

Spatial and Temporal Growth Opportunity for Juvenile Fall Chinook Salmon in the Snake and  
Clearwater Rivers, Idaho

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by

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### Authorization to Submit Thesis

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## Abstract

Understanding the conditions that produce diverse salmonid migration strategies is challenging in a large river network where life history trajectories arise from multiple biotic and abiotic factors. Because early growth is closely linked to migration initiation, identifying the growth conditions experienced by individual fish at a small time scale is crucial. Here, we paired a long-term otolith dataset with a detailed bioenergetic assessment of early growth opportunity in a population of Chinook salmon to identify how growth conditions related to migration initiation. In the Snake river population of fall Chinook salmon, juveniles historically migrated their first summer, but in recent years an overwintering migration strategy has emerged. Using otolith microchemistry and microstructure analysis, we determined that a significant proportion of fish from both the Clearwater and Snake rivers overwinter and migrate the following spring. Notably, Clearwater origin fish that migrated as yearlings performed a larger proportion of their freshwater growth in natal habitat than Snake origin fish. We also found higher growth and consumption during the early growth period for fish originating in the Snake river and downstream reservoir compared to the Clearwater river, by comparing relative growth and consumption using a daily time-step bioenergetics model. The combined bioenergetics and migration analysis demonstrates that while both Snake river and Clearwater origin fish express the overwintering strategy, their relative growth in natal habitats differ. These findings suggest that the yearling migration strategy may arise from different conditions throughout the population, though the net effect is the increasing prevalence of this strategy.

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### **Dedication**

For John, Kona and Bear, my adventure buddies and best friends. You three made this possible.

For Mom, Dad, and Lauren. See? I'm a scientist now.

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## CHAPTER 1

### A Bioenergetic Analysis of Growth Opportunity for Juvenile Chinook Salmon in the Snake River

#### **Abstract**

The early growth and movement of juvenile salmonids is related to the spatial and temporal distribution of rearing habitat in a river network. Habitat conditions are known to vary considerably between free-flowing rivers and the reservoirs that sometimes punctuate them, but implications of these differences for early growth of juvenile salmonids is unclear. Previous research in the Snake River basin (Idaho, USA) suggests that reservoir habitat represents a compromise for growth potential for rearing subyearling fall Chinook salmon. We used otolith-derived daily growth paired with a bioenergetics modeling framework to examine variation in subyearling growth rates in four river sections of the Snake and Clearwater Rivers. We hypothesized that habitat qualities such as temperature and prey energy density would vary between river sections and over time, and we predicted that this would result in lower growth rates for reservoir reared subyearlings. In contrast to our predictions, we found that between three river sections and one reservoir section examined, predicted growth and consumption were highest in the reservoir section, though growth was not significantly higher in the reservoir for the full duration of the study (overlapping 95% confidence intervals). We found that Julian date was the strongest predictor of growth and consumption (Generalized least squares model determined from model selection using  $\Delta AIC$  and  $AIC_w$ ), and that both growth and consumption decreased over the course of the study, even when accounting for allometric growth effects. These findings suggest that fish rearing in the reservoir section during their early growth period may have an ephemeral energetic

advantage relative to fish rearing in natal river sections, though future research must address that tradeoffs that reservoir rearing pose for migration and survival.

## **Introduction**

The uneven distribution of resources across the landscape drives spatial variation in occupancy and movement by animals. Individuals experience tradeoffs between growth opportunities and the costs of moving between habitats, which provides a mechanistic basis for the emergence of a diversity of dispersive or migratory strategies among individuals within a population (Stearns 1989). However, individual movement strategies may also result from genetic variation in evolved traits which manifest at the species level and are unrelated to individual-level variation in growth opportunity (Stenseth and Mysterud 2002; Durant et al. 2007). As a result, attributing the shifting composition of movement and migration strategies to changes in habitat conditions can be challenging, requiring an understanding of the contribution of evolved strategies and the relative plasticity of different strategies in the population (Crozier et al. 2008).

