were the most abundant in the estuary: West Cascade (fall and spring), Willamette River, Upper Columbia River summer/fall and Spring Creek. Snake River spring-run and fall-run, Upper and Mid-Columbia River spring-run and Deschutes River juvenile Chinook salmon were captured in much smaller numbers than other genetic reporting groups, but were still present in the estuary. The West Cascade fall-run juveniles inhabit the estuary year-round and increase in size at capture throughout the year. The lower river spring-run genetic reporting groups out-migrate at large sizes in March. The Upper Columbia River fall-run juvenile Chinook salmon are primarily captured in the freshwater tidal Columbia River estuary in the summer months, and reaches G and H.

Growth Check

Approximately 40% (N=237) of the juvenile Chinook salmon captured in the Columbia River freshwater tidal estuary exhibit a dramatic growth increase (25%) that may be associated with a habitat transition. Both wild and hatchery origin fish exhibited this growth check. This dramatic growth increase was exhibited in individuals from all reaches and capture groups as well as seven of the genetic reporting groups: West Cascade spring-run and fall-run, Willamette River spring-run, Spring Creek group, Upper Columbia River summer/fall-run, Snake River fall-run and Deschutes River fall-run. The ring number or age in days at which point a growth check was present varied, but was most often present around one month of age (Fig. 2).

DFA

All capture groups were best explained by four to five trends (Table 2). The growth trajectories of juvenile Chinook salmon in capture groups July 2010, July 2011, September 2010 and September 2011 were best explained by five trends. However, in capture groups May 2010 and May 2011 juvenile Chinook salmon were best described by four trends, despite containing the largest range of sizes of any capture group. In the DFA analysis, very few individuals load to a single growth trend, making interpretation difficult (Appendix). Additionally, individual growth time series load both negatively and positively to three to five trends in each capture group, further complicating interpretation. In general, there are four major patterns to which all trends can be described ecologically: (1) trends that vary around the mean, (2) trends that vary in time, but continuously increase in growth, (3) trends that vary in time, but continuously decrease in growth, and (4) trends that vary in time, but have one particularly extreme period of increased or decreased growth between emergence and capture in the freshwater tidal estuary.

The ordination of each individual juvenile Chinook salmon's loadings from the growth trends produced in the DFA analysis does not obviously align with genetic reporting group or capture location (Fig. 4). However, hatchery marked fish in May 2010 and May 2011 capture groups clustered together tightly (Fig. 5). Additionally, the DFA models took an incredible amount of time to converge (Table 3) and May 2010, m=5 would not converge (Table 2). This method may not be the most appropriate for otolith microstructure methods due to the large sample size. We also found that the closer the ratio of number of time series to the number of time steps (or days) reached 1:1 the longer the model took to converge (Table 3).

Discussion:

This study investigates the juvenile life history diversity of Chinook salmon rearing or migrating through the Columbia River freshwater tidal estuary by integrating (1) growth trajectories, as a proxy for habitat transitions (2) time, and (3) demographics or origin. We found a remarkable amount of diversity in freshwater tidal estuarine habitat use. Dynamic factor analysis estimated four to five growth trends are present among juvenile Chinook salmon caught in the Columbia River estuary (Table 2). Individual fish rarely load to a single trend and therefore we cannot assign particular categorical attributes (e.g., stock of origin or capture location) to any subset of trends or trend types. Additionally the growth check method was incredibly pervasive throughout these data and both hatchery origin and wild individuals exhibited a growth check. Regional stocks did not display divergent growth histories, but the DFA loading's ordination did cluster by hatchery or wild origin for some capture groups, suggesting that hatchery fish may not experience the same breadth of growth variability as wild fish. We were not able to quantify juvenile life history diversity, and this life history diversity remains difficult to catalog and integrate into species conservation and habitat restoration for resource management.

All juvenile Chinook salmon examined with otolith microstructure and DFA in this study are considered subyearlings or ocean-type by current fisheries standards for categorizing life history type (Dawley et al. 1986). However, we have shown that there is more diversity present among these individuals that is being coarsely grouped and simplified in many management practices. Genetically distinguishable groups do not conform to these standards of two primary categories for size and timing of out-migration (Teel et al. 2014), and some regional stock group's capture months and sizes suggest a wide range of freshwater habitat use (Fig. 2). For example, representatives of the Upper Willamette River stock were present in the freshwater tidal estuary most of the year (Fig. 2). This group enters and exits the estuary at large sizes in March (more typical of the stream-type and what we may expect from a spring-run juvenile Chinook salmon), as well as very small sizes early in the year and as subyearlings throughout the late summer, fall and winter (Fig. 2). The West Cascade spring-run juveniles show a similar pattern, suggesting at least three life history types exist in lower river spring-run populations. Both lower river fall-run populations (West Cascade fall-run and Spring Creek group) and Upper Columbia River fall-run juvenile Chinook salmon are present in the freshwater tidal estuary year-round at a variety of sizes. These regional stock groups increase in size at capture from spring to late summer. We know from Chapter one of this thesis that summer months support the fastest growth and no detectable relationship occurred between stock of origin and estuarine growth. Therefore summer estuarine rearing may be important for all fall-run juveniles. This descriptive approach to examining juvenile Chinook life history diversity, incorporating size, timing and genetic stock of origin reveals a variety of possible freshwater rearing patterns for juvenile Chinook salmon. However, this approach does not provide a quantitative method of categorizing life history types of juvenile Chinook salmon to be easily applied in management and habitat restoration.

Similarly to the estuarine growth estimates from Chapter one, we do not see a clear relationship with stock of origin and the growth trends produced from the DFA analysis (Fig. 4). The DFA analysis best explained all capture groups by four to five trends, supporting the descriptive results from the distribution of genetic groups captured throughout the estuary; that a number of life history types are present. However it remains unclear how growth and regional stock of origin relate to one another and influence life history diversity. It may be that many overlapping growth trajectories are present within each genetic reporting group, and that these growth trajectories represent relatively detailed variation from shifts in the duration of habitat transitions and resource availability for each individual. Even though the AICc values indicated that models with four or five trends were the most strongly supported, the way in which individual fish load to these trends is very complex. For example, some individuals positively or negatively loaded to the trends as well as loaded to several trends. The complexity in which these individuals related to the produced trends creates individual versions of the combinations of trends, increasing the number of trends for interpretation. These results provide insight into how variable juvenile Chinook salmon freshwater rearing can be, and the many possible ways they could be categorized for conservation. Several other studies have also concluded that Chinook salmon may complete their life cycles through a variety of pathways, and there can be a tremendous amount of variation in juvenile habitat use and timing in estuaries (Reimers 1971; Simenstad et al. 1982; Levings et al. 1986; Anderson 2006). However a clear characterization and quantitative tool for measuring this variation is difficult to provide with our DFA analysis.

The growth trends estimated by DFA do not have a clear relationship with hydrogeomorphic reach or habitat type in which they were captured in the freshwater tidal estuary (Fig. 4). This may in part be due to sampling design. The otolith samples were an opportunistic subsample of a larger study and we did not collect otoliths at every capture event in all 18 sites. Unfortunately, individual fish rarely load to a single trend and therefore we cannot assign particular attributes to any evidence of estuarine rearing. Additionally, other demographic changes, such as a release from gape limitation or pulses of high caloric prey items (e.g., larval fish) could be affecting our growth estimates. By comparing the estuarine residence methods from Neilson *et al.* 1985 we had hoped to speculate further into identifying estuarine residence, or a major habitat transition that could represent entrance into the freshwater tidal Columbia

River estuary. However, the growth check was observed in many fish in this study. A growth check was present in all months and reaches of capture, hatchery and wild origin individuals, as well as seven of the genetic reporting groups. In some capture periods the individuals exhibiting a growth check grouped with the ordination of trend loadings from the DFA analysis, but not exclusively.

Regional stocks and habitats did not display divergent growth histories, but the marked hatchery fish did ordinate very similarly in the trend loadings from the DFA analysis in May capture periods (Fig. 5). Additionally some of the hatchery marked individuals show a pattern we may predict from the known portion of their time rearing in freshwater: high initial growth (potentially when in the hatchery environment) followed by a steep but variable decline in growth and eventual leveling off (representing their transition into a wild more challenging environment) (Appendix). However, other hatchery fish show a pattern of growth that varies around the mean with no distinct changes. The strong grouping of hatchery fish within the DFA loading ordination plot may reveal an avenue for identifying unmarked hatchery fish, but was not tested in this study. It also suggests that hatchery fish may not experience the breadth of growth variability as wild fish. If the majority of an individual hatchery fish's life is experienced in a controlled environment it is plausible that it would experience less variability, despite being caught in the wild.

Finally, the dynamic factor analysis reveals considerable juvenile life history diversity in juvenile Chinook salmon that is not currently recognized in most management practices. However this complex continuum of life history diversity may not be a practical application for identifying juvenile life history types for managers, due to the complexity of the results and time intensive laboratory and statistical techniques (Table 3). It is important to continue to investigate a method for identifying freshwater tidal estuarine residence and explaining habitat use in the juvenile freshwater rearing phase. Nearly $170 million is spent annually to enhance the survival of juvenile Columbia River salmon populations in the freshwater phase of their life cycle (e.g., hatchery production and more natural habitat processes) (Naiman et al. 2012). To counter act havest declines and ameliorate rearing habitat loss, hatcheries target fast growth and large sized juveniles. Although growth has been shown to be an important indicator for juvenile salmon survival (Scheuerell and Williams 2005; Zabel et al. 2006, Duffy and Beauchamp 2011), there is no one optimum phenotype. Therefore, a better understanding of juvenile salmon life history diversity could improve hatchery management (Miller et al. 2010), which could work towards allowing the ecological expression of diversity instead of producing a single phenotype. Habitat restoration efforts could also integrate habitat complexity as a means for promoting species resilience, if juvenile habitat use could be better categorized and applied. Basin-wide water use practices, such as hydropower and flood control could also be improved by integrating a diversity of migration times and year-round estuarine habitat use. Additionally, many of these Chinook salmon populations are listed as threatened or endangered on the Endangered Species Act, and managers and habitat restoration practitioners have a responsibility to integrate diversity and resilience into salmon management and conservation as we prepare for the consequence of climate change on our natural resources.

