

**Salmon Life History in an Altered Landscape: Reconstructing Juvenile
Migration Using Chemical and Structural Analysis**

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Abstract

The understanding of movement is critical for the conservation of culturally and economically important migratory species. Migration, the act of moving periodically from one region to another, is taxonomically widespread throughout the animal kingdom (Webster et al. 2002) such that animals may exhibit migratory behavior owing to resource availability and/or reproductive opportunities. The “decision” to migrate can be viewed as a tradeoff between the survival and energetic costs of movement and the benefits gained in a new habitat (Lack 1954). These benefits include release from density dependent competition, increased growth potential in more productive habitats, and decreased risk of predation (Anholt 1995, Gross 1987).

Chinook salmon is one of several species that exhibit migratory behavior, whereby individuals are born in freshwater streams and rivers, move to the ocean to mature, and return to freshwater to spawn and die (i.e., anadromy). Unfortunately, several migrant populations have been severely impacted by human activities (Berger 2004). For example, the construction of hydroelectric impoundments in the Pacific Northwest, US, has blocked access to spawning and rearing habitat of Chinook salmon (NRC 1996) and thus resulted in decreased viability of these migrant populations.

Variability in migration timing within and among populations can have fitness implications (Drent et al. 2003). An individual change in fitness can lead to a deviation in a particular life history strategy and contribute to the expression of an

array of life histories, especially since environmental conditions are constantly changing (Stearns 1976). Life histories evolve in response to variation in fitness and underlying genetic differences among individuals, which drives natural selection. Chinook salmon exhibit high variability in migration timing within and among populations across their range.

Knowledge of animal movement has been constrained due to difficulties in tracking individuals over long distances for entire life cycles (Rubenstein and Hobson 2004). This lack of empirical data is an impediment to a greater understanding of dispersal and migration processes (Colbert et al. 2001, Webster et al. 2002). Recent technological advances in the use of natural tracers such as otolith microchemistry are now making it easier to determine the movement behavior of individuals (Webster et al. 2002).

Otolith microchemistry represents a technique for studying early Chinook salmon movement and habitat use that would be difficult to assess using traditional marking and tagging technologies (Kalish 1990, Thorrold et al. 1997, Campana 1999, Kennedy et al. 2000, Kennedy et al. 2002, Wells et al 2003). Otoliths are mineral structures located within the semicircular canals of the fish's inner ear, in which increments of calcium carbonate, as aragonite, are accreted daily as thin concentric rings (Kennedy et al. 2000, Kennedy et al. 2002). This daily deposition of calcified material reflects the distinct geochemical signature of the aqueous environment, and because otoliths are inert, this signature remains stable after deposition (Neilson and Geen 1982, Campana and Neilson 1985). The geochemical

signature of the water is influenced by variation in the age and composition of the underlying bedrock geology.

Using geochemical isotopic and elemental signatures from Chinook salmon otoliths I investigated the migratory patterns within the Willamette Basin. Specifically, my objectives were to quantify the representation of juvenile freshwater life history strategies in the Upper Willamette spring Chinook salmon population, and to develop a methodological test between scale and otolith juvenile life history interpretations, which was used to test the accuracy of scale assignment. I also reconstructed the juvenile rearing and migratory patterns of a sample of natural origin adult Chinook salmon that returned to the Middle Fork Willamette Basin.

Willamette Basin

The Willamette River is 300 kilometers long and located in Northwestern Oregon, U.S. The river flows north, between the Cascade and Coastal mountain ranges and through the Willamette valley, which contains over two-thirds of Oregon's population. It is a tributary to the Columbia River in Portland, Oregon's largest city (Figure 2). The basin is composed of 30% valley floor, 60% cascade mountains and foothills, and 10% coast range slopes. The river drains an area of 29,800 km² and has an average discharge of 900 m³/s. The headwater sub-basin bedrock geology is composed of primarily of andesite and basalt that was formed from the Oligocene to Miocene periods.

There are over 350 dams in the Willamette basin, including 18 non-federal hydropower projects and 25 major Federal Columbia River Power System (FCRPS)

dams (Keefer 2011). Included in the FCRPS dams are 11 single purpose hydroelectric projects and 13 U.S. Army Corps of Engineers (USACE) dams with reservoirs that provide flood control, irrigation, recreation, water supply, and hydroelectric generation. These impoundments, collectively the Willamette Valley Projects (WVP), were constructed starting in 1941 with Fern Ridge Dam on the Long Tom River to 1969 with Blue Ridge Dam on the McKenzie River. The watersheds in this study are the North Santiam, McKenzie, North Fork Middle Fork Willamette, and Upper Middle Fork Willamette sub-basins. Historically, these watersheds once contained large spring Chinook salmon populations, but now have a limited number of natural origin adult returns per year (NMFS 1999). Estimated habitat loss to migratory anadromous fish has been estimated at 70%-100% in the Middle Fork Willamette, and Santiam sub-basins, and 25% in the McKenzie sub-basin. These watersheds also all contain large impoundments and subsequent reservoirs (NMFS 2008).

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Chapter 1: Assessing the feasibility of geochemical signatures to distinguish early freshwater movement, habitat use, and life history of Chinook salmon (*Oncorhynchus tshawytscha*).

Abstract

Understanding movement behavior and habitat use in early life history stages is important for effective conservation and management of imperiled species. For threatened spring Chinook salmon (*Oncorhynchus tshawytscha*) of the Willamette River, quantifying freshwater habitat use can identify habitat and dam passage improvements that will assist in management strategies. Currently, in the Willamette river, offspring of ESA-listed adult Chinook salmon outplanted above project reservoirs may rear near outplant sites in natal spawning streams (natal tributaries), in reservoirs below natal tributaries, the mainstem and lower Willamette River, and/or the freshwater Columbia River Estuary. We sampled isotopic ratio $^{87}\text{Sr}/^{86}\text{Sr}$ and natural elemental tracers (Sr, Ba, Mg, Mn, and Ca) from water samples and otoliths in Chinook salmon juveniles and adults. Samples were collected from rearing and spawning habitats, respectively to address questions of movement, freshwater habitat use, and life history characteristics at multiple spatial scales within the Willamette Basin. Counter to expectations, we found that variation in otolith microchemistry was able to resolve several life history attributes at the finest scale (within headwater basin) and largest spatial scales (freshwater vs. marine), but had little resolving power at intermediate scales (among headwater basins or between headwaters and the mainstem Willamette River). Owing to this spatial variability in

otolith chemistry together with strong correlations between water and otolith chemistry, we estimated first year rearing habitat for adult Chinook. Our results suggest that 90% (n=18) of adults reared in Lookout Point reservoir and 10% (n=2) reared in the upstream natal stream habitat. This study highlights the utility of otolith microchemistry to reconstruct movement at multiple spatial scales and our results contribute to the limited body of research showing juvenile Chinook salmon successfully rearing in novel reservoir habitats.

Introduction

Movement influences ecological and evolutionary responses across a broad range of migratory taxa (Webster et al. 2002). For many migratory species movement during early life history, from natal to juvenile rearing habitats, is critical for species persistence and appears to be under strong selection (Gross et al. 1988; Drent et al. 2003). This early life stage movement may be a product of local and current differences between rearing habitats, such as temperature, growth opportunity, and density of conspecifics, but could also reflect genetic adaptation to past environments (Quinn and Unwin 1993). Early life stage movement is particularly important in some migratory species, such as salmon, where reaching a certain size threshold increases an individual's probability of survival (Zabel and Achord 2004)

Chinook salmon (*Oncorhynchus tshawytscha*) exhibit a wide array of movements, in the form of migration and dispersal behaviors, which contribute to variability in juvenile freshwater habitat use within populations (Quinn 2005, Hamman and Kennedy 2012). Anthropogenic alterations (particularly impoundments and associated reservoirs) affect the expression and relative fitness of alternative patterns in habitat use among individuals (Williams et al. 2008). For example, the lower Snake River fall run Chinook salmon population was thought to be composed solely of a sub-yearling life history type (i.e., juveniles that migrate to sea shortly after hatching) but recent evidence highlights the presence of a yearling "reservoir" life history type (i.e., juveniles that overwinter in lower Snake River reservoir habitats; (Hegg et al. 2013, Connor 2005). Reservoir-type juveniles migrate to the ocean during spring, at a larger body size, which may be

advantageous for survival to ocean entry and for the adult return to spawn in freshwater (Zabel and Achord 2004, Connor et al 2005). The larger size of the reservoir type life history may be influenced by dam-related altered temperature regimes, which provide growth opportunities (Connor et al. 2002, Hegg et al. in press).

In the Willamette Basin within the U.S. Pacific Northwest, substantial portions of Chinook salmon spawning and rearing habitats have been blocked due to the construction of large high-head dams from 1941-1969. Limited data was collected on juvenile Chinook salmon habitat use prior to dam construction in the Willamette River. However, from annual collections (1947-1951) made on the Willamette River upstream from Portland, Mattson (1962) identified three groups of juvenile Chinook salmon emigrating during two periods (late-spring and late-fall); a less common late-spring subyearling, a late-fall subyearling, and a more prevalent late-spring yearling group. Owing to the creation of impassable dams and mitigation efforts that manually place adult Chinook above project reservoirs into historic spawning reaches, there is indirect evidence of a reservoir-rearing life history strategy by juvenile spring Chinook salmon. In particular, there is evidence of prolonged residence in reservoirs possibly in response to favorable growth conditions that exist in combination with dam-related seasonal restrictions to downstream passage (Keefer et al. 2011).

Currently in the Willamette River, offspring of adult Chinook salmon outplanted above project reservoirs may rear in any of five locations; a) near outplant release sites in natal spawning streams (natal tributaries), b) in reservoirs

below natal tributaries, c) the tailrace and downstream of dams near the outplant collection site, d) the mainstem and lower Willamette River, and/or e) the freshwater Columbia River Estuary prior to saltwater entry (Figure 1). Knowledge of the degree to which juvenile Chinook utilize these different locations is critical for the effective management of this threatened species. But information about juvenile salmonid early life history movement has been constrained due to difficulties in tracking small individuals over long distances for extended periods of time (Kennedy et al. 2000, Rubenstein and Hobson 2004). Fortunately, natural markers in fish hard parts are increasingly used as a means to reconstruct individual movement and offer several advantages to traditional tagging studies (Campana 1999).

Fish otoliths are paired mineral structure located within the semicircular canals of the fish's inner ear, in which increments of calcium carbonate are accreted daily as thin concentric rings (Neilson and Geen 1982, Campana and Neilson 1985). This daily deposition of calcified material reflects the distinct geochemical signature of the aqueous environment, and because otoliths are inert, this signature remains stable after deposition (Kennedy et al. 2000, Kennedy et al. 2002). The geochemical signature of the water is influenced by variation in the age and composition of the underlying bedrock geology. For example, Felsic rocks (e.g. granite) lead to higher $^{87}\text{Sr}/^{86}\text{Sr}$ and Sr:Ca values compared to mafic rocks (e.g. basalt), and the uneven distribution of rocks derived from felsic and mafic sources drives spatial variability in geochemical markers (Hegg 2011). Therefore, the scale at which it is possible to distinguish movements of fish between different habitats is not only a product of the heterogeneity of the geochemical signatures (Kennedy et al. 2000, Barnett-Johnson

et al. 2010), but also the spatial and temporal resolution of the geochemical incorporation into the otolith (Hobson et al. 2009). Daily rings can be referenced to specific ages and changes in the elemental and isotopic composition across growth axes of the otolith, and can be used to reconstruct movements throughout the life of a fish.

The objectives of this study were to: 1) quantify the degree of geochemical variability at four spatial scales in the Willamette basin that correspond with important Chinook salmon habitat use and life history questions, and 2) to determine the early rearing habitat in a sample of natural origin returning adult Chinook salmon. A secondary goal of the study was to examine whether otolith geochemical markers could be used to detect straying among WVP populations in returning adult salmon. We hypothesized that otoliths would allow us to distinguish life history information at one or more of the four scales depending on the spatial variability of geochemical signatures in the Willamette basin (Figure 2)

Methods

Study Area

The Willamette River is 300 kilometers long and located in Northwestern Oregon, U.S. The river flows north, between the Cascade and Coastal mountain ranges and through the Willamette valley, which contains over two-thirds of Oregon's population. It is a tributary to the Columbia River in Portland, Oregon's largest city (Figure 2). There are over 350 dams in the Willamette basin, including 18 non-federal hydropower projects and 25 major Federal Columbia River Power System (FCRPS) dams (Keefer 2011). Included in the FCRPS dams are 11 single purpose hydroelectric projects and 13 U.S. Army Corps of Engineers (USACE) dams with reservoirs that provide flood control, irrigation, recreation, water supply, and hydroelectric generation. These impoundments, collectively the Willamette Valley Projects (WVP), were constructed starting in 1941 with Fern Ridge Dam on the Long Tom River to 1969 with Blue Ridge Dam on the McKenzie River.

Water Chemistry

To begin to understand the scale at which geochemical signatures could be applied to assess early juvenile Chinook salmon movement behavior and habitat use, we chemically analyzed water collected throughout habitats used by downstream migrating juveniles. We surveyed spatial and temporal variation in water chemistry by collecting a total of 26 water samples in 2010 during three separate sampling periods: July 9-11, August 18-19, and October 5-7, during the Chinook salmon growing season. Samples were collected in all major sub-basins in natal rearing tributaries, reservoirs, and below project dams during 2010 (Figure 1, Table 1). We also sampled Willamette River mainstem and lower Columbia River,

and we repeat sampled in May 2011 upper watershed and reservoir sites to examine annual variability in geochemical signatures (Figure 1).

Water samples were collected in pre-weighed, acid-washed 125 ml nalgene bottles, and acidified with ultra pure HNO₃ acid and re-weighed at the Washington State University Geoanalytical Laboratory in Pullman, WA. In January 2011, water samples were analyzed for elemental concentrations and ratios (Sr:Ca, Ba:Ca, Mg:Ca, and Mn:Ca) and strontium isotopic ratio (⁸⁷Sr/⁸⁶Sr). Strontium was separated using standard column chemistry (Kennedy et al. 2002). Sr isotopes (⁸⁷Sr/⁸⁶Sr) were analyzed using a Finnigan MAT 262 Multi-Collector Thermal Ionization Mass Spectrometer (TIMS). Elemental concentrations of Ca, Sr, Ba, Mg, and Mn were analyzed with an inductively-coupled plasma mass spectrometry (ICPMS – Finnigan-Thermo Element II).

We examined ⁸⁷Sr/⁸⁶Sr because this isotope ratio is found in direct proportion between fish otoliths and ambient water, with little biological fractionation (Kennedy 2002). We also examined a suite of elements (Sr, Ba, Mn, and Mg molar ratios) to calcium in water because these values correspond to otolith values despite biological and thermal fractionation (Wells 2003). We used non-parametric Wilcoxon signed rank and Kruskal-Wallis rank sum analysis with ⁸⁷Sr/⁸⁶Sr, Sr:Ca, and Ba:Ca to test for variability in water geochemical samples between sites at each of the four spatial scales (see below). These elements were the best indicators of discriminatory power in subsequent otolith analyses (Shaffler et al. 2008). Nonparametric tests were performed due to non-normal distributions and unequal variance, which violates the assumption of parametric tests (ANOVA, T-test). If only

one sample was analyzed, visual interpretations were reported. We focused our analyses on the following four spatial scales:

With-in Headwater Basin: we tested water geochemical variability between the Upper North Santiam River and Detroit reservoir in the North Santiam sub-basin, the South Fork McKenzie River and Cougar Reservoir in the McKenzie sub-basin, and the North Fork Middle Fork Willamette and Lookout Point reservoir in the Middle Fork sub-basin (Figure 1).

Inter-basin: we tested water geochemical variability between natal spawning reaches where spawning occurs in the Upper North Santiam, South Fork McKenzie, North Fork Middle Fork Willamette, and the Upper Middle Fork Willamette Rivers (Figure 1).

Headwater-Mainstem: we tested water geochemistry parameters between the headwater tributaries, mainstem Willamette River and the Freshwater Columbia River below the confluence with the Willamette River (Figure 1).

Freshwater-Marine: we visually analyzed water geochemical variability between fresh and brackish/marine environments in the Willamette migration corridor (Miller et al. 2011).

Otolith Sample Collection and Analysis

Juvenile samples – Left sagittal otoliths were collected over 3 years (2009-2011) from natural origin juvenile Chinook salmon ($n = 113$) (Table 1). Fish were collected by the Oregon Department of Fish and Wildlife, U.S. Army Corps of Engineers, and University of Idaho from adult outplant / natal tributaries, project reservoirs, tailrace

below project reservoirs, and the mainstem Willamette river at Willamette Falls. Fish were collected in three seasons (spring, summer, and fall), with rotary screw traps, fyke nets, trap nets, and hook and line sampling. All fish were euthanized with a lethal dose of MS-222 under NMFS permit W1-11-UI201. Scales were sampled from all fish at the time of otolith removal and analyzed by the Oregon Department of Fish and Wildlife to confirm age and interpret habitat specific structural patterns.