In Pacific salmon species, early growth is a quality which is both closely linked to migration and largely attributable to habitat conditions experienced by individuals, rather than to genetic variation (Perkins and Jager 2011). Because growth is closely linked with juvenile salmon migration initiation, understanding the relative growth potential of habitats used by a given population can help illuminate whether movements result from a plastic response to growth conditions or are an evolved strategy that is disjunct with current environmental conditions (Crozier and Hutchings 2014). Juvenile fall Chinook Salmon in the Snake River are known to express several distinct migration strategies that include some level of natal

river rearing followed by rearing and downstream movement in impounded reservoir habitats before ocean entry (Connor et al. 2003b). Understanding the variation in growth opportunity in natal river and downstream reservoir habitats could inform our understanding of how migration strategies are expressed within this population.

Juvenile Chinook salmon rear in impounded rivers throughout their range, including in many rivers which have been the focus of rearing habitat quality studies. In the John Day Reservoir on the Columbia river, Haskell et al. (2017) determined that higher energetic demands of warm summer water temperatures require juvenile Chinook salmon to switch from consuming low-quality zooplankton prey to higher energy juvenile fish. Additionally, previous research in the Snake River compared diet and growth in riverine and reservoir habitats within the basin and determined that juvenile Chinook salmon consume lower quality prey in reservoir habitat than riverine habitat and identified subsequent differences in juvenile growth (Tiffan et al. 2014). However, growth opportunity for Snake River fall Chinook salmon may also be related to the temporal variation in habitat experienced as fish progress downstream from natural free-flowing river habitat to impounded reservoir habitat, but at this time few prior studies have examined the earliest growth opportunity experienced by Snake River fall Chinook rearing in their natal habitat.

Because environmental variables like temperature can interact with the quality and quantity of prey to produce variable outcomes for growth, understanding their additive impact on individual fish can be challenging. Bioenergetics modeling is an approach which relies on a complex understanding of fish physiology and ambient habitat characteristics to generate predictions of growth or energy consumption by employing a series of mass balance equations (Ney 1993). By incorporating site-specific environmental variables such as prey energy

density and water temperature, bioenergetics modeling captures and aggregates the effects of both natural and anthropogenic variation (eg. Kennedy et al. 2008; Budy et al. 2011).

An additional challenge to understanding growth opportunity for juvenile salmonids is the temporal variability of systems. When habitat quality can change on a weekly or daily basis, traditional growth measurements that occur at the beginning and end of a study could be insufficient to identify changes in growth rate. Otolith-based growth reconstruction can be used in place of in-situ growth measurements to estimate growth rate over a long period of time without losing fine-scale resolution (Campana 1990). Otoliths are calcium-carbonate structures (aragonite) used by fish for hearing and orientation. Daily rings are formed by accretion of calcium-carbonate in layers and are directly related to the length of the fish (Francis 1990; Campana 1990, 1999). By measuring the distance between otolith rings, we can reconstruct daily growth for individuals from populations where fish-length to otolith-radius relationships are known, such as Snake River fall Chinook salmon (Zabel et al. 2010).

The overarching objective of this study is to quantify how spatial differences in rearing locations translate into performance differences for juvenile fall Chinook salmon, *Oncorhynchus tshawytscha*. We aim to understand how growth rates and opportunity varies throughout the basin by addressing two questions: First, do temperature and prey energy density variables vary significantly between the different river and reservoir reaches during a critical period for growth? Second, does observed growth in pre-migration fall Chinook vary between reservoir and river rearing areas? We addressed these questions using a spatially-explicit bioenergetics model and growth data collected from otoliths of juvenile fall Chinook salmon.

