AN ABSTRACT OF THE THESIS OF

<u>Gordon W. Rose</u> for the degree of <u>Master of Science</u> in <u>Marine Resource Management</u> presented on <u>September 29, 2015</u>.

Title: <u>Connecting Tidal-fluvial Life Histories to Survival of McKenzie River Spring</u> <u>Chinook Salmon (*Oncorhynchus tshawytscha*)</u>

Abstract approved:

Daniel L. Bottom

Chinook salmon returns to the Columbia River basin have declined due to impacts of a growing human population, despite significant mitigation expenditures.

Consequently, fisheries managers have become focused on recovery and long-term viability of at-risk populations. A viable population depends, in part, on the connectivity and quality of diverse habitat types salmon require to complete their anadromous life-cycles. The tidal-fluvial Columbia River estuary is one link in this chain of habitats, but was largely over-looked as important Chinook salmon habitat until recently. Habitat restoration projects are underway in the tidal Columbia River estuary with the goal of increasing survival benefits to juvenile Chinook salmon. However, knowledge gaps remain about stock-specific use of tidal-fluvial habitat and tracking these restoration efforts is largely subjective. This study has sought to quantify the importance of tidal-fluvial habitat for a critical population of Chinook salmon, from the McKenzie River in the upper Willamette River Basin. Using otolith micro-chemistry profile analysis, juvenile net growth in the tidal-fluvial Columbia River was back-calculated for 92

natural-origin McKenzie River Chinook salmon across outmigration years 2005 and 2006. All otoliths were sampled from McKenzie River adult salmon to draw inferences about the juvenile life histories of surviving spawners. Mean \pm SD net growth in the tidal fluvial estuary for all years was 5.48 ± 5.81 mm for subyearlings and 7.43 ± 8.32 mm for yearlings. Differences in mean net growth by juvenile life-history type were not significant despite a prevailing assumption that subyearlings rear longer in estuary habitat than yearlings. Emigration sizes and net-growth estimates were significantly greater for subyearlings in outmigration year 2005 than 2006; there was only suggestive evidence emigration sizes were greater for yearlings in outmigration year 2005 than 2006, and netgrowth estimates were similar between years. Sixteen percent (15 of 92) of McKenzie Chinook salmon grew between 10 and 43 mm over approximately 25-100 days in the tidal-fluvial Columbia River. Extended rearing in tidal-fluvial habitat provided an alternate life-history pathway for some yearling (12), fingerling (one), and fry (two) migrants. Subyearlings with intermediate-rearing or migratory life history pathways had greater net growth in tidal-fluvial habitat during 2005 than 2006, and in 2005 environmental conditions were unfavorable to overall salmon productivity. Fixed effects linear regression models suggest tidal-fluvial habitat supports McKenzie Chinook salmon life-history diversity, growth, and size, and therefore likely contributes to population resilience.

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Connecting Tidal-fluvial Life Histories to Survival of McKenzie River Spring Chinook Salmon (*Oncorhynchus tshawytscha*)

by Gordon W. Rose

A THESIS

Submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Master of Science

Presented September 29, 2015 Commencement June 2016 Master of Science thesis of Gordon W. Rose presented on September 29, 2015.

APPROVED:

Major Professor, representing Marine Resource Management

Dean of the College of Earth, Ocean, and Atmospheric Sciences

Dean of the Graduate School

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

Gordon W. Rose, Author

ACKNOWLEDGEMENTS

This study was only possible through collaboration of many individuals at Oregon State University, Oregon Department of Fish and Wildlife (ODFW), and NOAA Fisheries. My committee members at Oregon State, Dan Bottom, Jessica Miller, Mark Terwilliger, and Court Smith, each helped in unique ways greatly improving the final product. The Oregon Department of Fish and Wildlife was supportive of my research and shared archival otoliths for my study, and their existing analysis made this research possible. Kirk Schroeder, Ben Clemens, Kanani Bowden, Luke Whitman, Cameron Sharpe, Paul Olmsted and Brian Cannon each contributed with their prior work and help. The NOAA Northwest Fisheries Science Center's Estuarine and Ocean Ecology Program studying Chinook salmon in the Columbia River Estuary provided much support as well. Thanks to Laurie Weitkamp, David Teel's and Susan Hinton for sharing advice and Willamette River Chinook salmon data from their existing work. At the W.M. Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University thanks to Adam Kent, Andy Ungerer and Richard Bradshaw.

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1. Introduction

The primary purpose of this thesis is to quantify contributions of the tidal-fluvial Columbia River estuary to natural-origin McKenzie River Chinook salmon (Oncorhynchus tshawytscha), and the potential benefits of estuary restoration to salmon recovery. The portion of an estuary influenced by the tides, but upstream of saline intrusion, is termed the tidal-fluvial estuary. Chinook salmon populations have unique geographic, biological, and anthropogenic constraints (e.g., natal environmental conditions, genetic lineage, dams) affecting juvenile life history expression and viability. Life history refers to the sequence of traits that describe a fish's physiology and behavior throughout its life cycle. The McKenzie River spring Chinook salmon population, chosen for this study, is the only viable genetic legacy and core population from the Willamette River (Oregon), a major tributary of the tidal-fluvial Columbia River. Although long-term studies have described considerable variation in the size and timing of juvenile migrants leaving the Willamette River, the estuarine life histories of Columbia River Chinook salmon, including those of the McKenzie River population, and their contributions to adult returns are poorly known. In this general introduction I review the historic and geographic context for salmon recovery programs in the Columbia River basin and the importance of life history variations, including diverse estuarine life histories, to population viability. I then outline the objectives and structure of this thesis.

1.1 Decline of Columbia River Chinook Salmon

Many people value salmon for food, jobs, recreation, cultural identity, and other ecosystem services. Despite the inherent value of salmon resources and costly recovery efforts (USGAO 2002; Rieman et al. 2015), salmon returns to the Columbia River basin have declined substantially since European settlement in the mid-1800s (ISG 2000; NRC 2004). Pre-European salmon runs to the Columbia River have been estimated at 5-9 million returning salmon and steelhead (ISAB 2015), and the Columbia River was once the greatest Chinook salmon producing river in the world (Healey 1991; Lichatowich 1999; Williams et al. 2006). In 2011, average annual returns to the Columbia River basin were estimated at 1.7 million adult salmon and steelhead, and salmon returns over the last three decades were comprised of ~65-75% hatchery-origin fish (NMFS 2011).

Causes of Columbia River salmon declines vary among populations, but involve exploitation of the region's water and other natural resources. A common pattern has emerged: dams block quality habitat or impede salmon migrations, and reduce the hydrograph downstream; bank armaments and channelization reduce floodplain connectivity and habitat complexity; and aquatic productivity supporting salmon is reduced by development of the surrounding landscape (Bottom et al. 2005b; Williams et al. 2006; Maier and Simenstad 2009; Naiman 2013). The factors mentioned above have synergistic interactions that reduce the salmon ecosystem's carrying capacity and increase negative deterministic density effects (e.g., competition; McElhany et al. 2000; ISAB 2015). In addition, ecosystem processes, such as over-bank flow events and sediment transport, that restore and create quality salmon habitat have been impaired (Waples et al. 2009). Anthropogenic impacts reach beyond those discussed here, and are driven by an increasing human population in the Pacific Northwest (Lackey 2003; Naiman 2013).

A series of poor salmon returns in the 1990s culminated with a flurry of Endangered Species Act (ESA) listings. By the turn of the century, five Chinook salmon Evolutionarily Significant Units (ESUs) were listed under the ESA in the Columbia River basin. An ESU is a legal definition of the smallest population grouping that can be protected as a 'species' under the ESA. The two major criteria for determining an ESU are reproductive isolation from other conspecific population groups and significant evolutionary characteristics relative to the species as a whole (NMFS 1991). Each ESU is comprised of multiple independent population units used to evaluate viability and guide subsequent recovery plans (McElhany et al. 2000).

Salmon recovery efforts have now prioritized the long-term viability of natural salmon populations and are moving towards an ecosystem-based approach to management (ISG 2000; McElhany et al. 2000; Bottom et al. 2005b; Rieman et al. 2015). A viable salmon population depends, in part, on the connectivity and quality of diverse habitat types salmon require to complete their anadromous life-cycles (McElhany et al. 2000; Bottom et al. 2005b). Salmon life-history stages are a continuum and are not a series of independent stage-specific events. Therefore, Chinook salmon populations respond to the interactions of all their life-history stages across multiple landscapes and seascapes (Bottom et al. 2005b; Fresh et al. 2005).

The Columbia River estuary is an important link in the chain of Chinook salmon habitats. Until recently (~2000), the estuary was viewed as a source of mortality as opposed to a valuable rearing area, and was largely over-looked by Columbia River salmon recovery efforts (Bottom et al. 2005b; Fresh et al. 2005). Defined by the extent of tidal influence, the Columbia River estuary extends from the river mouth upstream to Bonneville Dam at river km 233 (Bottom et al. 2005; Fresh et al. 2005; NMFS 2011; Simenstad et al. 2011). The Columbia River estuary is unique in its large size and is predominantly driven by riverine processes. However, variation in the relative influence of the tide shapes physical and ecological gradients throughout long tidal-fluvial and then brackish estuarine reaches (Bottom et al. 2011; Simenstad et al. 2011).

Chinook are the most abundant salmon species in the Columbia basin (ISG 2000), and are dependent on estuarine habitats for their juvenile life history (Healey 1991; Bottom et al. 2005b). Chinook salmon juveniles often use wetlands and other shallow estuarine habitats to feed and grow for extended periods before entering the ocean (e.g., Reimers 1973; Healey 1980; Bottom et al. 2005a, 2005b; Volk et al. 2010). However, much of the historical wetland habitat in the Columbia River estuary has been lost to levee construction and other development (Marcoe and Pilson 2013).

Major development in the Columbia River estuary has resulted in poor consequences for the salmon ecosystem (Sherwood et al. 1990; Bottom et al. 2005b; Marcoe and Pilson 2013). These developments include both historic and recent modifications of the estuary: jetty construction at the Columbia River mouth began in 1885; the estuarine channel has been simplified via dredging; bank armaments have further reduced habitat complexity and impaired the ecological connection between the river and its floodplain; the floodplain has been developed decreasing productivity of the macro-detritus based food web; and dam operations have altered estuarine hydrology (Bottom et al. 2005b; Maier and Simenstad 2009; Marcoe and Pilson 2013).

The natural hydrology of the Columbia River estuary has been reduced in range, changed in timing, and no longer resembles the historic freshet regime (Bottom et al. 2005b). These effects culminated with completion of the Federal Columbia River Power System in the 1970s. Twenty-eight large dams, and hundreds of smaller dams, have been constructed in the Columbia River basin and now dominate estuarine hydrology. Flows are managed in a coordinated fashion for power production, navigation, flood control, water withdraws, and now fish passage (Sherwood et al. 1990; Bottom et al. 2005; NMFS 2011). Historical river discharge was much more variable ($\sim 2,200$ to 28,300 m³s⁻¹) compared to the modern hydrograph (~2, 800 to 14,200 m^3s^{-1}) controlled by the Federal Columbia River Power System (NMFS 2011). The spring freshet has shifted earlier by an average of two weeks, with a total reduction of 57% of the mean seasonal spring flow (Bottom et al. 2005b). The yearly mean flow of the Columbia River has decreased by roughly 17% since the late 1800s, equally attributable to water withdrawals and climate change (Bottom et al. 2005b). The estuary is naturally growing via sea-level rise and sediment filling. However, this process has been slowed by the hydro-system trapping 50% of fine sediment and all large wood behind reservoirs—two major contributors to island and marsh formation processes (Bottom et al. 2006).

The macro-detritus-based food web in the Columbia River estuary has been impaired by the cumulative effects of development (Bottom et al. 2005b; Maier and Simenstad 2009). Urban and industrial development as well as agriculture and forestry practices on the historic floodplain have had cascading effects on estuarine ecology (Bottom et al. 2005b; Marcoe and Pilson 2013). In total, roughly 70% of vegetated tidal wetlands and 55% of forested upland were lost throughout the historic Columbia River estuary and floodplain. Currently agriculture and urban development each make up about 25% of the historic floodplain, combining for 50% of the total area (Marcoe and Pilson 2013). Sherwood et al. (1990) estimated an 82% loss of emergent plants, which decreased the biological productivity of the lower estuary 12 fold, and drastically reduced the performance potential of an estuarine-rearing life history for Chinook salmon. The net loss of emergent plant production has been amplified by bank armaments and near-elimination of over-bank flood events—an important ecological linkage to the floodplain and its seasonal wetlands with high rearing potential (Teel et al. 2009) has been weakened (Bottom et al. 2005b).

Salmon restoration efforts in the Columbia River estuary began in earnest after ESA listings of many stocks in the 1990s. Federal agencies spent over ten million dollars from 2000-2010 on more than 100 restoration projects in the estuary, focused on shallow tidal wetlands (PNNL 2012). In 2008 the NOAA Biological Opinion on operation of the Federal Columbia River Power System further increased support for estuary restoration. From 2010-2018 the U.S. Army Corps of Engineers and the Bonneville Power Administration budgeted \$149.4 million for restoration, monitoring and evaluation in the Columbia River estuary (from www.salmonrecovery.gov). Stated goals of estuary restoration are to increase survival benefits by 9% for "ocean-type" (meaning subyearling dominant juvenile migrants) and 6% for "stream-type" (meaning yearling dominant juvenile migrants) Chinook salmon ESUs (NMFSa 2008). An adaptive management strategy has been developed to evaluate estuary restoration with the goal of assessing the cumulative impacts of many integrated projects (Diefenderfer et al. 2011; PNNL 2012). To date this strategy has not been able to directly detect or quantify the benefits of estuary restoration to survival of Chinook salmon populations (PNNL 2012).

1.2 Life History Variation in Columbia River Chinook Salmon

The terms "ocean-" and "stream-type" refers to the dominant juvenile outmigration age of a particular salmon ESU, and are based on a theory of two Chinook salmon lineages proposed by Healey (1991). He classified ocean-type populations as those that typically rear in freshwater for less than a year and outmigrate as subyearlings; stream-type populations typically rear in freshwater for over a year and outmigrate as yearlings. One problem associated with the ocean- and stream-type dichotomy is the tendency to assume that juvenile and adult life histories are fixed based on genetic lineages.

Genetic studies have since shown evolution of Chinook salmon lineages is more complicated than the simple ocean-type vs. stream-type dichotomy implies. Geographic boundaries explain more genetic variation than run-timing. Parallel evolution of dominant phenotypes has likely occurred in dozens of lineages (Waples et al. 2004; Moran et al. 2013). In the Columbia River basin at least two lineages exist that differ in run timing and the dominant juvenile outmigration age (Waples et al. 2004). Notably, the upper Willamette Chinook salmon ESU, often associated with the lower Columbia lineage, is sufficiently distinct to represent a novel heritage (Waples et al. 2004). While the concept of two Chinook salmon races is perhaps overly simplified the terminology is still widely used in management plans.

Chinook salmon populations in the Columbia River exhibit more genetic and lifehistory diversity than in any other basin in the species' range (Waples et al. 2004, 2008). Covering over 660,000 km², the Columbia River basin spans many different ecosystems and ecoregions. The Columbia River and its tributaries flow from alpine forests of the Rockies through high deserts in the basin's interior, forests of the Cascade mountain range, the Columbia River Gorge, and coastal rainforests before reaching the large estuary and entering the California current system of the Pacific Ocean. Across diverse riverine, estuarine, and ocean habitats, Chinook salmon populations have evolved many local adaptations expressed in the diversity of life-history pathways—i.e., different ages, periods, and migration routes—for adults returning to their spawning beds (Healey 1991).

A Chinook salmon life-history pathway is defined here as the sequence of lifehistory characteristics (i.e., phenotypes) through-out the life cycle. The classifications subyearling and yearling are a broad description of a Chinook salmon's juvenile lifehistory, although those terms are an age for the freshwater portion of a salmon's life. Chinook salmon life-history diversity exists within as well as between populations (Healey 1991). Life-history diversity in salmon can be attributed to genetic divergence, parallel evolution and phenotype plasticity (Beckman et al. 2003; Brannon et al. 2004; Waples et al. 2004, 2009). Studies have shown the natural-origin McKenzie River population of Chinook salmon may express an array of alternative juvenile life-history pathways through the river before reaching the estuary (Schroeder and Kenaston 2004; Schroeder et al. 2007). Some research suggests the definition of discrete life-history pathways, or "types", is an oversimplification because juveniles from the same population are capable of expressing a broad continuum of rearing and migration behaviors (Brannon et al. 2004; Volk et al. 2010). Juvenile Chinook salmon commonly outmigrate as fry (subyearlings < 60 mm FL), fingerlings (subyearlings > 60 mm FL), or yearlings. Most Chinook salmon outmigration occurs in pulses around the spring freshet of the first or second year, although can occur year-round (Healey 1991; Burke 2004; Schroeder and Kenaston 2004; Bottom et al. 2005; Schroeder et al. 2007; NMFSb 2008). Columbia River Chinook salmon generally return as three-, four-, five-, or six-year-olds. However, not all adult age classes and juvenile life histories are present in each population (Healey 1991).

Chinook salmon's complicated suite of life histories and intricate spatial population structure historically contributed to long-term species viability, or resilience, by spreading risks in time and space (Healey 1991; McElhany et al. 2000; Hilborn et al. 2003; Myers et al. 2006; Waples et al. 2009; Schindler et al. 2010). Species and population diversity in salmon create a stabilizing 'portfolio effect' through periods of short-term environmental variation. However, quantitative evaluations of the contributions of the 'portfolio effect' to salmon recovery efforts are lacking (Schindler et al. 2010). Moore et al. (2010) postulated that bolstering 'portfolio performance' for threatened species will depend upon protecting a diversity of populations and habitats.

Alternate Chinook salmon life-histories contribute to population viability by allowing individuals to utilize a variety of riverine, estuarine and ocean habitats, and to spread habitat use over time. Therefore, life-history diversity maximizes habitat productivity (Bottom et al. 2005b) and reduces detrimental density effects (McElhany et al. 2000; ISAB 2015) throughout continuous stages in the salmon life cycle. Life-history diversity is also indicative of a population's genetic diversity, which allows for adaptation during environmental changes over longer time-scales (McElhany et al. 2000; Waples et al. 2004).

1.3 The Estuarine Life Histories of Chinook Salmon

Chinook salmon depend on estuarine habitat during the outward migration of their juvenile life history. Previous studies have shown estuaries provide juvenile migration, refuge, foraging, and rearing opportunities (e.g., Reimers 1973; Healey 1980, 1991; Bottom et al. 2005a; Volk et al. 2010). In aggregate these factors support multiple estuarine life-history pathways for salmon linking freshwater and ocean habitats. Estuaries also allow for Chinook salmon to undergo physiological changes associated with the anadromous transition from fresh to salt water (Healey 1991). In a study of fall Chinook salmon from the Sixes River, a small Oregon coastal system, Reimers (1973) categorized five different subyearling life-history pathways through the river and estuary. He observed fry quickly migrating to the estuary in the spring, a peak of migration in the summer, and greatly reduced abundances by autumn. Healey (1980) concluded the Nanaimo River estuary, a small coastal system on Vancouver Island, B.C., was highly productive nursery habitat for subyearling Chinook salmon. A series of studies on the Salmon River estuary, a small coastal system in Oregon, similarly identified shallow tidal wetlands as productive Chinook rearing habitat and identified a diversity of subyearling life histories through the estuary (Gray et al. 2002; Bottom et al. 2005a; Hering et al.

2010; Volk et al. 2010). The Salmon River studies also observed juvenile Chinook salmon foraging in restored shallow tidal wetland habitat.

Long tidal-fluvial reaches of the Columbia River estuary and its seasonal floodplain wetlands may provide alternate low-velocity rearing habitat for juvenile Chinook salmon of many ESA listed stocks (Teel et al. 2009). Simenstad and Cordell (2000) introduced the concept of "realized function" as assessment criteria for restoration of salmon estuaries in the Pacific Northwest. The authors define realized function as the physiological or behavioral effects of habitat use contributing to a salmon's survival and fitness, including residence, growth, and foraging. However, within the tidal-fluvial region of the estuary, juvenile Chinook salmon residency patterns, realized function, and population survival are poorly understood.

The role of the Columbia River estuary to the survival of Chinook salmon has been debated long after the first comprehensive life history study found juveniles using the estuary (Rich 1920). Some authors have hypothesized the estuary supports juvenile Chinook salmon (e.g., Bottom et al. 2005b, 2011; Campbell 2010; Teel et al. 2014; Roegner et al. 2015), while others have suggested it is primarily a migration corridor and source of mortality (Dawley et al. 1986). These different views are partly based on a wide range of estimated estuarine residence times of days (Dawley et al. 1986) to months (Campbell 2010; Roegner et al. 2015) and may reflect sampling methodologies that target a small subset of salmon life histories and size classes. Due to the wide range of habitat types and depths, and the large size of the Columbia River, no one sampling technique can effectively capture all salmon life-history pathways through the tidal-fluvial reaches. Thus, the extent and variability of the Columbia River estuaries support to Chinook salmon stocks and the potential benefits of restoration are still unclear.