Adult samples – Otoliths were collected from adult post-spawn Chinook salmon of natural origin that had been outplanted to the North Fork of the Middle Fork River above the Dexter-Lookout Point Dam complex, in the Middle Fork Willamette basin (Figure 1, Table 1). Left sagittal otoliths (n = 20) were collected by Oregon Department of Fish and Wildlife spawning ground surveys, and University of Idaho personnel over 2 years (2009-2010). Scales and otoliths were sampled from all fish, and these were analyzed by the Oregon Department of Fish and Wildlife Scale Project to estimate age and juvenile freshwater life history.

All otolith samples were analyzed for elemental concentrations Sr:Ca, Ba:Ca, Mg:Ca, and Mn:Ca with a transect on the dorsal region from otolith edge to core. The region was chosen based on its repeatable and clear growth rings. Otoliths were mounted sulcus side down on glass slides using crystal bond resin, ground with a lapping wheel and slurries (grit sizes of 1 and 5 alumina micropolish) through the distal surface until nuclei were distinctly visible under a transmitted light microscope. Otoliths were then flipped and polished on the opposite side until nuclei were visible. Elemental ratios were quantified using a Finnigan Element2 high resolution single collector inductively coupled plasma mass spectrometer (HR-ICP-

MS) coupled with a New Wave UP-213 laser ablation system. Concentrations of all measured elements were calculated relative to a National Institute of Standards and Technology glass standard (NIST 612) and a gas blank. We laser ablated the otoliths at a constant speed (30 $\mu\text{m}/\text{second}$) and spot size (40 μm). Immediately prior to ICPMS analysis, polished otoliths were wiped with alcohol to remove any possible contamination accumulated during storage. Analyses were conducted at the Washington State University Geoanalytical Laboratory in Pullman, WA.

Juvenile and Adult Otolith Chemical Analysis

From edge to core transects of juvenile otoliths we focused our analyses on two otolith sections corresponding to an individuals' natal origin and capture location. The natal origin signature was quantified by averaging the first chemically stable point in the transect (generally located 110 μm to 200 μm from otolith core, and no smaller than 80 μm). We selected this region to estimate the geochemical signature during early growth in the natal stream because it is outside the area where maternal compounds associated with yolk sac absorption are known to influence natal signatures (Barnett-Johnson et al. 2008) yet not within the area associated with early post-emergence downstream movement (Zabel et al. 2010). The capture location chemical signature was quantified by averaging a stable signature located in the last 100 μm closest to otolith edge, and no smaller than 80 μm . This otolith edge signature was presumed to reflect the location from which an individual was collected. This otolith edge signature was located from ~ 300 μm from the otolith core in small individuals to ~ 1500 μm in larger individuals. We note that it is possible that some or all of the late-growth sections in individuals collected in

reservoirs may have accreted in tributaries if individuals moved downstream just prior to collection.

From edge to core transects of adult otoliths we estimated the rearing geochemical signature (i.e., growth that occurred during an individuals' first year of life) by averaging a stable region on the otolith transect from 500 - 650 μm from otolith core. The location of the rearing signature was based on previous calculations of an otolith size at length regression analysis in juvenile Chinook salmon Willamette populations, and on calculations from fall Chinook salmon in the Snake River where 250 – 800 μm from otolith core was considered first year rearing and past 800 μm from otolith core was considered an overwintering signature (Zabel et al. 2010).

Data Analysis: Spatial Variability in Capture Location

With-in Headwater Basin: We used a MANOVA to compare capture location derived geochemical signatures between natal streams and respective project reservoirs. Dependent variables used in this analysis were a suite of otolith element ratios; Sr:Ca, Ba:Ca, Mn:Ca, and Mg:Ca ($^{87}\text{Sr}/^{86}\text{Sr}$ was excluded because it showed low discriminatory power in water geochemical values, see Results), while independent variable was North Fork Middle Fork Willamette and Lookout Point reservoir otolith samples in the Middle Fork sub-basin (Figure 1). We also performed a linear discriminate function analysis (LDFA) with jack-knife leave one out cross-validation so as to test the accuracy with which individuals were classified to the location from which they were collected (Rencher 2003). McKenzie and North

Santiam sub-basin samples were excluded in this analysis because we lacked sufficient sample sizes.

Returning Adult Chinook salmon Classification: Within the headwater basin

The rearing habitat during their first year of life of individual adult fish was back-classified with linear discriminate function analysis (LDFA) using juveniles collected from known rearing locations (Hegg et al. in prep, Wells et al. 2003). We compared otolith samples from the North Fork Middle Fork Willamette and Lookout Point Reservoir capture location signatures based on MANOVA ($\alpha = 0.05$) using elemental ratios to calcium (Sr:Ca, Ba:Ca, Mn:Ca, and Mg:Ca). The juveniles from known rearing locations worked as the training set to generate the LDFA, which was used as a model to classify first year juvenile rearing habitat in returned adult natural origin fish in NFMF ($n = 20$). Due to limited sample sizes this reconstruction of rearing habitat for adults was limited to the within headwater basin.

Inter-basin: we compared the natal origin otolith geochemical elemental values (Sr:Ca, Ba:Ca, Mn:Ca, and Mg:Ca) from juveniles sampled in different natal rearing streams between sub-basins. Significance tests using MANOVA were used to compare the Upper North Santiam, South Fork McKenzie, North Fork Middle Fork Willamette, and the Upper Middle Fork Willamette rivers (Figure 1). Linear discriminate function analysis (LDFA) with jack-knife leave one out cross-validation was used to test classification accuracy in group membership. Differences would indicate potential to identify adults as out-of-basin strays.

Headwater-Mainstem: We used the capture location geochemical values in the margin of otoliths from juveniles sampled in 2009 at Willamette Falls downstream

trap (n=9) to represent the mainstem Willamette geochemical signature. No juveniles from the mainstem lower Columbia River were available for analysis. We compared Willamette Falls to upper watershed reservoir samples with ANOVA.

Freshwater-Marine: No juvenile Chinook salmon were sampled in the freshwater lower Columbia River below the confluence with the Willamette. We used geochemical signatures for juvenile Chinook salmon from Miller et al. (2011). These data were used in conjunction with our companion study (chapter 2) to estimate juvenile size and age at brackish water entry.

Results

Water Chemistry

$^{87}\text{Sr}/^{86}\text{Sr}$ and Sr:Ca ratios from sampled water did not differ significantly at two of the four investigated spatial scales; within headwater basin and inter basin. However, significant differences in $^{87}\text{Sr}/^{86}\text{Sr}$ were detected between mainstem Willamette and freshwater Columbia River (mean = 0.7109, standard deviation = 0.002; Kruskal-Wallis, chi-square = 3.860, $P = 0.04953$, $n = 6$) as well as between

freshwater mainstem water samples and the literature derived marine value (Table 2).

Otolith Geochemistry

Within Headwater Basin:

Elemental ratios (Sr:Ca, Ba:Ca, Mg:Ca, and Mn:Ca) sampled from otolith capture location geochemical signatures differed between reservoir and tributary habitats for juveniles collected at the end of the growing season in the North Fork Middle Fork Willamette sub-basin MANOVA ($F = 4.07$, $df = 4$, $p = 0.013$) (Figure 4). LDFA and jackknife cross-validation indicated that 70% of known origin juveniles were correctly classified to the location from which they were collected (either NFMF or LOP). When the otolith chemistry of known origin juveniles was used as the LDFA training set to estimate rearing location of adults (based on adult rearing otolith chemistry; $n = 20$) 90% of the adults were classified as rearing in reservoirs versus only 10% natal stream rearing (Table 3).

Inter-basin:

Using natal origin signatures (Sr:Ca, Ba:Ca, Mg:Ca, and Mn:Ca) from juvenile otoliths ($n = 77$), MANOVA indicated significant differences among the four major spawning sub-basins ($F = 4.16$, $df = 3$, $P = .000007$) (Figure 5). The LDFA and jackknife re-sampling indicated that 59% of known origin juveniles correctly classified.

Headwater-Mainstem *and* Freshwater-Marine:

No significant differences in capture location otolith chemistry were detected for fish collected from headwater and mainstem Willamette River, while few fish from freshwater Columbia River, brackish/estuary, or marine habitats, meant that a comparison between freshwater otolith signature and literature derived marine signature was not possible.

Discussion

The overall goal of this study was to assess the feasibility of using natural isotopic and elemental markers in Chinook salmon otoliths to identify key life history traits including movement and migration timing, freshwater habitat use, and the propensity of homing and straying. In order to accomplish this goal, we assessed the geochemical heterogeneity across the Willamette basin from fine (within-headwater basin) to broad (freshwater-marine) scales. Our data suggest multiple scales at which geochemical signatures could be employed to gain understanding in the spatial and temporal distribution of freshwater habitat use and life history in our study population. Recent monitoring shows increased variability in freshwater habitat use in the upper Willamette spring run population (Cramer et al. 1996; Beamesderfer et al. 2001; Friesen et al. 2007; Keefer et al. 2012), and our data show evidence that natural origin returning adult Chinook salmon are rearing in project reservoirs during their early life history.

The ability to reconstruct life history using otolith microchemistry requires adequate variability in geochemistry across the landscape. Water chemistry data revealed low variability in $^{87}\text{Sr}/^{86}\text{Sr}$ between sampling locations within the headwater basin scale (Figure 1, movement between natal stream and reservoir habitats) and in the inter-basin scale (Figure 1, distinguishing between natal streams at the sub-basin scale). These results were likely due to low geologic diversity across the study area, with high concentrations of basalt and andesite formed in the Oligocene to Miocene period. We also found that $^{87}\text{Sr}/^{86}\text{Sr}$ could be used in distinguishing the timing of movements and habitat use of juvenile Chinook salmon between mainstem

Willamette and Columbia Rivers (Figure 1, Headwater-mainstem). We found that a multivariate analysis of elemental ratios was able to distinguish natal tributary and reservoir habitats within basin despite the lack of variability in $^{87}\text{Sr}/^{86}\text{Sr}$.

There are a number of potential mechanisms that could explain why the within-headwater basin scale was applicable in using geochemical signatures to study Chinook salmon life history compared to broader scales. The mechanisms responsible for elemental incorporation into fish otoliths are understudied and research has suggested conflicting results in different elements (Campana 1999). One hypothesis in finding the within-headwater basin scale suitable in determining early Chinook salmon habitat use is that different environments fluctuate in the incorporation of otolith elemental values. Fish experience different temperature, growth, and physiological constraints in cool, relatively low productivity headwater streams compared to warmer, more productive reservoirs when moving between environments, which could explain why we found geochemical feasibility in juvenile salmon moving between natal tributary and reservoir habitats. Differences in biogeochemical cycling in lotic natal streams compared with lentic reservoirs may also affect elemental concentration in otoliths.

In the within headwater basin analysis, our objective was to evaluate the relative habitat use of juveniles between natal rearing streams and project reservoirs. Downstream movement of sub-yearling fry after emergence is fairly common among Chinook salmon populations where growth opportunities are heterogeneous between habitats (Connor et al. 2001, Keefer et al. 2011), but quantifying the relative timing of these movements and habitat use between natal

stream and reservoir habitats in individuals is critical for understanding life history characteristics in populations. Our results are direct evidence that reservoir rearing is occurring in a spring run Chinook salmon population, but more research is needed to determine if reservoir rearing increases survival to adulthood. Our results could be strengthened with an increased sample of adults from NFMF. Examining water chemistry data (Figure 3), this analysis would be possible in South Fork McKenzie/Cougar reservoir habitats with a sample of adult otoliths.

Quantifying straying and homing is important in understanding reproductive success in threatened populations of anadromous salmonids, and is difficult using traditional mark and tagging techniques (Hamman and Kennedy 2012). By comparing the natal origin signatures on adult otoliths to the geographic area where the otoliths were collected, otolith microchemical techniques have the potential to investigate straying rates (e.g. Hamman and Kennedy 2012). Our inter-basin analysis sought to collect preliminary data that could be used to investigate straying rates of natural origin adult Chinook salmon (Figure 1, inter-basin scale) in the Willamette basin. This was only possible if all 4 sub-basins, or a sub-set of sub-basins of the upper Willamette River spawning habitats contained distinct geochemical signatures. The inter-basin otolith data using a suite of elemental geochemical signatures showed significant variability between sub-basins (Figure 5), but when using LDA to build a training set with juvenile samples, jack-knife reclassification found only 59% classification accuracy in known origin samples. Given that stray rates in hatchery Chinook salmon range from 2.4% (Quinn and Fresh 1984) to 17% (Quinn et al. 1991), and natural origin Chinook salmon have

demonstrated stray rates on the order of 13% at coarse geographic scales (Hamman and Kennedy 2012), our data does not have the ability to accurately estimate straying and homing among the Willamette sub-basins.

The proposed objective for the headwater-mainstem scale was to distinguish movement and habitat use of juvenile Chinook salmon in the Willamette River headwaters, mainstem Willamette River, and Columbia Rivers (Figure 1, headwater-mainstem), and at the broadest level, sought to distinguish freshwater geochemical values from the marine environment. Although elemental analysis of otoliths revealed no significant variation between otoliths sampled at Willamette Falls, mainstem Willamette River and upper watershed reservoirs (Lookout point and Cougar reservoirs) (Figure 6), water chemistry $^{87}\text{Sr}/^{86}\text{Sr}$ values varied significantly between the mainstem Willamette and lower Columbia (freshwater) river locations (Table 2). Combining this data with the fact that Sr:Ca values in the lower Columbia are largely different compared to literature derived marine values (Table 2), the potential exists to use both geochemical tracers to distinguish between major sub-basin tributaries (e.g., Santiam River), the mainstem Willamette River, the freshwater lower Columbia River below the confluence with the Willamette River, and estuary and marine environments. Distinguishing fine scale habitat use of juvenile Chinook salmon in mainstem Willamette River, Columbia River, and brackish/marine habitats could be possible with otolith samples from these respective environments that are of known Willamette stock. Which would be possible through marking/tagging and/or genetic stock identification. Also, increased spatial and temporal water samples from these habitats would aid further research.

Otolith microchemical analysis presented a unique opportunity to investigate juvenile Chinook salmon movement behavior and habitat use in the Willamette system. Although we found low variability in geochemistry, multivariate analysis allowed us to distinguish juvenile habitat use at the finest spatial scale. A number of physiological and environmental variables likely contribute to juvenile Chinook salmon freshwater life history including predation, food availability, habitat conditions, and competition (Groot and Margolis 1991, Quinn 2005); however this study shows that juvenile Chinook salmon exhibit reservoir associated early habitat use. This research suggests a “reservoir rearing” life history type in the North Fork Middle Fork Willamette sub-basin.

Understanding migratory behavior of individuals at various spatial scales is essential for the conservation and management of Spring Chinook salmon in the Willamette valley. This research informs management operations pertaining to downstream survival; including safe bypass systems, fish collection facilities, and reservoir drawn-downs. Future research should focus closely on how juvenile salmon are using these reservoir habitats. Movements and depths fish encounter, inter and intra specific competition, feeding ecology, and predation risks in project reservoirs are important questions that would inform conservation and management of the study population. This research provides a framework for investigating fish life history characteristics at a variety of spatial scales. This is important for researchers looking to answer fish life history questions, but have limited by otolith or water samples. By combing individual habitat information with juvenile downstream passage data we can begin to assess the survival costs and benefits of various life

history pathways, as well as the relative fitness of specific juvenile Chinook life histories.

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Table 1. Sample distribution of water chemistry, juvenile, and adult Chinook salmon. Geographic locations of sampling are split up by sub-basin and habitat, and analysis refers to what scale questions we could ask with the samples that were collected from each sub-basin.

Sub-basin	Habitat	Water samples	Juvenile samples	Adult samples	Analysis (scale)
Upper Middle Fork Will.	natal stream	3	9	0	inter-basin
	reservoir	3	5		
North Fork Will.	natal stream	3	23	20	with-in headwater basin, inter-basin, headwater-mainstem
	reservoir	3	22		
South Fork McKenzie	natal stream	2	21	0	inter-basin
	reservoir	3	33		
Upper North Santiam	natal stream	1	2	0	inter-basin
	reservoir	2	5		
Mainstem Willamette		3	9	0	headwater-mainstem,

**Lower f.w.
Columbia**

3

0

0

headwater-mainstem,
freshwater-marine

Table 2. Summary of water geochemical data ($^{87}\text{Sr}/^{86}\text{Sr}$, Sr:Ca) for various locations in the Mainstem Willamette river, Lower freshwater Columbia river, and Marine environments.

Location	$^{87}\text{Sr}/^{86}\text{Sr}$	Sr:Ca (mmol/ mol)	River km from ocean	Source
Mainstem Willamette River - Buena Vista, OR	0.7042	2.73	333.1	This study
Mainstem Willamette River - Salem, OR	0.7041	2.93	300.9	This study
Mainstem Willamette River- Willamette Falls	0.7044	2.68	207.6	This study
Columbia River - below Bonneville Dam	0.7133	2.35	235	Miller et al. 2011
Columbia River - St. Helens, OR	0.7089	2.78	138.4	This study
Columbia River - Goble, OR	0.7104	2.64	117.5	This study
Marine - Southern Oregon Coast	0.7092	8.60	0	Miller et al. 2010

Table 3. Results of the LDFA analysis used to classify adult fish to their first year of life rearing habitat. Fish were collected on NFMF spawning ground surveys in 2009 and 2010.