## Methods

### Field Site

This study examined fall Chinook salmon originating in the Snake and Clearwater Rivers of western Idaho (Figure 1.1). These two rivers confluence in Lewiston, Idaho, and together comprise the majority of spawning habitat for the fall run Chinook salmon evolutionarily significant unit (Connor et al. 2002). Lower Granite Reservoir, formed by Lower Granite Dam, extends 39.3 miles downstream from the confluence of the Snake and Clearwater Rivers. The upstream range of salmon in the Snake River is bounded by Hells Canyon Dam, while movement in the mainstem Clearwater River is not prevented by impoundments. The North Fork Clearwater River confluences with the mainstem Clearwater River 41 miles upstream of the confluence. The North Fork Clearwater River is impounded by Dworshak Dam 1.9 miles upstream of the confluence and cold water releases from Dworshak Reservoir are used for summer temperature control in the downstream snake reservoir habitats (Connor et al. 1998).

### Fish collection

Juvenile fall Chinook salmon were collected from the Clearwater River, the Snake River, and the Lower Granite Reservoir between mid May and early June. We collected fish using a 100-meter seine set parallel to the shore by boat then pulled directly into the shore. Fish that were of possible hatchery origin were excluded based on either tags, clips or morphometric features (pupil diameter and body depth) identified by USGS staff. To determine diets, we performed gastric lavage on a sample of up to 20 captured wild juveniles at each sampling location (Table 1.1). Fish were anesthetized by submersion in Tricaine Methanesulfonate (MS222) buffered with sodium bicarbonate to a pH between 7.0-7.5,

weighed and measured, then pulsed gastric lavage induced fish to regurgitate stomach contents. Contents were collected in filter paper over a funnel then stored in whirlpaks with 70% ethanol solution. In addition to stomach samples collected from live fish, we lethally sampled fish in all reaches for otolith analysis (Table 1.1).

We collected daily average water temperature and discharge data for all river sections within the early rearing period of March - June 2017, which encompassed the period of time for which growth was reconstructed. For the Clearwater River and free-flowing sections of the Snake River, we used temperature and flow data from USGS gauge sites positioned closest to our collection sites. Because no USGS gauge sites were located within the reservoir reach, we used forebay temperature and discharge at Lower Granite Dam collected by the Columbia River DART network.

#### Diet

In total we sampled diets from 105 fish between May and June 2017 of which 30 were from the Clearwater (CW), 15 from the middle section of the Snake (MSK), 20 from the upper section of the Snake (USK), and 40 from the reservoir reach (LGR). We assumed fish captured in the reservoir reach originated in that habitat because some spawning is known to occur in the reservoir and they were captured prior to period when fish from this population initiate downstream movement for out-migration. We counted an average of 21.4 prey items per stomach from the Clearwater, 45.1 items per stomach in the Snake, and 9.5 items per stomach from the reservoir reach. Prey items were identified to lowest taxonomic level and enumerated by taxonomic group within samples. Aquatic and terrestrial invertebrates were identified to family in most cases and, in some cases where items were too broken apart or too rare to be identified consistently to family, samples were identified to order. Up to 10 items

from each taxonomic group were measured to nearest 0.1 mm in each diet sample. Prey items were pooled by river (Clearwater, Reservoir, Snake) to obtain average prey length for each taxonomic category and average prey lengths were converted to average wet weight using published relationships (Myrvold and Kennedy 2014). We calculated the proportional contribution of each prey group to an individual fish diet by multiplying the number of items by the average wet weight of that taxon and dividing that by the total wet weight of each diet sample. We determined diet energy density by multiplying the proportional contribution of each diet taxon by the published energy density value (Joules) of that taxon. For taxonomic groups with missing energy density values we borrowed values from close taxonomic groups. We calculated diet energy density from each diet sample collected, and averaged diet energy density values across river sections (LGR, MSK, USK, CW).