A synthesis of historic (circa 1920) and recent (circa 2000) data suggest anthropogenic factors, both outside and within the estuary, have reduced life-history diversity of Chinook salmon in the lower Columbia River estuary (Burke 2004). However, there is no pre-development research in the tidal-fluvial estuary from which to compare limited current observations. Chinook salmon life-history diversity, and thus population resilience, is maximized by diverse, functional, and connected habitat types (McElhany et al. 2000; Hilborn et al. 2003; Bottom et al. 2005b; Moore et al. 2010; Schindler et al. 2010). In theory reduced habitat complexity in the tidal-fluvial Columbia River may decrease salmon life-history expression, returning abundances, and hence viability. However, empirical evidence of this premise is sparse.

Most fish surveys have targeted the lower 100 km of the Columbia River estuary (e.g., Dawley et al. 1986; Campbell 2010; Bottom et al. 2011; Weitkamp et al. 2012; Roegner et al. 2015); therefore, Chinook salmon residence times and habitat use in the upper tidal-fluvial reaches are poorly understood. For example, recent otolith analyses relying solely on Sr/Ca indicators (Campbell 2010) can only depict residency in the brackish portion of the Columbia River estuary. In addition, estuarine life histories have rarely been evaluated for individual stocks. Teel et al. (2014) and others (e.g., Bottom et al. 2011; Roegner et al. 2012, 2015; Weitkamp et al. 2012) provided recent evidence of stock-specific differences in estuary habitat use, including variations in estuary migration timing, size at entry, and spatial distribution among different genetic stock groups. However, these interpretations are derived primarily from latitudinal catch data, or single

observations of individual fish that only indicate size, date, and presence in one location. Estimates of residency and performance at both habitat and landscape scales are necessary for a thorough understanding of the contemporary life-history pathways of individual Chinook salmon through the tidal-fluvial Columbia River estuary.

Recovery efforts seek to integrate understanding of Columbia River estuary habitat use with the more thoroughly studied life histories of Chinook salmon populations in their upriver habitats (NMFS 2011); yet life-history and population-specific analyses are limited by stock mixing and capture efficiency in the Columbia River estuary, as well as by the inability of the existing genetic baseline to resolve differences at scales finer than the ESU level (Teel et al. 2014). Trapping a representative sample of fish is problematic in such a large area. These above mentioned factors present difficulties in tracking migrants and cohorts from known source populations through the Columbia River estuary. Therefore, reliable estimates of abundance and survival in the Columbia River estuary are not available for Chinook salmon populations (Bottom et al. 2011).

Understanding the realized function of Columbia River tidal-fluvial landscapes is necessary to inform adaptive management of estuary restoration and salmon recovery programs. Estuarine habitat restoration is being incorporated into recovery plans for exploited Columbia River salmon populations; however, quantitative understanding of residency and growth throughout the estuarine life histories of Chinook is lacking (Simenstad and Cordell 2000; Bottom et al. 2005, 2011; NMFS 2011; PNNL 2012). Hence, the survival benefits of localized estuary habitat restoration projects to particular population groups of anadromous Chinook are poorly understood and not easily measured. Criteria and methods are needed for measuring the contribution of the estuarine landscape to individual performance and survival (i.e., realized function) of Columbia River Chinook salmon to then infer a population and ultimately ESU response to estuary restoration actions.

1.4 Objectives

The goal of my research is to determine the contributions of the tidal-fluvial Columbia River estuary to the survival and return of adult Chinook salmon in the McKenzie River basin. In the second chapter, my objectives are (1) to review knowledge of the tidal-fluvial life-history stage of the McKenzie River Chinook salmon population from the existing data and literature; (2) synthesize tidal-fluvial life-history pathways and their contributions to the McKenzie River Chinook salmon spawning population (i.e., survival); and (3) identify information gaps and testable hypotheses for the McKenzie River Chinook salmon tidal-fluvial life-history stage.

In the third chapter, my primary objectives are (1) to reconstruct juvenile lifehistory pathways represented among spawning McKenzie River Chinook salmon as indicated by time and size of entry and approximate residency in the tidal-fluvial Columbia River; (2) to quantify the net growth of juvenile Chinook salmon in tidalfluvial Columbia River habitats as an indicator of realized function; and (3) to determine the relative contributions of the tidal-fluvial estuary to survival and return of adult Chinook salmon in the McKenzie River. My secondary objectives are: (a) to explore factors influencing net-growth in the tidal-fluvial Columbia River estuary; (b) determine the feasibility of establishing a baseline of tidal-fluvial estuarine realized function; and (c) determine the feasibility of monitoring the cumulative effects of tidal-fluvial habitat restoration actions on a specific Columbia River Chinook salmon population.

- Beckman, B. R., D. A. Larsen, and W. W. Dickhoff. 2003. Life history plasticity in Chinook salmon: Relation of size and growth rate to autumnal smolting. Aquaculture 222(1-4):149–165.
- Bottom, D. L., A. Baptista, J. Burke, L. Campbell, E. Casillas, S. Hinton, D. A. Jay, M. A. Lott, G. Mccabe, R. Mcnatt, M. Ramirez, G. C. Roegner, C. A. Simenstad, S. Spilseth, L. Stamatiou, D. Teel, and J. E. Zamon. 2011. Estuarine habitat and juvenile salmon: current and historical linkages in the lower Columbia River and estuary: Final Report 2002-2008. National Marine Fisheries Service Report to the U.S. Army Corps of Engineers Contract W66QKZ20374382. Portland, OR.
- Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005a. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). Estuarine, Coastal and Shelf Science 64:79–93.
- Bottom, D. L., B. E. Riddell, and J. A. Lichatowich. 2006. The estuary, plume, and marine environments. Pages 507–569 *in* R. N. Williams, editor. Return to the River. Elsevier.
- Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005b. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. NOAA Technical Memorandum NMFS-NWFSC-68:246 pp.
- Bourret, S. 2013. Salmon life history in an altered landscape: reconstructing juvenile migration using chemical and structural analysis. Master's Thesis. University of Idaho (April).
- Brannon, E. L., M. S. Powell, T. P. Quinn, and A. Talbot. 2004. Population Structure of Columbia River Basin Chinook salmon and Steelhead trout. Reviews in Fisheries Science 12(2-3):99–232.
- Burke, J. L. 2004. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to the present. Master's Thesis. Oregon State University, Corvallis, Oregon.
- Campbell, L. A. 2010. Life histories of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary as inferred from scale and otolith microchemistry. Master's Thesis. Oregon State University, Corvallis, Oregon.
- Dawley, E. M., R. D. Ledgerwood, T. H. Blahm, C. W. Sims, J. T. Durkin, R. a Kirn, A. E. Rankis, and G. E. Monan. 1986. Migrational characteristics, biological

observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. National Marine Fisheries Service Final Report to Bonneville Power Administration (April 1986):256 pp.

- Diefenderfer, H. L., R. M. Thom, G. E. Johnson, J. R. Skalski, K. A. Vogt, B. D. Ebberts, G. C. Roegner, and E. M. Dawley. 2011. A levels-of-evidence approach for assessing cumulative ecosystem response to estuary and river restoration programs. Ecological Restoration 29(1-2):111–132.
- Fresh, K. L., E. Casillas, L. L. Johnson, and D. L. Bottom. 2005. Role of the estuary in the recovery of Columbia River basin salmon and steelhead: an evaluation of the effects of selected factors on salmonid population viability. NOAA Technical Memorandum NMFS-NWFSC-69:105 pp.
- Gray, A., C. A. Simenstad, D. L. Bottom, and T. J. Cornwell. 2002. Contrasting functional performance of juvenile salmon habit in recovering wetlands of the Salmon River estuary, Oregon, U.S.A. Restoration Ecology 10(3):514–526.
- Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon. Fishery Bulletin 77(3):653–668.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–394 in C. Groot and L. Margolis, editors. Pacific Salmon Life Histories. UBCPress.
- Hering, D. K., D. L. Bottom, E. F. Prentice, K. K. Jones, and I. A. Fleming. 2010. Tidal movements and residency of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) in an Oregon salt marsh channel. Canadian Journal of Fisheries and Aquatic Sciences 67(3):524–533.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the United States of America 100(11):6564–6568.
- ISAB (Independent Scientific Advisory Board). 2015. Density dependence and its implications for fish management and restoration programs in the Columbia River basin. ISAB 2015-1 (25 February 2015):246 pp.
- ISG (Independent Scientific Group). 2000. Return to the river. Northwest Power Planning and Conservation Council Document 2000-12 (1 January 2000).
- Lackey, R. T. 2003. Pacific Northwest salmon: forecasting their status in 2100. Reviews in Fisheries Science 11(1):35–88.

- Lichatowich, J. A. 1999. Salmon without rivers: a history of the pacific salmon crisis. Island Press, Washington D.C.
- Maier, G. O., and C. A. Simenstad. 2009. The role of marsh-derived macrodetritus to the food webs of juvenile Chinook salmon in a large altered estuary. Estuaries and Coasts 32(5):984–998.
- Marcoe, K., and S. Pilson. 2013. Habitat change in the lower Columbia River and estuary, 1870-2011. Lower Columbia River Estuary Partnership:57 pp.
- McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42:158 pp.
- Miller, J. A., V. L. Butler, C. A. Simenstad, D. H. Backus, A. J. R. Kent, and B. Gillanders. 2011. Life history variation in upper Columbia River Chinook salmon (*Oncorhynchus tshawytscha*): a comparison using modern and ~500-year-old archaeological otoliths. Canadian Journal of Fisheries and Aquatic Sciences 68(4):603–617.
- Moore, J. W., M. Mcclure, L. A. Rogers, and D. E. Schindler. 2010. Synchronization and portfolio performance of threatened salmon. Conservation Letters 3(5):340–348.
- Moran, P., D. J. Teel, M. A. Banks, T. D. Beacham, M. R. Bellinger, S. M. Blankenship, J. R. Candy, J. C. Garza, J. E. Hess, S. R. Narum, L. W. Seeb, W. D. Templin, C. G. Wallace, C. T. Smith, and E. Taylor. 2013. Divergent life-history races do not represent Chinook salmon coast-wide: the importance of scale in Quaternary biogeography. Canadian Journal of Fisheries and Aquatic Sciences 70(3):415–435.
- Myers, J., C. Busack, D. Rawding, A. Marshall, D. Teel, D. M. V. Dornick, and M. T. Maher. 2006. Historical population structure of Willamette and lower Columbia River basin Pacific salmonids. NOAA Technical Memorandum NMFS-NWFSC-73:311 pp.
- Naiman, R. J. 2013. Socio-ecological complexity and the restoration of river ecosystems. Inland Waters 3(4):391–410.
- NMFS (National Marine Fisheries Service). 1991. Policy on applying the definitions of species under the Endangered Species Act to Pacific salmon. Federal Register 56:224(20 November 1991):58612–58618.
- NMFS (National Marine Fisheries Service). 2011. Columbia River estuary ESA recovery plan module for salmon and Steelhead. NMFS Northwest Region. Portland, Oregon. Prepared for NMFS by the Lower Columbia River Estuary Partnership (contractor) and PC Trask & Associates, subcontractor. (January 2011):260 pp.

- NMFSa (National Marine Fisheries Service). 2008. Federal Columbia River power system biological opinion. Endangered Species Act Section 7(a)(2) And Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation F/NVVR/2005/05883 (5 May 2008).
- NMFSb (National Marine Fisheries Service). 2008. Willamette project biological opinion. Endangered Species Act Section 7(a)(2) and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation F/NWR/2000/02117 (11 July 2008).
- NRC (National Research Council). 2004. Managing the Columbia River: instream flows, water withdrawals, and salmon survival. National Academy Press, Washington D.C.
- PNNL (Pacific Northwest National Laboratory). 2012. Evaluation of cumulative ecosystem response to restoration projects in the lower Columbia River and estuary, 2010. Report to U.S. Army Corps of Engineers Contract DE-AC05-76RL01830 (May):389 pp.
- Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commision of Oregon 4(2):42 pp.
- Rich, W. H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento rivers. Bulletin of the Bureau of Fisheries 37, 1919-2(887):73 pp.
- Rieman, B. E., C. L. Smith, R. J. Naiman, G. T. Ruggerone, C. C. Wood, N. Huntly, E. N. Merrill, J. R. Alldredge, P. A. Bisson, J. Congleton, K. D. Fausch, C. Levings, W. Pearcy, D. Scarnecchia, and P. Smouse. 2015. A Comprehensive Approach for Habitat Restoration in the Columbia Basin. Fisheries 40(3):124–135.
- Roegner, C., D. Bottom, A. Baptista, L. Campbell, P. Goertler, S. Hinton, R. Mcnatt, C. Simenstad, D. Teel, and K. Fresh. 2015. Salmon habitat use of tidal-fluvial habitats of the Columbia River estuary, 2010-2013. National Marine Fisheries Service Final Report to U.S. Army Corps of Engineers, Portland District (April 2015):103 pp.
- Roegner, G. C., R. McNatt, D. J. Teel, and D. L. Bottom. 2012. Distribution, size, and origin of juvenile Chinook salmon in shallow-water habitats of the lower Columbia River and estuary, 2002–2007. Marine and Coastal Fisheries 4(1):450–472.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465(7298):609–612.

- Schroeder, R. K., and K. R. Kenaston. 2004. Spring Chinook salmon in the Willamette and Sandy rivers. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-09:64 pp.
- Schroeder, R. K., K. R. Kenaston, and L. K. McLaughlin. 2007. Spring Chinook salmon in the Willamette and Sandy rivers. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-11:62 pp.
- Sherwood, C. R., D. A. Jay, R. Bradford Harvey, P. Hamilton, and C. A. Simenstad. 1990. Historical changes in the Columbia River Estuary. Progress in Oceanography 25(1-4):299–352.
- Simenstad, C. A., J. L. Burke, J. E. O'Connor, and K. L. Cannon, C., Heatwole, D.W., Ramirez, M.F., Waite, I.R., Counihan, T.D., Jones. 2011. Columbia River estuary ecosystem classification - concept and application. U.S. Geological Survey Open-File Report 2011-1228:54p.
- Simenstad, C. A., and J. R. Cordell. 2000. Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific northwest estuaries. Ecological Engineering 15(283):302.
- Teel, D. J., C. Baker, D. R. Kuligowski, T. A. Friesen, and B. Shields. 2009. Genetic stock composition of subyearling Chinook salmon in seasonal floodplain wetlands of the lower Willamette River, Oregon. Transactions of the American Fisheries Society 138(1):211–217.
- Teel, D. J., D. L. Bottom, S. A. Hinton, D. R. Kuligowski, G. T. McCabe, R. McNatt, G. C. Roegner, L. A. Stamatiou, and C. A. Simenstad. 2014. Genetic identification of Chinook salmon in the Columbia River estuary: stock-specific distributions of juveniles in shallow tidal freshwater habitats. North American Journal of Fisheries Management 34(3):621–641.
- USGAO (U.S. General Accounting Office). 2002. Columbia River basin salmon and steelhead: federal agencies' recovery responsibilities, expenditures and actions. Report to U.S. Senate GAO-02-612(July 2002):86 pp.
- Volk, E. C., D. L. Bottom, K. K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139(2):535–549.
- Waples, R., T. Beechie, and G. R. Pess. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific salmon populations? Ecology and Society 14(1):3.

- Waples, R. S., G. R. Pess, and T. J. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications 1(2):189–206.
- Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution; international journal of organic evolution 58(2):386–403.
- Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fishery Bulletin 110(4):426–450.
- Williams, R. N., J. A. Stanford, J. A. Lichatowich, W. J. Liss, C. C. Coutant, W. E. McConnaha, R. R. Whitney, P. R. Mundy, P. A. Bisson, and M. S. Powell. 2006. Return to the river: strategies for salmon restoration in the Columbia River basin. Elsevier.

2. Evaluating Tidal-fluvial Life Histories for a Population of Columbia River Chinook Salmon (*Oncorhynchus tshawytscha*)

2.1 Introduction

Life-histories of anadromous Chinook salmon (*Oncorhynchus tshawytscha*) through tidal-fluvial reaches of the Columbia River estuary are largely unknown, and their contributions to adult returns are poorly understood. However, limited evidence suggests tidal-fluvial habitat is capable of supporting fitness and life-history diversity of Columbia River Chinook salmon.

The Columbia River estuary is defined by the entire area where varying tides influence habitat structure and ecosystem processes (Simenstad et al. 2011). By this definition the Columbia River estuary encompasses a vast complex of tidal-freshwater (hereafter "tidal-fluvial") habitats that extend ~200km from the dynamic brackish water interface (~rkm 20-40) to the tailrace of Bonneville Dam (rkm 233) (Bottom et al. 2005b; Fresh et al. 2005). Nearly 70% of vegetated tidal wetland and 55% of forested upland habitat area has been lost to development throughout the Columbia River estuary and its historical floodplain (Marcoe and Pilson 2013). Federal agencies have spent more than ten million dollars from 2000-2010 on >100 restoration projects in the Columbia River estuary, focused on shallow tidal wetlands (PNNL 2012). From 2010-2018 the U.S. Army Corps of Engineers and the Bonneville Power Administration budgeted another \$149.4 million for restoration, monitoring and evaluation (from www.salmon-recovery.gov).

Stated goals of Columbia River estuary restoration are to increase survival benefits by 9% for "ocean-type" and 6% for "stream-type" Chinook salmon Evolutionarily Significant Units (ESUs) (NMFSa 2008). However, the survival benefits of tidal-fluvial estuary habitat restoration projects to particular Columbia River ESUs of Chinook salmon are poorly understood (PNNL 2012). The terminology "ocean-" and "stream-type" refers to the dominant juvenile outmigration age of a particular salmon ESU and is based on a theory of two Chinook salmon lineages proposed by Healey (1991). Recent genetic evidence has identified many more than two historic Chinook lineages (Waples et al. 2004; Moran et al. 2013), and suggests abandoning the ocean- and stream-type dichotomy in favor of the terms subyearling (for ocean-type) and yearling (for stream-type) (Moran et al. 2013).

Population-specific analyses are needed to directly connect estuarine life histories to Chinook salmon returns, and ultimately, to assess the survival benefit of estuary restoration to a particular Columbia River salmon ESU. Focusing on Chinook salmon population units is important from an ecological perspective, but also from an operational perspective. The recovery of salmon in the Columbia River basin may be the largest and most complex ecological restoration ever attempted (ISG 2000, ISAB 2011). Proper classification and evaluation of independent population units is a launching point for viability analysis and Endangered Species Act (ESA) de-listing (McElhany et al. 2000; Myers et al. 2006). Each independent Chinook salmon population has unique constraints affecting life-history expression and the viability of various life histories, including during the estuarine life stage (McElhany et al. 2000, NMFS 2011). Studies have shown Chinook salmon distributions in the tidal-fluvial Columbia River are stockspecific, and suggest estuarine life histories may also vary by stock (Teel et al. 2014).

The natural-origin McKenzie River Chinook salmon population, from the Willamette River basin (Oregon), is an ideal candidate for estuarine life-history analysis. The McKenzie-Willamette-Columbia River migration corridor has few large dams. Therefore, juvenile McKenzie River Chinook salmon may be able to utilize estuarine habitat and express a diversity of tidal-fluvial life histories (Bottom et al. 2005b, 2011). Specifically, the Willamette River basin has been shown to provide fry (subyearlings) <60mm), fingerling (subyearlings >60mm), and yearling Chinook salmon migrants to the tidal-fluvial Columbia River (Friesen et al. 2007) in a wide range of sizes, habitats, and seasons (Weitkamp et al. in press; Bottom et al. 2011; Roegner et al. 2012, 2015). However, areas where known Willamette juvenile Chinook salmon have been observed in the highest abundances are also areas where many Colombia River salmon stocks mix (Teel et al. 2009, 2014). The McKenzie Chinook salmon population is well studied in the Willamette and McKenzie rivers (e.g., Schroeder et al. 2005, 2007, Myers et al. 2006, ODFW and NMFS 2011), allowing for analysis of the juvenile life histories of spawning adults.

In this chapter, my objectives are (1) to review knowledge of the tidal-fluvial lifehistory stage of the McKenzie River Chinook salmon population from the existing data and literature; (2) synthesize tidal-fluvial life-history pathways and their contributions to the McKenzie River Chinook salmon spawning population (i.e., survival); and (3) identify information gaps and testable hypotheses for the McKenzie River Chinook salmon tidal-fluvial life-history stage.

2.2 Background of the McKenzie River Chinook Salmon Population

The natural-origin McKenzie River Chinook salmon population is critical to survival of the Willamette River Chinook salmon ESU, classified as threatened under the ESA in 1999 (Myers et al. 2006; NMFSb 2008; Ford et al. 2010; ODFW and NMFS 2011). The McKenzie River population is the only one of six historical upper Willamette River spring Chinook salmon populations deemed to have a low 100-year extinction risk. Three of the six historic populations from the Molalla, Calapooia, and Middle-Fork Willamette rivers may have been extirpated, and the remaining high-risk populations in the North and South Santiam rivers are compromised by large dams and hatchery influences (ODFW and NMFS 2011). The largest natural-origin (i.e., born in the wild) Chinook salmon run on record to the McKenzie River was 46,000 in 1941. Predevelopment, circa 1850, abundances are thought to have been a similar, although variable (NMFSb 2008). One recent report estimated a strong pre-development run as ~110,000 returning adults (ODFW and NMFS 2011).