<i>Sample Location</i>	<i>Sample size</i>	<i>Natal stream rearing</i>	<i>Reservoir rearing</i>
North Fork Middle Fork Willamette Spawning Grounds	20	2 (10%)	18 (90%)

Willamette Basin

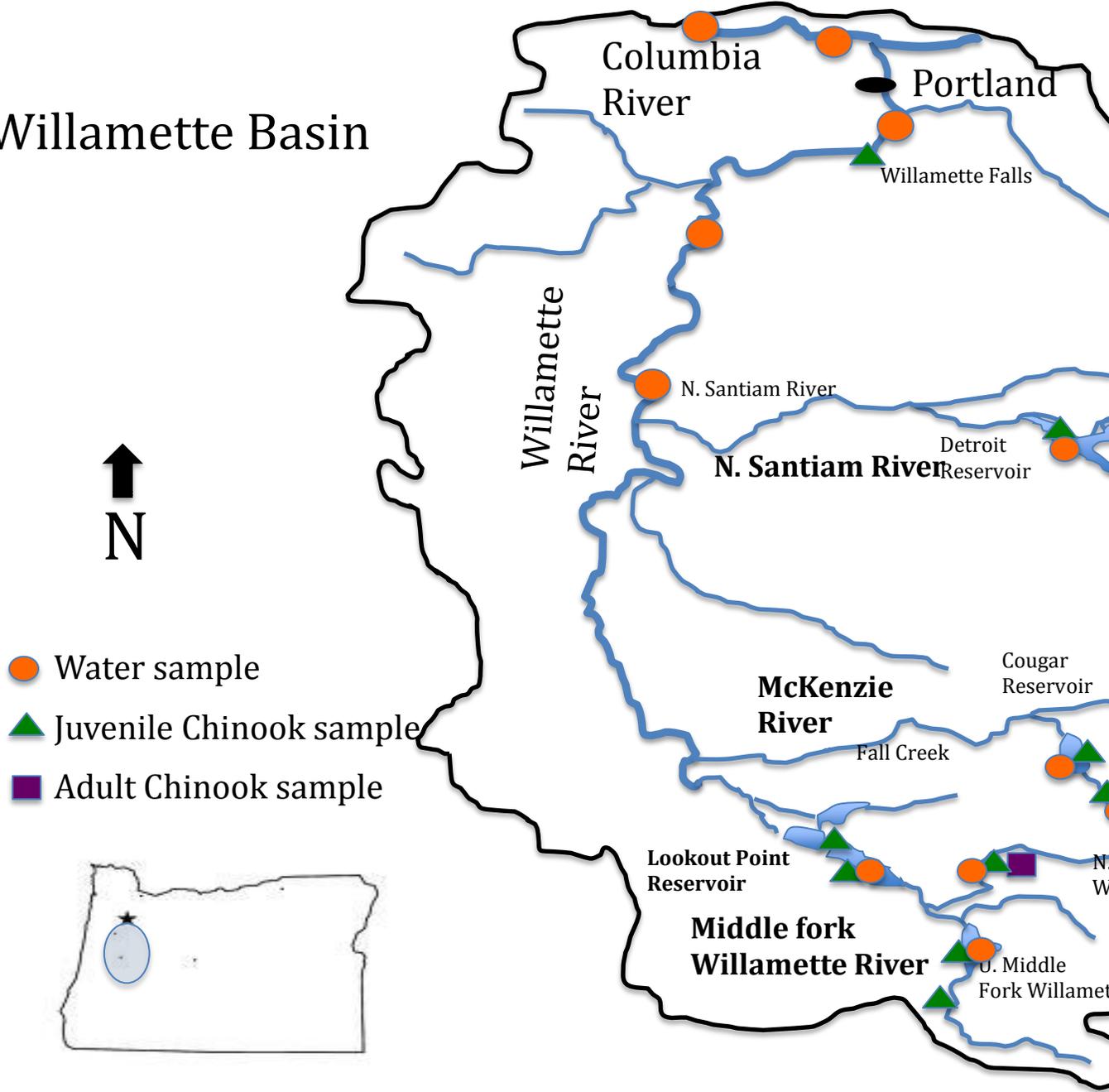
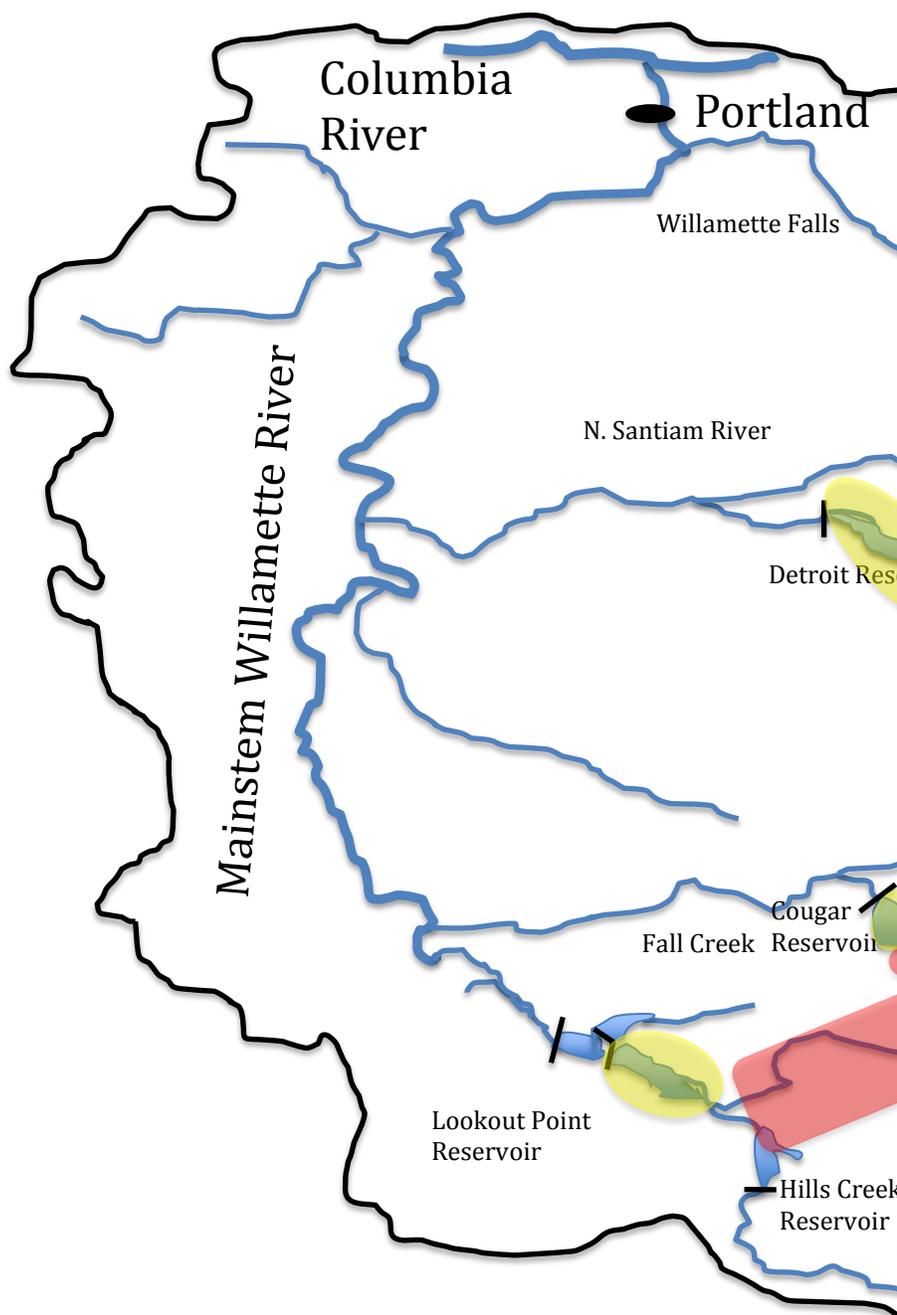


Figure 1. General location of the Willamette Valley with four major sub-basins (North Santiam, McKenzie, North Fork Middle Fork Willamette, and Upper Middle Fork Willamette). Locations of water samples (●), juvenile Chinook salmon samples (▲), and adult Chinook salmon samples (■) identified.

a)

With-in headwater basin

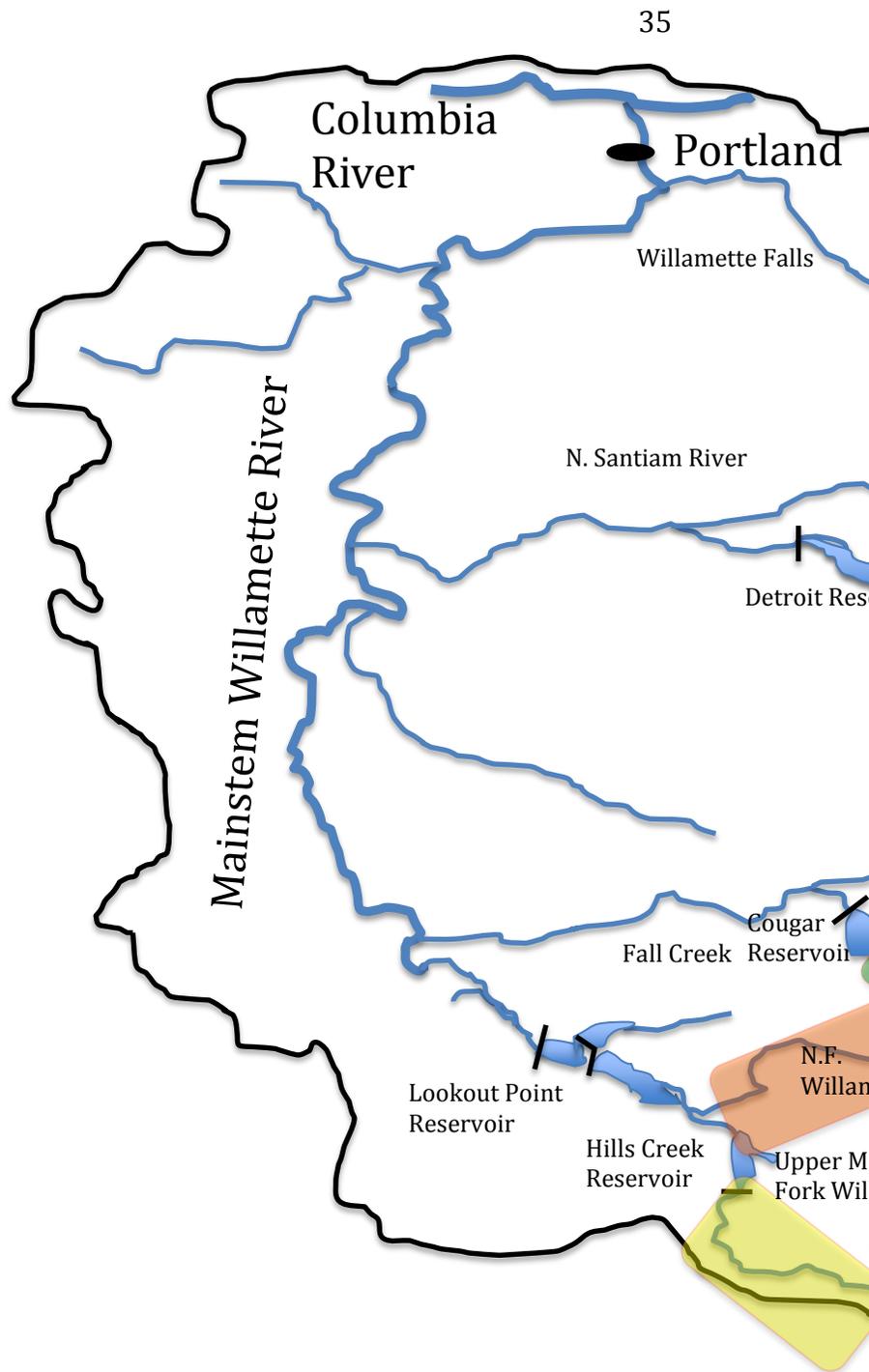
Each natal rearing
stream is
geochemically
distinct from
downstream
reservoirs



(b)

Inter-basin

4 natal sub-basins
have
distinct geochemical
signatures



(c)

Headwater-mainstem

Upper tributaries, mainstem Willamette, and freshwater Columbia rivers are geochemically distinct