Tables/Figures:

Table 1: Regional stock of origin abbreviations.

Abbreviation	Source Tributary(s)	Adult Return Timing
Desch_F	Deschutes River	fall
MCR&UCR_Sp	Mid and Upper Columbia River Region	spring
SCG_F	Spring Creek	fall
Snake_F	Sanke River	fall
Snake_Sp	Sanke River	spring
UCR_Su/F	Upper Columbia River	summer or fall
WC_F	West Cascade Range	fall
WC_Sp	West Cascade Range	spring
WR_Sp	Willamette River	spring

Table 2: Summary of AICc and R-squared values for each number of trends and capture group.

	May 2010		July 2010		Sept. 2010		May 2011		July 2011		Sept. 2011	
# of trends	Δ AICc	R^2	Δ AICc	R^2	Δ AICc	R^2	Δ AICc	R^2	Δ AICc	R^2	Δ AICc	R^2
1	148	0.09	1024	0.09	430	0.13	438.3	0.09	810	0.09	671	0.12
2	36	0.14	648	0.14	224	0.22	134.2	0.16	468	0.14	453	0.19
3	15	0.18	351	0.17	75	0.28	56.21	0.21	235	0.17	290	0.25
4	**0**	0.21	197	0.2	30	0.31	**0**	0.25	88	0.21	93	0.31
5	51	0.24	**0**	0.23	**0**	0.33	NA	NA	**0**	0.23	**0**	0.34

Table 3: Summary of the approximate time to convergence for each loop of models for m = 1 to 5, by capture group.

Capture group	Number of time series	Number of time steps	~ Time to converge
May 2010	152	205	4 weeks
July 2010	115	188	3 weeks
September 2010	13	245	< 1 day
May 2011	128	206	4 weeks
July 2011	100	220	3 weeks
September 2011	16	295	1.5 days

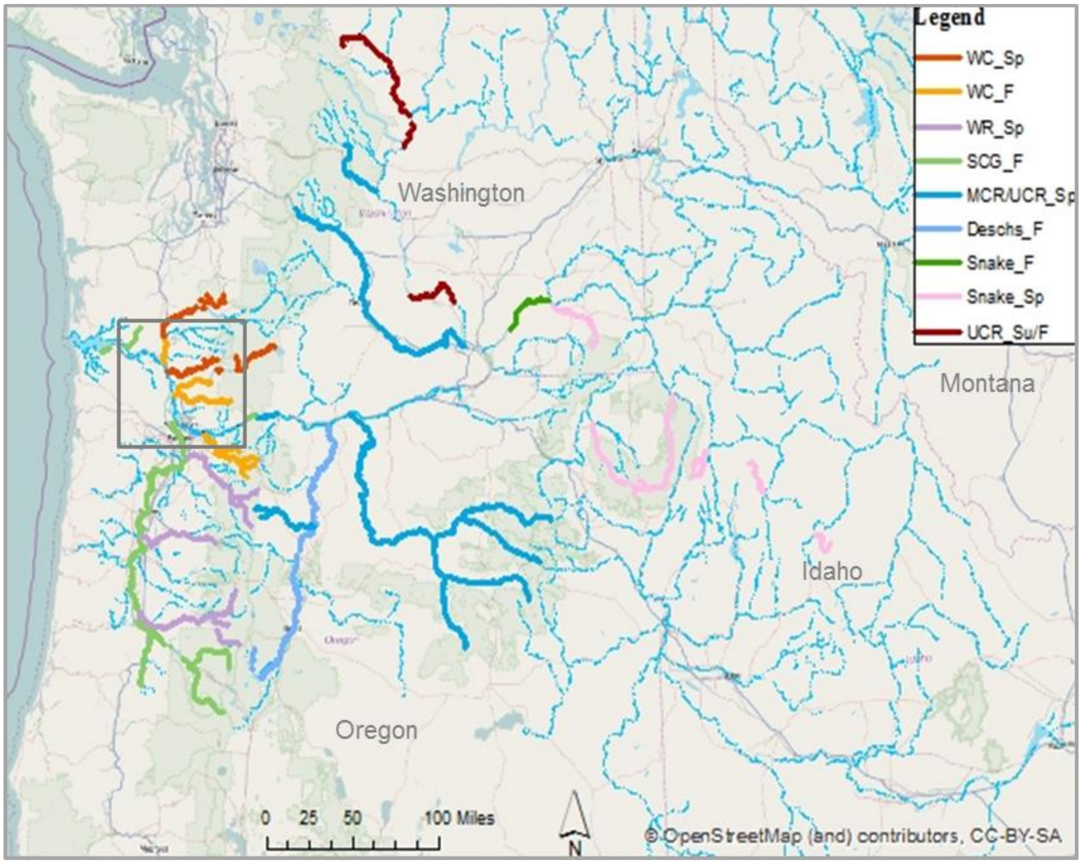


Figure 1: Columbia River basin (in aqua) and the locations of Chinook salmon populations (see legend) used as baseline data for genetic stock identification analysis in this study (adapted from Teel et al. 2014). Grey box: freshwater tidal estuarine region sampled, reaches C-H from the CREEC (Simenstad et al. 2011).

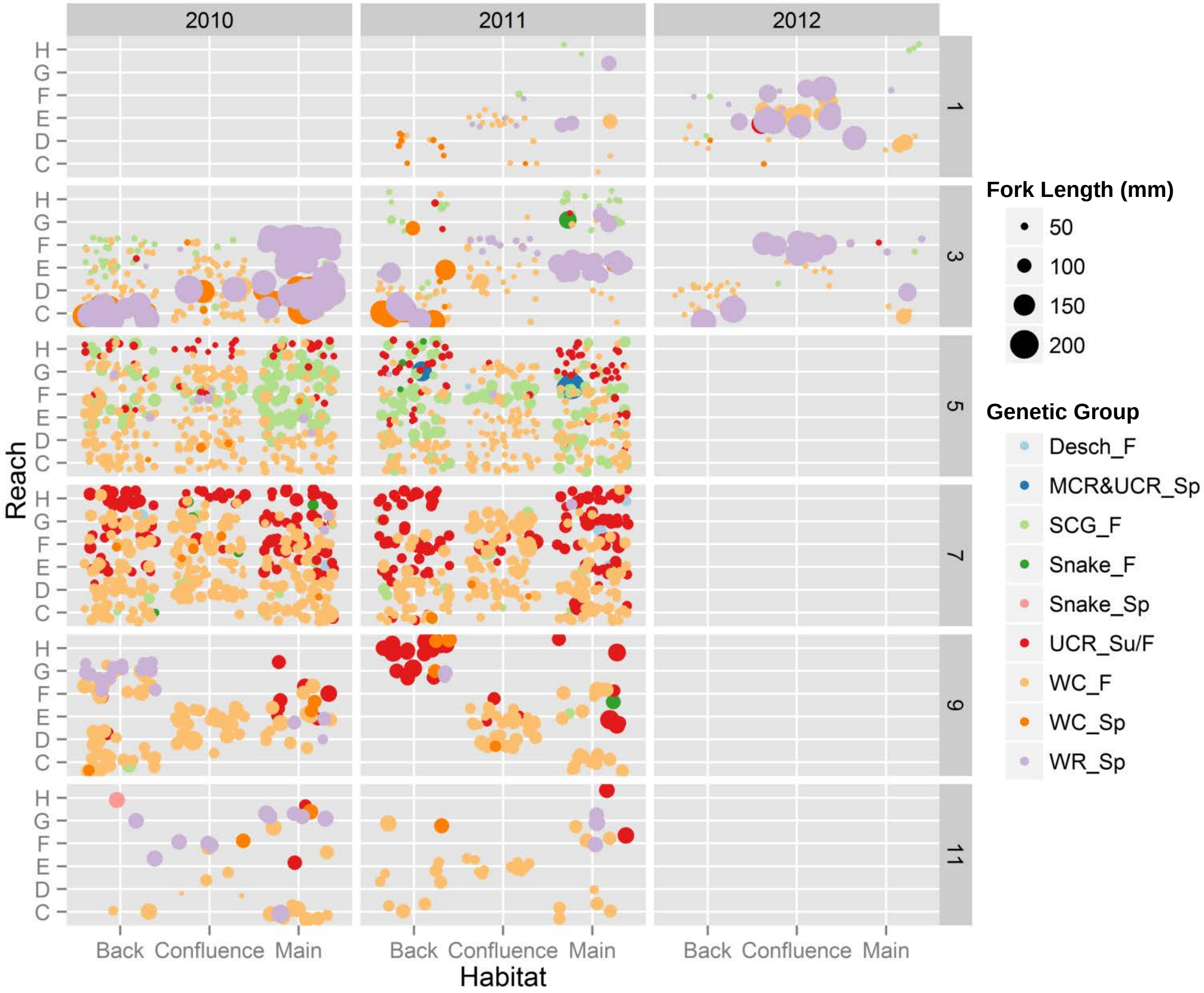


Figure 2: The distribution of size, timing and genetic group of juvenile Chinook salmon over space and time in the Columbia River estuary (adapted from Teel et al. 2014). The inner grid represents space: the intersection of each line is one of the 18 locations from which we sampled. The outer grid represents time: each larger grid cell is a combination of month and year.