Natural-origin McKenzie River Chinook salmon returns have been between 1000-5000 fish since ESA listing, and on average have composed >50% of all natural-origin Chinook salmon returning to the Willamette River basin since natural/hatchery determinations became possible in 2002 (ODFW 2013). Recent returns of McKenzie River Chinook salmon have fallen below replacement levels for the population (see Table 2.1 described later in this chapter). The prognosis for upper Willamette Chinook salmon populations outside of the McKenzie River watershed is deemed 'high risk' for extinction
within 100 years; in part, because the highest quality habitats are now inaccessible. Overall the Willamette Chinook salmon ESU status has not improved since ESA listing, and is considered likely to move from a threatened to an endangered status (Ford et al. 2010; ODFW and NMFS 2011).

Approximately 5.5 million hatchery Chinook salmon are released in the Willamette River basin annually (Paquet et al. 2011) with ~1.2 million produced from the McKenzie River salmon hatchery (www.dfw.state.or.us/resources/visitors/-McKenzie_hatchery.asp). From 2002-2012, an estimated 49-81% of the total adult Chinook salmon annual returns to the McKenzie River were of hatchery origin, and the percentage was higher for the total Chinook salmon returns to the Willamette River basin (ODFW 2013). Hatchery-origin Chinook salmon can affect natural-origin populations through genetic introgression; predator attraction (e.g., humans, pinnipeds, birds, fish) (ODFW and NMFS 2011; Paquet et al. 2011); and competition or other density-related effects (McElhany et al. 2000; ISAB 2015) . However, these influences are largely unquantified in the basin and are beyond the scope of this review.

The McKenzie River originates in the Three Sisters Mountains wilderness area and flows down the forested slopes of the Cascade Mountain range 145 km to its confluence with the Willamette River near Eugene, OR. The Willamette River meanders north through a fertile and populated valley flanked on the east by the Cascades and to the west and south by the Coast Range Mountains. After traversing 239 km from the mouth of the McKenzie River, the Willamette River drops over a 12 m basalt shelf known as Willamette Falls and enters the upstream extent of tidal influence. Over the next 43 km, the Willamette River passes through the city of Portland before joining the tidal-fluvial Columbia River estuary. The Columbia River passes 163 km through a wide floodplain, skirting the Coast Range to the Pacific Ocean where the Columbia River forms a dynamic plume out into the California Current system of the Pacific Ocean (Bottom et al. 2006). Critical habitat for Willamette River spring Chinook salmon has been designated through the ESA and includes the entire freshwater migration corridor described above (Figure 2.1).

Figure 2.1 The McKenzie River watershed (orange), Willamette River basin (green), and Columbia River estuary (red) with ESA designated critical habitat for Willamette River Chinook salmon (light blue).



The Columbia River estuary is a large river dominated system where varying tidal ranges shape gradients in habitat structure and ecosystem processes. Simenstad et al. (2011) classified eight hydro-geomorphic reaches in the Columbia River estuary lettered A at the mouth through H at Bonneville Dam. These classifications differ from earlier schemes in that they place greater emphasis on tributary, floodplain, and tidal-fluvial processes.

Willamette River basin Chinook salmon utilize the lower six hydro-geomorphic estuarine reaches (Figure 2.2) on their outmigration, and of these reaches C to F are classified as tidal-fluvial. The confluence of the Willamette and Columbia rivers forms the upstream boundary of Reach F (rkm 137-165), which has the broadest floodplain in the tidal-fluvial estuary. This reach includes Multnomah Channel, a protected back-water route to the Columbia River that many Willamette River salmon follow during their juvenile migration (NMFSb 2008). In Reach E (rkm 119-137) the tidal floodplain narrows between valley walls, alluvial terraces and volcanic outwash. Reach D (rkm 103-119) is constrained upstream near the Kalama River, and the floodplain widens downstream near the Cowlitz River, both rivers draining the Washington State Cascade Mountains. Reach C (rkm 61-103) is in a narrow valley constricted by the Coast Range on the north bank and a floodplain terrace on the south bank. Tidal currents reverse flow direction as far upriver as Reach C during low river discharge. Reach B (rkm 23-61) transitions from a river valley into an open complex of bays, deltas, islands, shoals, and channels. The maximum extent of salinity intrusion is roughly midway through Reach B. In Reach A (rkm 0-23) marine influence dominates ecosystem processes (e.g., storm

surges, tidal cycles, upwelling, estuarine mixing). Reach A is completely brackish and has bays on both the north and south of the main channels with prominent low-velocity flats (Simenstad et al. 2011).

Figure 2.2 Willamette River spring Chinook salmon utilize the lower six Columbia River estuary hydro-geomorphic reaches during their juvenile outmigration, lettered F at the Columbia-Willamette River confluence to A at the Columbia River mouth. The upper half of Reach B and reaches C-F are tidal-fluvial. Reach A and the roughly the lower half of Reach B are brackish.



2.3 Review of McKenzie River Chinook Salmon Data

A comprehensive understanding of Chinook salmon estuarine life histories and their spawning contributions must consider population-specific constraints upriver. Extensive surveys have been conducted in the McKenzie and Willamette rivers; sample sizes are large and life histories are well documented, including juvenile size distribution and timing of estuarine entrance, and age classes of the adult spawning population. Cross-sectional catch studies within the Columbia River estuary have occurred less frequently and capture a mixture of genetic stock groups, of which Willamette River basin Chinook salmon are typically a small proportion.

The ocean survival of Chinook salmon from different estuarine life-history pathways may vary. For example, Waples et al. (2004, 2008) suggested Columbia River Chinook salmon stocks with wide oceanic distributions, a trait the authors deemed fixed by genetic lineage, may be most successful when marine entry occurs in the early spring at a large size; the authors speculated this may be due to a longer migration distance to oceanic rearing areas and the timing of oceanic bio-productivity cycles. Therefore, sizes and times Chinook salmon leave the estuary may have population-specific effects on ocean survival. In the marine environment, studies of natural- and hatchery-origin Columbia River Chinook salmon stocks provide limited data on marine entry and oceanic distributions of Willamette River basin Chinook salmon.

The ability to distinguish juvenile Chinook salmon from the McKenzie River population diminishes with distance from the natal spawning grounds down the migration corridor as other stocks mix, spatial scales increase, and samples become less representative. In the McKenzie River and Willamette River above the Santiam River confluence (rkm 174), unclipped Chinook salmon are assumed to be from the naturalorigin McKenzie River population (Schroeder et al. 2007, in review; NMFSb 2008; ODFW 2013). Below the Santiam River confluence in the Willamette River, naturalorigin Chinook can only be classified to the ESU level. Once fish approach and pass the Columbia River confluence group assignment to ESU requires genetic analysis (Teel et al. 2009, 2014) or a rare PIT-tag detection from a known location (Roegner et al. 2015; Schroeder et al. in review). Therefore inferences about the McKenzie River Chinook salmon population must be based on observations of the broader Willamette River Chinook salmon ESU that could be confounded by population-specific differences in lifehistory expression and survival (i.e., from the North and South Santiam rivers Chinook salmon populations; Schroeder et al. 2007).

The Oregon Department of Fish and Wildlife (ODFW) has compiled a large data set describing the life history of Chinook salmon in the Willamette River basin (Schroeder and Kenaston 2004; Schroeder et al. 2007, in review). ODFW researchers surveyed all known Chinook salmon spawning habitat in the Willamette River tributaries since the late 1990s, analyzed scales from all carcasses recovered from spawning grounds (Clemens et al. 2013; Borgerson et al. 2014), and monitored juvenile life histories since the mid-2000s (Schroeder et al. 2007; in review). Scale analyses identified the age classes of all McKenzie River Chinook salmon spawners and reconstructed the brood year affiliations of all cohorts (Schroeder et al. 2007, in review). Oregon Department of Fish and Wildlife scale data from 2002 to 2012 shows nine different age classes contributed to the McKenzie River Chinook salmon spawning population (Table 2.1). Age classes are determined based on adult age-at-return (three to six years) and outmigration age (subyearling, yearling, and possibly a novel reservoirrearing type). The mean percent subyearling migrant juvenile life history of all Chinook analyzed was 22%, but the percent varies from five to 51% for the period of record. Most fish (97%) returned as four- or five-year-olds (Schroeder et al. 2007; in review). Table 2.1 displays the estimated contributions of these nine age classes to returns from the 1996-2006 broods. Age classes are described in Gilbert-Rich notation with the total age, followed by a subscript to denote the number of winters in freshwater (including the first winter in the gravel: 1 for subyearlings, 2 for yearlings, and X for reservoir rearing) (Borgerson et al. 2014). This is a conservative estimate of life-history variation because scale analysis can only resolve subyearling, yearling, and possibly reservoir-rearing juvenile life histories. Table 2.1 Estimated natural- and hatchery-origin spawner abundances (left) and age classes for 1999–2006 broods of natural-origin McKenzie River Chinook salmon (right) show two major points: (1) spawning abundances are not replacing (in bold); and (2) most natural-origin fish come from four age classes (4₁, 4₂, 5₁, 5₂), and the numbers of each vary annually. Age classes are in Gilbert-Rich notation: the first digit is total age, and the subscript digit is juvenile winters spent in freshwater including the first winter in the gravel (1=subyearling, 2=yearling, X=possible reservoir rearing). Natural- or hatchery-origin determination of each brood's parental spawning population (shown on the left) was not possible prior to 2002. Estimated natural-origin return of each brood is shown on the far right. Data are expanded by annual adult abundances, such that proportions vary from text. Data modified from: Schroeder et al. in review, ODFW Willamette Spring Chinook and Life History Analysis Projects.

Spawn		Estimated riv	er spawner	s	Brood				1	Age clas	s				Estimated
year	Natural	Hatchery	Total	% Natural	year	31	32	41	42	$4_{\rm X}$	51	52	$5_{\rm X}$	62	natural return
1998	NA	NA	2,302	NA	1999	12	-	717	416	-	291	3,389	-	102	4,928
1999	NA	NA	2,278	NA	2000	23	-	-	1,112	-	51	2,322	-	41	3,549
2000	NA	NA	3,251	NA	2001	-	-	171	273	-	108	1,327	-	147	2,027
2001	NA	NA	4,878	NA	2002	17	17	257	867	-	49	2,886	49	127	4,269
2002	4,201	2,898	7,099	59%	2003	27	-	353	285	20	28	1,864	56	102	2,736
2003	5,689	5,142	10,831	53%	2004	-	-	113	621	169	93	680	19	20	1,715
2004	4,845	5,060	9,905	49%	2005	127	-	1,052	270	9	79	1,359	20	10	2,926
2005	2,954	800	3,754	79%	2006	19	-	118	827	39	177	1,488	21	215	2,689
Total:	17,689	13,900	44,298			225	17	2,782	4,671	238	877	15,315	165	765	24,839
Annual															
mean:	4,422	3,475	5,537	60%		1%	0%	11%	19%	1%	4%	62%	1%	3%	2,516

A continuum of juvenile Chinook salmon migration past Willamette Falls and into tidal-fluvial habitat has been observed; yearling and subyearling fry (<60 mm FL) pass the falls in the winter and spring, followed by later spring and summer subyearling fingerlings (>60mm FL), and fall/winter subyearling fingerlings (Friesen et al. 2007; Schroeder et al. 2007, in review; Teel et al. 2009). To supplement understanding of juvenile life histories, ODFW began PIT-tag and observation studies in 2004. The scope of the juvenile monitoring has gradually increased and now tags ~18,000 individual salmon per year. Juvenile McKenzie River Chinook salmon display a wide range of emergence times beginning in January. A diversity of migration, rearing and overwintering patterns have been observed in the McKenzie and Willamette rivers (Schroeder et al. 2007). PIT-tag detection data from 2005 through spring 2015 show a continuous juvenile Chinook salmon migration past Willamette Falls (Figure 2.2). However, the data must be interpreted carefully: tagging effort has varied by year, season, and location; the PIT-tag detection array has periodically failed; detections are influenced by hydrology over the falls and through the Sullivan hydro-electric plant; and it is possible subyearlings migrate through the Sullivan plant and past the PIT detection arrays in a higher proportion or greater abundance than that of yearlings (G. R. and L. Whitman, ODFW unpublished data).





The lower Willamette River below the falls (rkm 0-43) is tidally influenced, and estuarine by the standards of Simenstad et al. (2011) and others (e.g., Bottom et al. 2005b; Fresh et al. 2005). Friesen et al. (2007) found juvenile Chinook salmon, including fry, fingerlings, and yearlings in the Willamette River below the falls in 34 of 35 months from May 2000 to July 2003 with the highest abundances from January to May. Mean migration rates through the lower 43 km of the Willamette River for radio tagged (>100 mm FL) and unclipped yearling Chinook salmon were 8.4 km/day, with significant individual and temporal variability. Lengths and weights were significantly greater at downstream than at upstream sampling sites in the lower 43 km of the Willamette River for the Willamette River for both subyearling and yearling Chinook salmon. The results imply that juvenile Chinook salmon delay their migrations long enough to feed and grow in the tidal-fluvial portion of the lower Willamette River before migrating further downriver (Friesen et al. 2007).

Willamette River Chinook salmon PIT-tag detections in the Columbia River estuary have been sparse considering the intensive tagging effort in recent years. However, this is not surprising given the small number of detection sites in the lower Columbia River. Off-channel detection arrays in a few small secondary channels at Russian Island (rkm 36), lower Sauvie Island (rkm 139), and the upper Multnomah Channel (~rkm 165) yielded 8 detections of natural-origin McKenzie River Chinook salmon from 2008 to 2013. The mean \pm SD migration rate was 6.7 ± 7.0 km/day, and rates ranged from one to 21 km/day from the most recent detection. However, these rates were based on release locations that were 230 to 296 rkm upstream of tidal influence, and it is not clear when these fish migrated into the tidal-fluvial estuary (Roegner et al. 2015; R. McNatt, NOAA Fisheries, personal communication). However, their detection at offchannel sites indicates these fish were rearing in the estuary for at least some period of time.

The other estuary PIT-tag detection area for tagged upper Willamette River spring Chinook salmon is between rkm 61 and 83, where a mobile pair-trawl array operates from March to June (Magie et al. 2008). From 2004-2014, 17 subyearling and 14 yearling McKenzie River Chinook salmon were detected at both Willamette Falls and at the pair-trawl detection area. Mean \pm SD migration rate was 27.6 \pm 8.9 km/day for subyearlings and 30.0 \pm 9.2 km/day for yearlings, with the fastest individual rates at ~40 km/day (K. Schroeder, ODFW consultant, personal communication). The differences in observed migration rates likely reflect the habitats and juvenile life-history types sampled by each survey method. The off-channel arrays sample shallow secondary channels year round and likely characterize the behaviors of slowly migrating juveniles that feed and grow before migrating seaward. The main-stem pair-trawl operation samples deeper main-stem habitats during spring and summer months and likely targets active tidalfluvial migrants. The Columbia River estuary PIT-tag studies demonstrate multiple estuarine life-history pathways expressed by Willamette River Chinook salmon.

Beach seining coupled with genetic analysis in shallow tidal-fluvial portions of the Columbia River estuary has provided insight into distribution patterns of naturalorigin Willamette River Chinook salmon (Teel et al. 2014). Synoptic sampling was conducted bi-monthly at 18 sites in estuary hydro-geomorphic reaches A (rkm 0-23) and C-H (rkm 61-233) from January 2010 to April 2012. Upper Willamette River spring Chinook salmon of a range of sizes were observed during various seasons; fry were documented in hydro-geomorphic estuarine reaches E and F (rkm 119-163) from January through March (Teel et al. 2014). Fry and fingerlings were also observed on seasonal floodplain habitat near the Willamette-Columbia River confluence (Columbia rkm 163) as part of another related study (Teel et al. 2009). In March yearlings were captured in reaches C through F (rkm 61-163), and in September and November fingerlings were found in reaches E and F (Teel et al. 2014). A total of 25 fry, 37 fingerling, and 37 yearling unclipped upper Willamette River spring Chinook salmon were caught in the synoptic genetic survey (Teel et al. 2014). These results confirm variability in juvenile Chinook salmon life histories, but the surveys were infrequent (bimonthly) and characterized a limited variety of near-shore habitats. For example, Teel et al. (2014) noted the small seine size (3 m by 38 m variable mesh bag seine) likely explained a lack of summer yearlings noted in earlier studies (Dawley et al. 1986) which sampled slightly deeper habitat.

Roegner et al. (2012) conducted monthly beach seines (3 m by 50 m variable mesh beach seine) at seven sites in the lower 61 km of the Columbia River estuary from January 2002 to September 2007. The authors caught 11,988 juvenile Chinook salmon of all sizes (both clipped and unclipped) and collected genetic data from 2,174 individuals. From the genetic analysis, only five unclipped fish were confidently identified (with a genetic probability >80%) as upper Willamette River spring Chinook salmon including two fry caught in March, two fingerlings caught in April and July, and one yearling caught in May (Roegner et al. 2012, personal communication).

Additional data on size and timing of Willamette River Chinook salmon exiting the tidal-fluvial estuary comes from Weitkamp et al. (2012, in press). Fish were sampled every two weeks with a 10.6 m by 155 m fine mesh purse seine and targeted water eight to ten m deep in both the north (rkm 17) and south (rkm 13) main channels in reach A of the Columbia River estuary. Genetic data were collected for 2013 Chinook salmon juveniles; 20 of these were unclipped Willamette River Chinook salmon including seven yearlings (135-178 mm FL) from mid-April through early June, and 13 subyearlings (85-129 mm FL) from late May through mid-July (L. Weitkamp, NOAA Fisheries, personal communication).

Juvenile Chinook salmon growth rates in the Columbia River estuary estimated from three separate studies ranged from 0.11 to 0.82 mm/day (Campbell 2010; Bottom et al. 2011; Goertler et al. 2015). Campbell (2010) estimated growth rates of 91 fish beach seined just below the brackish-freshwater interface in Columbia River estuary reach A. Growth rate was derived from the average otolith increment width for 30 days prior to capture. Mean growth rate was 0.4 mm/day with a range from 0.11 to 0.67 mm/day. Willamette River Chinook made up only two of 91 fish used for this estimate—both fry with a mean FL at capture of 38 mm and estimated mean residence time in saline waters of 40 days (Bottom et al. 2011; Roegner et al. 2012). Goertler et al. (2015) found no significant differences in juvenile Chinook growth rates by stock of origin in a similar study conducted in Columbia River estuary reaches C to F (rkm 61-165). The authors analyzed a subsample (n= 608) of juvenile Chinook salmon otoliths collected during the above mentioned genetic synoptic survey from 2010-2012 (Teel et al. 2014). Growth rate was estimated by the mean otolith increment width 14 days prior to capture; mean growth rate was 0.23 mm/day with a range from 0.11 to 0.43 mm/day. In another study, instantaneous growth rates were measured for fish residing in shallow tidal-fluvial emergent marsh habitat for at least one week in Columbia River estuary Reach B (rkm 23-61) during 2006 and 2008. Growth rates ranged from 0.65 to 0.82 mm/day, although none of the Chinook salmon used for this estimate were identified as the Willamette River genetic group (Bottom et al. 2011).

Juvenile Willamette River Chinook salmon, on average ~80% yearlings, migrate to the ocean early and disperse quickly relative to other Columbia River stocks. Oceanic distribution has largely been inferred from observations of hatchery-origin fish marked with coded wire tags (Myers et al. 2006; Fisher et al. 2014), and recent genetic analysis of clipped and unclipped fish (Teel 2004; Weitkamp et al. in press). The idea that hatchery- and natural-origin fish share similar oceanic distributions is supported by: genetic similarities between hatchery- and natural-origin Chinook salmon stocks in the Willamette River basin (Myers et al. 2006; NMFSb 2008; Ford et al. 2010; ODFW and NMFS 2011); genetic constraint on Chinook salmon oceanic distributions (Healey 1991; Waples et al. 2004); and by similarities in patterns of ocean entrance between hatcheryand natural-origin Chinook salmon (Weitkamp et al. in review). Willamette River basin hatchery-origin Chinook salmon were caught off coastal British Columbia but 30% were recovered off Alaska, indicating Willamette River Chinook salmon have a wider oceanic distribution than other lower Columbia River Chinook salmon ESUs (Myers et al. 2006). In the Columbia River, Willamette River basin yearling Chinook were the earliest to enter the lower estuary and ocean from 2007-2011 (Weitkamp et al. in review). They were present in their highest abundances in marine waters near the Columbia River mouth when sampling commenced in April, and had the highest estimated oceanic growth rates in May at ~1.6 mm/day (including both hatchery- and natural-origin fish). The high reported growth rates for Willamette River Chinook salmon in this study may have been due to prolonged exposure to favorable oceanic growth conditions, or due to underestimated ocean residence by missing the peak migration before the April sampling commenced (Weitkamp et al. in review). Hatchery-origin Willamette River basin Chinook salmon have one of the highest ocean dispersal rates of any Columbia River Chinook salmon ESU, surpassed only by interior spring run groups (Fisher et al. 2014); they were observed in the Pacific Ocean as early as March, from southern Oregon to Alaska by June, and were mostly north of Vancouver Island by August. Another oceanic genetic study of natural-origin Chinook salmon found Willamette River Chinook were largely absent from coastal waters off of Washington State and the Columbia River by June (Teel 2004).