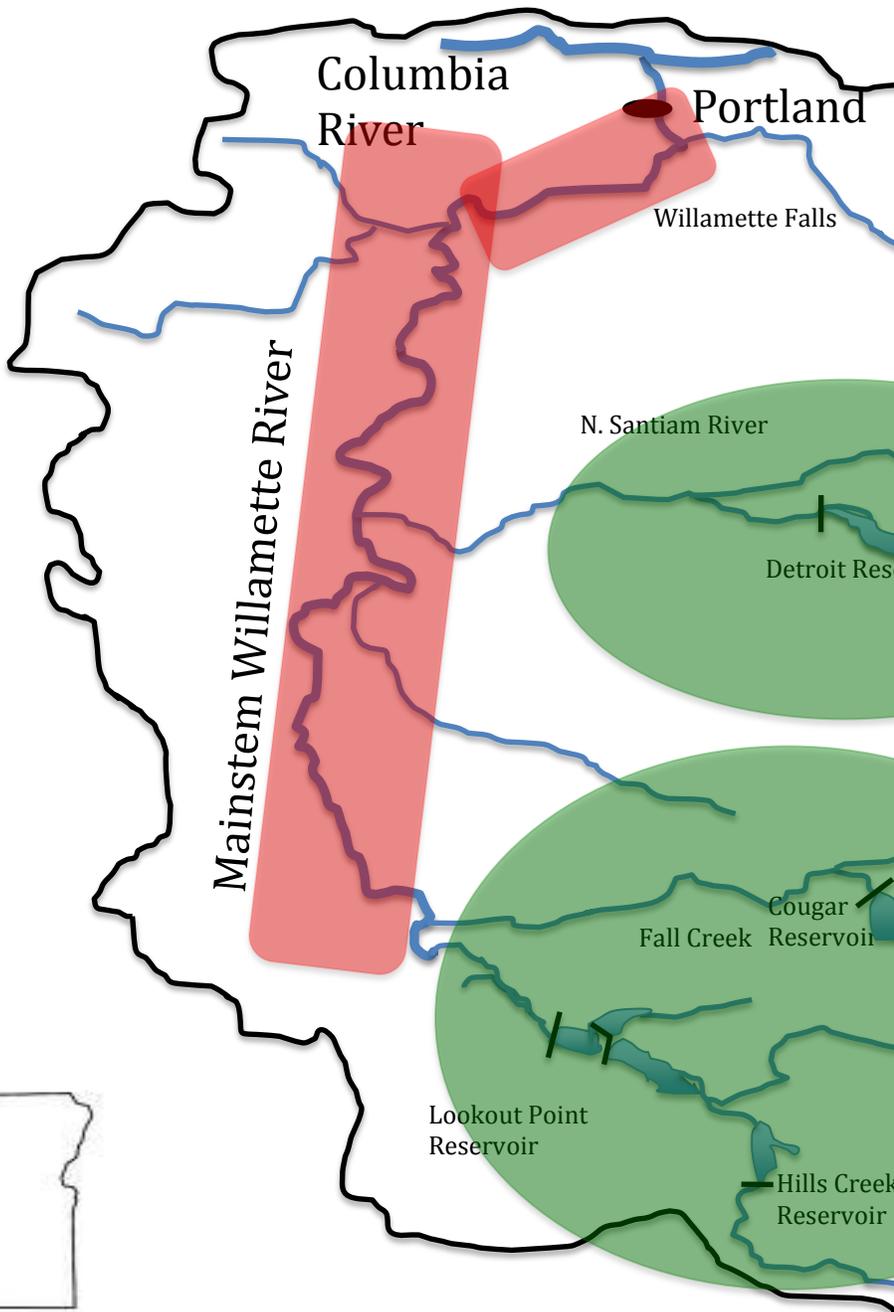
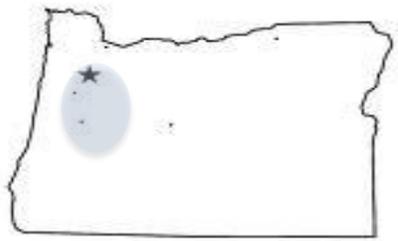
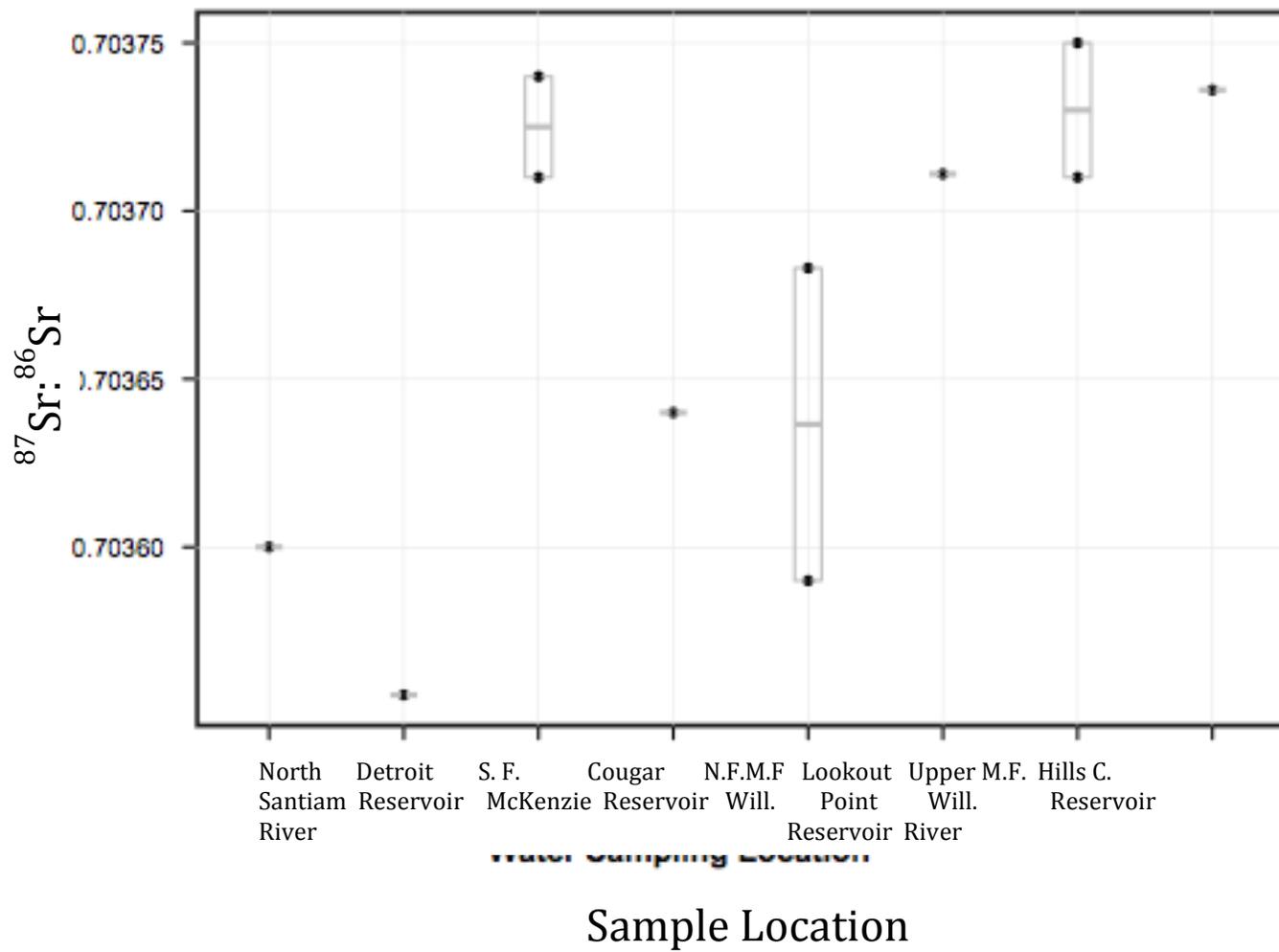
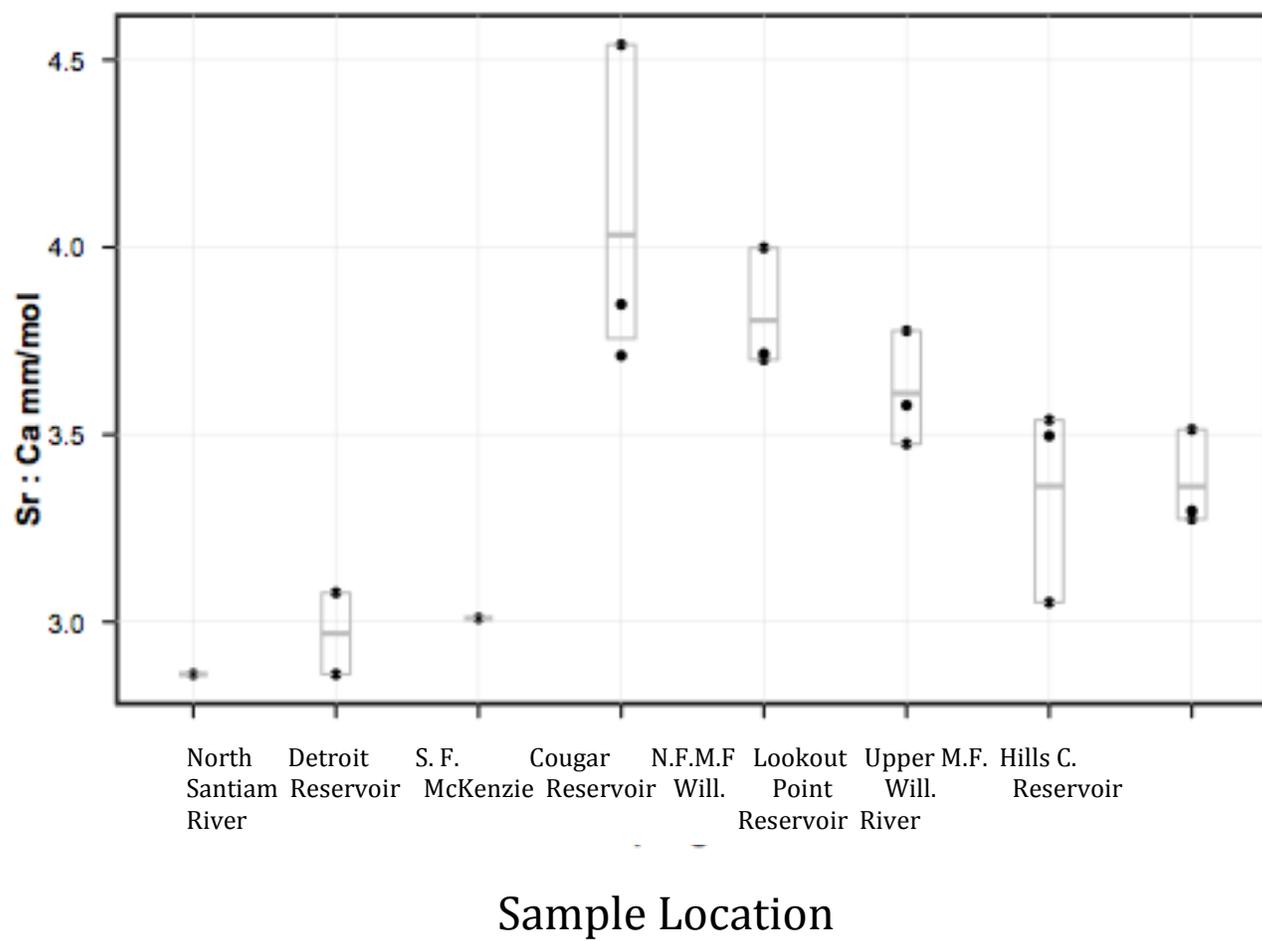
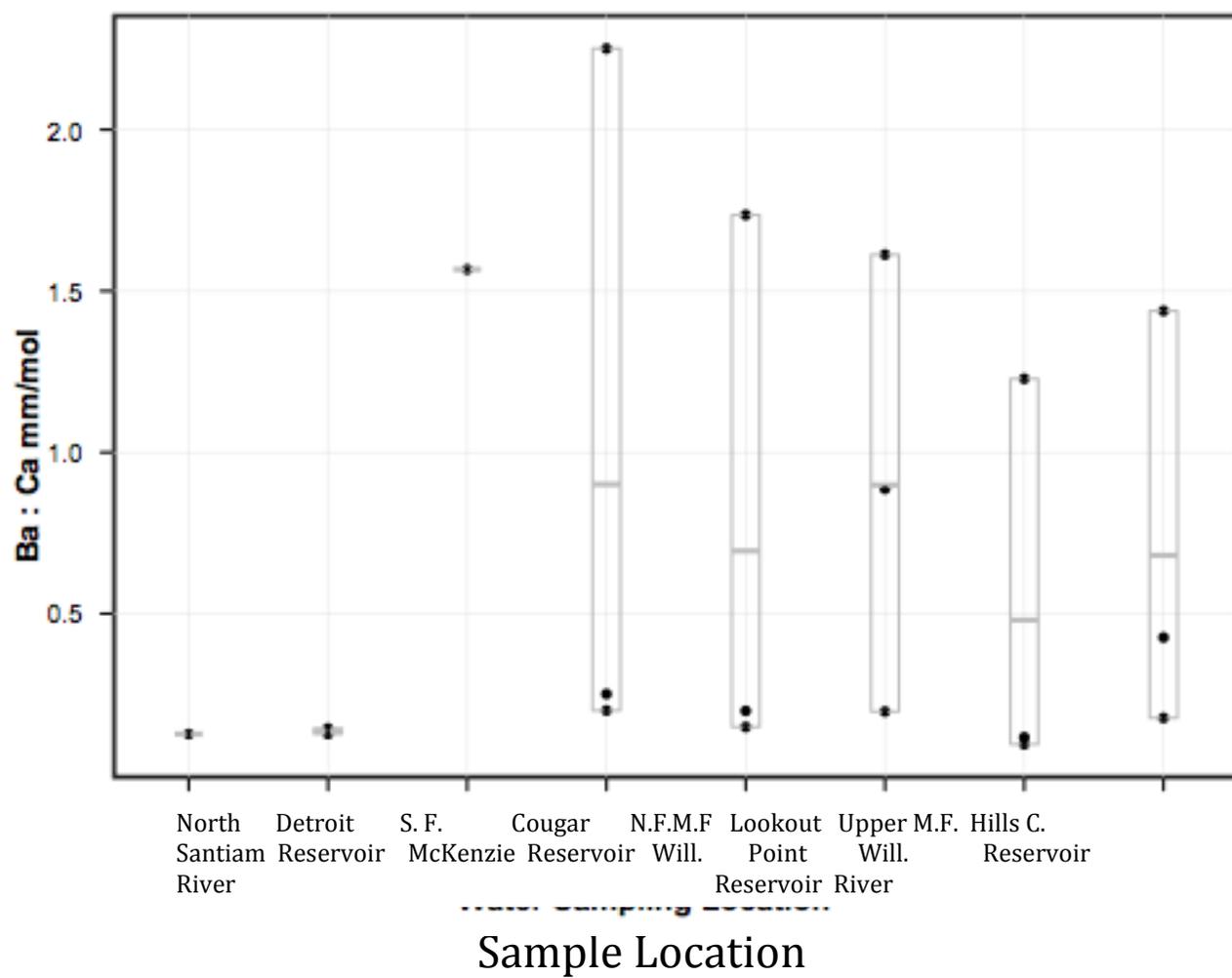
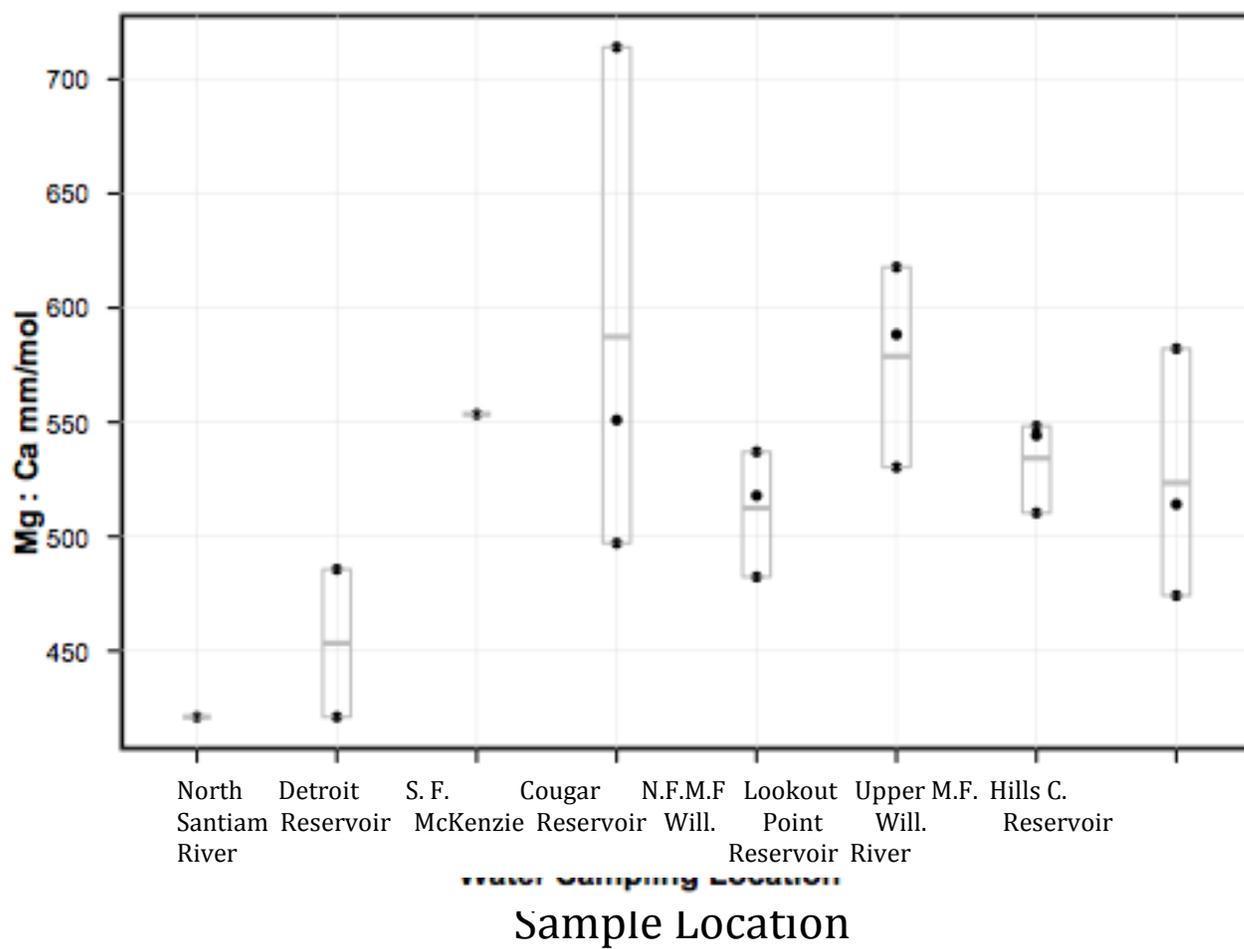


Figure 2. Three possible spatial scales that were hypothesized to investigate juvenile Chinook salmon habitat use and movement patterns, (a) with-in headwater basin, (b) inter-basin, and (c) headwater-mainstem. Different colors represent habitat types with geochemically distinct signatures.









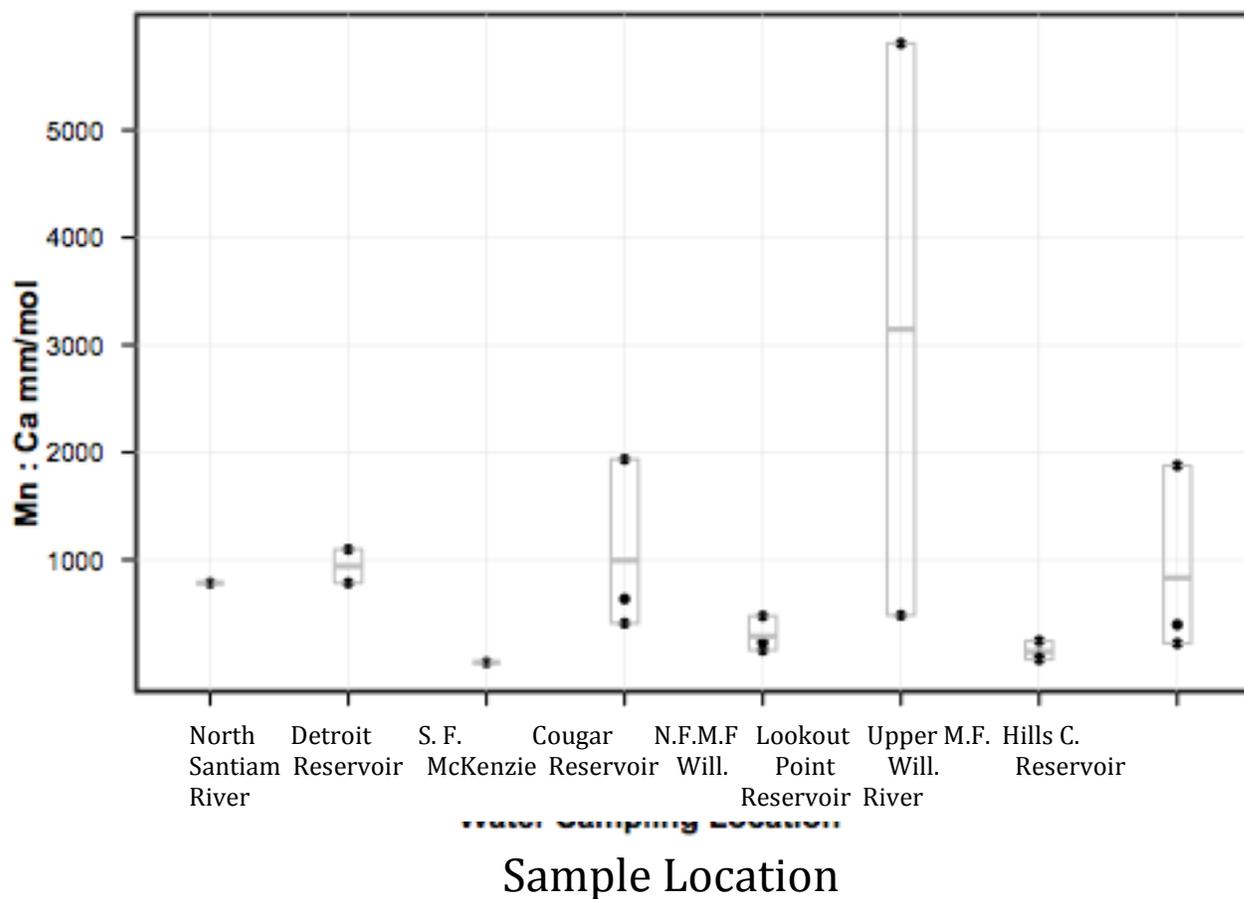


Figure 3. Water geochemical values ($^{87}\text{Sr}/^{86}\text{Sr}$, Sr:Ca, Ba:Ca, Mg:Ca, and Mn:Ca) in 4 natal rearing sub-basins in the Willamette system and the respective natal rearing tributary and downstream reservoir habitats. The central mark is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme values not considered outliers, and the number of dots represent sample size.