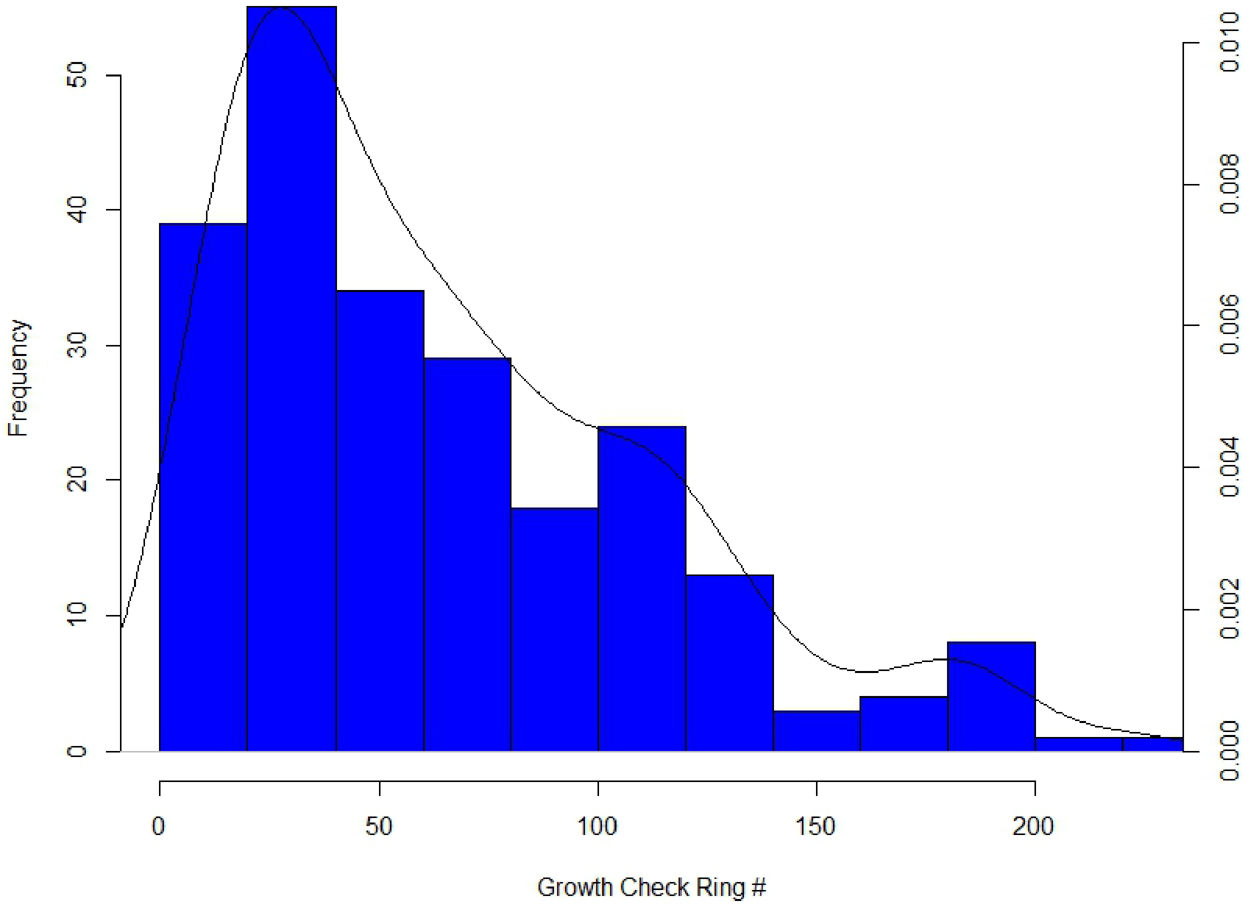
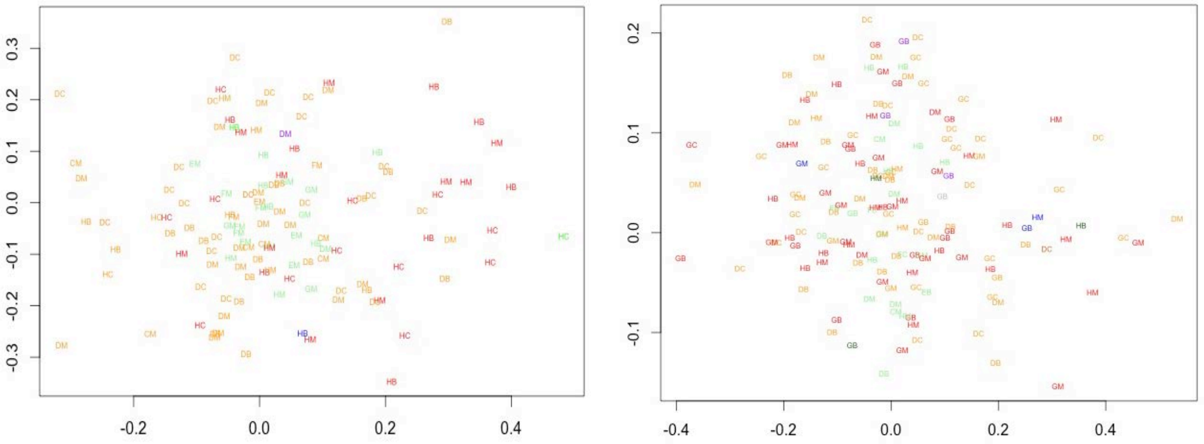
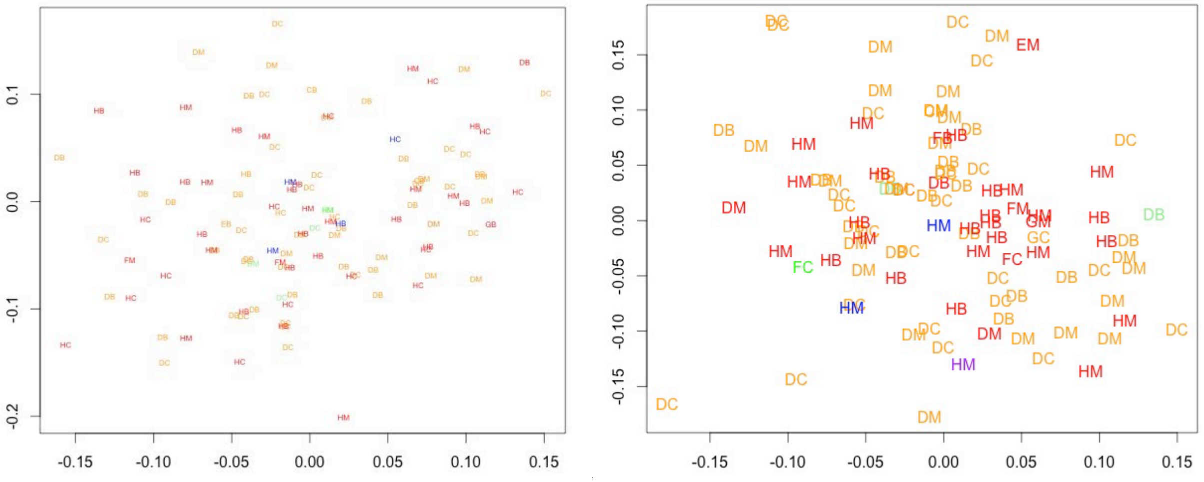


Figure 3: The frequency of the ring number or age in days at which point a growth check was present for all juvenile Chinook salmon exhibiting a growth check.