In order to broaden our sample size for diet contents, we included energy density values estimated for Snake River fall Chinook salmon subyearlings in Tiffan et al. 2104 in the bioenergetics model. In the Tiffan et al. (2014) study diets were collected over the course of three years (2009-2011) during the same seasonal growth period as the fish used in this study. Tiffan et al. (2014) found that diet energy densities varied between the reservoir and free flowing river sections of the Snake River. We used monthly-averaged values for both river- and reservoir-type diets from their study to generate a normally distributed set of energy density values. These values were sampled randomly within our bioenergetics model on a daily time step.

## Otolith Preparation

Sagittal otoliths from all sacrificed fish were extracted and mounted on petrographic slides using thermoplastic cement, then polished on a lapping wheel using 2400 and 6000 regular Micro-mesh™ cushioned abrasive sanding paper to reveal otolith microstructure. Polished otoliths were digitally photographed at 20X magnification using a Cybernetics camera mounted on a Zeiss microscope (Thornwood, NY, U.S.A). Otolith radius was measured in the same location on each otolith using Image Pro image analysis software (MediaCybernetics, Bethesda, MD, U.S.A.). Along the otolith radius a contiguous section of discernable daily growth rings was identified, and widths between daily growth rings were measured. Due to variation in otolith preparation and capture date, number of daily growth rings varied between fish.

## Growth Analysis and Bioenergetics Model

We used the quadratic growth relationship developed by Zabel et al. (2004) to predict fish length from otolith radius for each measured ring, resulting in a daily length estimates for each fish. We used Equation 1 and river specific Chinook length and weight data for 2017 downloaded from PTAGIS to calculate mass at age for each otolith ring (Isely & Grabowski 2007, PTAGIS Data).

$$\log_e W = a + b \log_e L \quad (1)$$

Where L is fish length (mm), M is fish mass (g). Because we calculated individual masses for each day, we were able to distinguish individual growth trajectories and parse individual growth patterns between distinct time periods and rearing areas.



We also used these data to populate an individual-based bioenergetics model that was used to estimate consumption rates (Equation 2). By supplying the model with observed growth and known non-growth energy uses, the user can generate estimates of ration (g) or consumption (Joules).

$$\textit{Consumption} = \textit{Metabolism} + \textit{Growth} + \textit{Waste} \quad (2)$$

Our daily bioenergetics model was adapted from the R model designed by Chittaro et al. (2014) and used parameters from the Wisconsin Bioenergetics Model 3.0 (Hanson 1997), fish-specific estimates of mass (g) and growth ( $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ , hereafter “growth”), and river-specific estimates of diet energy density ( $\text{Joules}\cdot\text{g}^{-1}$ ) and temperature ( $^{\circ}\text{C}$ ). In cases where juvenile Chinook parameter estimates were unavailable, we used values from adult Chinook (Stewart and Ibarra 1992). Modeling was performed on daily time steps for the period of March 31<sup>st</sup> to May 10<sup>th</sup>. Output for each day included consumption (g), consumption (J), growth, and the proportion of maximum consumption (P). P was estimated iteratively within the model until observed growth (from the otoliths) most closely matched model estimated growth for each day.

### Statistical Analysis

For each river section, we averaged consumption (g), consumption (Joules), and growth (g) over five-day periods from March 31<sup>st</sup> to May 10<sup>th</sup> to account for day to day variability in growth conditions and lag times related to environmental effects. Additionally, we chose not to directly compare these estimates between rivers because average fish mass varied between river and growth is known to scale with mass. Instead, we standardized weekly average consumption (g), consumption (Joules), and growth (g) for fish from each

river section using the mean mass (g) pooled across river sections. We used non-linear regression to generate regression models between total pooled estimate of mass ( $M$ ) and the response variables consumption (g), consumption (Joules), and growth across river. These models were constructed in the form of Equation 3.  $Y_p$  represents the pooled parameter of consumption (g), consumption (Joules), or growth, and  $M_p$  represents pooled estimates of mass across river section and growth period.

$$Y_p = a * \exp(-bM_p) \quad (3)$$

From each predicted model, we used estimates of the  $a$  and  $b$  parameters and the overall average fish mass to scale each response parameter to a fish of 1.7 grams, the average size of fish collected in our study (Equation 4). This method is discussed in greater detail in by Chittaro et al. (2014).