Figure 4. Otolith edge chemistry (Sr:Ca, Ba:Ca, Mg:Ca, Mn:Ca) comparing Lookout Point reservoir (LOP) and North Fork Middle Fork Willamette (NFMF) rearing habitats, located in the Middle Fork Willamette sub-basin. The central mark is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme values not considered outliers, and the above numbers represent sample size.

30 12 29 6

30 12 29

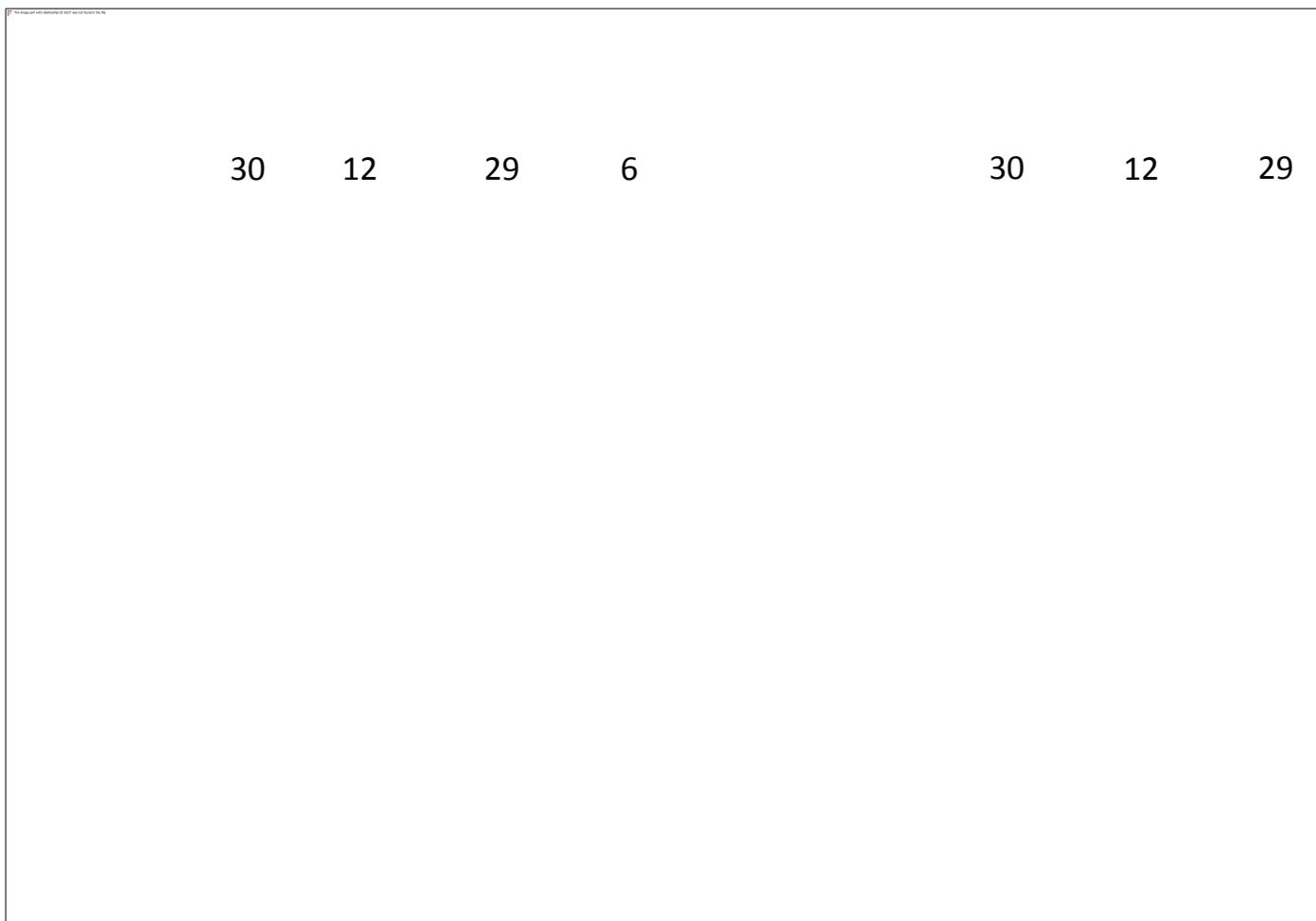


Figure 5. Natal origin geochemical signatures determined from otolith chemicals (Sr:Ca, Ba:Ca, Mg:Ca, Mn:Ca) in 4 natal rearing sub-basins in the Willamette system. The central mark is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme values not considered outliers, and the above numbers represent sample size.

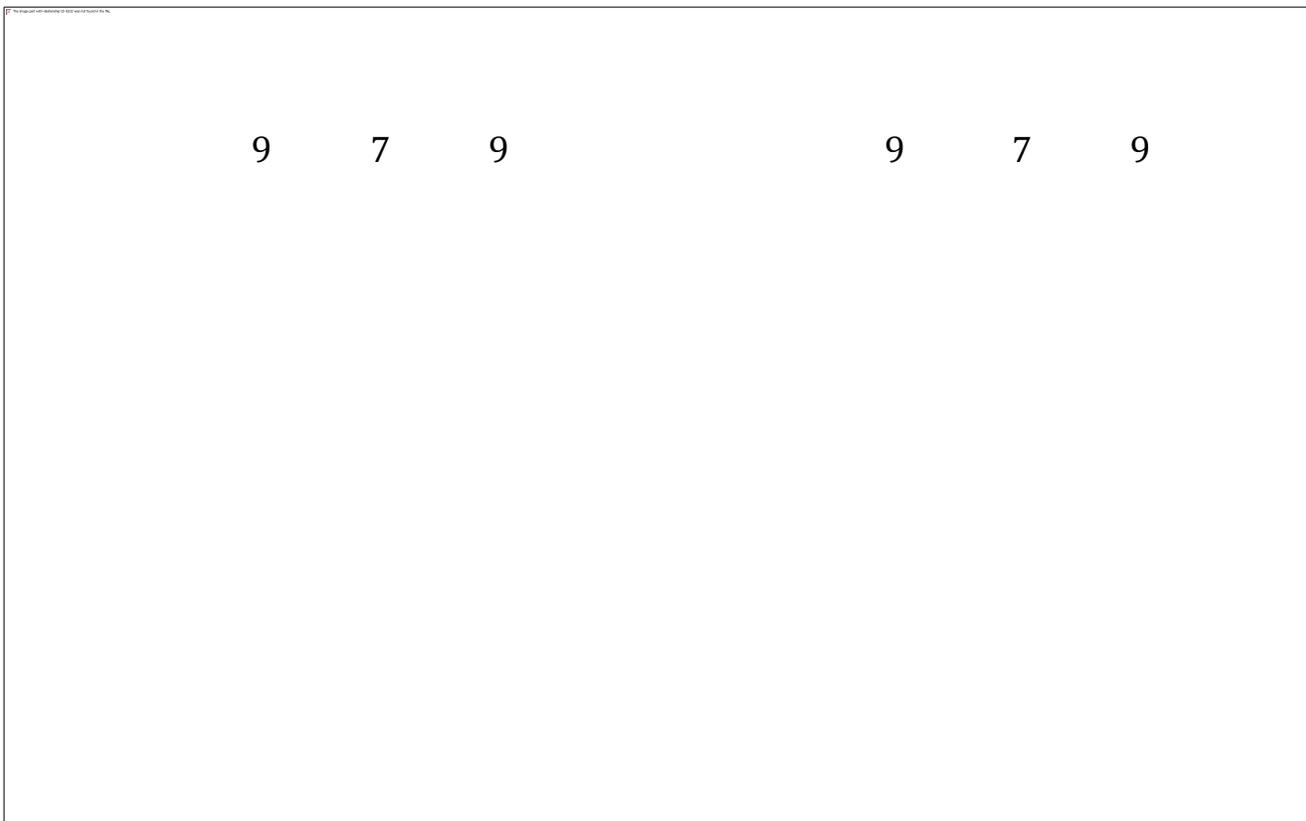


Figure 6. Habitat geochemical signatures determined from otolith chemicals (Sr:Ca, Ba:Ca) in Cougar reservoir (CGR), Lookout Point reservoir (LOP), and Main-stem Willamette river (MSW) capture locations. The central mark is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme values not considered outliers, and the above numbers represent sample size.

Chapter 2: Influence of Anthropogenic Alterations on Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) Life History

Abstract

Pacific salmon populations have suffered declines and local extirpations in the Pacific Northwest over the last century as a result of physical and functional changes to their freshwater environments. Understanding the distribution, abundance and relative performance of life history types is critical for ensuring population persistence. Recent analyses of screw trap data suggest that juvenile Chinook salmon life history strategies are variable within and among Willamette Valley populations, including traits that resemble both an ocean-type life history with subyearling emigration in summer or fall as well as a stream-type life history with yearling emigration the following spring. Our objective was to quantify the representation of juvenile freshwater life history strategies in the Upper Willamette spring Chinook salmon population, and to develop a methodological test of the accuracy of scale analysis in identifying life history strategies. Specifically, otolith isotope and elemental ratios $^{87}\text{Sr}/^{86}\text{Sr}$ and Sr:Ca combined with otolith and scale structural patterns were used to characterize juvenile life histories, estimate juvenile size and age at freshwater emigration, and assess relative growth between natal rearing habitats. We found a substantial portion of juvenile Chinook salmon reared in project reservoirs and emigrate from freshwater at large sizes. Our comparison of scale structure and otolith chemical derived life history determination indicated a high correspondence between the two methods. The results of this study highlight

the potential for further research that assesses relative fitness of juvenile life history types in the Willamette Basin. Determining the juvenile rearing habitat and patterns of emigration for these populations will enhance the understanding of the interaction between life history variation and anthropogenic disturbance and assist in developing appropriate management strategies.

Introduction

Freshwater ecosystems are experiencing substantial anthropogenic alterations in order to sustain the growing human population (Naiman and Dudgeon 2011). Human induced aquatic alterations are one of the largest causes of biodiversity loss in freshwater ecosystems (Moyle and Cech 2004). Alterations to rivers in the form of water withdrawal, changes in land use, and dams, disrupt habitat, flow, and chemical regimes important to ecosystem function (Arthington et al. 2009). Human disruptions to natural ecosystem processes and functions are altering species movement and growth in habitats critical for their survival (Moyle and Cech 2004). When human alterations change the conditions under which populations have evolved, average fitness can be decreased (Zabel and Williams 2002). One obvious mechanism by which fitness consequences are experienced is the changing nature of habitat connectivity and associated impacts on migration. Hence, it is paramount to study life history strategies by freshwater species and how they are influenced by anthropogenic alterations (Clarke et al., 2007).

River impoundments and the resulting reservoirs that they create have been implicated in the development of alternative life histories in Chinook salmon populations (Williams et al. 2008). For example, lower Snake River Fall Chinook salmon population, thought to be historically composed of an obligate sub-yearling life history type, now contains a yearling juvenile Chinook salmon life history that overwinter in lower Snake River reservoir (Connor et al. 2005, Hegg et al. 2013). Reservoir-type juveniles migrate to the ocean during spring, at a larger size, which has potential to be advantageous for survival to saltwater and adulthood (Zabel and

Achord 2004, Connor et al 2005). Reservoir habitat use as part of juvenile life history is hypothesized to provide favorable temperatures and/or resource availability that create growth opportunities (Connor et al. 2002, Hegg et al. 2013), Alternatively, reservoir life history types may be expressed because of seasonally poor passage conditions (e.g., Keefer et al. 2012).

For threatened and endangered Chinook salmon populations, understanding life history strategies is critically important for persistence and resilience.

Quantifying life history strategies is essential for managers to select among potential alternative management strategies including developing downstream passage improvements at dams and juvenile by-pass strategies. Since individuals with variable life history traits (e.g. size, age, and juvenile migration timing) may experience differential survival to adulthood, juvenile life history strategies could contribute variably to the adult population (Hillborn 2003, Bottom et al. 2005, Claiborne et al. 2011)). Quantifying the contribution of juvenile Chinook salmon life history strategies to adult production (or relative survival to reproduction) will inform managers and dam operators where to focus juvenile by-pass improvements with the ultimate goal of increasing natural origin adult escapement.

In annual collections made on the Willamette River mainstem from 1947-1951, Mattson (1962) reported three life history strategies of juvenile Chinook salmon passing during two periods (late-spring and late-fall runs). Based on timing and age at outmigration, the three major historical groups identified were a late-spring subyearling, a late-fall subyearling, and a late-spring yearling group (Figure 2). Since impassable impoundments currently block adult access to a large

proportion of historic spawning habitats, adult Chinook salmon are manually outplanted—collected and transported above project reservoirs into historic spawning reaches.

In the Willamette River basin, recent data highlights that juvenile Chinook salmon vary in outmigration timing, size, and age and impoundments may influence several of these key life history traits (Cramer et al. 1996; Beamesderfer et al. 2001; Friesen et al. 2007; Keefer et al. 2011). It is unknown if life history variability in the Willamette basin is a response to favorable growth conditions in project reservoirs or seasonally-restricted access to downstream passage routes caused by variation in reservoir elevation and discharge, or a combination of both mechanisms.

We used chemical and morphometric components of fish scales and otoliths to study life history traits of Chinook salmon in the Willamette basin. The use of scale structural and morphometric techniques to interpret life history characteristics in salmonids has been employed by fish scientists for over 100 years (Gillbert 1913, Rich 1920, Dhsपोवालॉव and Taft 1954, Connor et al. 2005). Interpreting individual salmonid life history characteristics from scales relies on distinct structural patterns in circuli spacing and checks that correspond with habitat transitions associated with varying growth opportunities. Assumptions about scale circuli patterns include: 1) narrow spacing represents relatively slow growth rate in freshwater, 2) medium spacing coincides with increased growth in estuarine or reservoir/lake growth, and 3) wide spacing occurs during high growth in productive ocean environments (Rich 1920, Dhsपोवालॉव and Taft 1954, Connor et al. 2005). Unfortunately, scale structural and morphometrical techniques in life history interpretations for salmonids

are rarely validated (Beamish and MacFarlane 1983, Carlander 1987), and few studies have used independent life history measures to verify scale interpretations.

Otolith microchemistry provides a unique method of reconstructing aspects of individual juvenile Chinook salmon life history (Kennedy et al. 2000, Kennedy et al. 2002, Wells et al. 2003, Volk et al. 2010) and can be used to validate scale interpretations when comparing information from a single individual (Campbell et al. 2010, thesis). Fish otoliths are calcified mineral structures that record the daily growth and chemical environment an individual inhabits. Strontium ($^{87}\text{Sr}/^{86}\text{Sr}$ and Sr:Ca) becomes incorporated in the calcium carbonate matrix of the otolith in the same abundances that are found in the individuals environment. Reconstructing fish life history with otolith microchemistry assumes a positive relationship between otolith and water strontium composition (Kennedy et al. 1997), and has been a reliable geochemical marker in studying diadromous fish migrations (Volk et al. 2010, Miller et al. 2011, Walther and Limburg 2012). Otoliths remain chemically and structurally stable after material is deposited, thus otoliths can be used to determine fine scale movement, habitat use, age, and growth in individuals (Campana et al. 1997).

Our objective was to quantify the relative composition of juvenile freshwater life history strategies in the Upper Willamette spring Chinook salmon population. By reconstructing the size, age, and habitat use of juvenile Chinook salmon in successful returning adults we attempted to answer two questions: What is the composition of juvenile life histories represented in this natural origin Chinook salmon population? And how can this inform impending management actions

regarding juvenile by-pass strategies? Our hypothesis is that the exploitation of reservoir habitats provides juvenile Chinook salmon increased growth opportunities compared to upstream and downstream lotic habitats. To address these questions, we compared life history classifications derived from independent scale and otolith techniques. The goal of this objective is to develop an otolith validation life history test that could be used in other anadromous populations, and also evaluate whether fisheries scientists in the Willamette basin can quantify juvenile life history strategies with scales alone.