May 2010 May 2011



July 2010 July 2011



September 2010 September 2011

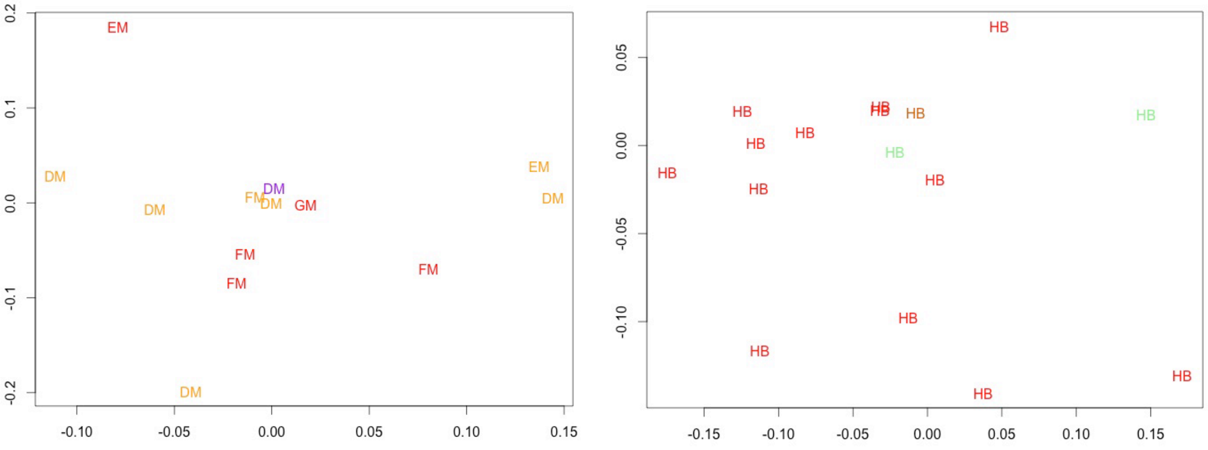
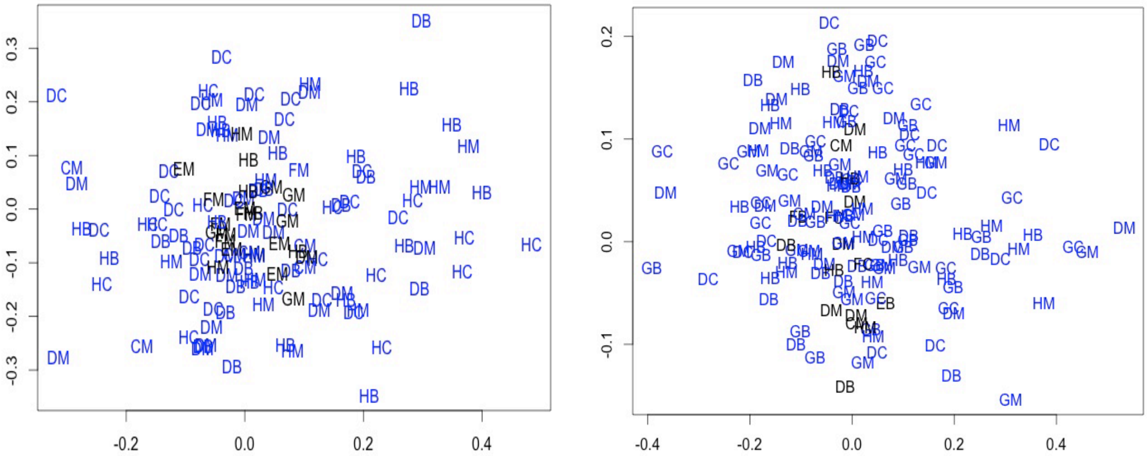


Figure 4: Ordination plots of trend loadings for each fish. Colors represent regional stock of origin. Each point represents the acronym for capture location in the estuary and each plot separates the year and month of capture in the estuary.

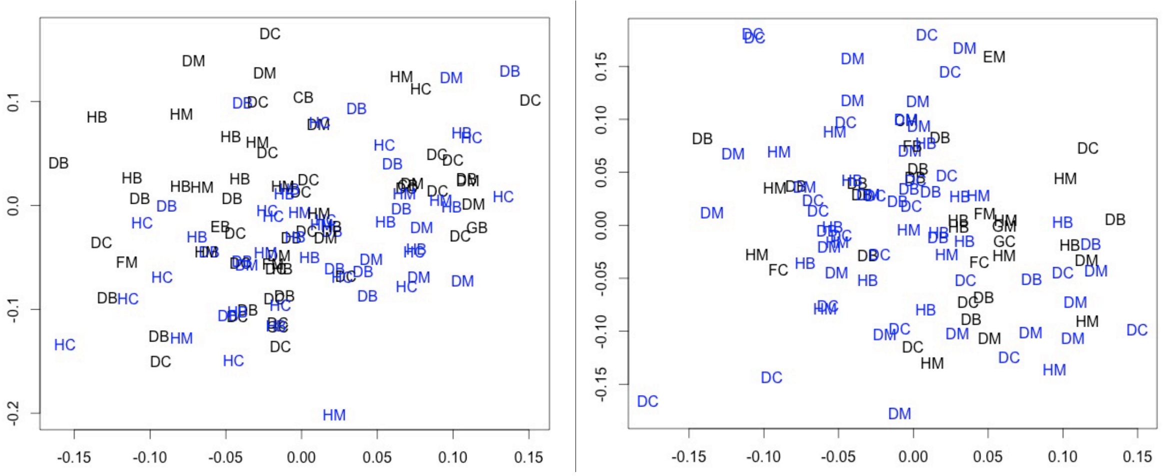
May 2010

May 2011



July 2010

July 2011



September 2010

September 2011

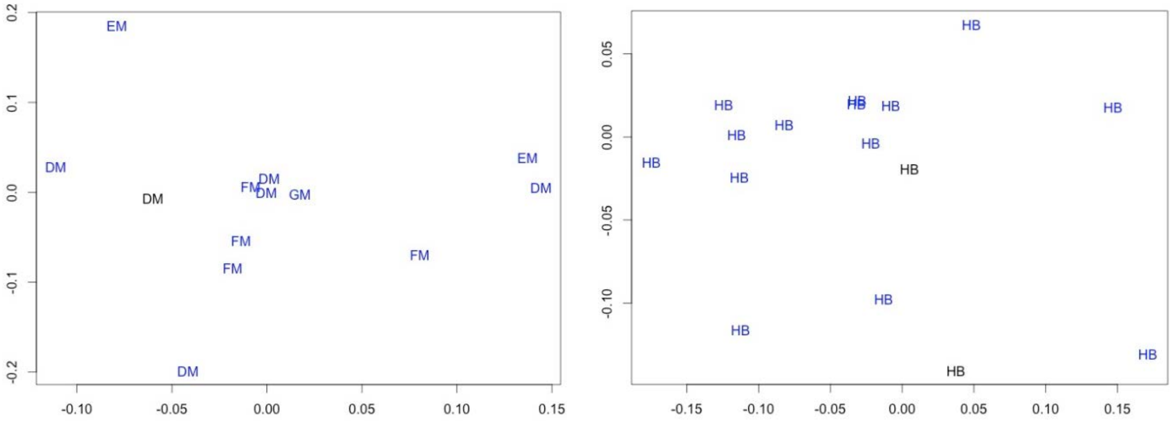
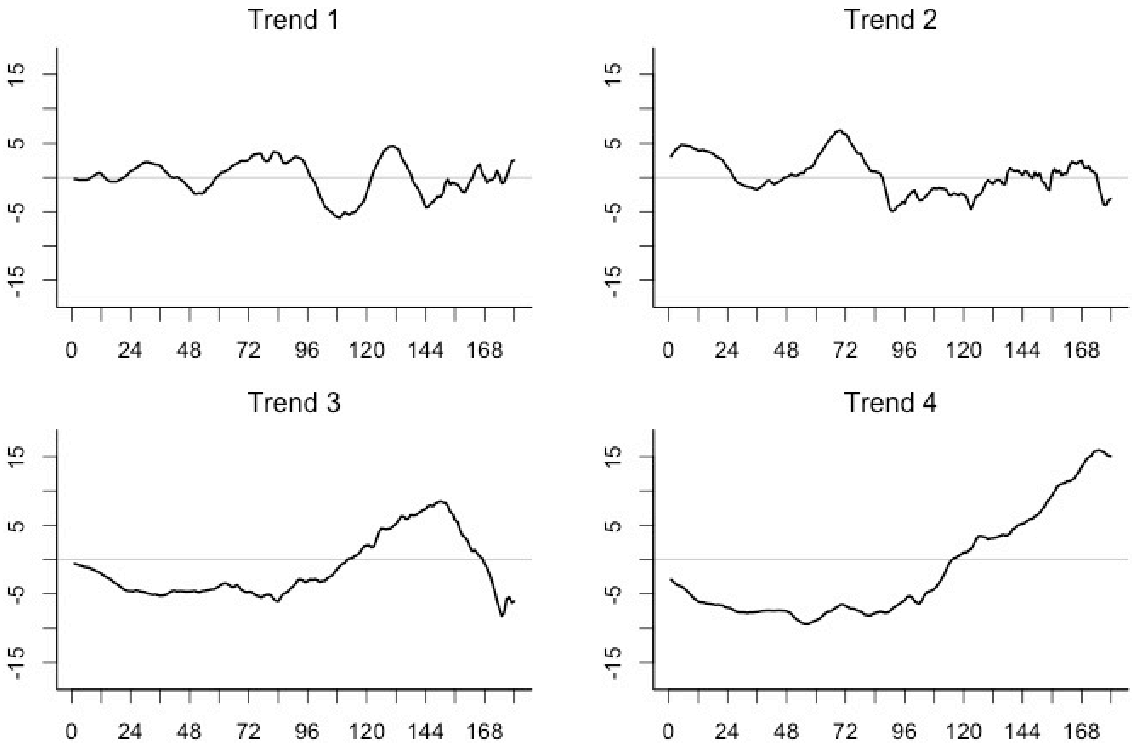
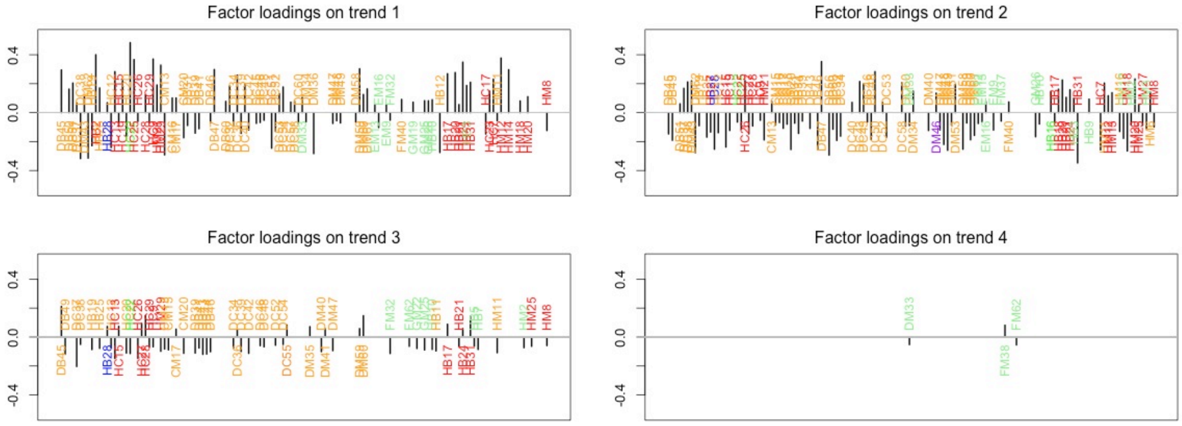


Figure 5: Ordination plots of trend loadings for each fish. Colors represent hatchery (black) or wild (blue) origin. Each point represents the acronym for capture location in the estuary and each plot separates the year and month of capture in the estuary.