$$\bar{Y}^* = \bar{Y} - \hat{a} * \exp(-\hat{b} * M) + \hat{a} * \exp(-\hat{b} * 1.7) \quad (4)$$

We used generalized least squares (GLS) regression to understand how growth, consumption, and ration varied by stream and date. Individual fish were considered replicates for river section and we included first-order autocorrelation in the error term to account for repeated measures on individuals. For each response variable we constructed GLS models with the following predictor variables: river, date as the continuous variable Julian date. For each response variable we tested a null model, a model with only date or river, and models with the interaction of date and river. Model selection was performed using Akaike's Information Criterion (AIC). Top ranking models were used to generate predictions of growth, consumption, and ration for each river section.

## Results

### Reach level environmental variables

Temperature and diet energy density varied between reaches over the course of the study. Water temperature in CW was generally 2-4° C lower than other sites, with greater temperature differences developing later in the study (Figure 1.2). These patterns were consistent with our hypothesis that the thermal landscape varied across the landscape. Further, these results underscored the necessity of testing for the effect of degree day on growth and consumption.

Mean diet energy density (expressed in Joules/gram) varied significantly between river reaches (Figure 1.3b) however, pairwise comparison revealed significant differences only between USK-MSK and MSK-LGR (Tukey-Kramer Honestly Significant Difference,  $\alpha = 0.05$ ).

### Otolith Increment Analysis

We collected otoliths from between 9 and 36 individuals across river sections. Fish collected from MSK and USK were larger on average than fish from the other river sections (Table 1.1) and fish collected from CW were the smallest on average. Average increment width varied significantly by river section and Julian date ( $P < 0.05$ ), with the largest increment widths observed in USK and the smallest increment widths observed in CW. Otolith increments were narrower early in the study, relative to widths observed later in the study.

## Bioenergetics

We detected significantly different growth and consumption over the course of the study within all study reaches. Mean standardized growth and consumption showed a downward trend over the course of the study, with mean growth occurring in the 5-day period following March 31 being  $0.048 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  while mean standardized growth in the five day period after May 10 was  $0.046 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ . This trend was present in all river sections, with the most pronounced difference observed in Upper Snake River section where mean growth following March 31 was  $0.065 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  and mean standardized growth after March 31 was  $0.051 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ .

Standardized growth and consumption varied significantly between the Clearwater river and the other reaches throughout the study. Standardized consumption also varied significantly between the Upper Snake River and other reaches throughout the study, though this difference diminished over the course of the study. In general, standardized growth and consumption were lower in the Clearwater and higher in the upper Snake River throughout the course of the study, and growth and consumption in the reservoir reach and the middle Snake reach were not significantly different throughout the study (based on confidence intervals).

The generalized least squares regression model with most support for all response variables included Julian date, river section, and the interaction between Julian date and river. (Table 1.2).

## Discussion

Growth opportunity for Juvenile Snake River fall Chinook in this study exhibited temporally explicit patterns in four important rearing reaches of the Snake River drainage. We found that mean river temperature was lower in the Clearwater River relative to other reaches, and that mean diet energy density varied between reaches. Standardized growth rate varied significantly between the upper Snake reach, the Clearwater reach, and the other sections of the river during the first half of the study, with highest growth present in the upper Snake section, but this difference diminished during the latter half of the study (overlapping 95% confidence intervals). Throughout the study, standardized growth and consumption were significantly lower in the Clearwater reach than in the other study sites. Our findings suggest that growth opportunity is as least as high in the reservoir as in adjacent free-flowing Snake River. Additionally, our results provide support for the hypothesis that the Clearwater River confers lower growth opportunity than other rearing areas used by fall Chinook.