The return migration for Willamette River basin Chinook salmon commences in February and March when three-to-six-year-old adults first enter the Columbia River (Myers et al. 2006). Most Chinook salmon ascend Willamette Falls from April to May when temperatures rise above 10° C and when historic river flows were highest. Passage through the Willamette River is rapid, with fish holding in natal tributaries until the fall. Spawn timing is dependent on river conditions, although generally begins in August, peaks in September, and has finished by October (Myers et al. 2006; NMFSb 2008; ODFW and NMFS 2011).

River temperature in the spawning and natal rearing environment is the dominant driver of phenotypic plasticity for Chinook salmon (Brannon et al. 2004), and temperature almost certainly affects the tidal-fluvial life-history stage—both by carry-over effects from previous life-history stages (Schroeder and Kenaston 2004; Schroeder et al. 2005, 2007) and directly (Bottom et al. 2005b). Chinook salmon spawn timing and spawning locations are affected by environmental cues, including temperature and hydrologic regime, which can co-vary between spawning, freshwater and oceanic life-history stages. Early life history of Chinook salmon broods can be influenced by parental spawning conditions via emergence timing and locations (Brannon et al. 2004; Williams et al. 2006). Higher temperatures can speed incubation, emergence, and metabolism, causing more subyearling juvenile phenotypes (Beckman et al. 2003, 2007; Brannon et al. 2004; Schroeder et al. 2007).

In the Columbia River estuary, warmer temperatures may increase ecosystem productivity and juvenile Chinook salmon metabolism to a point. Temperatures above 18° C can be harmful to salmonids. These high temperature conditions occur during summer months in the lower Willamette River (NMFSb 2008), and in the Columbia River tidal-fluvial reaches, especially in shallow habitat with poor circulation and low shade (NMFS 2011). 2.4 Synthesis of McKenzie River Chinook Salmon Tidal-fluvial Life Histories

Migration of juvenile McKenzie River Chinook salmon into the tidal-fluvial Columbia River estuary occurs year round, and includes fry migrants from winter to summer (Friesen et al. 2007; Teel et al. 2009, 2014), fingerling migrants from spring to winter (also see Figure 2.4), and yearling migrants from winter to spring (Friesen et al. 2007). Migration rates are highly variable (Roegner et al. 2015; R. McNatt, NOAA Fisheries and K. Schroeder, ODFW consultant, personal communiactions), and Chinook salmon of all sizes have been found in a variety of estuarine habitats (e.g., main channel, shallow-tidal, off-channel, seasonal wetlands) (Teel et al. 2009, 2014)

Recent surveys report size-related differences in the estuarine distributions of juvenile Willamette River Chinook salmon. Fry were most commonly observed in reaches E-F from January to March, fingerlings in reaches E-F in September and November, and yearlings in reaches C-F in March (Teel et al. 2014). Fewer Willamette River Chinook salmon were captured in reaches A-B, despite greater sampling effort; although it is possible some sampling beginning in April in these reaches may have begun after the peak of migration. Sampling frequency throughout the estuary was biweekly to bi-monthly and not comprehensive. However, the abundance data suggest both yearling and subyearling Willamette River Chinook salmon may predominantly utilize the upper tidal-fluvial Columbia River estuary and pass quickly through the lower estuary. Geographic survey locations are scattered, sampled infrequently, and the estuarine residence times of individual fish from known populations are rarely reported. Studies in smaller coastal and predominantly brackish estuaries suggest some fry or fingerlings pass directly to the ocean, some forage or seek refuge briefly, and some reside for extended periods (Reimers 1973; Healey 1980; Bottom et al. 2005a; Volk et al. 2010). However evidence of subyearling residency patterns are lacking in the large tidal-fluvial Columbia River estuary, and there is very little basis to make assumptions about residency patterns of yearling migrants.

Variations in estuarine life histories of juvenile McKenzie River Chinook salmon, and their contributions to adult survival, are poorly understood (Figure 2.3). Ocean entry timing for yearlings appears to be predominantly in early spring, and for subyearlings in the early summer (Weitkamp et al. in press), however the fate of subyearlings observed in the estuary in the fall is unknown; do they enter the ocean in the fall or winter, or do they overwinter in the estuary to leave the basin as yearlings the following spring? Or do fall migrants rarely survive? Both subyearlings and yearlings contribute to the McKenzie River Chinook salmon spawning population, however the contributions are not consistent across years (Schroeder et al. 2007). It is unclear what life-history stages, or interactions between them, are driving variable survival to the spawning life stage. Figure 2.4 Observed McKenzie River Chinook salmon estuarine life-history pathways are summarized down the rows by estimated entrance timing from January 1. Columns represent broad juvenile life-history stages and estimated survival contributions. Uncertainties are denoted by question marks and italics. Data from: Friesen et al. 2007; Schroeder et al. 2007; Teel et al. 2009, 2014; Weitkamp et al. 2012, in press; and ODFW Willamette Spring Chinook and Fish Life-History Analysis Projects.



2.5 Information Gaps for McKenzie River Chinook Salmon in the Tidal-fluvial Columbia River Estuary

Monitoring cumulative effects of habitat restoration on Chinook salmon in the Columbia River estuary requires some baseline knowledge of estuarine life-histories, performance, and their relationship to survival. However, there are five major issues with connecting tidal-fluvial estuarine life-history pathways to survival of Columbia River Chinook salmon: (1) Chinook salmon immigration into and emigration out of the estuary are largely unquantified—therefore survival estimates are not available and do not seem feasible to quantify at reach and landscape scales (Simenstad and Cordell 2000; Bottom et al. 2011; Roegner et al. 2015); (2) mixing of Chinook salmon stocks in the lower Columbia River confounds monitoring of population-specific performance or survival (McElhany et al. 2000; Teel et al. 2014); (3) the identification of Chinook salmon estuarine life-history pathways without large sample sizes requires multiple observations of individual fish; (4) the contributions of specific estuarine life-history pathways to Chinook salmon spawning populations are unknown; and (5) interactive effects across Chinook salmon life stages limit understanding of survival benefits or mortality factors at any one stage (Simenstad and Cordell 2000).

Direct observations have shown McKenzie and Willamette River Chinook salmon in the Columbia River estuary at a variety of sizes and times; but sample sizes are low, the proportion of McKenzie River Chinook salmon is unconfirmed, and recaptures are rare (Bottom et al. 2011; Roegner et al. 2012, 2015; Weitkamp et al. 2012). The current knowledge base does not provide a baseline of Chinook salmon performance and residency in the tidal-fluvial Columbia River (NMFS 2011). Consequently, monitoring the cumulative effects of habitat restoration in the tidal-fluvial Columbia River estuary is challenging and remains subjective. Reconstructing juvenile Chinook salmon life histories with adult otoliths from known source populations can circumvent some of above mentioned difficulties, and provide a connection to population survival (Campana 1999; Miller et al. 2011). Figure 2.3 suggests five uncertainties and hypotheses otolith analysis could address to improve understanding of McKenzie River Chinook salmon life histories in the tidal-fluvial Columbia River estuary: (1) to what extent do the majority of spring yearling migrants reside and grow; (2) to what extent do the majority of spring/summer subyearling migrants reside and grow; (3) do fry migrants to the estuary rear for extended periods and contribute to the spawning population; (4) do fall/winter migrants to the estuary rear for extended periods and contribute to the spawning population; (5) does tidal-fluvial habitat support alternative juvenile life-history pathways? This information could benefit Willamette River Chinook salmon recovery efforts and improve assessment of the cumulative effects of Columbia River estuary restoration on Chinook salmon populations. In the next chapter, Chinook salmon otoliths from the McKenzie River spawning population are analyzed to address these uncertainties.

- Beckman, B. R., B. Gadberry, P. Parkins, K. A. Cooper, and K. D. Arkush. 2007. Statedependent life history plasticity in Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate smolting and early male maturation. Canadian Journal of Fisheries and Aquatic Sciences 64(2):256–271.
- Beckman, B. R., D. A. Larsen, and W. W. Dickhoff. 2003. Life history plasticity in Chinook salmon: Relation of size and growth rate to autumnal smolting. Aquaculture 222(1-4):149–165.
- Borgerson, L., B. Clemens, K. Bowden, and S. Gunckel. 2014. Fish Life History Analysis Project: methods for scale analysis. Oregon Department of Fish and Wildlife Information Report 2014-10 (September):41 pp.
- Bottom, D. L., A. Baptista, J. Burke, L. Campbell, E. Casillas, S. Hinton, D. A. Jay, M. A. Lott, G. Mccabe, R. Mcnatt, M. Ramirez, G. C. Roegner, C. A. Simenstad, S. Spilseth, L. Stamatiou, D. Teel, and J. E. Zamon. 2011. Estuarine habitat and juvenile salmon: current and historical linkages in the lower Columbia River and estuary: Final Report 2002-2008. National Marine Fisheries Service Report to the U.S. Army Corps of Engineers Contract W66QKZ20374382. Portland, OR.
- Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005a. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). Estuarine, Coastal and Shelf Science 64:79–93.
- Bottom, D. L., B. E. Riddell, and J. A. Lichatowich. 2006. The estuary, plume, and marine environments. Pages 507–569 *in* R. N. Williams, editor. Return to the River. Elsevier.
- Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005b. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. NOAA Technical Memorandum NMFS-NWFSC-68:246 pp.
- Brannon, E. L., M. S. Powell, T. P. Quinn, and A. Talbot. 2004. Population Structure of Columbia River Basin Chinook salmon and Steelhead trout. Reviews in Fisheries Science 12(2-3):99–232.
- Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263–297.

- Campbell, L. A. 2010. Life histories of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary as inferred from scale and otolith microchemistry. Master's Thesis. Oregon State University, Corvallis, Oregon.
- Clemens, B. K., K. Bowden, and L. Borgerson. 2013. Fish life history analysis project: project description. Oregon Department of Fish and Wildlife (July 2013):6 pp.
- Dawley, E. M., R. D. Ledgerwood, T. H. Blahm, C. W. Sims, J. T. Durkin, R. a Kirn, A. E. Rankis, and G. E. Monan. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. National Marine Fisheries Service Final Report to Bonneville Power Administration (April 1986):256 pp.
- Fisher, J. P., L. A. Weitkamp, D. J. Teel, S. A. Hinton, J. A. Orsi, E. V. Farley, J. F. T. Morris, M. E. Thiess, R. M. Sweeting, and M. Trudel. 2014. Early ocean dispersal patterns of Columbia River Chinook and Coho salmon. Transactions of the American Fisheries Society 143(1):252–272.
- Ford, M., T. Cooney, P. Mcelhany, N. Sands, L. Weitkamp, J. Hard, M. Mcclure, R. Kope, J. Myers, A. Albaugh, D. Teel, P. Moran, and J. Cowen. 2010. Status review update for Pacific salmon and Steelhead listed under the Endangered Species Act. NOAA Technical Memorandum NMFS-NWFSC-113:346 pp.
- Fresh, K. L., E. Casillas, L. L. Johnson, and D. L. Bottom. 2005. Role of the estuary in the recovery of Columbia River basin salmon and steelhead: an evaluation of the effects of selected factors on salmonid population viability. NOAA Technical Memorandum NMFS-NWFSC-69:105 pp.
- Friesen, T. a., J. S. Vile, and A. L. Pribyl. 2007. Outmigration of juvenile Chinook salmon in the lower Willamette River, Oregon. Northwest Science 81(3):173–190.
- Goertler, P. A. L., C. A. Simenstad, D. L. Bottom, S. Hinton, and L. Stamatiou. 2015. Estuarine habitat and demographic factors affect juvenile Chinook (*Oncorhynchus tshawytscha*) growth variability in a large freshwater tidal estuary. Estuaries and Coasts:18 pp.
- Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon. Fishery Bulletin 77(3):653–668.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–394 in C. Groot and L. Margolis, editors. Pacific Salmon Life Histories. UBCPress.

- ISAB (Independent Scientific Advisory Board). 2011. Using a comprehensive landscape approach for more effective conservation and restoration. ISAB-2011-4 (30 September 2011):179 pp.
- ISAB (Independent Scientific Advisory Board). 2015. Density dependence and its implications for fish management and restoration programs in the Columbia River basin. ISAB 2015-1 (25 February 2015):246 pp.
- ISG (Independent Scientific Group). 2000. Return to the river. Northwest Power Planning and Conservation Council Document 2000-12 (1 January 2000).
- Magie, R. J., A. S. Cameron, R. D. Ledgerwood, B. P. Sandford, and G. M. Matthews. 2008. Development of pair-trawl detection systems for monitoring PIT-tagged juvenile salmonids in the Columbia River estuary, 2007. National Marine Fisheries Service Report to Bonneville Power Administration, Contract 36723 (July 2008):37 pp.
- Marcoe, K., and S. Pilson. 2013. Habitat change in the lower Columbia River and estuary, 1870-2011. Lower Columbia River Estuary Partnership:57 pp.
- McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42:158 pp.
- Miller, J. A., V. L. Butler, C. A. Simenstad, D. H. Backus, A. J. R. Kent, and B. Gillanders. 2011. Life history variation in upper Columbia River Chinook salmon (*Oncorhynchus tshawytscha*): a comparison using modern and ~500-year-old archaeological otoliths. Canadian Journal of Fisheries and Aquatic Sciences 68(4):603–617.
- Moran, P., D. J. Teel, M. A. Banks, T. D. Beacham, M. R. Bellinger, S. M. Blankenship, J. R. Candy, J. C. Garza, J. E. Hess, S. R. Narum, L. W. Seeb, W. D. Templin, C. G. Wallace, C. T. Smith, and E. Taylor. 2013. Divergent life-history races do not represent Chinook salmon coast-wide: the importance of scale in Quaternary biogeography. Canadian Journal of Fisheries and Aquatic Sciences 70(3):415–435.
- Myers, J., C. Busack, D. Rawding, A. Marshall, D. Teel, D. M. V. Dornick, and M. T. Maher. 2006. Historical population structure of Willamette and lower Columbia River basin Pacific salmonids. NOAA Technical Memorandum NMFS-NWFSC-73:311 pp.
- NMFS (National Marine Fisheries Service). 2011. Columbia River estuary ESA recovery plan module for salmon and Steelhead. NMFS Northwest Region. Portland, Oregon. Prepared for NMFS by the Lower Columbia River Estuary Partnership (contractor) and PC Trask & Associates, subcontractor. (January 2011):260 pp.

- NMFSb (National Marine Fisheries Service). 2008. Willamette project biological opinion. Endangered Species Act Section 7(a)(2) and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation F/NWR/2000/02117 (11 July 2008).
- ODFW (Oregon Department of Fish and Wildlife). 2013. Fisheries management and evaluation for 2012 Willamette River spring Chinook. ODFW Ocean Salmon and Columbia River Program (January 2013):24 pp.
- ODFW (Oregon Department of Fish and Wildlife), and NMFS (National Marine Fisheries Service). 2011. Upper Willamette River conservation and recovery plan for Chinook salmon and Steelhead (5 August 2011):462 pp. plus executive summary and appendices.
- Paquet, P. J., T. Flagg, A. Appleby, J. Barr, L. Blankenship, D. Campton, M. Delarm, T. Evelyn, D. Fast, J. Gislason, P. Kline, D. Maynard, L. Mobrand, G. Nandor, P. Seidel, and S. Smith. 2011. Hatcheries, conservation, and sustainable fisheries—achieving multiple goals: results of the Hatchery Scientific Review Group's Columbia River basin review (February 2013):547–561.
- PNNL (Pacific Northwest National Laboratory). 2012. Evaluation of cumulative ecosystem response to restoration projects in the lower Columbia River and estuary, 2010. Report to U.S. Army Corps of Engineers Contract DE-AC05-76RL01830 (May):389 pp.
- Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commision of Oregon 4(2):42 pp.
- Roegner, C., D. Bottom, A. Baptista, L. Campbell, P. Goertler, S. Hinton, R. Mcnatt, C. Simenstad, D. Teel, and K. Fresh. 2015. Salmon habitat use of tidal-fluvial habitats of the Columbia River estuary, 2010-2013. National Marine Fisheries Service Final Report to U.S. Army Corps of Engineers, Portland District (April 2015):103 pp.
- Roegner, G. C., R. McNatt, D. J. Teel, and D. L. Bottom. 2012. Distribution, size, and origin of juvenile Chinook salmon in shallow-water habitats of the lower Columbia River and estuary, 2002–2007. Marine and Coastal Fisheries 4(1):450–472.
- Schroeder, R. K., and K. R. Kenaston. 2004. Spring Chinook salmon in the Willamette and Sandy rivers. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-09:64 pp.
- Schroeder, R. K., K. R. Kenaston, and Krentz L. K. 2005. Spring Chinook salmon in the Willamette and Sandy rivers with 1996 – 2004 summaries. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-10:90 pp.

- Schroeder, R. K., K. R. Kenaston, and L. K. McLaughlin. 2007. Spring Chinook salmon in the Willamette and Sandy rivers. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-11:62 pp.
- Schroeder, R. K., L. D. Whitman, B. Cannon, and P. Olmsted. (n.d.). Juvenile life history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon. Canadian Journal of Fisheries and Aquatic Science.
- Simenstad, C. A., J. L. Burke, J. E. O'Connor, and K. L. Cannon, C., Heatwole, D.W., Ramirez, M.F., Waite, I.R., Counihan, T.D., Jones. 2011. Columbia River estuary ecosystem classification - concept and application. U.S. Geological Survey Open-File Report 2011-1228:54p.
- Simenstad, C. A., and J. R. Cordell. 2000. Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific northwest estuaries. Ecological Engineering 15(283):302.
- Teel, D. J. 2004. Genetic mixed stock analysis of juvenile Chinook salmon in coastal areas of western North America. North Pacific Anadromous Fish Commission Technical Report (5):47–48.
- Teel, D. J., C. Baker, D. R. Kuligowski, T. A. Friesen, and B. Shields. 2009. Genetic stock composition of subyearling Chinook salmon in seasonal floodplain wetlands of the lower Willamette River, Oregon. Transactions of the American Fisheries Society 138(1):211–217.
- Teel, D. J., D. L. Bottom, S. A. Hinton, D. R. Kuligowski, G. T. McCabe, R. McNatt, G. C. Roegner, L. A. Stamatiou, and C. A. Simenstad. 2014. Genetic identification of Chinook salmon in the Columbia River estuary: stock-specific distributions of juveniles in shallow tidal freshwater habitats. North American Journal of Fisheries Management 34(3):621–641.
- Volk, E. C., D. L. Bottom, K. K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139(2):535–549.
- Waples, R. S., G. R. Pess, and T. J. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications 1(2):189–206.
- Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution; international journal of organic evolution 58(2):386–403.

- Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fishery Bulletin 110(4):426–450.
- Weitkamp, L. A., D. J. Teel, M. Liermann, S. A. Hinton, D. M. Van Doornik, and P. J. Bentley. (n.d.). Stock-specific size and timing at ocean entry of Columbia River juvenile salmon and Steelhead: implications for early ocean growth. In Review at Marine and Coastal Fisheries.
- Williams, R. N., J. A. Stanford, J. A. Lichatowich, W. J. Liss, C. C. Coutant, W. E. McConnaha, R. R. Whitney, P. R. Mundy, P. A. Bisson, and M. S. Powell. 2006. Return to the river: strategies for salmon restoration in the Columbia River basin. Elsevier.

3. Back-calculating Emigration Sizes and Net Growth in the Tidal-fluvial Columbia River for Surviving Spring Chinook Salmon (*Oncorhynchus tshawytscha*) from the McKenzie River, OR

3.1 Introduction

Intact estuarine habitat has been shown to support juvenile Chinook salmon and their life-history diversity (Reimers 1973; Healey 1980; Gray et al. 2002; Bottom et al. 2005a, 2005b; Hering et al. 2010; Volk et al. 2010) while contributing to population survival (Magnusson and Hilborn 2003). Restoration of estuarine habitat is being incorporated into recovery plans for exploited Columbia River salmon, although little is known about how estuarine habitats support individual Chinook salmon populations (Fresh et al. 2005; PNNL 2012). The Columbia River estuary is a large river-dominated ecosystem defined by the entire area where tidal variations shape gradients in habitat structure and ecosystem processes (Simenstad et al. 2011). By this definition the estuary encompasses a vast complex of tidal-freshwater (hereafter "tidal-fluvial") habitats that extend ~200 km from the dynamic brackish water interface (~rkm 20-40) to the tailrace of Bonneville Dam (rkm 233) (Bottom et al. 2005b; Fresh et al. 2005). Nearly 70% of vegetated tidal wetland and 55% of forested upland habitat area has been lost to development throughout the Columbia River estuary and its historic floodplain (Marcoe and Pilson 2013). From 2010-2018 the U.S. Army Corps of Engineers (USACE) and the Bonneville Power Administration budgeted ~\$150 million for restoration, monitoring and evaluation of salmonid habitat in the Columbia River estuary (from

www.salmonrecovery.gov) with goals to increase survival benefits of 9% for "oceantype" (predominantly subyearling) and 6% for "stream-type" (predominantly yearling) Chinook salmon Evolutionarily Significant Units (ESUs) (NMFSa 2008).