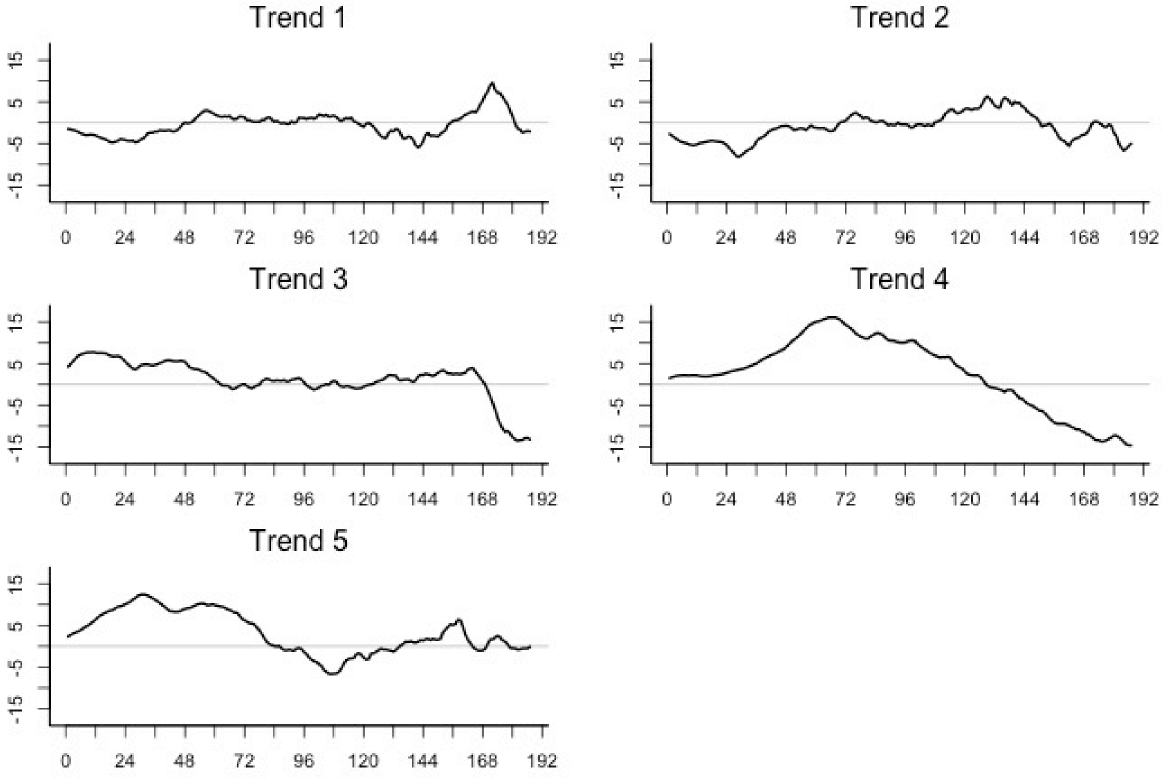
Appendix: Trends and factor loadings for every sampling month and year. The color of each fish number represents the same genetic groups as the colors in all other figures, fish numbers correspond to site of capture.

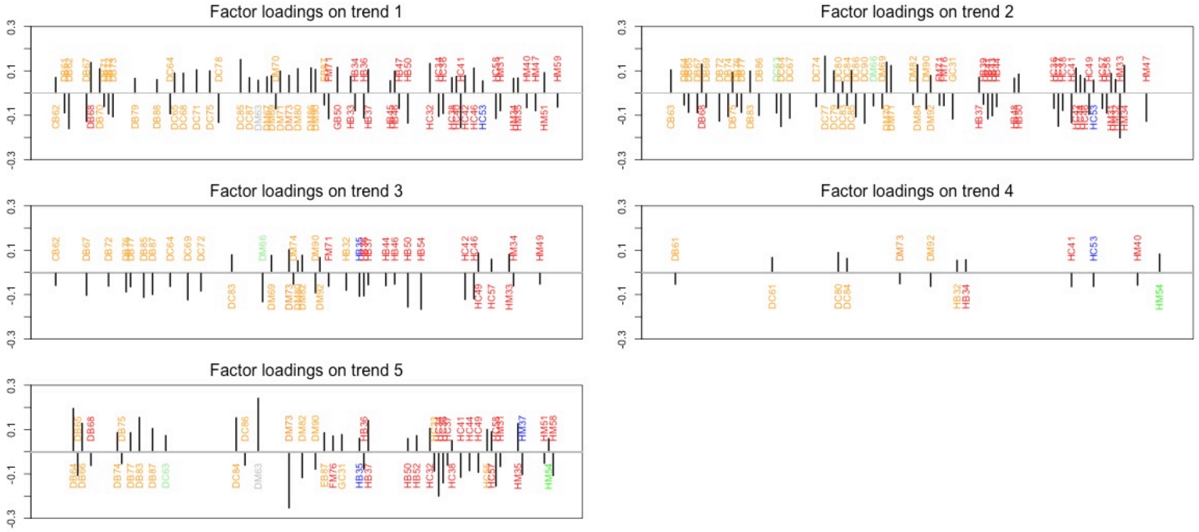
May 2010 capture group:





July 2010 capture group:





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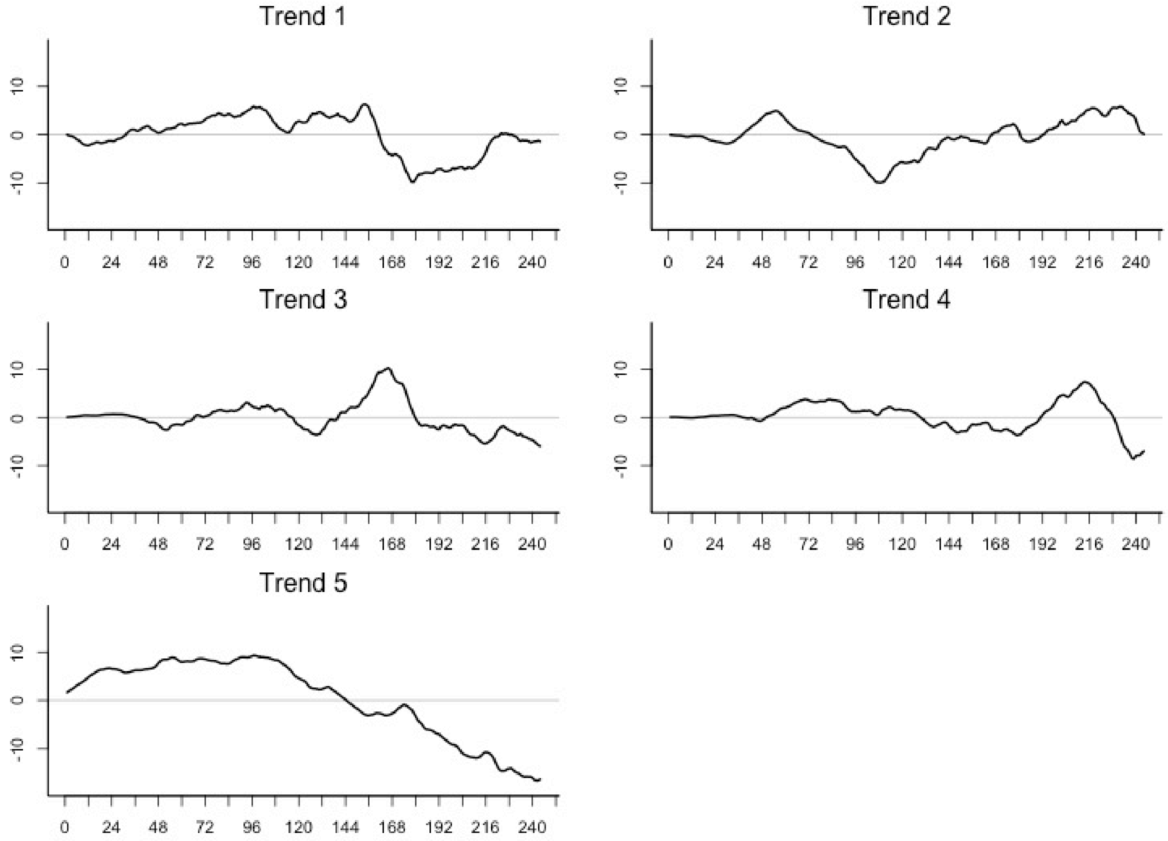