Chinook salmon rearing in the Snake River experience a variety of human-altered habitat conditions related to the downstream progression from riverine to reservoir habitat, including composition of prey species assemblages and localized species introductions (Tiffan et al. 2014), and variable water temperature between impounded and free-flowing river sections (Connor et al. 2003a). These habitat qualities were known to vary between the river and reservoir reaches in our study, and our research confirmed these differences. We found that water temperature was significantly lower in the Clearwater River than in the reservoir and other river reaches throughout the study. We also observed variation in diet composition and diet energy density between the four river sections (Figure 1.3a), similar to those observed by Tiffan et al. (2014): reservoir diets were dominated by dipterans, *N. Mercedis*

and *Corophium* species while riverine diets consisted of mostly Ephemeropteran, dipteran, and trichopteran species. Despite these observed differences, growth and consumption did not reflect the potentially “lower” energetic quality of rearing habitat in the reservoir. For example, fish captured in the reservoir rearing area experienced a significantly colder thermal regime to those in the Snake River reaches ( $p>0.05$ ), but their growth rate was similar to other river sections for the majority of the study. These results suggest that observed habitat differences in the reservoir reach do not confer a growth disadvantage to rearing subyearlings relative to fish in river reaches.

We observed a significant decrease in growth and consumption in all river sections over the course of the study. These results were confirmed by the importance of the Julian date variable in all significant generalized least squares models. Interestingly, these results contradict the expectation that growth and consumption rates would increase with the increase in water temperature observed in the study. Chittaro et al. (2014) observed diminishing daily growth rates in a population of spring/summer Chinook salmon in the Salmon River basin in Idaho, a pattern the authors attribute to decreasing temperature and photoperiod over the course of the study. Growth in Chinook salmon juveniles feeding maximally increases with temperature between 5° and 15°C (Brett et al. 1982), and through the course of our study, temperature in all sites rose from below 5°C to above 10°C. Temporal variation in prey quality could partially account for the observed differences, and Tiffan et al. (2014) observed fluctuations in energy density of prey items which included lower values in late spring than early spring for two of three study years. We did not include this prey quality trend in our values of energy density derived from the bioenergetics model but if prey energy density

fluctuated downward over the course of the study, it may have manifested in reduced observed growth even though it was not directly included in the bioenergetics analysis.

An additional consideration for the decreasing growth rate over the course of the study is bias in growth calculations resulting from the use of otoliths to determine daily growth rate. Bias in fish length/ otolith radius relationships can result from growth rate effects and have been observed in numerous studies as reviewed by (Campana 1990). Slower growing fish tend to have fish length/otolith radius relationship which is lower than the average relationship for the population, and faster growing fish tend to have higher than average relationship. While our model allowed for time-varying growth rates, it is possible subpopulation level variation in fish length/otolith radius relationship within the basin impacted the reconstruction of growth rates and contributed to the observed decreasing growth rate pattern (Campana 1990, Zabel et al. 2010).

Early downstream movement of juvenile Chinook salmon has been observed in many populations, including the Snake River fall Chinook population (Roper and Scarnecchia 1999; Connor et al. 2005; Bottom et al. 2005; Roddam and Ward 2017). Our findings suggest that Subyearling fall Chinook salmon that move downstream to reservoir habitat in the Snake River may encounter equivalent growth opportunity to that afforded by their natal habitat. Our results also demonstrate that growth varies temporally within sites, suggesting that predictions of optimum growth opportunity by site type (river versus reservoir) are inadequate for understanding population level trends. Instead, we recommend that time spent in various habitats and the timing of habitat use be considered.

The findings in this study are important in the context of recovery efforts for the Snake River fall Chinook population where early growth is known to be related to migration timing

and survival (Connor et al. 2002, Connor and Tiffan 2012). Our results confirm previous findings in the basin that growth is spatially distributed throughout the major rearing areas with potential implications for migration timing. Fish that grow to migration size more quickly can initiate migration earlier, with the potential to escape stressful summer water temperatures and exploit ocean habitat with its higher growth opportunity. Additionally, if reservoir growth opportunity is comparable or higher than riverine growth opportunity, fish that move into reservoir habitat later in the year and residualize to river rearing may take advantage of continued growth opportunity, accounting for the emergence of the reservoir overwintering strategy observed in this population (Connor et al. 2001, Hegg et al. 2013).