The survival benefits of localized estuarine habitat restoration projects to particular population groups of anadromous Chinook salmon are poorly understood and not easily measured, in part because juvenile Chinook salmon are inherently migratory and transient through estuarine habitats (Healey 1980, 1991; Simenstad and Cordell 2000; Bottom et al. 2005a). In addition, representatively sampling juveniles across temporal and spatial scales in the Columbia River estuary has been problematic because of its large size and diverse habitat types (Bottom et al. 2005b, 2011; Roegner et al. 2015). Existing Chinook salmon abundance data provides only cursory evaluations of estuarine habitat use and performance (Simenstad and Cordell 2000). Furthermore, mixing of Chinook salmon stocks in the estuary presents major challenges for tracking cohorts from individual populations (Teel et al. 2014). Finally, tracing Chinook salmon performance in any one life stage to survival is confounded by their anadromous life cycles with many stages, which possibly have interacting effects on survival (Simenstad and Cordell 2000; PNNL 2012).

Criteria and methods are needed for measuring the contribution of estuarine habitats to the performance and survival (i.e. realized function) of juvenile salmon, and ultimately to assess the viability of Columbia River Chinook salmon populations. Simenstad and Cordell (2000) defined three estuarine assessment criteria—habitat capacity, opportunity, and realized function—for evaluating a habitat's support of juvenile salmon. However, survival and growth in restored estuarine habitats are rarely measured directly, and estuarine assessments must consider the broader habitat landscape integrated by salmon (Simenstad and Cordell 2000) and its overall contributions to adult returns. Reliable metrics for evaluating the support of estuarine landscapes to Chinook salmon could help to assess the cumulative effects of Columbia River estuary restoration programs (Simenstad and Cordell 2000; Naiman 2013; Rieman et al. 2015). This research measures contributions of the tidal-fluvial estuarine landscape to life-history diversity, growth, and survival in a known population of Columbia River Chinook salmon.

New approaches using genetic and otolith data have partially addressed the uncertainties mentioned above. A recently developed genetics baseline enabled investigators to distinguish the upriver sources (i.e., ESUs) of unmarked Columbia River salmon collected in the estuary (Teel et al. 2009, 2014). Otolith micro-chemical techniques can identify the environmental transitions that Chinook salmon experience during their anadromous migrations. Otoliths methods can reconstruct juvenile life history characteristics, and can estimate their relative contributions to the adult survivors from a specific population by sampling carcasses from known spawning grounds (Bacon et al. 2004; Miller et al. 2010, 2011; Volk et al. 2010). Sr/Ca elemental ratios are commonly used to identify the transition from fresh to brackish water. However, the Sr/Ca method cannot account for fish residency in the tidal-fluvial portions of a riverdominated system like the Columbia River estuary. Strontium isotopic methods have expanded the capabilities of otolith analysis (Campana 1999; Bacon et al. 2004; Elsdon et al. 2008; Miller et al. 2011), but have not been applied to the tidal-fluvial Columbia River estuary. This study uses Sr/Ca and Sr isotopic methods to back-calculate juvenile net growth within the tidal-fluvial region of the Columbia River estuary for spawning Chinook salmon from a specific population.

A long-term monitoring program in the McKenzie and Willamette rivers (Oregon) provides a comprehensive data set and otolith collection to estimate contributions of the tidal-fluvial estuary to a spawning population of adult spring Chinook salmon. The Oregon Department of Fish and Wildlife (ODFW) has monitored juvenile and adult populations of McKenzie River Chinook salmon since the late 1990s (Schroeder and Kenaston 2004, Friesen 2005, Schroeder et al. 2005, 2007; in review, NMFSb 2008, Teel et al. 2009, ODFW and NMFS 2011, ODFW 2013). The results reveal a diverse continuum of juvenile life histories, including variations in migration timing, sizes, and ages (Teel et al. 2006, 2009; Friesen et al. 2007; Schroeder et al. 2007). Juveniles enter the estuary at all times of the year but peak abundance occurs in the spring (Friesen et al. 2007). A wide range of sizes and ages of Willamette River juveniles have been observed in the Columbia River estuary, including fry (subyearlings < 60 mm FL), fingerlings (subyearlings > 60 mm FL), and yearlings (Bottom et al. 2011; Teel et al. 2014). Aquatic habitat along the migration corridor for McKenzie River Chinook salmon is relatively intact from natal reaches to the main-stem Willamette River and the tidal-fluvial Columbia River estuary. Furthermore, the Willamette River intersects the Columbia River estuary in the upper reaches below Bonneville Dam, providing a useful example for distinguishing the population response to the tidal-fluvial Columbia River estuary.

The McKenzie River Chinook salmon population is critical to survival of the Willamette River spring Chinook salmon ESU, classified as threatened under the Endangered Species Act (ESA) in 1999 (Myers et al. 2006, NMFSb 2008, Ford et al. 2010, ODFW and NMFS 2011). The Willamette River Chinook salmon ESU status has not improved since ESA listing, and is considered likely to move from a threatened to an endangered ESA rating (Ford et al. 2010, ODFW and NMFS 2011). The five upper Willamette River Chinook salmon populations outside of the McKenzie River (Mollala, North and South Santiam, Calapooia, and Middle-fork Willamette River populations) are deemed high risk for extinction within 100 years. Although the McKenzie River population has been rated as having a low extinction risk (ODFW and NMFS 2011), recent population reproduction has been below replacement levels (see bold summary statistics in Table 2.1, bottom rows).

In the Willamette River basin, environmental differences among salmon-bearing tributaries highlight the need for both population-specific data and a landscape approach to monitoring estuary restoration. Willamette River Chinook salmon populations are genetically similar (Waples et al. 2004; Myers et al. 2006), yet juvenile phenotypes are highly plastic (McElhany et al. 2000; Beckman et al. 2003, 2007; Waples et al. 2004, 2008; Schroeder et al. 2007). Among Willamette River tributaries with Chinook salmon populations, the McKenzie River is the least modified by watershed development and most closely resembles its historic environmental conditions (Myers et al. 2006; ODFW and NMFS 2011).

In this study I used otolith micro-chemical techniques to measure the realized function of the tidal-fluvial Columbia River estuary among adult survivors in the naturalorigin (i.e., born in the wild) spawning population of McKenzie River Chinook salmon. My primary objectives were (1) to reconstruct juvenile life-history pathways represented among spawning McKenzie River Chinook salmon as indicated by time and size of entry and approximate residency in the tidal-fluvial Columbia River; (2) to quantify the net growth of juvenile Chinook salmon in tidal-fluvial Columbia River; (2) to quantify the net indicator of realized function; and (3) to determine the relative contributions of the tidalfluvial estuary to survival and return of adult Chinook salmon in the McKenzie River. My secondary objectives are (a) to explore factors influencing net-growth in the tidalfluvial Columbia River estuary; (b) determine the feasibility of establishing a baseline of tidal-fluvial estuarine realized function; and (c) determine the feasibility of monitoring the cumulative effects of tidal-fluvial habitat restoration actions in the Columbia River for a specific Chinook salmon population.

3.2 Methods

This study analyzed otolith chemical markers from McKenzie River Chinook salmon to infer the juvenile life histories of returning adults at the transition from the Willamette River to the main-stem Columbia River estuary and from the tidal-fluvial to the brackish estuary. Two chemical indices were used to define these transitions: Sr isotope ratios at Willamette River emigration and Sr/Ca at freshwater emigration. Strontium and Ca are both alkaline earth metals with similar chemical and physical properties, and Sr substitutes for Ca in otolith formation. Regression models were used to develop a juvenile otolith-width to fork-length relationship for back-calculating juvenile sizes at each migration event. Finally adult otolith data were analyzed to assess the overall contributions of the tidal-fluvial Columbia River estuary to the return of adult Chinook salmon in the McKenzie River.

3.2.1 Willamette River to Tidal-fluvial Columbia River Transition

Differences in geology across the Columbia River basin produce variations in water chemistry that, in turn, are reflected in Chinook salmon otoliths. Spatial variability in riverine ⁸⁷Sr:⁸⁶Sr is recorded on Chinook salmon otoliths at values nearly identical to ambient water (Campana 1999; Kennedy et al. 2000, 2002; Campana and Thorrold 2001; Bacon et al. 2004; Elsdon et al. 2008; Miller et al. 2011). The value of ⁸⁷Sr:⁸⁶Sr is remarkably consistent in marine water (Viezer 1989; Campana 1999). In freshwater environments, seasonal changes in riverine Sr flux do not significantly affect isotopic ratios of Sr in the water, or in otoliths (Campana 1999; Bacon et al. 2004; Elsdon et al. 2008; Miller et al. 2011).

Riverine ⁸⁷Sr:⁸⁶Sr at a specific location is similar to the integral of the upriver watershed geology from three main Sr sources in the Columbia River basin (Faure 2001; Bacon et al. 2004; Miller et al. 2011). Strontium 87 is formed from the radioactive decay of Rubidium 87, with a half-life of ~49 billion years (Faure 2001; Miller et al. 2011). The oldest basement rock in the Columbia occurs in the upper basin on the ancient granitic continental craton with high ⁸⁷Sr:⁸⁶Sr (mean \pm 1 SD = 0.8847 \pm 0.1028, n = 77) (Faure 2001; Madin 2009; Miller et al. 2011). In contrast, the surface geology of the interior plateau is dominated by Columbia River flood basalts with lower ⁸⁷Sr:⁸⁶Sr (mean \pm 1 SD = 0.7046 \pm 0.001, n = 224) (Faure 2001; Madin 2009; Miller et al. 2011). In the southern Willamette River basin including the McKenzie River watershed, more recently formed Cascade igneous rocks have low ⁸⁷Sr:⁸⁶Sr (mean \pm 1 SD = 0.70340 \pm 0.0004, n = 99) (Faure 2001; Madin 2009; Miller et al. 2011).

Literature values reveal a substantial difference in strontium isotopic ratios for the Willamette and Columbia rivers, enabling a potential indicator of juvenile McKenzie River Chinook salmon emigration from the Willamette River into the upper tidal-fluvial portion of the main-stem Columbia River (Table 3.1). Strontium isotopic ratios show a significant increase (~three orders of magnitude over detection precisions) from the lower Willamette River to the Columbia River below Bonneville dam, from 0.7045 to 0.71328 (Miller et al. 2011; Bourret 2013). Water ⁸⁷Sr:⁸⁶Sr values mixed to 0.70890 by St. Helens (Bourret 2013), at the downstream end of Multnomah Channel (Columbia rkm 119) approximately 44 rkm downstream from the Willamette-Columbia River confluence (rkm 163). Therefore, it was assumed Columbia River estuary hydro-geomorphic reaches E-F (from St. Helens to the Willamette-Columbia River confluence) was a reasonable estimate for the zone of mixing between Willamette and Columbia River water masses. However, the precise interface boundary is likely to vary with relative discharge of the two large rivers. The Willamette River makes up on average $\sim 15\%$ of the Columbia River flow below their confluence, but during the winter can spike to over 40% (USGSb,

no date). The transition of ⁸⁷Sr:⁸⁶Sr from the lower Columbia River to Pacific Ocean is less clear, with the middle estuary values straddling the global marine value of 0.70198 (Viezer 1989; Miller et al. 2010, 2011).

Table 3.1 Strontium elemental and isotopic ratios at Columbia River locations above the Willamette River confluence, in the Willamette River basin, in the Columbia River below the Willamette River confluence, and the global marine values.

Water Sampling Location	87Sr:86Sr	Sr:Ca (mmol/mol)	Source
Columbia River below John Day Dam	0.71391	2.36	Miller et al. 2011
Columbia River below The Dalles Dam	0.71304	2.32	Miller et al. 2011
Columbia River below Bonneville Dam	0.71328	2.35	Miller et al. 2011
South Fork McKenzie River	0.70380	3.20	Bourret 2013
Willamette River at Salem	0.70410	2.93	Bourret 2013
Willamette Falls	0.70450	2.70	Bourret 2013
Willamette River at Portland	NA	2.89	USGSb; this study
Lower Columbia River near St Helens, OR	0.70890	2.80	Bourret 2013
Lower Columbia River near Goble, OR	0.71050	2.60	Bourret 2013
Lower Columbia River at Beaver Army Terminal	NA	2.48	USGSb; this study
Global marine values	0.70918	8.54	Miller et al 2010, de Villiers 1999

3.2.2 Columbia River Tidal-fluvial to Brackish Transition

Otolith analysis of Sr/Ca elemental ratios has been a proven indicator of anadromy in fishes based on the chemical gradients encountered as individuals migrate from freshwater to marine environments (Campana 1999; Zimmerman 2005; Elsdon et al. 2008; Miller et al. 2010; Volk et al. 2010); and specifically for Chinook salmon in the Columbia River (Bacon et al. 2004; Campbell 2010; Miller et al. 2011; Roegner et al.
2015). Uptake of Sr from ambient water to the otolith is highly regulated in Chinook salmon. However, its discrimination is somewhat predictable: Chinook salmon otolith Sr/Ca ratios are typically ~0.4 to 0.2 (the distribution coefficient, D_{Sr}) of values from ambient water (Campana 1999; Bacon et al. 2004; Zimmerman 2005). Strontium has a conservative mixing profile and Sr/Ca is related to salinity (Campana 1999), reported here in practical salinity units (a dimensionless ratio of conductivities). In lab-based salinity treatments D_{Sr} in Chinook salmon ranged from ~0.4 at zero salinity and moved to ~0.2 at salinities of 6.3 to 33 (Zimmerman 2005). Strontium to calcium ratios increased to ~7.4 to 8.6 mmol/mol at salinites of 5 in an Oregon coastal estuary (Volk et al. 2010), approximately reaching marine values. Intermediate salinity (~13) caused a steep inflection on Chinook salmon otolith Sr/Ca profiles from around 1.0 to 1.5 mmol/mol in lab experiments (Zimmerman 2005) and in Columbia River field studies (Bacon et al. 2004; Campbell 2010; Bottom et al. 2011; Roegner et al. 2015).

Literature values for freshwater Sr/Ca in the Columbia River are variable (Table 3.1) but significantly lower in the tidal-fluvial portion of the estuary (mean ± 1 SD of 2.48 ± 0.144 mmol/mol; USGSb, no date) than in marine waters (8.51 \pm 0.0384 mmol/mol; de Villiers 1999). Salinities of 10 are common at Point Ellice (rkm 22) during flows lower than 5500 m³/s, but salinity intrusion is highly variable in the Columbia River estuary (Baptista et al. 2005; Bottom et al. 2005b; Simenstad et al. 2011). An estimated 68-86% of ~300 juvenile Chinook salmon captured near the brackish interface of the lower Columbia River (Point Adams Beach, near rkm 20) in 2003-05 (Campbell et al. 2010, Bottom et al. 2011) showed a Sr/Ca chemical inflection on their otoliths. Therefore, Point

Adams represents an approximate brackish water transition where otolith Sr/Ca would be expected to sharply increase for McKenzie Chinook salmon in this study.

3.2.3 Juvenile Otolith Width to Fork Length Relationship

Accurately back-calculating fish length at key chemical inflections along the otolith growth axis depends on a reliable model of the juvenile otolith-size to fork-length relationship. Otolith width has been shown to be a more reliable indicator of fish length than otolith length (Miller et al. 2010, 2011) and was the metric used in this study. The intention was to create a model with the greatest explanatory power for the transition between the Willamette River to the Columbia River tidal-fluvial and then brackish water masses. Therefore, for my back-calculation model I sought to cover a range of Columbia River estuary habitat, sampling years, seasons, and age classes of McKenzie River spring Chinook salmon.

Sagittal otoliths from juvenile Willamette River spring Chinook salmon were used to establish the otolith-width to fish-length relationship, and were obtained from other studies conducted within or bounding Columbia River estuary habitat. This included purse seine studies at the mouth of the estuary in brackish waters (Weitkamp et al. 2012), beach seine studies in the tidal-fluvial estuary (Roegner et al. 2015), and ODFW samples from the bypass trap at the Sullivan hydro-electric plant at Willamette Falls (the upper extent of tidal influence in the Willamette River). All samples used in the relationship that were collected in the Columbia River were genetically identified as the upper Willamette River Chinook salmon stock group with a probability of > 0.80 (Weitkamp et al. in press; Teel et al. 2014; Roegner et al. 2015). Origin could only be identified to the level of ESU, due to sampling locations and the resolving power of the current stock identification baseline. Sampling dates for otolith collections ranged from 2007 to 2013, with one fish from 2002. All fish in the final sample were unclipped. Presumably most of these were naturally spawned since over 95% of Willamette River hatchery salmon are marked before release (Schroeder et al. 2007, ODFW 2013); however, in recent surveys $\sim 2 - 25\%$ of returning Chinook salmon were hatchery-origin adults (Johnson and Friesen 2010), and unclipped Willamette River juveniles could have a slightly higher proportion of hatchery-origin individuals.

Otolith width measurements were taken from 69 juvenile Chinook salmon including seven spring fry, 17 spring/summer subyearling, 12 fall/winter subyearling and yearling, and 33 spring yearling migrants. Age class was determined by size and date of capture (Weitkamp et al. 2012; Roegner et al. 2015). I measured otolith width along the entire growth axis, following the methods of Miller (et al. 2010, 2011), which have proven more repeatable and robust than otolith radius length methods. However, analyzing the entire growth axis can be more time consuming and therefore may reduce sample size. Otolith widths were measured using a Leica® stereo-scope and Image Pro Plus® software. The otolith length axis was first identified as the longest transect between the posterior edge and rostral tip of the otolith, roughly parallel and close to the sulcus. The width was determined along the widest axes passing through the core region and perpendicular to the length axis (Figure 3.1). Figure 3.1 Juvenile Chinook salmon otolith width (solid arrow) is measured along the widest growth axis through the core and perpendicular to the length axis (dashed arrow).



A generalized fixed-effects linear regression analysis was used to fit the otolithwidth to fork-length relationship. The models with the lowest AIC scores used a samplegroup parameter and involved weighting the relationship by 1/otolith-width². This created tapered fork-length prediction intervals, narrower for smaller fish. Although weighting resulted in higher adjusted R^2 values, preliminary analysis of data from 2015 indicates this may be inappropriate; variable growth rates can alter the otolith-width to fork-length growth trajectory even for subyearling migrants (G.R. unpublished data). The samplegroup parameter for juvenile data explained much of the variability as an interaction or a main-effect term but was not applicable to the adult otolith collections, and therefore not useful for back-calculating sizes or estimating net growth in the tidal-fluvial estuary. Only 'otolith width' (OW: continuous) and 'freshwater age' (FWage: categorical, either subyearling or yearling) parameters were available for both juvenile modeling and adult back-calculation of juvenile fork length (FL).

I identified three back-calculation models that seemed appropriate: (1) the simple model without a "freshwater age" parameter (FL ~ OW), (2) a parallel lines model using a "freshwater age" parameter (FL ~ OW + FWage), and (3) the separate slopes model (FL ~ OW : FWage). Polynomial parameters of otolith width were not significant. The FWage parameter was not significant (P = 0.331) in the parallel lines model, but was significant (P < 0.0001) in the separate slopes model. However there was no evidence for using the separate slopes model instead of the simple model (two-way ANOVA, $F_{1,66} = 1.01$, P = 0.318). Slope parameters for FWage in the separate slopes and simple model were very similar, with 97.3% agreement. Therefore the simple model (Figure 3.2) was chosen to use in back-calculations from adult otoliths.

Figure 3.2 Otolith-width to fork-length relationship was similar for subyearling and yearling Chinook salmon sampled at various locations between the lower Columbia River estuary and Willamette Falls in 2002 and 2007-12. The mean slope is shown (blue line) with the slopes 95% confidence interval (dark grey) and the 95% prediction (light gray). * note the 'T-F estuary 2012' sample group includes one yearling sample from 2002 (the only grey triangle).



3.2.3 Adult Data Collection and Sample Selection

Oregon Department of Fish and Wildlife has collected Chinook salmon otolith and scale samples from all carcasses recovered during spawning surveys in the McKenzie River watershed since 2002 (Schroeder and Kenaston 2004; Schroeder et al. 2005, 2007). Sampling protocols are similar to those described for the Clackamas and Sandy River watersheds (ODFW, no date). Otoliths from unclipped fish were examined for evidence of hatchery-origin thermal marks. Confirmed natural-origin fish had scales analyzed for total age (three to six years old at return), and freshwater age at juvenile outmigration (subyearling or yearling) to identify an age class (Clemens et al. 2013; Borgerson et al. 2014).

I selected 100 adult otolith samples from the most common age classes in the McKenzie River Chinook salmon spawning population from 2002 to 2012. These included samples from four age classes representing ninety-five percent of all McKenzie River spawners: subyearling and yearling migrants from four- and five-year-old returning adults (Figure 3.3). I excluded from the analysis the less common reservoir-rearing juvenile types, three-year-olds, and six-year-olds to maximize group sample sizes and statistical power. Four-year-old subyearlings averaged 19% of the annual returns, and in two return years, accounted for > 40% of the returning adults. All otoliths in the analysis were selected from the 2005 and 2006 outmigration years. From the 2005 group, a high proportion of subyearling migrants returned as four-year-old adults; in the 2006 oumigration group, a higher number of yearling migrants returned as 5-year-old adults. Based on these age class differences, the analysis tested the hypothesis that freshwater growth was greater in the 2005 than 2006 outmigrant group. By sampling years with different age class proportions, I hoped to capture much of the variation in tidal-fluvial life histories for the bulk of the reproductive population. I characterized outmigration years instead of brood years to compare subyearlings and yearlings under similar environmental conditions in the tidal-fluvial estuary. The total sample size of 100 otoliths was constrained by budget and to minimize the number of archival samples sacrificed for these analyses.