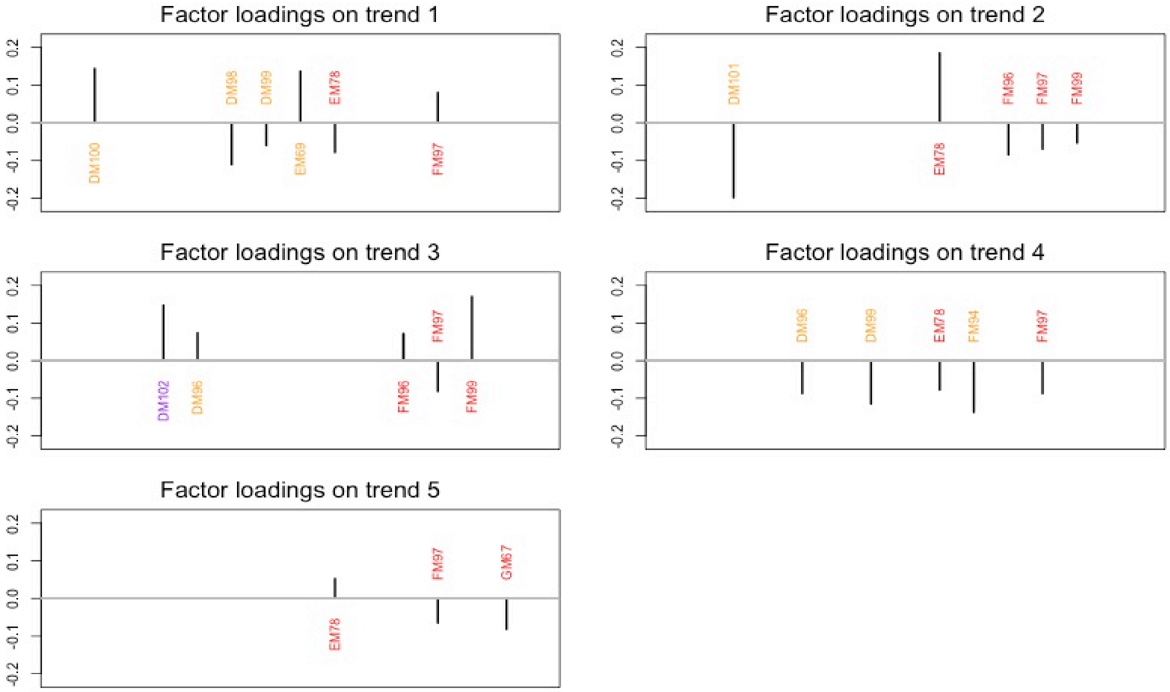

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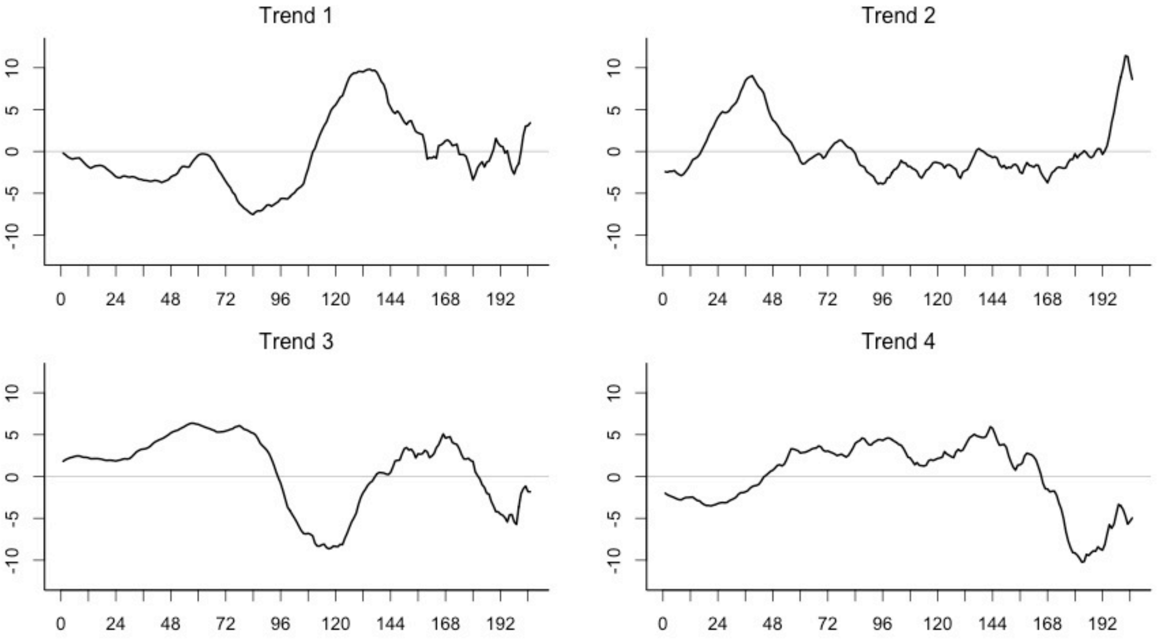

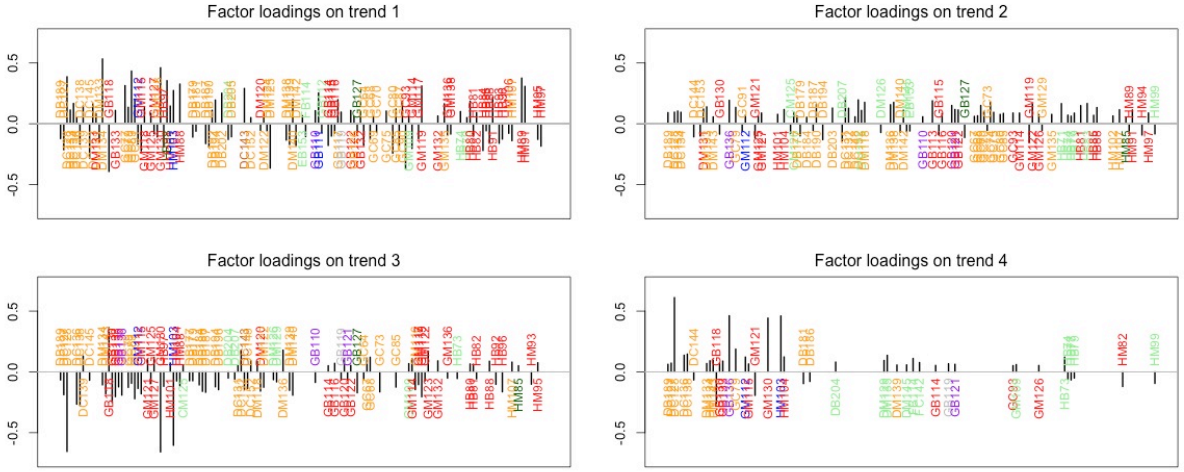

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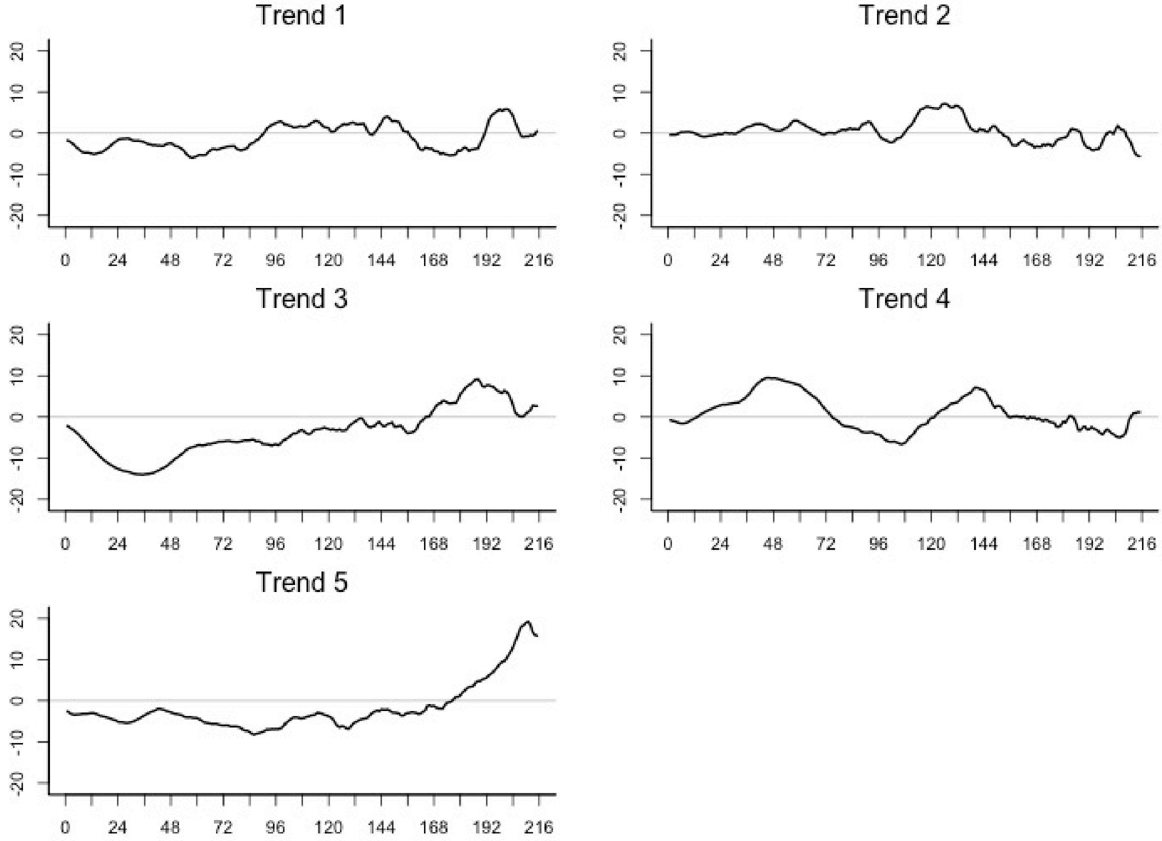