Methods

Study site

The upper Willamette River is a highly impounded system located in western Oregon (Figure 1). The Willamette Valley Project (WVP) dams were constructed from 1941-1969, and are composed of 11 hydroelectric projects and 13 U.S. Army

Corps of Engineers (USACE) dams with reservoirs that provide flood control, irrigation, recreation, water supply, and hydroelectric generation. The WVP dams block access to major portions of historic spring Chinook salmon (*Oncorhynchus tshawytscha*) spawning and rearing habitats. Habitat loss has been estimated at 70%-100% in the Middle Fork Willamette, and Santiam sub-basins, and 25% in the McKenzie sub-basin (Keefer 2011). Other human induced alterations include overharvest, hatchery inputs, introductions of non-native fishes, and habitat destruction, which have had deleterious effects on other salmonid populations (Lichatowich 1999). Numbers of spring Chinook salmon returning to the Willamette River and headwater tributaries were near historic low levels in recent years, and the population was listed as threatened under the U.S. Endangered Species Act in 1999 (NMFS 2008).

Water chemistry

Interpreting variation in otolith chemical information is supported by geochemical data from the freshwater habitats that migrating fish experience. We collected 6 water samples in the lower mainstem of the Willamette River and in the Columbia River below the confluence with the Willamette River (Figure 1). Samples were collected in pre-weighed, acid-washed 125 ml nalgene bottles, and acidified with ultra pure HNO₃ acid and re-weighed at the Washington State University Geoanalytical Laboratory in Pullman, Washington. We analyzed water samples for elemental ratios Sr:Ca and strontium isotopic ratios (⁸⁷Sr/⁸⁶Sr). Strontium was separated using standard column chemistry (Kennedy et al. 2002). Sr isotopes (⁸⁷Sr/⁸⁶Sr) were analyzed using a Finnigan MAT 262 Multi-Collector Thermal

Ionization Mass Spectrometer (TIMS). Elemental concentration Sr:Ca was analyzed with an inductively-coupled plasma mass spectrometry (ICPMS – Finnigan-Thermo Element II).

Scale analysis

The purpose of our scale analysis was to associate ages and particular structure patterns of juvenile Chinook salmon with the habitat they were sampled, so as to estimate juvenile life history strategy in adult scale samples. We collected scales over three years (2009 – 2011) from returning non-marked (presumed wild) adult Chinook salmon. Scales from adult Chinook were obtained during spawning ground surveys on the North Fork Willamette River and Fall Creek from carcasses, and from fish trap collections at Dexter Dam on the Middle Fork Willamette River (Figure 1). During the same years scales from juvenile Chinook (presumed wild) were obtained from a variety of habitats so as to investigate habitat specific scale structure patterns. Scales were collected by the United States Army Core of Engineers (USACE) and the Oregon Department of Fish and Wildlife (ODFW) rotary screw traps, ODFW reservoir sampling, and hook and line methods from North Santiam, McKenzie, and Middle Fork Willamette sub-basins, as well as Willamette Falls (Figure 1). Sampling natal (adult outplant) streams, project reservoirs, and directly below project dams in the tailrace (assumed reservoir habitat).

A total of 210 adult and 95 juvenile Chinook salmon scales were analyzed by the Oregon Department of Fish and Wildlife Life History Research Lab. Scales were mounted on gummed paper and impressed in plastic for viewing with a microfiche projector or using image analysis software. Standard QA/QC methods employed by

the ODFW Scale Project were used; scales were read by two experienced readers (trained using scales of known origin) and without knowledge of sample location or data for each analyzed set of scales from individual fish. Any discrepancies were resolved during a joint reading. Juvenile life histories were interpreted from circuli patterns in the freshwater zone on the scale of juveniles collected from known habitats and ages. These circuli patterns were then referenced to scales from adults to infer juvenile freshwater life history (Figure 3).

Otolith chemical analysis

The purpose of our otolith chemical analysis was to determine life history traits and then to compare this with estimates derived from scales in the same individuals. We sampled otoliths from a sub-sample of adult Chinook salmon ($n = 70$) that were also assigned a juvenile life history with scale techniques. Otoliths from North Fork Middle Fork Willamette and Fall Creek spawning grounds, from brood years 2005, 2006, 2007, and 2008 were analyzed for $^{87}\text{Sr}/^{86}\text{Sr}$ ratios and concentrations of Sr:Ca with a transect on the dorsal region from otolith edge to core. Otoliths were mounted on glass slides using crystal bond resin, polished with a lapping wheel to expose daily growth increments, and were analyzed using a Finnigan Neptune multicollector inductively coupled plasma mass spectrometer (Thermo Scientific), coupled with a New Wave UP-213 laser ablation sampling system (MC-LA-ICPMS) at the Washington State University Geoanalytical Laboratory in Pullman, WA. To evaluate the internal precision of the instrument, a marine carbonate standard was used to correct each measurement (Hegg et al. 2013).

Otolith growth analysis

The purpose of the otolith growth analysis was to determine relative somatic growth differences between reservoir and natal tributary habitats. Daily increments in fish otoliths are a product of an endogenous circadian rhythm for which the relative widths between increments covary in a consistent manner with fish growth, thus providing an accurate record of an individual's growth (Neilson and Geen 1985). Otolith microstructure analysis was used to compare relative juvenile growth opportunities of Chinook salmon between reservoir and natal outplant tributaries.

Relative growth estimated from samples collected in Cougar ($n = 4$) and Lookout reservoirs ($n = 10$), was compared to samples from the South Fork McKenzie ($n = 7$) and the North Fork of the Middle Fork Willamette River ($n = 8$). Sample sizes were small because of the ESA listed status. Fork length and mass were measured before removal of the left otolith. Otoliths were mounted on glass slides using Crystalbond resin (<http://www.crystalbond.com>), and polished in a sagittal plane using a grinding wheel and water based alumina grit slurries (sizes 600, 400, 100 μm). Polishing ceased when central primordial and daily microstructure increments were visible with a compound light microscope. Otoliths were then re-heated and flipped, and polishing continued on the opposite side until microstructure was visible. Polished otoliths were photographed using a digital camera (Moticam 2300) mounted on a compound microscope (Zeiss; 20x magnification). Image Pro software (MediaCybernetics) was used to measure daily increment width along the ventral transect perpendicular to the longest longitudinal axis. Total otolith radius was also measured on the same axis. If daily increments

were not clear from the otolith core to edge, the transect was shifted slightly. The mean width of 5-10 consecutive daily growth increments at 100, 200, 300, 400, 500, 600, and 700 μm from the primordium were calculated. We assumed discrete measurements from otolith core were comparable between fast and slow growing fish. A constant number of 10 increments could not always be measured due to variable visual quality of preparations. Otolith microstructure increments were compared with a Welch two sample t-test (which does not assume equal variance) between reservoir and natal stream sampled otoliths at each measurement from otolith core.

Life history determination and size comparison

To test the accuracy of scale life history we compared life history classifications obtained from otolith chemical transects ($^{87}\text{Sr}/^{86}\text{Sr}$ and Sr:Ca) and structural patterns derived from scales from the same fish. Freshwater life history classifications were determined for 70 adult otoliths from brood years 2005, 2006, and 2007 collected from North Fork Middle Fork Willamette and Fall Creek spawning grounds. First, we identified the time of freshwater emigration (i.e. the point of brackish-oceanic entry) by the inflection point of $^{87}\text{Sr}/^{86}\text{Sr}$ and Sr:Ca, (see Miller et al. 2010, 2011). Next, Based on the location of the Sr:Ca inflection compared to the first annulus (i.e. before or after freshwater emigration), fish were classified as sub-yearling or yearling. We measured otolith width at inflection point, and used a juvenile otolith width and fork length back calculation model to estimate juvenile size at freshwater emigration (Figure 4). The juvenile back calculation model was constructed with a sample of $n = 67$ juvenile Chinook salmon sampled in the North

Santiam, McKenzie, Middle Fork Willamette sub-basins; in natal rearing streams, project reservoirs, and below project reservoirs, as well as Willamette Falls trapping facility (Figure 8). The back calculation model consists of a linear regression analysis of juvenile fork length (FL) and otolith width (OW). FL was measured prior to preservation and OW was measured along the dorsal-ventral growth axis at the widest point.

We compared freshwater age estimated from otolith and scales (Figure 7). This analysis sought to gain detailed age information of each scale life history pathway. We also compared size at freshwater emigration to scale derived life history pathway (Figure 9). We used ANOVA and Tukey's HSD to test the hypothesis that average size at freshwater emigration is larger in reservoir reared juveniles in each age class.

Results

Water chemistry

Water samples from mainstem Willamette and lower freshwater Columbia Rivers generally exhibited low Sr:Ca values (2.35-2.93 mmol/mol) compared to marine samples from the southern Oregon coast (Table 1). The $^{87}\text{Sr}/^{86}\text{Sr}$ water chemistry values, of mainstem Willamette river samples were lower (0.7041-0.7044) than lower Columbia River samples (0.7089-0.7104), and the $^{87}\text{Sr}/^{86}\text{Sr}$ global marine value (0.7092) was lower compared to lower Columbia River samples (Table 1). Thus, we were able to distinguish between freshwater and marine habitats.

Life history classification using scale analysis

Scales collected from juvenile Chinook salmon from habitats throughout the Willamette basin showed distinct structural patterns associated with a variety of age classes and habitat use (Figure 3). Sub-yearling, yearling, and 2 year old juvenile Chinook salmon ranged in back-calculated size from 67-251 mm (sub-yearling), 139-256 mm (yearling), and one 315mm 2 year old individual. Sub-yearling individuals were collected in natal streams and ranged from 60-105mm. Yearlings collected in the Willamette falls trapping facility were 126-146mm (Figure 5).

Life history determination using otoliths

All otoliths showed a consistent pattern of chemical composition across the growth axis. Sr:Ca and $^{87}\text{Sr}/^{86}\text{Sr}$ exhibited the expected pattern of increased values at the core of the otolith, due to maternal influence, declined to a steady value during freshwater residence in the Willamette valley, and abruptly increased to a stable value during marine residence (Figure 4, upper panel). For Sr:Ca, freshwater values were <1.3 mmol/mol and marine values ranged from 1.5-2.4 mmol/mol. For $^{87}\text{Sr}/^{86}\text{Sr}$, freshwater values ranged from 0.7039-0.7042 and marine values were stable at the global marine value (0.70918).

Otolith growth analysis

Juvenile Chinook salmon sampled in project reservoirs (n=14) had wider average growth increments (mean 4.85-5.25 μm) compared to juveniles sampled in natal streams (n=14) (mean 3.25-4.15 μm). Both natal stream and reservoir salmon otoliths showed consistent trends of decreasing in average otolith increment width from 100-400 μm from otolith core, and both increasing at 500 μm (Figure 6). For

reservoir samples, average otolith width increased past 500 μm , however no otoliths were wider than 559 μm in natal stream samples, so no measurements were possible. Significant differences were found for the 100 μm ($t=2.52$, $df=15.48$, $p=0.023$), 200 μm ($t=3.3$, $df=17.90$, $p=0.004$), and 400 μm ($t=3.22$, $df=14.88$, $p=0.006$) measurements when comparing average microstructure width between reservoir and natal stream habitats (Figure 6).

Back-calculation of juvenile size

Juvenile fork length (FL) (mm) was positively and linearly related with otolith width (OW) (μm), ($r^2=0.850$, $n=67$). Hence, we used the following relationship to estimate FL based on OW:

$$\text{FL} = 0.196 \times \text{OW} - 16.73$$

The estimated fork length at freshwater emigration ranged from 69.60-239.72 mm. Juvenile size at freshwater emigration ranged from 69.59-171.43 mm in the O life history strategy, 143.22-215.57mm in OR, 140.50-222.93mm in 1S, 101.89-239.72mm in 1R, and 223.94-238.61mm in 2S. Mean estimated length at freshwater emigration was significantly different among the five life history pathways ($F=8.977$, $n=70$, $p<.0001$). Among age classes, there was a significant difference between O and OR (Tukey's HSD $p=0.0002$), where size of reservoir reared fish were larger; 1R were also larger than 1S, though this difference was not significant (Tukey's HSD $p=0.166$; Figure 9).

Life history determination using scales and otoliths

Comparison of scales obtained from juvenile Chinook salmon from known locations to adults returning to the same sub-basin revealed evidence of a variety of life history pathways. Juvenile Chinook salmon freshwater life histories were categorized into the following life history pathways: **0** (subyearling, natal stream resident), **0R** (subyearling, reservoir habitat use), **1S** (yearling, natal stream resident), **1R** (yearling, reservoir use), **2S** (yearling plus, natal stream resident), and **1S1R** (yearling plus, natal stream resident in first year of life and moving to the reservoir habitat in second year of life) (Figure 2).

When analyzing adult natural origin scales (n=210) from brood years 2005-2008, collected on NFMF and Fall Creek spawning grounds, we found all six life history pathways. The most common life history pathway was 1R (48%), followed by 0R (27%), 1S (17%), 0 (5%), 1S1R (2%), and 2S (1%) (Figure 10).

Freshwater age based on otolith chemical and structural analysis revealed sub-yearling (0), yearling (1), and two year old (2) age classes. We compared the freshwater age classifications based on otoliths to those from scale life history classifications. There was not complete correspondence in terms of life history type between otolith and scale. Specifically, for the 0 scale life history classification, 66% fish (n=3) matched the 0 otolith classification, however 100% of the 0R scale life history fish (n=26) were in the yearling otolith age group. In the yearling scale life history classifications, 95% (n=22) of the 1S scale group and 94% (n=18) of the 1R scale group were in the yearling otolith class. 100% of the 2S scale class was in the otolith freshwater 2 age class (Figure 7).

Discussion

Using a combination of scale and otolith techniques, we found evidence of six juvenile Chinook salmon life history strategies in the upper Willamette River spring Chinook salmon population, with the yearling reservoir (1R) and sub-yearling reservoir (0R) representing the highest proportions (48% and 27% respectively) (Figure 10). Immediately following dam construction in the Willamette Valley, three juvenile life history pathways were observed, with the most common demonstrating a yearling strategy and two less common sub-yearling life histories emigrating in their first spring and fall (Mattson 1962). Our results indicate increased variability in life history strategies in the upper Willamette spring Chinook salmon population, likely induced by novel reservoir rearing habitats created by human manipulation of the rearing and migration corridor.

We found faster relative growth rates in juvenile Chinook salmon that dispersed into project reservoirs, compared to those that were sampled in natal streams (Figure 6), which was also found in past monitoring (Monzyk, 2011 personal communication). Growth rates were relatively faster throughout the early life history of juvenile Chinook salmon in our growth analysis (Figure 6), which suggests juveniles dispersed to project reservoirs soon after hatching. Early growth opportunity is an important factor in juvenile life history characteristics including size, age, and timing of smoltification (Quinn 2010). Heterogeneity in freshwater growth opportunities has been linked to early downstream dispersal (Healey 1991, Quinn 2010), and research has found variability in the propensity of juvenile Chinook salmon to disperse downstream and use all available freshwater rearing habitats.

Our results indicate that novel reservoir habitats have allowed for a diversity of growth opportunities, hence a continuum of ages and sizes of juvenile Chinook salmon throughout rearing habitats (Figure 5). Juvenile Chinook salmon have shown behavioral thermoregulation in Columbia reservoirs, and Tiffan et al. (2009) suggested that this behavior could enhance growth opportunity and life history diversity in Chinook salmon populations. In the Willamette basin, reservoir habitats are highly variable between sub-basins due to elevation, temperature, and temporal water regulation. These habitat characteristics could explain the variability in juvenile growth and size that we found.

Growth rate and residence time in rearing habitats are a function of juvenile Chinook salmon size, prior to migration. Fish size has been shown to confer a selective survival advantage in many populations of fishes (Sogard 1997). A broad array of ages (0-2 years) and sizes (67-315mm) in juvenile Chinook salmon were found in reservoir habitats, contrary to a small size (55-148mm) and age range (0-1 year) found in natal stream sampling (Figure 5). This could be a product of temporal sampling bias or low sample size, but similar trends were found in a dam influenced survival and behavioral study of Willamette River juvenile salmonids (e.g. Keefer et al. 2011). Our results support the conclusion that larger juveniles have higher survival probability in freshwater. However, poor downstream survival of larger smolts through project dams (Keefer 2011) contradicts the conclusion that reservoir rearing is an adaptive strategy.

Miller et al. 2011 estimated the juvenile fork length of returning adult upper Columbia River spring Chinook salmon, and found a size range of 110-170mm, with

the majority estimated at 130-139mm. Our data show a broader size range of juvenile Chinook salmon fork length at freshwater emigration: from 85-270mm, with the majority estimated at 170mm. Comparatively, this suggests that upper Willamette spring Chinook salmon are experiencing higher growth opportunities and emigrating from freshwater at larger sizes.