Figure 3.3 Yearling juvenile Chinook salmon migrants make up on average 80% of the McKenzie River spawning population, but can vary from 50-95% of spawners. Proportions of the four most common age classes are shown from the 2002-2011 mean (top left), all juveniles outmigrating in 2005 (top center) and 2006 (top right). Samples for this study were taken from 2005 and 2006, and are shown below their respective outmigration years (bottom center and right). Age class is total age at adult return (four or five) followed by juvenile outmigration age subyearling (sub) or yearling (yr). Sample size is labeled over bars. Data modified from Schroeder et al. in review; and ODFW Willamette Spring Chinook and Fish Life History Analysis Projects.



Analysis of climate and water data revealed major differences in environmental conditions experienced by McKenzie River Chinook salmon between 2005 and 2006. Discharge was lower and water temperatures were warmer in 2005 relative to 2006 at the McKenzie River at Vida, the Willamette River at Portland, and the Columbia River at Beaver Army Terminal. In the McKenzie River, the winter of 2004-2005 had a flat hydrograph with only one discharge event >200 m³s⁻¹. In the winter of 2005-2006

discharge was generally >300 m³s⁻¹ from December through February, with one event >500 m³s⁻¹ (USGSb, no date). The relative low winter flows in the McKenzie River in 2004/2005 coincided with low flows throughout the Willamette River basin, a lower spring freshet in the Columbia River in 2005, a late spring upwelling transition off the Oregon and Washington Coast, and a weak upwelling season (www.cbr.washington.edu/status/trans; Tomaro et al. 2012). Summer time low flows were similar between 2005 and 2006. The Pacific Northwest Index (PNI) (http://www.cbr.washington.edu/status/pni) uses negative values to indicate wet-cool

conditions on land and a cool productive local ocean; conversely positive values indicate warm-dry conditions on land and a warm, less-productive local ocean. The PNI values for 2004, 2005 and 2006 were 0.94, 0.91 and -0.71 respectively.

3.2.4 Otolith Analysis

Chinook salmon otoliths were prepared for chemical profile analysis following the methods of Miller (2009), Miller and Kent (2009), and Miller et al. (2010, 2011). All water used throughout the process was filtered by a Dionex Ion Chromatograph (Dionex ICS-1500 with Autosampler) system operated by Oregon State University Institute of Water and Watersheds Collaboratory. Otoliths were mounted sulcus side up on standard microscope slide using Crystalbond[™] ceramic resin and hand-ground using 3M[™] Wet or dry sandpaper stepping from 300 to 2000 grit with water until the core was nearly exposed. Otoliths were then polished with 3M[™] lapping film and two µm alumina slurry. The otolith was heated, flipped, air cooled, and ground and polished down to the core plane on its ventral side to create thin sections. Microscopic slides with otolith thin sections were cut down to small rectangles using an isometric saw and cleaned in an ultra-sonic bath for five minutes. Individual otoliths were mounted, roughly ten to a standard microscope slide, for laser ablation.

Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS) was conducted at the W.M. Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University. Methodologies were adopted from Woodhead et al. (2005), Miller (2009), Miller and Kent (2009), and Miller et al. (2010, 2011). Two different plasma mass-spectrometers were used for measurements: Sr/Ca elemental ratios on a Thermo X-Series II Quadropole and ⁸⁷Sr:⁸⁶Sr isotopes on a Nu Plasma Multi-Collector. Both massspectrometers operate with a Photon Machines Analyte G2 laser and use He as a carrier gas. Two laser passes were made on each otolith parallel and in close proximity to each other ($<75 \,\mu$ m). Laser transects were set through the otolith core, visually identified as the dominant primordia near the center of the sulcus. Transects were set perpendicular to the length axis and visually identified (when possible) by otolith increments outside the zone of first feeding to the first annulus or check. Transects spanned the dorsal edge to the proximity of the ventral edge (see Figure 3.4). Exact transect orientation was altered on otoliths with imperfect surfaces (i.e. chips, cracks, pits). Nu Plasma instrument sensitivity was lower, so spot size had to be increased slightly for ⁸⁷Sr:⁸⁶Sr data. Also, laser speed had to be increased for ⁸⁷Sr:⁸⁶Sr readings because of instrument failures and time constraints.

Figure 3.4 Two parallel laser ablation transects were set through the adult Chinook salmon otolith core from edge to edge and perpendicular to growth increments along the dorsal-ventral growth axis to create chemical life-history profiles for each fish. The multi-collector mass spectrometer generated ⁸⁷Sr:⁸⁶Sr profiles (left transect, dotted line) and back-calculated juvenile size at entry to the tidal-fluvial Columbia River (5159 μ m for this sample). The quadropole mass spectrometer (right transect, solid line) generated Sr:Ca profiles and back-calculated size at exit from the tidal-fluvial Columbia River (5125 μ m for this sample).



Strontium isotopic ratios collected on the multi-collector were taken at ten Hz at a speed of ten μ m/s with a 50 μ m spot size. Background counts were subtracted and Krypton and Rubidium corrections followed the methods of Woodhead (et al. 2005). A marine gastropod (AP-Gastro) and a natural clinopyroxene (BBcpx-1) standard were run before and after every unknown sample. Mean ⁸⁷Sr/⁸⁶Sr was calculated for AP-Gastro standards and compared to the known solution measured mean value of 0.709190 (Miller and Kent 2009), and a small correction factor was applied to all data. The mean ⁸⁷Sr/⁸⁶Sr of BBcpx-1 measured here (mean \pm two SE, ⁸⁷Sr/⁸⁶Sr = .070447 \pm 0.00006) was identical

to the known value (mean \pm two SE, 87 Sr/ 86 Sr = .070447 \pm 0.00002) (A. Kent, Oregon State University, personal communication).

Elemental ratios of Sr to Ca obtained on the quadropole were taken at seven Hz with a five μ m/s speed and a spot size of 40 μ m. National Institute of Standards and Technology (NIST) 612 glass standards were analyzed before and after every four samples for data corrections and calibrations. For data processing, background values were first calculated and subtracted from all standards and samples. Measurements from known standards were averaged throughout a run and applied as a correction factor to all samples from that run. Otolith Sr/Ca, $\frac{C_{Sr}^{0}}{C_{Oa}^{0}}$, was determined by the formula:

$$\frac{C_{Sr}^{O}}{C_{Ca}^{O}} = \frac{C_{Sr}^{NIST} / C_{Ca}^{NIST}}{I_{86Sr}^{NIST} / I_{43Ca}^{NIST}} \times \frac{I_{86Sr}^{O}}{I_{43Ca}^{O}}$$

where *I* represents measured ion counts of otoliths (I^{O}) and standards (I^{NIST}). Concentrations for the otoliths (C^{O}) were determined by multiplying I^{O} by a correction factor of known standard values, C^{NIST} (Jochum et al. 2011), divided by I^{NIST} . Relative standard error of normalized ⁸⁶Sr counts measured from NIST 612 ($I_{86Sr}^{NIST}/I_{43Ca}^{NIST}$) between all nine runs was less than one percent.

Aligning micro-chemistry profiles from two transects and calculating profile distances was a multi-step process. Corrected and zeroed raw counts were plotted, and the ablation portion was visually identified by the sudden increase and drop off of Ca and/or Sr counts. Transect distance was recorded from the laser software during data collection, and ablation troughs were measured using a Leica® stereo-scope and Image

Pro Plus® software (see Figure 3.4). Distances recorded during transect setting were used for calculations, unless comparisons indicated a transcription error had occurred. Total transect distance was applied to the ablation data assuming equal distance between data points. Raw data were smoothed by taking a running ten-point mean value (Volk et al. 2010), corresponding to ~15 μ m from the center of each bounding data point. Using the otolith-width to fork-length relationship described earlier, 15 μ m would on average represent 0.9 mm of somatic fork-length growth in the tidal-fluvial Columbia River estuary. The core was visually identified and its position on each profile was set to zero. The two profiles were plotted, and ⁸⁸Sr voltage on the multi-collector profile was aligned with Sr/Ca on the quadropole profile to finely adjust the two transects.

Chemical inflection points along the two otolith transects were identified visually. The Sr/Ca inflection points were defined as the sharp increase from values near 1.0 mmol/mol to sustained values >1.5 mmol/mol; the otolith width at these inflection points was determined as the point of freshwater emigration. Willamette emigration was defined as the otolith width where 87 Sr/ 86 Sr rose from natal reach water values (~0.7035) to more than our detection efficiency (two SE of BBcpx-1 = 0.00006) above the lower Willamette value (~0.7045, Bourret 2013). Otolith width at Willamette emigration was subtracted from width at freshwater emigration to determine the width of otolith deposition while the juvenile was within the tidal-fluvial Columbia River.

Otolith widths were used to test for differences between groups (freshwater ages subyearling and yearling, outmigration years 2005 and 2006, and total ages four and five), although results were nearly identical when tests were applied to estimated forklengths. Otolith widths were used to estimate fork length and net growth for summary statistics. In addition, tidal-fluvial net growth was calculated as a proportion of size at both Willamette River and freshwater emigrations points. Data were first examined for the normality and constant variance assumptions of parametric tests. All parameters appeared to meet the constant variance assumption between groups. The normality assumption appeared to be met for emigration sizes and corresponding otolith widths, allowing for T-tests, fixed effects linear regression, and two-way Analysis of Variance (ANOVA) procedures on nested fixed effects linear regression models. However, all net growth data were positively skewed and did not meet the normality assumption. Transformations of net growth did not appear to meet the normality assumption, and Mann-Whitney rank-sum tests (MW), Kruskal-Wallis chi-squared tests (KW), and Kolmogorov-Smirnov distribution tests (KS) were used. Net growth was also added as a continuous fixed effect to two sets of regression models with emigration sizes as the response variable. All statistical analyses were performed in $\mathbb{R}^{\mathbb{C}}$.

Of the 100 adult McKenzie River Chinook salmon otoliths prepared for analysis, six were removed because of polishing plane errors (i.e., core plane not fully exposed, major surface cracking, or otolith ground past core plane). Another otolith was removed for apparent misclassification of a possible reservoir-rearing migrant that did not meet the selection criteria for a typical subyearling or yearling used for this analysis. One stray adult was excluded, identified by a mean ± 1 SD natal ⁸⁷Sr/⁸⁶Sr of 0.70574 ± 0.00002 ; Bourret (2013) found the range of ⁸⁷Sr/⁸⁶Sr in all major Cascade origin Willamette tributaries (including the McKenzie) to be 0.70355 to 0.70380 (n=11), consistent with the values of Cascade basalts (Miller et al. 2011). When back-calculated freshwater emigration size was used to independently classify emigration age, results agreed 96% with age assignments from ODFW scale analysis. Four fish that were outliers for freshwater emigration size in their original scale-assigned age classes were reclassified: three fish classified as subyearlings were reclassified as yearlings, and one yearling was reclassified as a subyearling. None of the reclassified fish showed signs of extended tidal-fluvial rearing (net growth ranged from 0.5 to 4 mm).

3.3 Results

The Willamette River and freshwater emigration transitions were successfully identified on all 92 otoliths analyzed from spawning McKenzie River Chinook salmon that outmigrated in 2005 or 2006. Otolith deposition corresponding to net growth in the

tidal-fluvial Columbia River was also detected, and 15 of 92 Chinook salmon showed evidence of extended tidal-fluvial rearing. The range of back-calculated Chinook tidalfluvial net growth is 0.1 to 42.3 mm, consistent with previous Chinook salmon growth and migration research (see discussion). Thirteen of fifteen otolith profiles with extended tidal-fluvial rearing had ⁸⁷Sr:⁸⁶Sr values intermediate between lower Willamette and Columbia River values, consistent with observations of Willamette Chinook salmon concentrated in hydro-geomorphic Reaches E-F (rkm 139-163) (Teel et al. 2009, 2014) where the two rivers mix.

3.3.1 Classification of Tidal-fluvial Estuarine Life-history Pathways

Although otolith profile patterns and net-growth estimates were continuous, seven juvenile life-history pathways through the tidal-fluvial Columbia River estuary were classified to aid descriptions (Figure 3.5). Juvenile age class (subyearling fry, subyearling fingerling, and yearling) was determined by previous ODFW scale analysis and with freshwater emigration size estimates from this study. Tidal-fluvial life-history pathway was determined by age class and tidal-fluvial Columbia River net growth; zero to four mm of net growth is classified as migratory, four to ten mm of net growth is classified as intermediate rearing, and over ten mm of net growth is classified as extended rearing. Nearly half (47%) of the samples selected in this study were subyearlings, however natural-origin McKenzie River Chinook salmon returns averaged ~20% subyearlings from 2002 to 2012 and varied from five to 50% of the natural-origin spawning population (see Figure 3.3 for age classes proportions in this study compared

with ten-year mean proportions collected on spawning grounds).

Figure 3.5 Seven tidal-fluvial life-history pathways were identified from 92 adult McKenzie River Chinook salmon that outmigrated in 2005 and 2006. The most common pathway for subyearlings and yearlings was migratory. Yearlings with intermediate-toextended tidal-fluvial rearing and subyearlings with intermediate rearing were also common. Although subyearlings with extended tidal-fluvial rearing were rare, two subyearling fry were classified as extended-rearing types. Estimated tidal-fluvial Columbia River residence time for each pathway is shown in parentheses.



Net growth differences likely represent size-related differences in residency within the tidal-fluvial Columbia River. Emigration from the Willamette River at a small size relative to age class, and possibly early time, is associated with greater net growth in tidal-fluvial habitat (see section 3.3.4). Therefore, residence times were estimated based on size and growth data from this study and previous Chinook salmon catch and growth rate studies in the Columbia River estuary. Estuarine entrance dates of the migratory and intermediate-rearing life histories most represented in these results were assumed to follow peak abundance trends in survey data. For subyearlings, estuarine entry observations of Willamette River Chinook salmon peak in late spring or summer (Figure 2.2) (Friesen et al. 2007; Teel et al. 2014). Yearlings have been observed in the Columbia River estuary in highest abundances from early to late spring (Friesen et al. 2007, Teel et al. 2014, Weitkamp et al. in press).

Yearlings with higher net growth, and assumed longer residency, could have entered the estuary in the fall as subyearlings, or possibly in early winter as yearlings. If winter Chinook salmon growth rates were on the slower end of the observed estuarine range of 0.11 to 0.82 mm/day (Bottom et al. 2011; Goertler et al. 2015), net growth estimates of 10 to 43 mm for yearlings with extended rearing life histories could equate to residence times of several months in the tidal-fluvial Columbia River.

Subyearlings with extended tidal-fluvial rearing were represented by two fry and one fingerling migrant. The two fry migrants experienced an estimated 23 mm and 32 mm of tidal-fluvial net growth or roughly 30% of each individual's estimated length at freshwater emigration. Fry have been observed in the tidal-fluvial Columbia River in the late winter to spring and these could have resided for on the order of ~two months. Fingerlings have been observed in the estuary from spring to winter, and the individual with extended rearing likely had over one month of tidal-fluvial residency (based on observed growth rates, see discussion). Otolith ⁸⁷Sr:⁸⁶Sr profiles were consistent with known water chemistry values throughout the McKenzie River Chinook salmon migration corridor. The otolith core had elevated ⁸⁷Sr:⁸⁶Sr from the mother's residence in marine water. Outside of the core region ⁸⁷Sr:⁸⁶Sr stabilized between ~0.7035 and ~0.7045, the known values in the McKenzie and Willamette rivers (Bourret 2013). Fifty-one percent of profiles showed a steep ascent in ⁸⁷Sr:⁸⁶Sr from ~0.7040 to the global marine value of 0.70918 (Viezer 1989) and were classified as migratory through the tidal-fluvial Columbia River. Thirtythree percent of profiles showed an intermediate ascent from lower Willamette River to marine ⁸⁷Sr:⁸⁶Sr values. Sixteen percent of profiles showed a broken ascent from lower Willamette River to marine ⁸⁷Sr:⁸⁶Sr values, indicating extended rearing in the tidalfluvial Columbia River.

Variations in chemical profiles depicting different life-history pathways are illustrated by representative samples classified as subyearling migratory (Figure 3.6a), yearling migratory (Figure 3.6b), and yearling extended-rearing (Figure 3.6c). The migratory otolith profiles had similar otolith widths during Willamette emigration (Figure 3.6, vertical dashed pink lines on lower ⁸⁷Sr:⁸⁶Sr graphs) and freshwater emigration (Figure 3.6, vertical dashed red lines on upper Sr/Ca graphs). The extended tidal-fluvial rearing profile had a conspicuous stair-step (e.g., Figure 3.6c black arrows) or spike feature in the ⁸⁷Sr:⁸⁶Sr profile after rising above the lower Willamette Value (horizontal solid pink line in lower ⁸⁷Sr:⁸⁶Sr), but before the Sr/Ca steeply rose in the corresponding upper graph. Otolith width during Willamette emigration was noticeably narrower than

during freshwater emigration in rearing (3.6c) relative to migratory patterns (3.6a and b). Strontium voltage (i.e., otolith Sr concentration) on the lower graph independently supports alignment with the Sr/Ca profile in the upper graph indicating that the Sr isotopic ratio increased before fish reached brackish water (with higher Sr concentration). However, Sr voltage is not normalized by Ca concentration, so the data are less reliable and more variable than Sr/Ca for measuring otolith widths. Figure 3.6 Examples of Chinook salmon otolith chemical profiles for subyearling migratory (3.6a), yearling migratory (3.6b), and yearling extended-rearing (3.6c) tidal-fluvial life histories. On all graphs the x-axis denotes position along the otolith profile. Zero approximates the otolith core, values to the left are the dorsal growth axis, and values to the right are the ventral growth axis. In each pane the top graph depicts otolith Sr/Ca profile (blue), and otolith width at freshwater emigration is marked with a dashed vertical red line. The lower graph depicts profiles of ⁸⁷Sr/⁸⁶Sr (green) and ⁸⁸Sr voltage (yellow), the global marine ⁸⁷Sr/⁸⁶Sr value of 0.70918 (dark horizontal line), the lower Willamette River ⁸⁷Sr/⁸⁶Sr value of 0.7045(pink horizontal line), and otolith width at Willamette emigration is similar in the migratory profiles (3.5a and b). Otolith width at Willamette emigration is smaller than at freshwater emigration and has a stair-step feature (3.5c black arrows) in the extended-rearing profile.



3.6a





3.6c



3.3.3 Estimated Juvenile Sizes at Tidal-fluvial Migratory Transitions

Emigration sizes were affected by outmigration year. Data were fit into two sets of fixed effects linear regression models using Willamette River and freshwater emigration sizes as the response and freshwater emigration age as a fixed effect (discrete: subyearling or yearling) in the reduced model. Outmigration year (discrete: 2005 or 2006) was added to the full model as an additional fixed effect. Two-way Analysis of Variance (ANOVA) tests compared the full and reduced regression models, and indicated outmigration year affected Willamette emigration size ($F_{1,89}$ = 4.59, P = 0.035) and freshwater emigration size ($F_{1,89}$ = 10.7, P = 0.0015). The regression models indicated 2005 had greater emigration sizes than in 2006: 4.2 mm larger at Willamette emigration and 5.7 mm larger at freshwater emigration.

Outmigration year influenced subyearling more than yearling emigration sizes (Figure 3.7, Table 3.2). One-sided tests evaluated the hypothesis that freshwater growth for each age class was faster in 2005 than in 2006. When the above data were split into subsets by freshwater age, distributions for Willamette emigration size were greater in 2005 than in 2006 for both subyearlings and yearlings (KS; for subyearlings D = 0.465, P = 0.012; and for yearlings D = 0.355, P = 0.046). Freshwater emigration size distributions were greater in 2005 than in 2006 for subyearlings (KS, D = 0.592, P = 0.0006), but not for yearlings (KS, D = 0.312, P = 0.093). However a two sample *T*-test showed: weak evidence yearling freshwater emigration size was 4.4 mm greater in 2005 than in 2006 (T = 1.67, df = 46.5, P = 0.051); strong evidence subyearling Willamette emigration size was 4.9 mm greater in 2005 than in 2006 (T = 2.06, df = 40.1, P = 0.023);

and convincing evidence subyearling freshwater emigration size was 7.27 mm greater in

2005 than in 2006 (*T* = 3.18, df = 33.5, *P* = 0.0016).

Figure 3.7 Back-calculated juvenile sizes were greater during 2005 than 2006 outmigration years among returning adult Chinook salmon in the McKenzie River. Upper panel depicts the estimated juvenile size distributions at the transition from the Willamette River to the Columbia River. Lower panel depicts the estimated juvenile size distributions at the transition from the tidal-fluvial to the brackish Columbia River.



Table 3.2 Emigration sizes (Willamette River emigration = WE, freshwater emigration = FE) and net growth estimates in the tidal-fluvial Columbia River were greater for yearlings than subyearlings, greater in outmigration (Om.) year 2005 than 2006, and greater for four-year-old than five-year-old returning McKenzie River Chinook salmon.