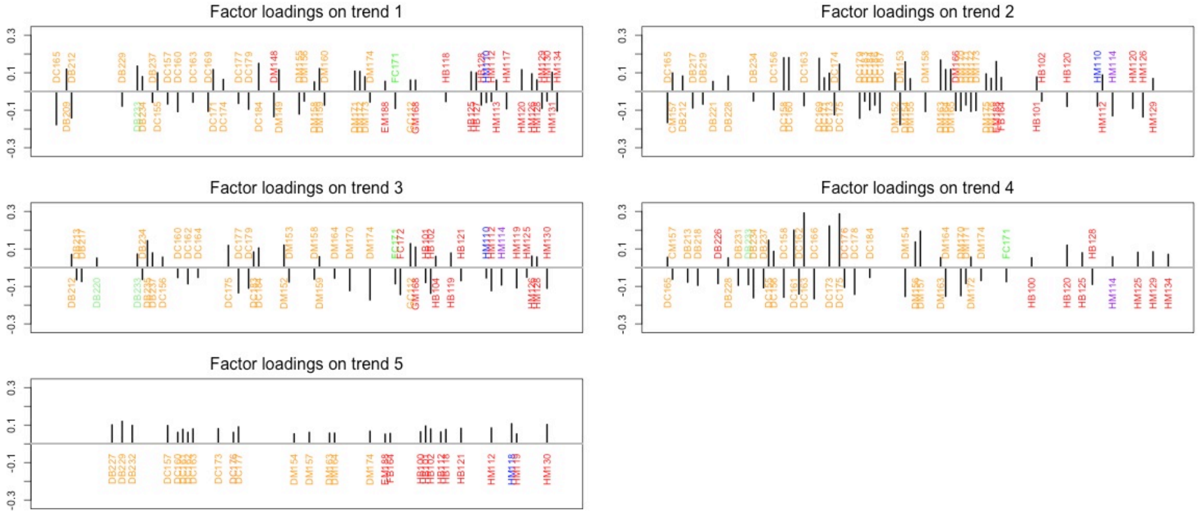
Trend 1

Trend 2

Trend 3

Trend 4

Trend 5



Factor loadings on trend 1

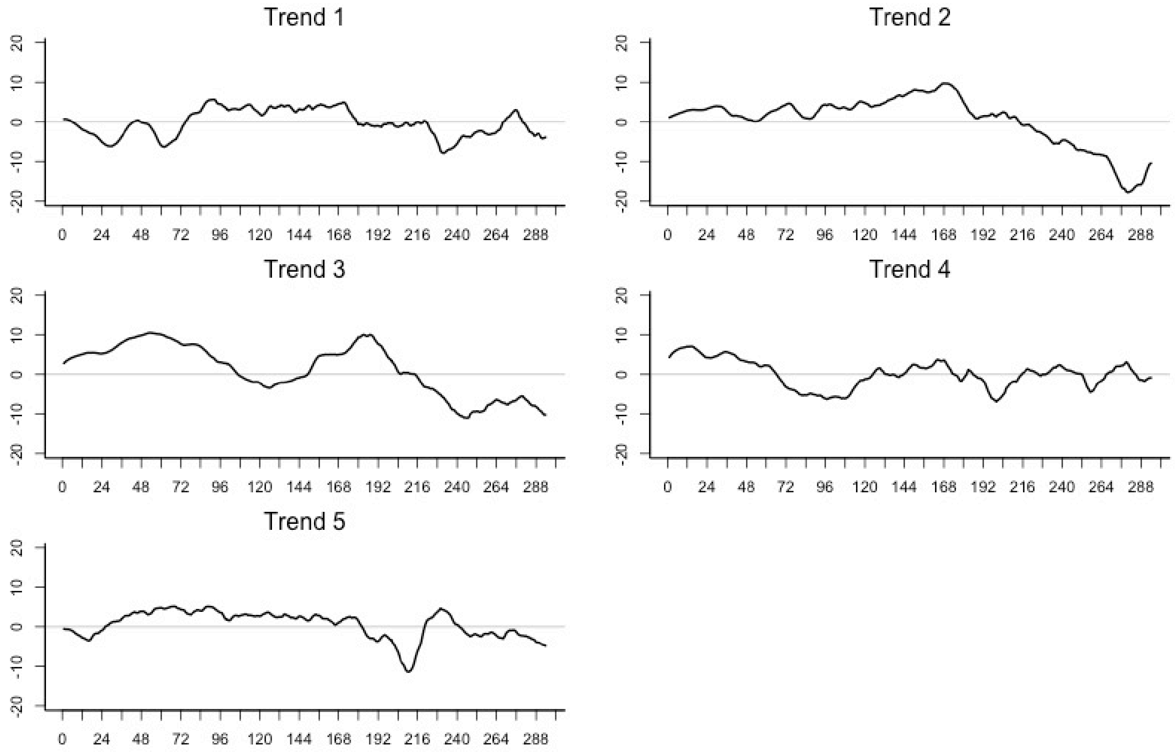
Factor loadings on trend 2

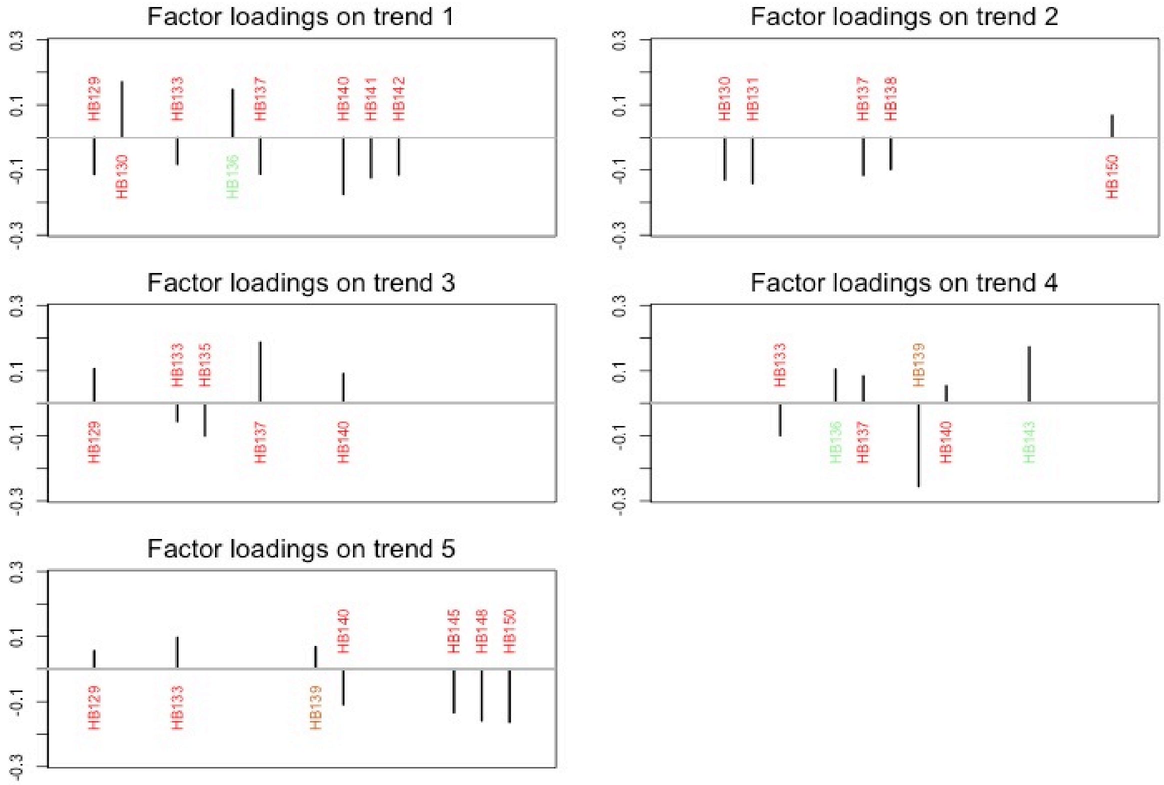
Factor loadings on trend 3

Factor loadings on trend 4

Factor loadings on trend 5

September 2011 capture group:





Conclusions

My study addressed the relative contributions of a range of temporal, environmental and demographic factors affecting juvenile Chinook salmon estuarine growth rate, however no one group of factors best represented these data. Both short-term estuarine-specific explanatory variables and predetermined or permanent explanatory variables were included, but habitat of capture and an interaction between length and month best explained the variability in estuarine growth. I also found a remarkable amount of diversity in freshwater tidal estuarine habitat use. Dynamic factor analysis estimated four to five growth trends were present in juvenile Chinook salmon caught in the Columbia River estuary. However I was not able to quantify juvenile life history diversity, and this life history diversity remains difficult to catalog and integrate into species conservation and habitat restoration for resource management. My thesis incorporates a number of metrics to examine juvenile Chinook salmon over a range of genetically distinct stocks, sizes, seasons, years and freshwater tidal habitats to assess many of the primary factors that may be influencing growth. These results would support a restoration-planning framework focused on landscape scale juvenile Chinook diversity and habitat quality across a range of estuarine habitats.