Variation in life history strategy has been associated with complex habitat and environmental conditions (Healy and Prince 1995, Bottom et al. 2010). In the upper Columbia River spring Chinook salmon population human alterations have reduced habitat complexity and rearing opportunities, and life history variability is much less complex than was observed in the past (Burke 2004, Bottom et al. 2005b). Although similar alterations have occurred in the upper Willamette basin, our results indicate that the reservoir habitats are promoting life history diversity by providing a productive rearing environment

The influence of human alterations on Chinook salmon life history variability has implications for population level consequences, and subsequent management decisions. Life history variability in pacific salmon populations spreads risk and can avoid brood failure by acting as a bet-hedging mechanism against stochastic environmental rearing and migrating conditions (Healy 2009, Schindler et al. 2010). This provides resilience in populations because all individuals do not rear in the same habitats over time or space, and allows for at least some individuals to survive unfavorable conditions (Bottom et al. 2009). The variability in size and age of juvenile Chinook salmon outmigrating in the Willamette basin shows a continuum of rearing and migration behaviors that must be conserved for population recovery.

Future work should focus on the relative fitness of life histories, and how life history diversity is influenced by future downstream passage projects at Willamette River dams.

Summary

This study validates the accuracy of scale morphometric patterns in discerning juvenile life history classifications. Using scales for accurate juvenile life history classification in adult Chinook salmon enables researchers to obtain large sample sizes of scales from migrating juveniles and successful post-spawn adults in the Willamette basin. This represents the baseline data for assessing the relative fitness among life history types with a matrix modeling framework, and potential benefits to Chinook salmon of implementing dam passage vs. head-of-reservoir collection and transport operations. The modeling approach could provide information on stage or life history type specific mortality and survival rates that affect overall population growth. Specifically, this data will assist in estimating the contribution of reservoir-reared juveniles to the population growth rate, identifying thresholds where environmental conditions will have affects on the population, and describing important knowledge gaps and parameter uncertainties. There is also potential to assess historic life history type fitness frequency and how population growth rate has changed over time, with archival scale collections that many agencies have collected historically.

Although human habitat alterations in the Willamette basin have decreased the Spring Chinook salmon population to the point of ESA listing, investigating the influence of dams and novel reservoir habitats on juvenile life history is crucial in

rebuilding the natural population for a sustainable future. This study provides Willamette basin scientists with frequency estimates of juvenile life histories in returning adults, and accuracy validation of scale patterns to be used as a tool in reconstructing juvenile life history. This is imperative because recovery efforts and dam passage engineering in the Willamette basin should focus on increasing survival of all juvenile life histories, in an effort to establish population resilience. This research is a framework to study how non-natural habitat manipulations affect early life history in fishes, and has broad applications where freshwater ecosystems are experiencing human manipulations.

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Table 1. Summary of water geochemical data ($^{87}\text{Sr}/^{86}\text{Sr}$, Sr:Ca) for various locations in the Mainstem Willamette river, Lower freshwater Columbia River, and Marine environments.

Location	$^{87}\text{Sr}/^{86}\text{Sr}$	Sr:Ca (mmol/ mol)	River km From Ocean	Source
Mainstem Willamette River - Buena Vista, OR	0.7042	2.73	333.1	This study
Mainstem Willamette River - Salem, OR	0.7041	2.93	300.9	This study

Mainstem Willamette River- Willamette Falls	0.7044	2.68	207.6	This study
Columbia River - below Bonneville Dam	0.7133	2.35	235	Miller et al. 2011
Columbia River - St. Helens, OR	0.7089	2.78	138.4	This study
Columbia River - Goble, OR	0.7104	2.64	117.5	This study
Marine - Southern Oregon Coast	0.7092	8.60	0	Miller et al. 2010

Willamette Basin

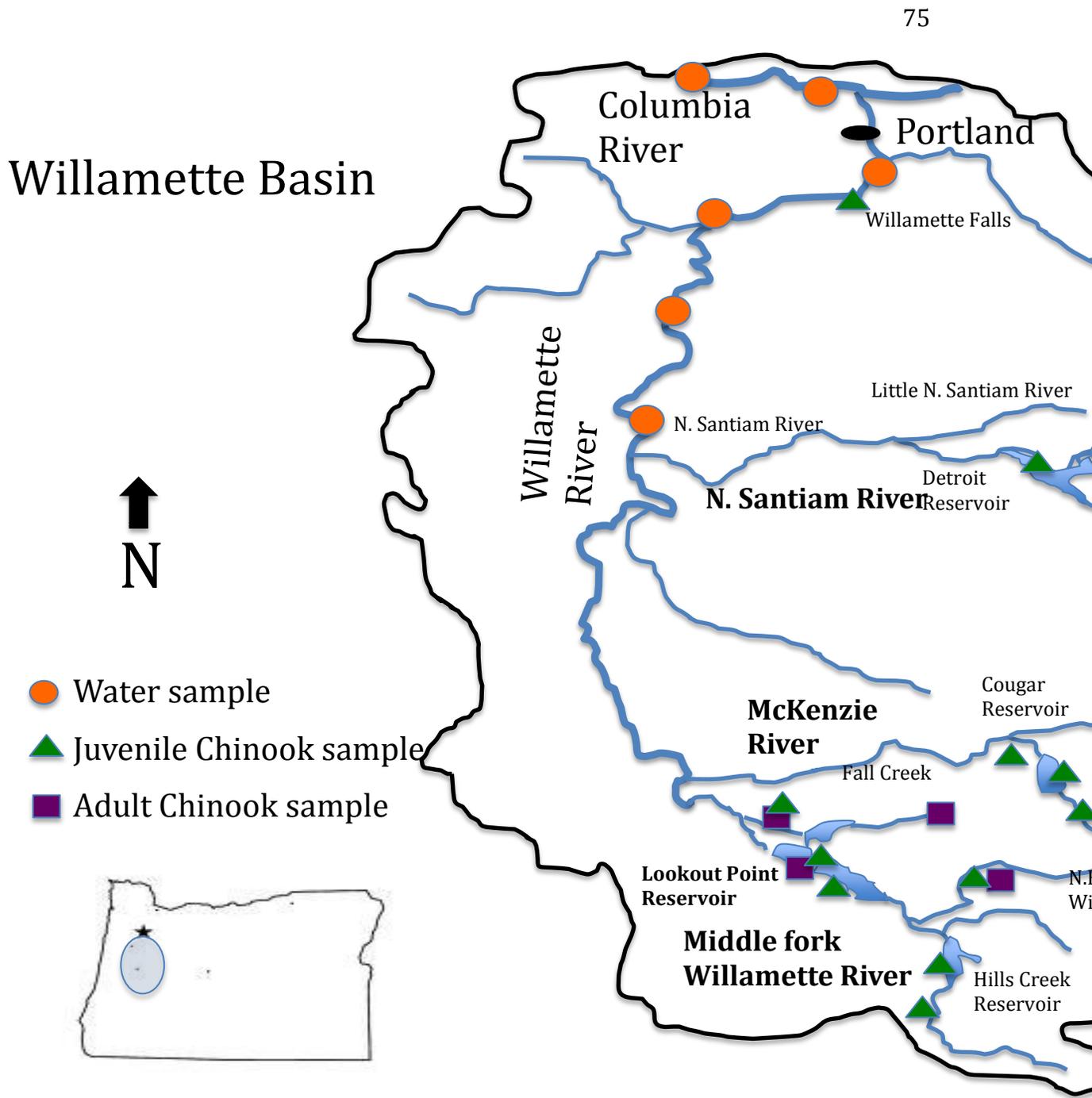


Figure 1. Location of the Willamette Valley with three major sub-basins (North Santiam, McKenzie, and Middle Fork Willamette). Locations of water samples (●),

juvenile Chinook salmon samples () , and adult Chinook salmon samples ()
identified.

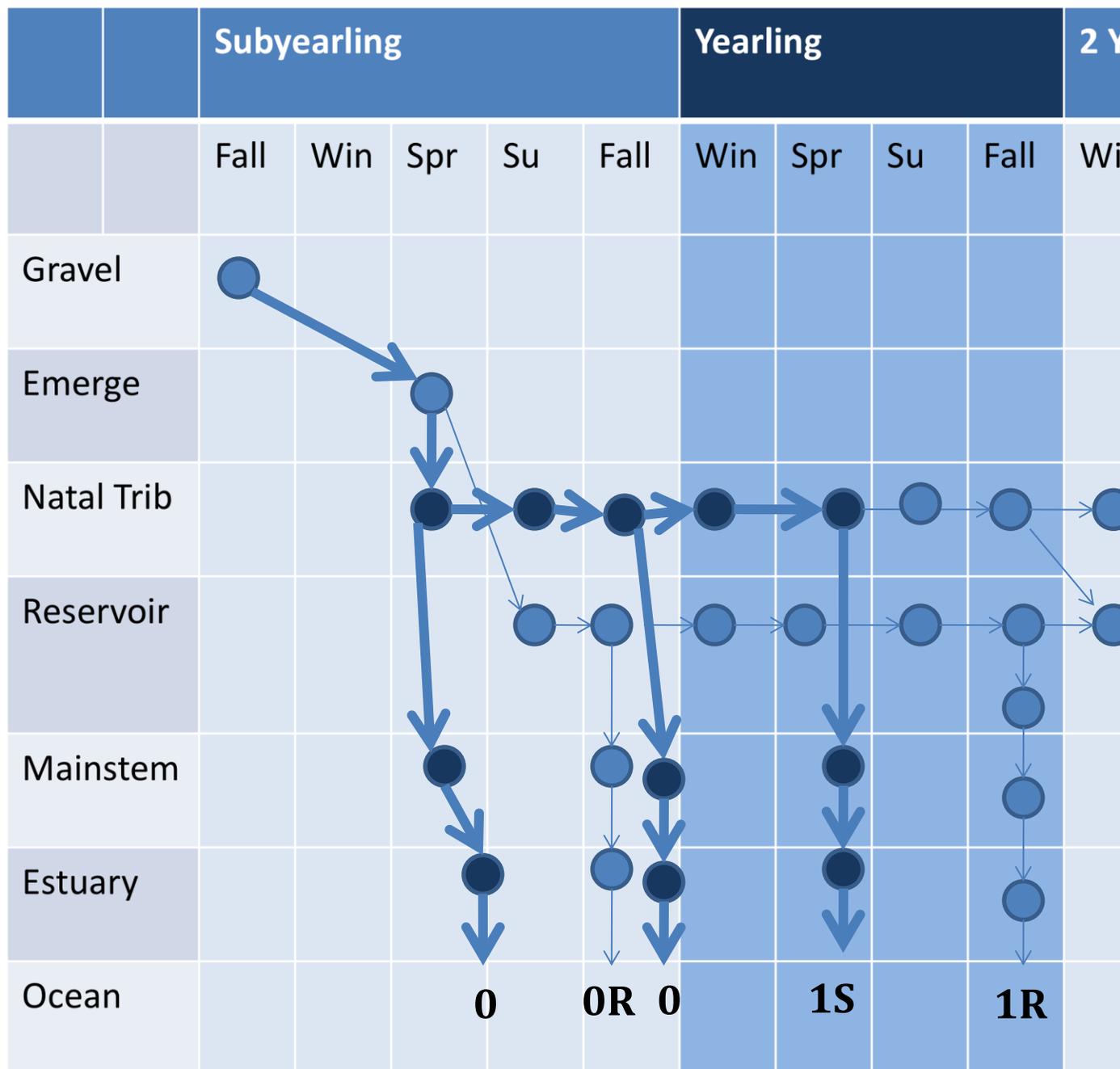


Figure 2. Six juvenile life history pathways described in scale analysis (light blue and dark blue dots). 0 = subyearling, 0R = subyearling rearing in reservoir, 1S = yearling rearing in natal stream, 1R = yearling rearing in reservoir, 2S = yearling + natal stream rearing, 1S1R = rearing 1 year in natal stream and 1 year in reservoir. Dark blue dots represent historical life history types (Mattson, 1962).

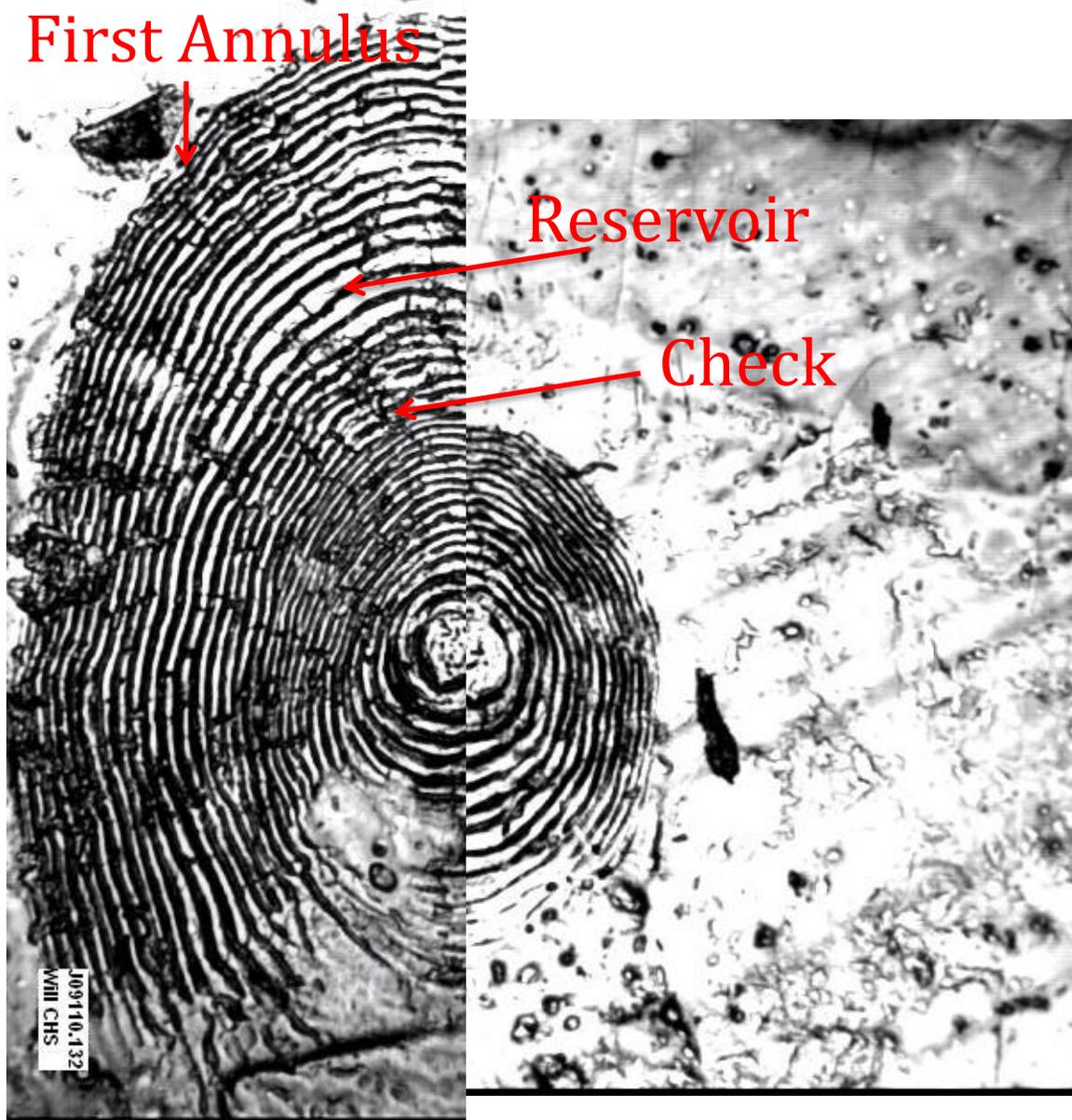


Figure 3. Comparison of two juvenile Chinook salmon scales from the NFMF basin. Left panel: juvenile Chinook salmon sampled on 9/10/09 in Lookout Point Reservoir, aged as a yearling with its first annulus forming on the edge. Brood year = 2007. Right panel: juvenile Chinook salmon sampled on 9/22/09 in the NFMF Willamette, aged as a sub-yearling based on the timing of collection and scale size, Brood year = 2008. The two images were taken at the same magnification and were cropped, but are otherwise unaltered. The area of intermediate growth just after the first annulus on the older fish may represent spring growth in the stream followed by summer growth in the reservoir.