Subyearlings	ubyearlings Growth (mm)		WE size (mm)		FE size (mm)		Growth/WE-size		Growth/FE-size	
Subset:	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
All	5.48	5.80	82.95	8.33	88.43	8.02	7.0%	9.1%	6.1%	6.2%
Om. year 2005	6.53	7.00	85.11	9.24	91.64	6.39	8.6%	11.4%	7.1%	7.6%
Om. year 2006	4.15	3.56	80.23	6.24	84.37	8.17	5.1%	4.1%	4.7%	3.5%
four-year-olds	6.10	6.48	84.16	8.50	90.25	6.89	7.9%	10.3%	6.7%	7.0%
five-year-olds	3.67	2.51	79.45	7.03	83.12	9.02	4.5%	2.7%	4.2%	2.4%
Yearlings	Growth	(mm)	WE size	(mm)	FE size (mm)	Growth/W	VE-size	Growth/F	E-size
Yearlings Subset:	Growth (mean	(mm) SD	WE size mean	(mm) SD	FE size (mean	mm) SD	Growth/V mean	VE-size SD	Growth/F mean	E-size SD
Yearlings Subset:	Growth mean	(mm) SD	WE size mean	(mm) SD	FE size (mean	mm) SD	Growth/V mean	VE-size SD	Growth/F mean	E-size SD
Yearlings Subset: All	Growth mean 7.43	(mm) SD 8.32	WE size mean 122.01	(mm) SD 10.52	FE size (mean 129.44	mm) SD 9.47	Growth/V mean 6.5%	VE-size SD 8.2%	Growth/F mean 5.6%	E-size SD 6.2%
Yearlings Subset: All	Growth mean 7.43	(mm) SD 8.32	WE size mean 122.01	(mm) SD 10.52	FE size (mean 129.44	mm) SD 9.47	Growth/V mean 6.5%	VE-size SD 8.2%	Growth/F mean 5.6%	E-size SD 6.2%
Yearlings Subset: All Om. year 2005	Growth mean 7.43 7.83	(mm) SD 8.32 9.37	WE size mean 122.01 123.78	(mm) SD 10.52 12.47	FE size (mean 129.44 131.60	mm) SD 9.47 9.95	Growth/V mean 6.5% 7.0%	VE-size SD 8.2% 9.8%	Growth/F mean 5.6% 5.9%	E-size SD 6.2% 7.0%
Yearlings Subset: All Om. year 2005 Om. year 2006	Growth mean 7.43 7.83 7.02	(mm) SD 8.32 9.37 7.25	WE size mean 122.01 123.78 120.17	(mm) SD 10.52 12.47 7.86	FE size (mean 129.44 131.60 127.18	mm) SD 9.47 9.95 8.58	Growth/V mean 6.5% 7.0% 6.0%	VE-size SD 8.2% 9.8% 6.3%	Growth/F mean 5.6% 5.9% 5.3%	E-size SD 6.2% 7.0% 5.3%
Yearlings Subset: All Om. year 2005 Om. year 2006	Growth mean 7.43 7.83 7.02	(mm) SD 8.32 9.37 7.25	WE size mean 122.01 123.78 120.17	(mm) SD 10.52 12.47 7.86	FE size (mean 129.44 131.60 127.18	mm) SD 9.47 9.95 8.58	Growth/V mean 6.5% 7.0% 6.0%	VE-size SD 8.2% 9.8% 6.3%	Growth/F mean 5.6% 5.9% 5.3%	E-size SD 6.2% 7.0% 5.3%
Yearlings Subset: All Om. year 2005 Om. year 2006 four-year-olds	Growth mean 7.43 7.83 7.02 8.62	(mm) SD 8.32 9.37 7.25 10.28	WE size mean 122.01 123.78 120.17 123.65	(mm) SD 10.52 12.47 7.86 11.68	FE size (mean 129.44 131.60 127.18 132.27	mm) SD 9.47 9.95 8.58 9.01	Growth/V mean 6.5% 7.0% 6.0% 7.7%	VE-size SD 8.2% 9.8% 6.3% 10.9%	Growth/F mean 5.6% 5.9% 5.3% 6.4%	FE-size SD 6.2% 7.0% 5.3% 7.5%
Yearlings Subset: All Om. year 2005 Om. year 2006 four-year-olds five-year-olds	Growth mean 7.43 7.83 7.02 8.62 6.80	(mm) SD 8.32 9.37 7.25 10.28 7.17	WE size mean 122.01 123.78 120.17 123.65 121.14	(mm) SD 10.52 12.47 7.86 11.68 9.94	FE size (mean 129.44 131.60 127.18 132.27 127.94	mm) SD 9.47 9.95 8.58 9.01 9.50	Growth/V mean 6.5% 7.0% 6.0% 7.7% 5.9%	VE-size SD 8.2% 9.8% 6.3% 10.9% 6.5%	Growth/F mean 5.6% 5.9% 5.3% 6.4% 5.2%	FE-size SD 6.2% 7.0% 5.3% 7.5% 5.4%

3.3.4 Estimated Juvenile Net Growth in the Tidal-fluvial Columbia River Estuary

Net growth estimates were continuous in positively skewed distributions by age class (Figure 3.10). For all Chinook salmon analyzed, the range of estimated net growth was 0.1 to 42.7 mm, median net growth was 4.0 mm, and mean ± 1 SD net growth was 6.5 ± 7.3 mm. Estimated mean ± 1 SD net growth in the tidal-fluvial Columbia River was 5.5 ± 5.8 mm for subyearlings and 7.43 ± 8.32 mm for yearlings (Table 3.2). The upper quartile of estimated net growth for all Chinook salmon analyzed was above 7.4 mm. Net-growth mean values and SDs were greater for yearlings than for subyearlings, greater in outmigration year 2005 than in 2006, and greater for four-year-olds than five-year-

olds. Net growth as a percent of emigration sizes followed a similar pattern, except those mean values were slightly greater for subyearlings than for yearlings.

Figure 3.8 McKenzie River Chinook salmon net growth estimates in the tidal-fluvial Columbia River during 2005 and 2006 outmigration years were positively skewed. Although distributions were continuous, seven tidal-fluvial life-history pathways were categorized to aid in descriptions based on outmigration age, size, and tidal-fluvial net growth. Approximate tidal-fluvial residence timings are given in parenthesis.



Outmigration year had a greater effect on subyearling than yearling net-growth estimates; however, estimated net growth was not significantly different between subyearlings and yearlings (MW, Z = -0.301, two-sided P = 0.766), and the distributions were similar for the age classes (KS, D = 0.236, two-sided P = 0.155). When subyearlings and yearlings were grouped, net growth was not significantly greater in outmigration year 2005 than in 2006 (Figure 3.8) (MW, Z = 1.43, one-sided P = 0.077).

When analyzed separately, subyearlings had significantly more net growth in 2005 than in 2006 (MW, Z = 1.77, one-sided P = 0.039), and yearling net growth was similar in 2005 and 2006 (MW, Z = 0.520, one-sided P = 0.3).

Figure 3.9 Estimated net growth in the tidal-fluvial Columbia River was greater in outmigration year 2005 than 2006 for juvenile subyearlings, but was similar for yearlings, among returning adult Chinook salmon in the McKenzie River.



Net-growth estimates were added to fixed effect linear regression models as a continuous explanatory variable. In order to meet normality assumptions of linear regression, emigration sizes were used as the response variables. After accounting for freshwater age (subyearling or yearling) and outmigration year (2005 or 2006), Willamette emigration size was inversely proportional to net growth, which was a highly significant parameter in the full model (Figure 3.10, $\beta = -0.67$, $P = 1.9 \times 10^{-7}$). Adding net growth improved the full Willamette emigration size model (with freshwater-age, outmigration-year, and net-growth parameters) over the reduced model (with freshwater-

age, and outmigration-year parameters) (ANOVA, $F_{1,88} = 31.99$, $P = 1.9 \times 10^{-7}$). Again after accounting for freshwater age and outmigration year, freshwater emigration size was directly proportional to net growth, which was a highly significant parameter in the full model ($\beta = 0.33$, P = 0.0059). Adding net growth also improved the full freshwater emigration size model over the reduced model (ANOVA, $F_{1,88} = 7.35$, P = 0.0059).

Figure 3.10 Willamette River emigration size is inversely proportional tidal-fluvial net growth within subyearling and yearling age classes.



3.3.5 Relationships between Juvenile and Adult Characteristics

I compared total ages with emigration size and net-growth estimates to explore the effects of juvenile Chinook salmon growth conditions on adult phenotypes. All alternative hypotheses were one-sided to test that four-year-olds had faster freshwater juvenile growth than five-year-olds. Tidal-fluvial Columbia River net-growth estimates were not significantly greater for four-year-olds than five-year-olds when combining all fish or comparing subyearlings or yearlings only (MW: Z = 1.19, P = 0.1181; Z = 1.41, P= 0.082; Z = 0.567, P = 0.29 respectively). However, for subyearlings mean Willamette emigration size was 4.71 mm greater for four- than five-year-olds and the difference was significant (MW, Z = 2.09, P = 0.018). Subyearling mean freshwater emigration size was 7.13 mm greater for four- than five-year-olds and the difference was also significant (MW, Z = 2.51, P = 0.0056). Yearling Willamette emigration size was similar for fourand five-year-olds (MW, Z = 1.10, P = 0.1375). However, there was suggestive evidence yearling freshwater emigration size was greater for four-year-old than five-year-old (MW, Z = 1.5649, P = 0.060).

Estimated tidal-fluvial data from this study were compared with adult Chinook salmon return length, return location, and sex. Adult return length was not related to netgrowth or emigration sizes in any tested linear regression models. Net growth was similar between carcass recovery locations (Below Leaburg, Leaburg to S. Fork, S. Fork, and Above S. Fork; KW, $\chi^2 = 3.10$, df = 3, *P* = 0.39). Net growth was not significantly different between males and females (MW, *Z* = -1.49, two-sided *P* = 0.14).

3.4 Discussion

This is the first study to document Chinook salmon life-history pathways through the tidal-fluvial Columbia River estuary and their contributions to a specific spawning population. Diverse patterns of estuary use contribute to overall phenotypic diversity of McKenzie River Chinook salmon. By approximating realized function (Simenstad and Cordell 2000) of tidal-fluvial habitat, which incorporates growth and residency, this study supplements understanding of McKenzie River Chinook salmon life-histories described by Schroeder et al. (2007, in review) and their contributions to survival. Tidal-fluvial netgrowth estimates and approximate rearing location were consistent with previous studies, and implied residence times of days to months in the upper tidal-fluvial Columbia River estuary. The methods developed were successful in distinguishing growth in the tidalfluvial estuary and could be used as a quantitative metric for evaluating realized function of natural or restored habitats. These results suggest tidal-fluvial habitat should benefit life-history diversity and support recovery efforts of the Willamette River Spring Chinook salmon ESU.

The tidal-fluvial Columbia River estuary contributes to life-history diversity of McKenzie Chinook yearlings, and likely serves as over-wintering habitat for some. Tidal-fluvial net-growth estimates did not vary significantly between 2005 and 2006 for yearlings despite weak evidence of larger emigration sizes in 2005. In addition environmental differences between 2005 and 2006 were substantial, suggesting an estuary rearing life history may consistently contribute to population reproduction. Nearly one half (24 of 49) of all McKenzie River adult survivors from the dominant yearling juvenile age class (~80% of returns from 2002-2011; Schroeder et al. in review) showed evidence of intermediate to extended tidal-fluvial rearing. McKenzie River Chinook salmon, via active migration, competitive pressure, or passive displacement during high flow events, possibly enter the Columbia River estuary in the fall or winter. Once in the estuary individuals may rear, feed, or take refuge until making the transition to salt water as yearlings in the spring. Recent acoustic tagging studies indicate that other stocks of juvenile Chinook salmon also overwinter in the tidal-fluvial estuary (Johnson et al. 2015).

Net growth results suggest that intermediate tidal-fluvial rearing was common for subyearlings but extended rearing was rare. Subyearlings had higher tidal-fluvial netgrowth estimates in 2005 relative to 2006; and the 2005 subyearling cohort composed an unusually large proportion, ~47%, of the spawning population in 2009 (Schroeder et al. in review). This suggests the tidal-fluvial habitat may be particularly important to subyearlings during low overall salmon productivity conditions (e.g., in 2005 or other years with poor McKenzie Chinook yearling success and high PNI values) and could confer resilience to the spawning population by providing alternative feeding habitats. Increased subyearling net growth in the tidal-fluvial Columbia River in 2005 over 2006 could have been affected by increased temperatures speeding metabolism and habitat productivity, lower discharge slowing migration rates, or both (NMFSb 2008).

To my knowledge, these results provide the first documentation that fry migrants contribute to the McKenzie River Chinook salmon spawning population. Willamette River fry have been observed in the Columbia River estuary early in the year (Friesen et al. 2007; Teel et al. 2009, 2014); however little is known about their estuarine residency or survival to adulthood. The contribution of fry migrants to the McKenzie River spawning population verifies an alternative estuarine-dependent life-history pathway that could directly benefit from estuary restoration, and possibly contribute to population resilience.

Fixed effect linear regression models suggest the tidal-fluvial Columbia River supports freshwater emigration size and presumably greater fitness and survival of McKenzie River Chinook salmon. After accounting for differences between subyearlings and yearlings, and outmigration years 2005 and 2006, Willamette emigration size was inversely and freshwater emigration size directly proportional to estimated net growth in the tidal-fluvial Columbia River. Together these results suggest tidal-fluvial habitat directly supports McKenzie River Chinook salmon: individuals that entered the tidalfluvial Columbia River estuary at a relatively smaller size had greater net growth, and those that have a greater net growth, exited the tidal-fluvial Columbia River at a relatively larger size.

My net-growth estimates are consistent with expectations based on Chinook salmon growth and migration rate data from the Columbia River estuary. Migration rates estimated for Willamette River Chinook salmon in the tidal-fluvial Columbia River span from ~3 km/day (Roegner et al. 2015) to 40 km/day (Schroeder et al. in review). Chinook salmon growth rates estimated from otolith increments and direct observations in the Columbia River estuary range from 0.11 to 0.82 mm/day (Campbell 2010; Bottom et al. 2011; Goertler et al. 2015). The tidal-fluvial Columbia River estuary extends on average 140 total km (rkm 23 – rkm 163) below the Willamette River confluence. Assuming that the fastest migrants likely consume the least food and experience the slowest growth rates, then the least net growth we might expect in the tidal-fluvial Columbia River is ~ 0.4 mm (i.e., (140 km / 40 km/day) x (0.11 mm/day), and the highest predicted net growth should be ~50 mm (i.e., (140 km / 3km/day) x (0.82 mm/day). These back-of-the-envelope calculations are similar to the 0.1 mm to 42.7 mm range in net growth estimated by the otolith methods in this study.

Residence time estimates can be made by dividing net growth by an approximate growth rate, although this requires multiple assumptions and should be interpreted cautiously. Research suggests the slowest growth rates were likely more typical of active migrants, and the fastest growth rates more typical of juveniles that rear in off-channel habitats (Goertler et al. 2015; Roegner et al. 2015). However, growth rates in the Columbia River estuary vary by season, year, and habitat type (Campbell 2010; Bottom et al. 2011; Goertler et al. 2015; Roegner et al. 2015) and range almost an order of magnitude from 0.11 mm/day to 0.82 mm/day. Recent Chinook salmon otolith increment analyses measured growth increments for the 14 days prior to capture and estimated growth rates of ~0.1 to 0.4 mm/day in the tidal-fluvial Columbia River estuary (Goertler et al. 2015). Applying these rates across the range of net growth observed in this study (0.1 to 42.7 mm) yields residence times ranging from a few days to >3 months. Strontium isotopic signatures during tidal-fluvial rearing indicated residence in the zone of mixing between Willamette and Columbia River water masses; this is consistent with observations of relatively high proportions of Willamette Chinook salmon distributed in

the upper Columbia River estuary, including large numbers of January fry and March yearlings near the Willamette-Columbia River confluence (Teel et al. 2014).

The techniques developed in this study could be applied to more years of data to establish a baseline of the tidal-fluvial Columbia River estuary's realized function for Chinook salmon, and to evaluate the cumulative effectiveness of estuary restoration actions. The Annual difference in net growth was not significant for yearling migrants. However, two years of data are not enough to characterize natural variability of tidalfluvial life-history expression in Chinook salmon. Subyearlings showed significant variation between outmigration years, and inclusion of the 2005 outmigration year as half of my sample likely biased the subyearling mean and variance estimates of net growth.

Despite successfully identifying tidal-fluvial rearing otolith profiles, the techniques developed have four weaknesses. (1) The micro-chemistry proxies used do not account for the lower 42 km of tidal-fluvial Willamette River habitat, and therefore net growth calculations are a conservative estimate of tidal-fluvial habitat use. However, restoration of tidal-fluvial habitat has been largely focused on the Columbia River, and therefore assessing the realized function of that region is most germane to management actions. (2) Sizes at emigration measured by otolith chemical markers represent transitions between shifting water masses rather than fixed geographic locations in the Columbia River estuary. However, marking the first rise above lower Willamette River Sr isotopic ratios and the steep increase of Sr/Ca as the points of emigration likely minimizes noise associated with this variability. (3) The otolith technique cannot independently resolve the date of entry into the tidal-fluvial Columbia River and the

duration of residency without an extensive time-series water sampling regime. However, previous studies have shown peak migration times and documented growth rates that allow for reasonable assumptions about timing. (4) The otolith-growth to somatic-growth relationship varies among individuals and with environmental conditions. This has been established in the literature and the general premise is that slower growing fish have larger otoliths per fish size than faster growing fish (Francis 1990, Campana 1999). Considering growth conditions were faster in 2005, these variations may have been underestimated. However, increasing net-growth estimates in 2005 would strengthen test differences, and is not likely to change tidal-fluvial life history calculations, except to change a few fish from migratory to intermediate-rearing and from intermediate- to extended-rearing classifications.

Otolith analysis allows for virtual recaptures, or repeated measurement from individual fish, and a reliable sample from specific Chinook salmon spawning populations. It is important to remember this study only sampled the returning adults, not all juvenile phenotypes sampled during outmigrant surveys. Comparing the proportions of successful phenotypes with all those observed could help identify recovery opportunities to support the life-histories that are missing or underrepresented in the spawning population. Using multiple otolith chemical proxies allows for multiple "observations" per individual to integrate the entire tidal-fluvial Columbia River landscape and reconstruct individual life histories. Finally, otolith analysis allows for estimates of realized function without experimental manipulation effects; such as those caused by tagging and from monitoring transported and confined hatchery-origin fish in estuary restoration sites (Simenstad and Cordell 2000). These methods could be directly applied to other salmon populations spawning in Cascade Mountain reaches, or possibly modified for interior Columbia River basin salmon stocks. For interior stocks, it is possible a decrease in Sr isotopic signature could be detected as juveniles migrate past the major Cascade tributaries (i.e., the Willamette and Cowlitz rivers); however, this would require validation of water chemistry and would exclude the upper portion of the tidal-fluvial estuary between these locations and Bonneville Dam. A time-series water sampling regime throughout a specific salmon population's migration corridor could uncover useful indices such as: variable Sr/Ca, Ba/Ca, and O isotopes (18 and 16). Combining the methods developed here with mass otolith marking of juvenile Chinook salmon, either during trap-and-haul operations around main-stem dams or during passage at Bonneville dam bypass facilities could also isolate tidal-fluvial otolith growth for at-risk interior Chinook salmon stocks.

In summation, these results demonstrate tidal-fluvial Columbia River habitats contribute to the performance and life-history diversity of a Chinook salmon population—suggesting restoration in tidal-fluvial habitat may benefit recovery of Columbia River Chinook salmon ESUs. This study quantified the tidal-fluvial habitat's realized function as indicated by net growth and improved understanding of estuarine life-history pathways and their reproductive contributions to the McKenzie River Chinook salmon population. This knowledge could help to guide recovery programs targeting the Columbia River estuary and the Willamette River Chinook salmon ESU. Uncertainty about the potential benefits of Columbia River estuary restoration to large yearling migrants is reflected in lower target survival benefits for stream-type or yearling
(6%) than ocean-type or subyearling (9%) Chinook salmon ESUs. This study has demonstrated that yearling life-history types, previously considered rapid estuarine migrants, can reside in the tidal-fluvial Columbia River estuary for extended periods before entering the ocean. These findings raise the possibility that restoration may offer greater-than-anticipated benefits to yearlings from other Columbia River Chinook salmon stocks.