In my first chapter I found that the variability in estuarine growth rate is best explained by season, habitat and an interaction between size and month of capture. However, I had little explanatory power with the variables and sample sizes measured in this study. When summarized by mean estuarine growth rate, the explanatory variables from the most representative model, exhibited patterns among their associated categories. These patterns across months and habitat types seemed to be explained by estuarine temperature, river discharge, and possibly by stomach contents. I also evaluated the use of DFA to estimate common growth trends obtained from otolith microstructural analysis, and identify major habitat transition that may be associated with freshwater wetland entrance or residency. I found a method for illuminating the complexity of estuarine Chinook salmon growth histories, an expression of diversity currently being simplified in many management practices. However, the application remains difficult to integrate into species conservation and habitat restoration, due to the complexity of the results and time intensive laboratory and statistical techniques. For example, we could not identify discrete categories that may have been used as diversity targets for hatcheries or habitat transition times that could be integrated into the timing or frequency of water release mandates for the hydropower system.

My first chapter examined juvenile Chinook salmon growth over a range of wetland habitats reaches in the freshwater tidal Columbia River estuary. I employed a generalized linear model (GLM) to test three hypotheses: juvenile Chinook growth was best explained by (1) temporal factors, (2) habitat use, or (3) demographic characteristics, such as stock of origin. This study incorporated otolith microstructure, individual assignment to stock of origin, GIS habitat mapping and diet composition in three habitats (mainstem river, tributary confluence and backwater channel) along ~130 km of the upper estuary. I found that variation in growth was best explained by habitat and an interaction between size and month of capture. Juvenile Chinook salmon grew faster in backwater channel habitat and later in the summer. Backwater sites also had higher percentages of emergent prey in the diet composition analysis, and possibly a stronger connection to wetland food-webs. I also found that mid-summer and late summer/fall subyearlings had the highest estuarine growth rates. When compared to other studies in the basin these juvenile Chinook grew on average 0.23, 0.11-0.43 mm/d in the freshwater tidal estuary, similar to estimates in the brackish estuary, but ~4 times slower than those documented for juvenile Chinook in the plume and upstream reservoirs. Survival studies from the system elucidated a possible tradeoff between growth and survival in the Columbia River basin. Therefore there may be no one optimum rearing habitat for habitat restoration design. These findings present two applicable recommendations for estuarine habitat restoration: (1) improve or maintain habitat connectivity, and (2) maintaining a mosaic of rearing and migratory habitats may be an important factor for juvenile Chinook salmon growth. My hope is that these results will be integrated into restoration design and habitat recovery efforts which focus on juvenile Chinook salmon rearing habitat in altered systems.

In my second chapter, I used otolith microstructure and growth trends produced in a dynamic factor analysis (DFA) to identify the life history variation in juvenile Chinook salmon caught in the Columbia River estuary over a two year period (2010-2012). Structural and chemical analysis of otoliths have been found useful in illuminating the age, growth and major migratory movements of individuals over their life-time (Campana and Neilson 1985). However over 75% of the Columbia River estuary is freshwater tidal and to date there is no known chemical signature for freshwater estuarine entrance (Bath et al. 2000). Therefore, I used genetic assignment of fish to stock of origin and capture location and date with growth trajectories, as a proxy for habitat transitions, to classify juvenile life history types. Dynamic factor analysis estimated four to five growth trends among juvenile Chinook salmon caught in the estuary, more diversity than is currently being accounted for in many management practices. Regional stocks and habitats did not display distinctive growth histories, but marked hatchery fish did ordinate very similarly in the trend loadings from the DFA analysis, suggesting that hatchery fish may not experience the same breadth of growth variability as wild fish. I was not able to quantify overall juvenile life history diversity, and juvenile Chinook life history diversity remains difficult to catalog and integrate into species conservation and habitat restoration for resource management. However, by expanding our understanding of how juvenile Chinook salmon experience their freshwater rearing environment we improve our capacity to conserve and manage salmon populations. For example, a better understanding of juvenile salmon life history diversity could provide a blueprint for more natural hatchery rearing, and restoration efforts could integrate habitat complexity as a means for promoting species resilience, as well as integrating a diversity of migration times and year-round estuarine habitat use when managing hydropower and flood control.

The application of these results for rearing habitat restoration design should consider several factors: (1) managing for mechanisms of diversity; and, (2) strengthening the connectivity of main channel sites to wetland food-webs. For example, the diet composition analysis shows that backchannel sites, which have been associated with faster growth rates, had higher percentages of emergent prey and main channel sites had higher percentages of planktonic prey items. This may be due to a loss of connectivity to wetland habitats for juvenile Chinook salmon in the more channelized main river shipping canal in the Columbia River estuary. Therefore, enhanced growth performance for juvenile Chinook salmon in restoration sites may depend on making wetland food-webs more available to out-migrating juvenile salmon. Additionally, the diet composition analysis suggested that fish were not receiving a flux of terrestrial material during the flooding event experienced in this study (May or July of 2011). I also describe that the percent digested material in May 2011 was five times higher than the previous low water year (May 2010), suggesting that the May 2011 fish may not have been eating continuously. The increased water discharge may have dispersed the prey, decreasing foraging opportunity for these fish. Therefore, increased connectively to wetland habitats may provide more access to low-energy shallow-water habitat during flooding periods.

I also present evidence for the importance of integrating the mechanisms of diversity (e.g. habitat complexity, juvenile life history variation and a more natural disturbance regime) within hatchery practices, habitat restoration and hydrological regulation. The dynamic factor analysis estimated four to five growth trends are present in juvenile Chinook salmon caught in the Columbia River estuary, more diversity than is currently being accounted in most approaches to salmon management. Similar to results from Chapter I, regional stocks did not display divergent growth histories. Interestingly, in some capture periods marked hatchery fish did ordinate very similarly in the trend loadings from the DFA analysis. Hatchery marked fish did not display the same breadth of ordination as wild fish, suggesting that hatchery fish may not experience the same extent of growth variability as wild fish. Hatchery produced fish are meant to curb harvest declines, and bred for increased growth and large sizes, in many cases a single phenotype across many hatcheries. However the increase in the hatchery production of Chinook salmon since the 1950s (Naish et. al 2008) has not returned adult abundances to historic levels (Bottom et al. 2005). Therefore, if hatchery origin fish, which make up approximately 80% of the Columbia River juvenile Chinook salmon basin-wide, have depressed biocomplexity, their presence may be reducing species resilience. This may be evidence for maintaining a mosaic of rearing and migratory habitats to increase the variability experiences by juvenile Chinook salmon, as well as integrating juvenile life history variation into hatchery rearing practices. Although the realities of implementation are an inevitable constraint, restoration projects should also consider promoting habitat complexity. A mosaic of rearing and migratory habitats may provide juvenile Chinook salmon with a range of growth opportunities and risks. My comparisons between growth and survival studies throughout the Columbia River basin showed that no one region may provide the best alternatives for juvenile Chinook salmon. Opportunities for both growth and refuge throughout these environmental gradients could balance the tradeoffs and challenges presented to juvenile Chinook salmon while out-migrating. Additionally, the relationship between juvenile Chinook salmon estuarine growth rate and size and timing within the estuary was complex, but the strength of this relationship may be additional evidence for the importance of promoting a diversity of out-migration timing and juvenile rearing habitat use in salmon conservation and management. In conclusion, the results from my thesis present evidence for the importance of integrating variation within juvenile Chinook salmon use of the Columbia River estuary through hatchery practices, habitat restoration and hydrological regulations, and improved habitat connectivity between the shipping channel and wetland food-webs.

Broader Impacts and Intellectual Merit: The approach employed in this study consists of well documented financially responsible methods, and clear descriptions and techniques available for simple use and replication. This study addressed the knowledge gaps associated with the spatial and temporal variation of juvenile salmon estuary growth. Additionally, this project integrated a landscape ecology perspective and diversity, with genetics, growth and life history diversity. The integration of these methods built a more comprehensive description of juvenile Chinook salmon estuarine growth.

The dissemination of these data will benefit both the scientific and management communities by outlining the relationship between estuarine rearing habitat and salmon population structure, diversity and growth; to provide insights to collective species stability. The results from this study have been and will be distributed to the scientific community and general public through peer-reviewed journal publications and conference presentations. These data have also contributed to a federal Tidal Fluvial Annual Report through the Columbia River estuary project. This study is directly applicable to the management of the Chinook salmon populations within the Columbia River basin and could be relevant for the identification of valuable juvenile salmon estuarine rearing habitat in other systems. Furthermore, this examination of salmon growth variability could be used to inform habitat management of a wide range of estuaries and guide restoration projects throughout the Pacific Northwest. Chinook salmon are commercially, historically and culturally iconic species for the Pacific Northwest as well as Columbia River communities. Additionally this study informs federal mandates, which aspire to secure the stability and resilience of Chinook populations in the Columbia River protected under the Endangered Species Act. This data can be integrated into the restoration of watersheds impacted by human disturbance and populations stifled by declining habitat and other stressors. In addition to contributing to the management of an ESA listed and culturally important natural resource, results from this study can be integrated into management targeting resilience in an exploited species, which is vital in view of the effects of climate change on natural resources.

This research also contributed to the mentorship of young scientists. I mentored six undergraduate students in field and laboratory research through the course of this Master’s thesis. This project has encompassed one capstone research project through the School of Aquatic and Fishery Sciences and one School of the Environment internship. In addition to four field volunteers, who have all successfully graduated with bachelor degrees and obtained employment in aquatic research.

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