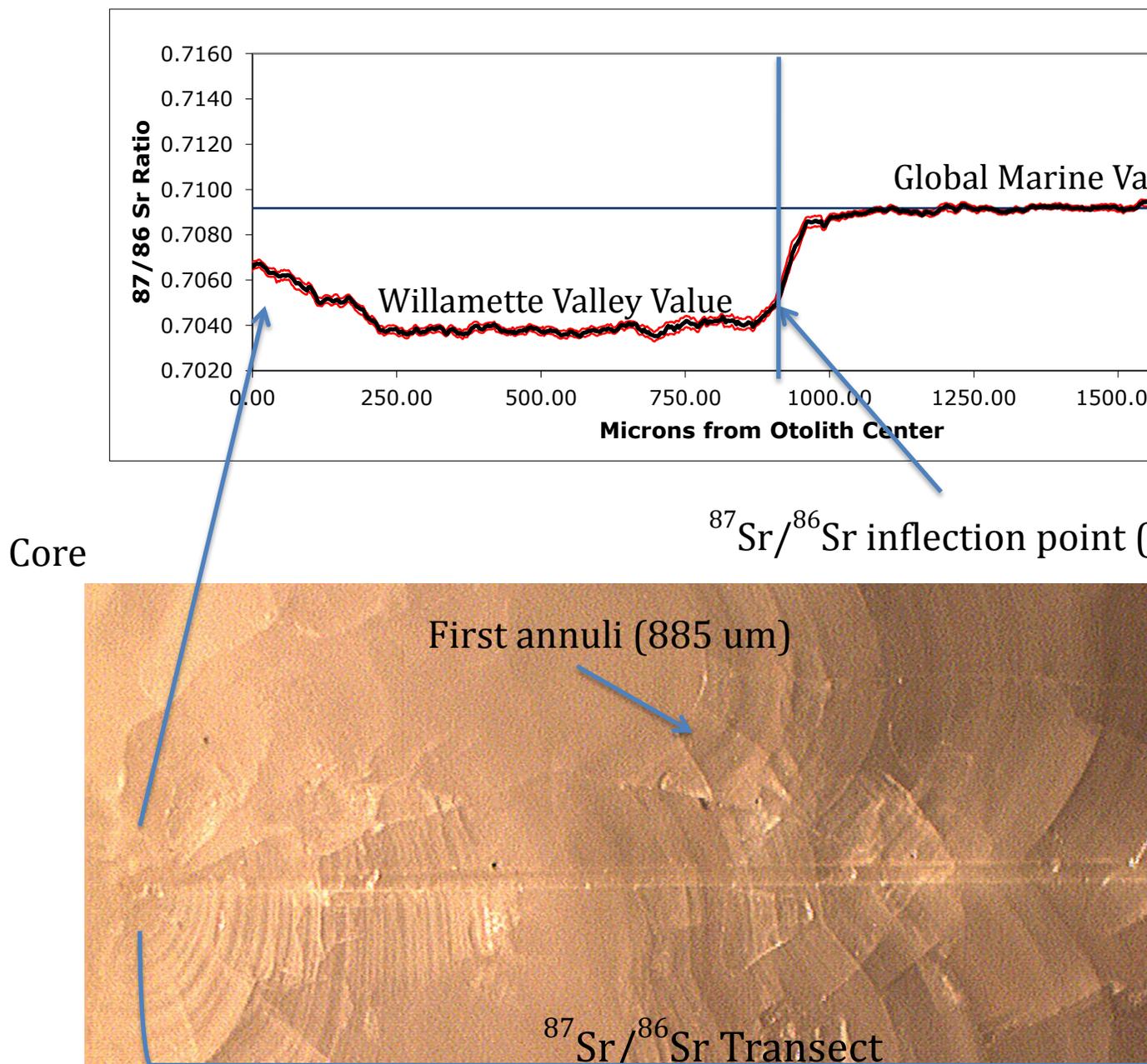


Figure 4. Chemical profile of an adult Chinook salmon otolith showing the $^{87}\text{Sr}:^{86}\text{Sr}$ inflection point in the top panel and the respective microscope image with the laser ablated transect and first annuli, in the bottom panel.

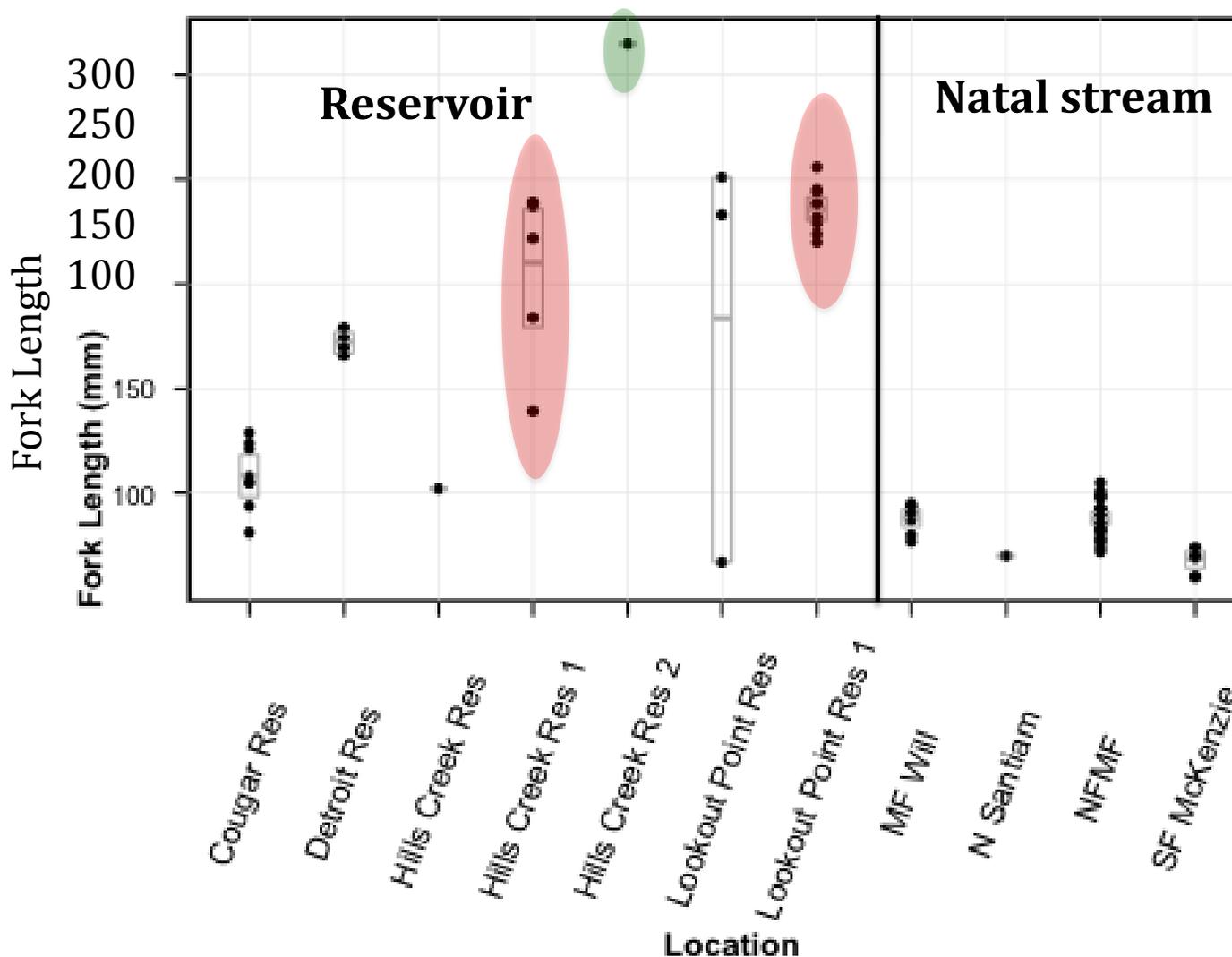


Figure 5. Juvenile Chinook salmon collected from 2009-2010, from throughout multiple habitats in the Willamette basin plotted by fork length (n=86). Reservoir sampled individuals in the left panel, natal stream juveniles in the middle panel, and individuals collected at Willamette Falls collection facility in the right panel. No shading represents sub-yearling, red shading represents age 1, and the green shading represents age 2.

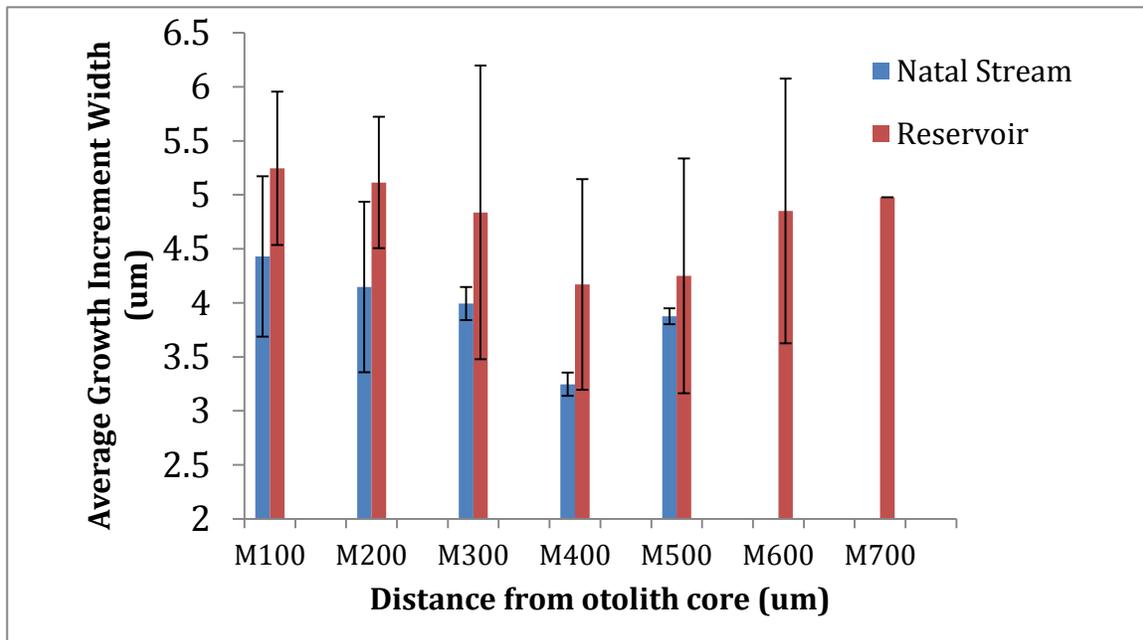


Figure 6. Average microstructure increment width in juvenile otoliths sampled from natal stream (blue bars) and reservoir habitats (red bars). Each distance increment on the x-axis represents the M (measurement) or the average of 5-10 daily growth rings.

Scale Life History Classifications

Otolith Freshwater Age		0	0R	1S	1R	
	0		66%		5%	6%
1		33%	100%	95%	94%	
2						
Sample		3	26	22	18	

Figure 7. Comparison between life history classification in scale analysis and freshwater age from otolith analysis. Otoliths and scales were sampled from the same individual adult Chinook salmon (n=70, brood year 2005, 2006, 2007, and 2008). Blue boxes represent an age match between scale life history and otolith freshwater age. The percentages show the proportion of each scale life history that falls into otolith age classifications.

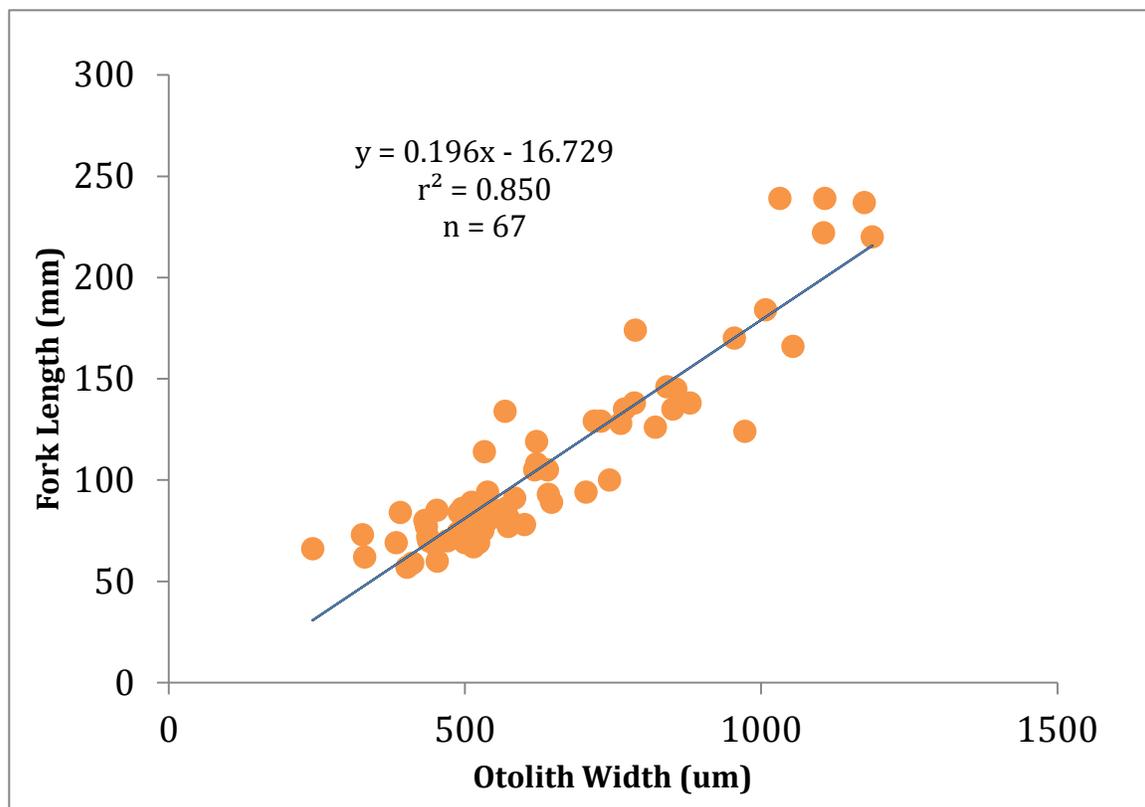


Figure 8. Juvenile Chinook salmon back calculation model. Juvenile fork length was positively and linearly related to otolith width. Juveniles were collected to represent a variety of sizes and age classes.

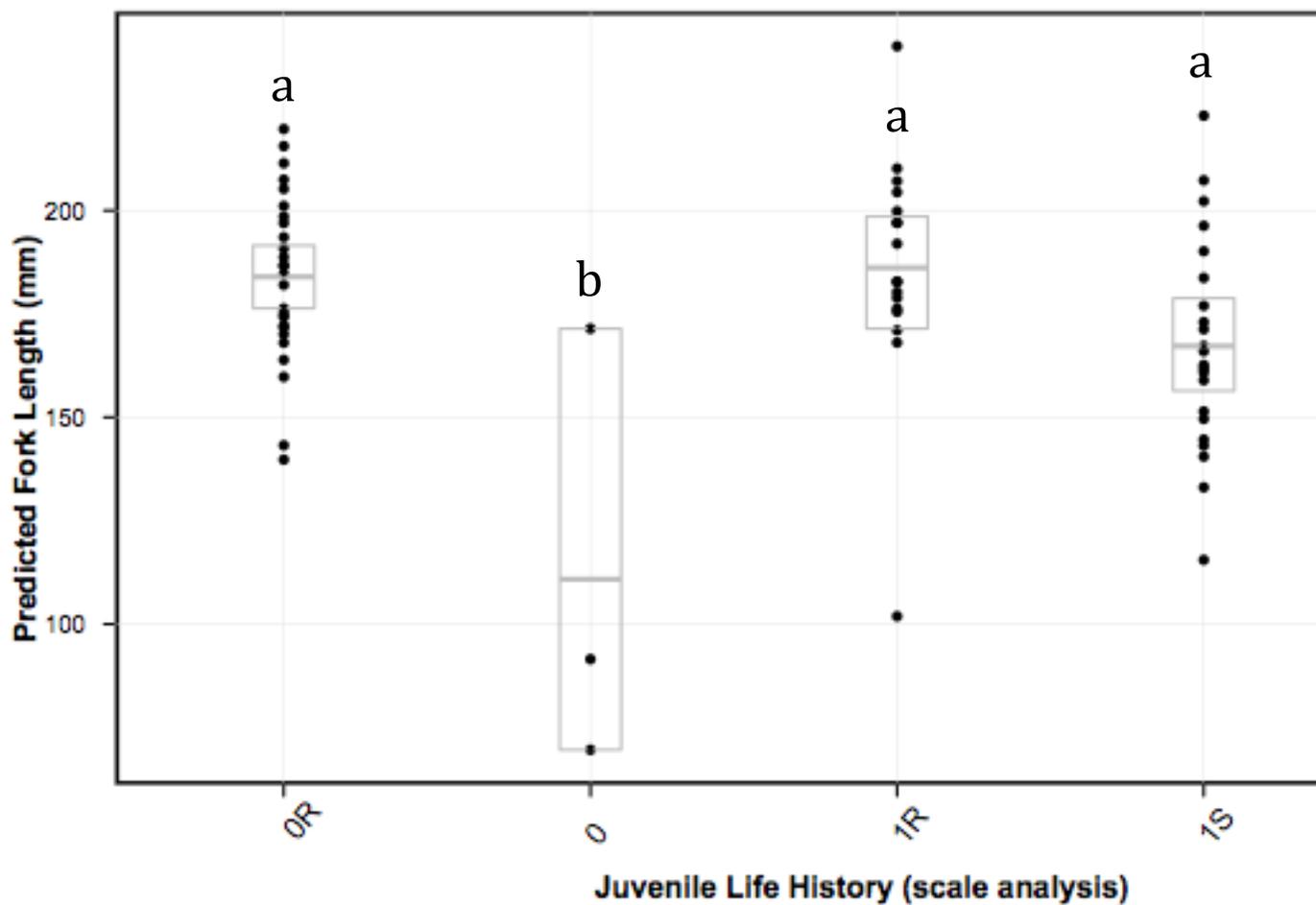


Figure 9. Predicted fork length of juvenile Chinook salmon at freshwater emigration from adult otolith analysis, plotted by juvenile life history from adult scale analysis. Otoliths and scales were sampled from the same individual adult Chinook salmon ($n=70$, brood year 2005, 2006, 2007, and 2008). Bars represent mean and 95% confidence interval.



Figure 10. The number of juvenile life history types in natural origin adults (n=210, brood years 2005-2008), collected on NFMF and Fall Creek spawning grounds found with scale analysis.