References:

- Bacon, C. R., P. K. Weber, K. A. Larsen, R. Reisenbichler, J. A. Fitzpatrick, and J. L. Wooden. 2004. Migration and rearing histories of Chinook salmon (*Oncorhynchus tshawytscha*) determined by ion microprobe Sr isotope and Sr/Ca transects of otoliths. Canadian Journal of Fisheries and Aquatic Sciences 61(12):2425–2439.
- Baptista, A. M., Y. Zhanga, A. Chawlaa, M. Zulauf, C. Seatona, E. P. M. Iijab, J. Kindlec, M. Wilkina, M. Burlaa, and P. J. Turnera. 2005. A cross-scale model for 3D baroclinic circulation in estuary-plume-shelf systems: II. Application to the Columbia River. Continental Shelf Research 25:935–972.
- Beckman, B. R., B. Gadberry, P. Parkins, K. A. Cooper, and K. D. Arkush. 2007. Statedependent life history plasticity in Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate smolting and early male maturation. Canadian Journal of Fisheries and Aquatic Sciences 64(2):256–271.
- Beckman, B. R., D. A. Larsen, and W. W. Dickhoff. 2003. Life history plasticity in Chinook salmon: Relation of size and growth rate to autumnal smolting. Aquaculture 222(1-4):149–165.
- Borgerson, L., B. Clemens, K. Bowden, and S. Gunckel. 2014. Fish Life History Analysis Project: methods for scale analysis. Oregon Department of Fish and Wildlife Information Report 2014-10 (September):41 pp.
- Bottom, D. L., A. Baptista, J. Burke, L. Campbell, E. Casillas, S. Hinton, D. A. Jay, M. A. Lott, G. Mccabe, R. Mcnatt, M. Ramirez, G. C. Roegner, C. A. Simenstad, S. Spilseth, L. Stamatiou, D. Teel, and J. E. Zamon. 2011. Estuarine habitat and juvenile salmon: current and historical linkages in the lower Columbia River and estuary: Final Report 2002-2008. National Marine Fisheries Service Report to the U.S. Army Corps of Engineers Contract W66QKZ20374382. Portland, OR.
- Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005a. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). Estuarine, Coastal and Shelf Science 64:79–93.
- Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005b. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. NOAA Technical Memorandum NMFS-NWFSC-68:246 pp.

- Bourret, S. 2013. Salmon life history in an altered landscape: reconstructing juvenile migration using chemical and structural analysis. Master's Thesis. University of Idaho (April).
- Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263–297.
- Campana, S. E., and S. R. Thorrold. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries and Aquatic Sciences 58(1):30–38.
- Campbell, L. A. 2010. Life histories of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary as inferred from scale and otolith microchemistry. Master's Thesis. Oregon State University, Corvallis, Oregon.
- Clemens, B. K., K. Bowden, and L. Borgerson. 2013. Fish life history analysis project: project description. Oregon Department of Fish and Wildlife (July 2013):6 pp.
- Elsdon, T. S., B. K. Wells, S. E. Campana, B. M. Gillanders, C. M. Jones, K. E. Limburg, D. H. Secor, S. R. Thorrold, and B. D. Walther. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: Hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology: an Annual Review 46(1):297–329.
- Faure, G. 2001. Origin of igneous rocks: the isotopic evidence. Springer, New York.
- Ford, M., T. Cooney, P. Mcelhany, N. Sands, L. Weitkamp, J. Hard, M. Mcclure, R. Kope, J. Myers, A. Albaugh, D. Teel, P. Moran, and J. Cowen. 2010. Status review update for Pacific salmon and Steelhead listed under the Endangered Species Act. NOAA Technical Memorandum NMFS-NWFSC-113:346 pp.
- Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology 36:883–902.
- Fresh, K. L., E. Casillas, L. L. Johnson, and D. L. Bottom. 2005. Role of the estuary in the recovery of Columbia River basin salmon and steelhead: an evaluation of the effects of selected factors on salmonid population viability. NOAA Technical Memorandum NMFS-NWFSC-69:105 pp.
- Friesen, T. A. 2005. Biology, behavior and resources of resident and anadromous fish in the lower Willamette River. Oregon Department of Fish and Wildlife Final Report of Research 2000-2004, to City of Portland (March):246 pp.
- Friesen, T. a., J. S. Vile, and A. L. Pribyl. 2007. Outmigration of juvenile Chinook salmon in the lower Willamette River, Oregon. Northwest Science 81(3):173–190.

- Goertler, P. A. L., C. A. Simenstad, D. L. Bottom, S. Hinton, and L. Stamatiou. 2015. Estuarine habitat and demographic factors affect juvenile Chinook (*Oncorhynchus tshawytscha*) growth variability in a large freshwater tidal estuary. Estuaries and Coasts:18 pp.
- Gray, A., C. A. Simenstad, D. L. Bottom, and T. J. Cornwell. 2002. Contrasting functional performance of juvenile salmon habit in recovering wetlands of the Salmon River estuary, Oregon, U.S.A. Restoration Ecology 10(3):514–526.
- Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon. Fishery Bulletin 77(3):653–668.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–394 in C. Groot and L. Margolis, editors. Pacific Salmon Life Histories. UBCPress.
- Hering, D. K., D. L. Bottom, E. F. Prentice, K. K. Jones, and I. A. Fleming. 2010. Tidal movements and residency of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) in an Oregon salt marsh channel. Canadian Journal of Fisheries and Aquatic Sciences 67(3):524–533.
- Jochum, K. P., U. Weis, B. Stoll, D. Kuzmin, Q. Yang, I. Raczek, D. E. Jacob, A. Stracke, K. Birbaum, D. A. Frick, D. Günther, and J. Enzweiler. 2011. Determination of reference values for NIST SRM 610-617 glasses following ISO guidelines. Geostandards and Geoanalytical Research 35(4):397–429.
- Johnson, G. E., G. R. Ploskey, N. K. Sather, and D. J. Teel. 2015. Residence times of juvenile salmon and steelhead in off-channel tidal freshwater habitats, Columbia River, USA. Canadian Journal of Fisheries and Aquatic Science 696(January):684– 696.
- Johnson, M. A., and T. A. Friesen. 2010. Spring Chinook salmon hatcheries in the Willamette Basin: existing data, discernable patterns and information gaps. Final Report to U.S. Army Corps of Engineers, Task Order NWPPM-09-FH-05:87 pp.
- Kennedy, B. P., J. D. Blum, C. L. Folt, and K. H. Nislow. 2000. Using natural strontium isotopic signatures as fish markers: methodology and application. Canadian Journal of Fisheries and Aquatic Sciences 57(11):2280–2292.
- Kennedy, B. P., A. Klaue, J. D. Blum, C. L. Folt, and K. H. Nislow. 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. Canadian Journal of Fisheries and Aquatic Sciences 59(6):925–929.

- Madin, I. P. 2009. Oregon: a geologic history. Oregon Department of Geology and Mineral Industries Interpretive Series Map 28 available: www.oregongeology.org/sub/publications/ims/ims-028/ (accessed 10 July 2015).
- Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (Oncorhynchus kisutch) and chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. Estuaries 26(4):1094–1103.
- Marcoe, K., and S. Pilson. 2013. Habitat change in the lower Columbia River and estuary, 1870-2011. Lower Columbia River Estuary Partnership:57 pp.
- McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42:158 pp.
- Miller, J. A. 2009. The effects of temperature and water concentration on the otolith incorporation of barium and manganese in black rockfish Sebastes melanops. Journal of Fish Biology 75(1):39–60.
- Miller, J. A., V. L. Butler, C. A. Simenstad, D. H. Backus, A. J. R. Kent, and B. Gillanders. 2011. Life history variation in upper Columbia River Chinook salmon (*Oncorhynchus tshawytscha*): a comparison using modern and ~500-year-old archaeological otoliths. Canadian Journal of Fisheries and Aquatic Sciences 68(4):603–617.
- Miller, J. A., A. Gray, and J. Merz. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. Marine Ecology Progress Series 408:227–240.
- Miller, J. A., and A. J. R. Kent. 2009. The determination of maternal run time in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) based on Sr/Ca and 87Sr/86Sr within otolith cores. Fisheries Research 95(2-3):373–378.
- Myers, J., C. Busack, D. Rawding, A. Marshall, D. Teel, D. M. V. Dornick, and M. T. Maher. 2006. Historical population structure of Willamette and lower Columbia River basin Pacific salmonids. NOAA Technical Memorandum NMFS-NWFSC-73:311 pp.
- Naiman, R. J. 2013. Socio-ecological complexity and the restoration of river ecosystems. Inland Waters 3(4):391–410.
- NMFSa (National Marine Fisheries Service). 2008. Federal Columbia River power system biological opinion. Endangered Species Act Section 7(a)(2) And Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation F/NVVR/2005/05883 (5 May 2008).

- NMFSb (National Marine Fisheries Service). 2008. Willamette project biological opinion. Endangered Species Act Section 7(a)(2) and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation F/NWR/2000/02117 (11 July 2008).
- ODFW (Oregon Department of Fish and Wildlife). (n.d.). Clackamas and Sandy River Spawning Surveys. www.oregonstate.edu/dept/ODFW/willamettesalmonidrme/clackamas-sandy-riverspawning-surveys, accessed 2015-08-08.
- ODFW (Oregon Department of Fish and Wildlife). 2013. Fisheries management and evaluation for 2012 Willamette River spring Chinook. ODFW Ocean Salmon and Columbia River Program (January 2013):24 pp.
- ODFW (Oregon Department of Fish and Wildlife), and NMFS (National Marine Fisheries Service). 2011. Upper Willamette River conservation and recovery plan for Chinook salmon and Steelhead (5 August 2011):462 pp. plus executive summary and appendices.
- PNNL (Pacific Northwest National Laboratory). 2012. Evaluation of cumulative ecosystem response to restoration projects in the lower Columbia River and estuary, 2010. Report to U.S. Army Corps of Engineers Contract DE-AC05-76RL01830 (May):389 pp.
- Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commision of Oregon 4(2):42 pp.
- Rieman, B. E., C. L. Smith, R. J. Naiman, G. T. Ruggerone, C. C. Wood, N. Huntly, E. N. Merrill, J. R. Alldredge, P. A. Bisson, J. Congleton, K. D. Fausch, C. Levings, W. Pearcy, D. Scarnecchia, and P. Smouse. 2015. A Comprehensive Approach for Habitat Restoration in the Columbia Basin. Fisheries 40(3):124–135.
- Roegner, C., D. Bottom, A. Baptista, L. Campbell, P. Goertler, S. Hinton, R. Mcnatt, C. Simenstad, D. Teel, and K. Fresh. 2015. Salmon habitat use of tidal-fluvial habitats of the Columbia River estuary, 2010-2013. National Marine Fisheries Service Final Report to U.S. Army Corps of Engineers, Portland District (April 2015):103 pp.
- Schroeder, R. K., and K. R. Kenaston. 2004. Spring Chinook salmon in the Willamette and Sandy rivers. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-09:64 pp.
- Schroeder, R. K., K. R. Kenaston, and Krentz L. K. 2005. Spring Chinook salmon in the Willamette and Sandy rivers with 1996 – 2004 summaries. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-10:90 pp.

- Schroeder, R. K., K. R. Kenaston, and L. K. McLaughlin. 2007. Spring Chinook salmon in the Willamette and Sandy rivers. Annual Progress Report Oregon Department of Fish and Wildlife F-163-R-11:62 pp.
- Simenstad, C. A., J. L. Burke, J. E. O'Connor, and K. L. Cannon, C., Heatwole, D.W., Ramirez, M.F., Waite, I.R., Counihan, T.D., Jones. 2011. Columbia River estuary ecosystem classification - concept and application. U.S. Geological Survey Open-File Report 2011-1228:54p.
- Simenstad, C. A., and J. R. Cordell. 2000. Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific northwest estuaries. Ecological Engineering 15(283):302.
- Teel, D. J., C. Baker, D. R. Kuligowski, T. A. Friesen, and B. Shields. 2009. Genetic stock composition of subyearling Chinook salmon in seasonal floodplain wetlands of the lower Willamette River, Oregon. Transactions of the American Fisheries Society 138(1):211–217.
- Teel, D. J., D. L. Bottom, S. A. Hinton, D. R. Kuligowski, G. T. McCabe, R. McNatt, G. C. Roegner, L. A. Stamatiou, and C. A. Simenstad. 2014. Genetic identification of Chinook salmon in the Columbia River estuary: stock-specific distributions of juveniles in shallow tidal freshwater habitats. North American Journal of Fisheries Management 34(3):621–641.
- Teel, D., T. Lundrigan, and P. Moran. 2006. Genetic analysis of Chinook salmon juveniles sampled in 2003 and 2004 at the Sullivan hydroelectric plant fish bypass in the Willamette River. NOAA Northwest Fisheries Science Center Report to Portland General Electric (1 February 2006):15 pp.
- Tomaro, L. M., D. J. Teel, W. T. Peterson, and J. A. Miller. 2012. When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. Marine Ecology Progress Series 452:237–252.
- USGSb (United States Geologic Survey). (no date). National Stream Quality Accounting Network. http://water.usgs.gov/nasqan/, accessed 2015-08-08.
- Viezer, J. 1989. Strontium isotopes in seawater through time. Annual Review of Earth and Planatary Sciences (3):141–167.
- De Villiers, S. 1999. Seawater Sr and Sr/Ca variability in the Atlantic and Pacific oceans. Earth and Planetary Science Letters 171:623–634.
- Volk, E. C., D. L. Bottom, K. K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary, Oregon, using

otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139(2):535–549.

- Waples, R. S., G. R. Pess, and T. J. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications 1(2):189–206.
- Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution; international journal of organic evolution 58(2):386–403.
- Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fishery Bulletin 110(4):426–450.
- Weitkamp, L. A., D. J. Teel, M. Liermann, S. A. Hinton, D. M. Van Doornik, and P. J. Bentley. (n.d.). Stock-specific size and timing at ocean entry of Columbia River juvenile salmon and Steelhead: implications for early ocean growth. In Review at Marine and Coastal Fisheries.
- Woodhead, J., S. Swearer, J. Hergt, and R. Maas. 2005. In situ Sr-isotope analysis of carbonates by LA-MC-ICP-MS: interference corrections, high spatial resolution and an example from otolith studies. Journal of Analytical Atomic Spectrometry 20(1):22.
- Zimmerman, C. E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62(1):88–97.

4. General Conclusions

Connectivity between populations, habitats, and ecological processes contribute to the viability and resilience of Chinook salmon (Bottom et al. 2005b, 2011); however, this connectivity has been altered by development of the Columbia River basin (Bottom et al. 2005b; Healey 2009). Anthropogenic development has likely simplified life-history expression of Chinook salmon, at the expense of their abundances and resilience (Burke 2004; Bottom et al. 2005b, 2011; Williams et al. 2006; Schindler et al. 2010).

Historically, Chinook salmon phenotypic plasticity allowed for life-history diversity through a continuum of ecologically functional habitats (Healey 1991, McElhany et al. 2000, Waples et al. 2004, Bottom et al. 2005b). The benefits of lifehistory diversity to long-term population survival and to buffer short term environmental variations (i.e., the portfolio effect) have been established for salmonids generally (Healey 1991; McElhany et al. 200; Hilborn et al. 2003; Myers et al. 2006; Gustafson et al. 2007; NMFSb 2008; Moore et al. 2010; Schindler et al. 2010), and specifically for the McKenzie River population of Chinook salmon (Schroeder et al. 2007, in review). However, prior to this study, the estuarine life histories of McKenzie River Chinook salmon were poorly understood.

Otoliths provide a 'natural tag' for Sr that can be used to back-calculate movements, age, and size of anadromous fishes throughout their life histories (Campana 1999; Campana and Thorrold 2001; Elsdon et al. 2008). Yet this technology has not previously been applied to the tidal-fluvial Columbia River estuary. Non-lethal sampling of otoliths, which can be accomplished by sampling adults after spawning, is beneficial when studying threatened salmon species. Otolith techniques can also detect estuarine chemical indicators from specific salmon spawning populations. Individual migratory histories may be discriminated at a fine resolution from known water chemistry changes and through the use of multiple otolith chemical proxies (Bacon et al. 2004).

The methods developed here provide a metric of the realized function of tidalfluvial Columbia River estuary habitat. Quantification of tidal-fluvial Columbia River net growth for surviving McKenzie Chinook was successful for the years analyzed, but not sufficient for a monitoring baseline. Future studies could expand analysis years and include rare age classes (e.g., three-year-old subyearlings, six-year-old yearlings). The resolution of otolith analysis also could be further refined by collecting additional timeseries environmental data to track temporal and spatial changes in water chemistry.

Determining emigration timing and identifying more emigration points may be possible by monitoring riverine conditions and chemistry. However, this would require sampling at least five years in advance of collecting otoliths. Analyzing water temperature and ¹⁸O:¹⁶O isotope levels with otolith O isotope profiles has potential to back-calculate water temperature profiles and emigration dates in conjunction with the proxies used in this study. River Sr, Ba, and Ca concentration vary temporally and could be aligned with otolith profiles to refine analysis capabilities (Campana 1999; Elsdon et al. 2008). Specifically, Sr/Ca ratios in the upper McKenzie River watershed are highly variable and reach values of ~four mmol/mol (Bourret 2013); this signal could be used to match dates with Sr/Ca peaks during the freshwater portion of otolith profiles to identify natal rearing locations.

This study could support adaptive management of Chinook salmon restoration efforts in the Columbia River estuary by addressing the critical uncertainty of populationspecific use of estuary habitat and assessing the impact on adult returns—the ultimate measure of success. Although I have chosen the McKenzie River population as a case study, the methodologies developed here could be applied to other Cascade origin Chinook salmon populations. With additional water sampling and possibly massmarking otoliths, these methods could be modified to study interior Columbia River Chinook salmon stocks.

McKenzie River Chinook salmon net growth in tidal-fluvial estuarine habitat was similar if not greater for yearlings than subyearlings. This contrasts with the results of many lower-estuary surveys indicating that subyearling migrants linger in shallow, nearshore habitats while larger yearlings move more rapidly seaward in deeper channels (e.g., Dawley et al. 1986; Bottom et al. 2011; Weitkamp et al. 2012). Such results have raised questions about the likely benefits of restoring shallow estuarine habitat for yearling migrants, as reflected in the greater survival goals for subyearling, or "ocean-type", than for yearling, or "stream type", Chinook salmon ESUs. Yearlings, by definition, reside for longer periods in fresh water. However, in this case the freshwater migration corridor happens to be tidal-fluvial for the lower 183 river km, including the lower Willamette River, and the period of estuarine residency extends to fall and winter seasons after typical subyearling migrants have entered the ocean. The premise that subyearlings are estuarine dependent is supported by a breadth of literature (i.e., Reimers 1973; Healey 1980, 1991; Bottom et al. 2005a; Volk et al. 2010), which may not represent the full range of Chinook salmon rearing behaviors in larger river-dominated systems. In the Columbia River estuary, long tidal-fluvial reaches and floodplain access may afford alternative low-velocity areas for juvenile salmon rearing. This study has demonstrated that Chinook salmon yearling juvenile migrants (or "ocean-type") can reside in the tidal-fluvial Columbia River estuary for extended periods before entering the ocean. Finally these results suggest benefits of estuary restoration may be possible for yearlings from other Columbia River Chinook salmon stocks, including migrants from the interior basin. In conclusion, I was initially surprised to find more yearlings with tidal-fluvial rearing than subyearlings; upon more thorough analysis I believe the results are real, and consistent with previous studies.

References:

- Bacon, C. R., P. K. Weber, K. A. Larsen, R. Reisenbichler, J. A. Fitzpatrick, and J. L. Wooden. 2004. Migration and rearing histories of Chinook salmon (*Oncorhynchus tshawytscha*) determined by ion microprobe Sr isotope and Sr/Ca transects of otoliths. Canadian Journal of Fisheries and Aquatic Sciences 61(12):2425–2439.
- Bottom, D. L., A. Baptista, J. Burke, L. Campbell, E. Casillas, S. Hinton, D. A. Jay, M. A. Lott, G. Mccabe, R. Mcnatt, M. Ramirez, G. C. Roegner, C. A. Simenstad, S. Spilseth, L. Stamatiou, D. Teel, and J. E. Zamon. 2011. Estuarine habitat and juvenile salmon: current and historical linkages in the lower Columbia River and estuary: Final Report 2002-2008. National Marine Fisheries Service Report to the U.S. Army Corps of Engineers Contract W66QKZ20374382. Portland, OR.
- Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005a. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). Estuarine, Coastal and Shelf Science 64:79–93.
- Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005b. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. NOAA Technical Memorandum NMFS-NWFSC-68:246 pp.
- Bourret, S. 2013. Salmon life history in an altered landscape: reconstructing juvenile migration using chemical and structural analysis. Master's Thesis. University of Idaho (April).
- Burke, J. L. 2004. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to the present. Master's Thesis. Oregon State University, Corvallis, Oregon.
- Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263–297.
- Campana, S. E., and S. R. Thorrold. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries and Aquatic Sciences 58(1):30–38.
- Elsdon, T. S., B. K. Wells, S. E. Campana, B. M. Gillanders, C. M. Jones, K. E. Limburg, D. H. Secor, S. R. Thorrold, and B. D. Walther. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: Hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology: an Annual Review 46(1):297–329.

- Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon. Fishery Bulletin 77(3):653–668.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–394 in C. Groot and L. Margolis, editors. Pacific Salmon Life Histories. UBCPress.
- Healey, M. C. 2009. Resilient salmon, resilient fisheries for British Columbia, Canada. Ecology and Society 14(1).
- Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commision of Oregon 4(2):42 pp.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465(7298):609–612.
- Volk, E. C., D. L. Bottom, K. K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139(2):535–549.
- Williams, R. N., J. A. Stanford, J. A. Lichatowich, W. J. Liss, C. C. Coutant, W. E. McConnaha, R. R. Whitney, P. R. Mundy, P. A. Bisson, and M. S. Powell. 2006. Return to the river: strategies for salmon restoration in the Columbia River basin. Elsevier.