Across their range, Pacific salmon species inhabit habitats that have been altered by human construction and agriculture, and substantial energy has been committed to understanding how these habitats impact individual and population level outcomes. Several studies have found that anthropogenically altered habitats can provide comparable or superior growth opportunity than adjacent river habitats. For example, Chinook salmon rearing in the Yolo bypass of the Sacramento River in California grew significantly faster than fish rearing in the adjacent river section (Sommer et al. 2001; Katz et al. 2017). Similarly, Koehler et al. (2006) found that Chinook salmon rearing along the highly developed shoreline of Lake Washington grow as well as fish reared in non-lake habitats. Finally, juvenile salmon rearing in Columbia River reservoir habitat have diets that are distinct from fish rearing in riverine habitat, but that confer comparable energy density (Rondorf et al. 1990). Our findings agree with these previous studies that found anthropogenically constructed habitats can provide quality rearing opportunities for juvenile salmonids in terms of nutrition and growth rates.

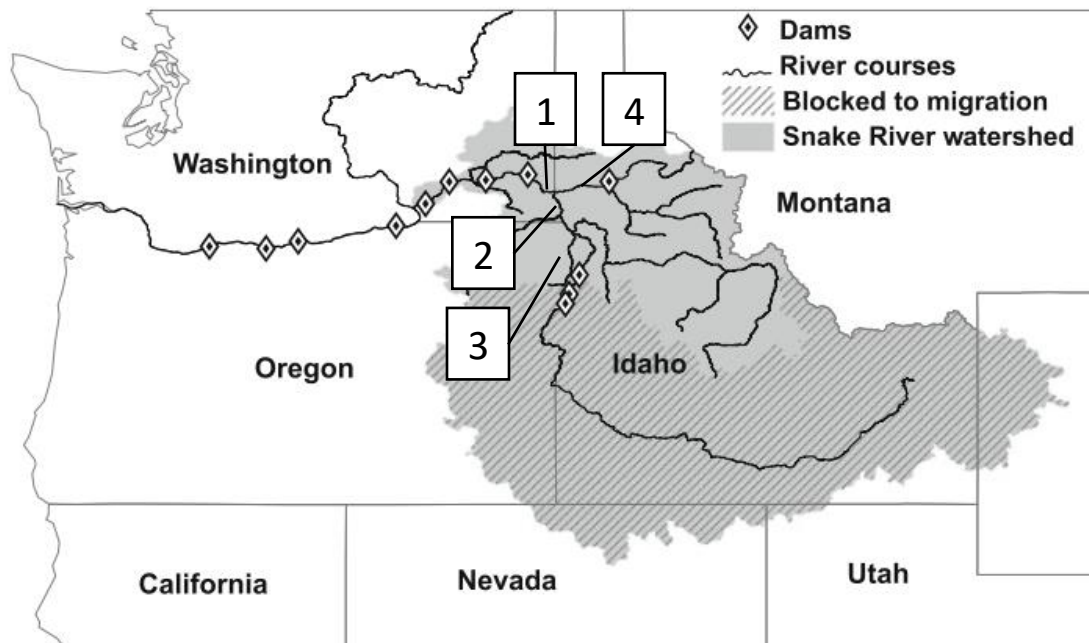


Our study broadens our understanding of reservoir habitat quality and confirms previous research which found that rearing in Snake River reservoir habitat can confer a growth advantage to juvenile Chinook salmon. Future research that examines the timing of movements into reservoir habitat by pre-migration juveniles could increase our understanding of the importance of this habitat in the rearing and migration of Snake River fall Chinook salmon.

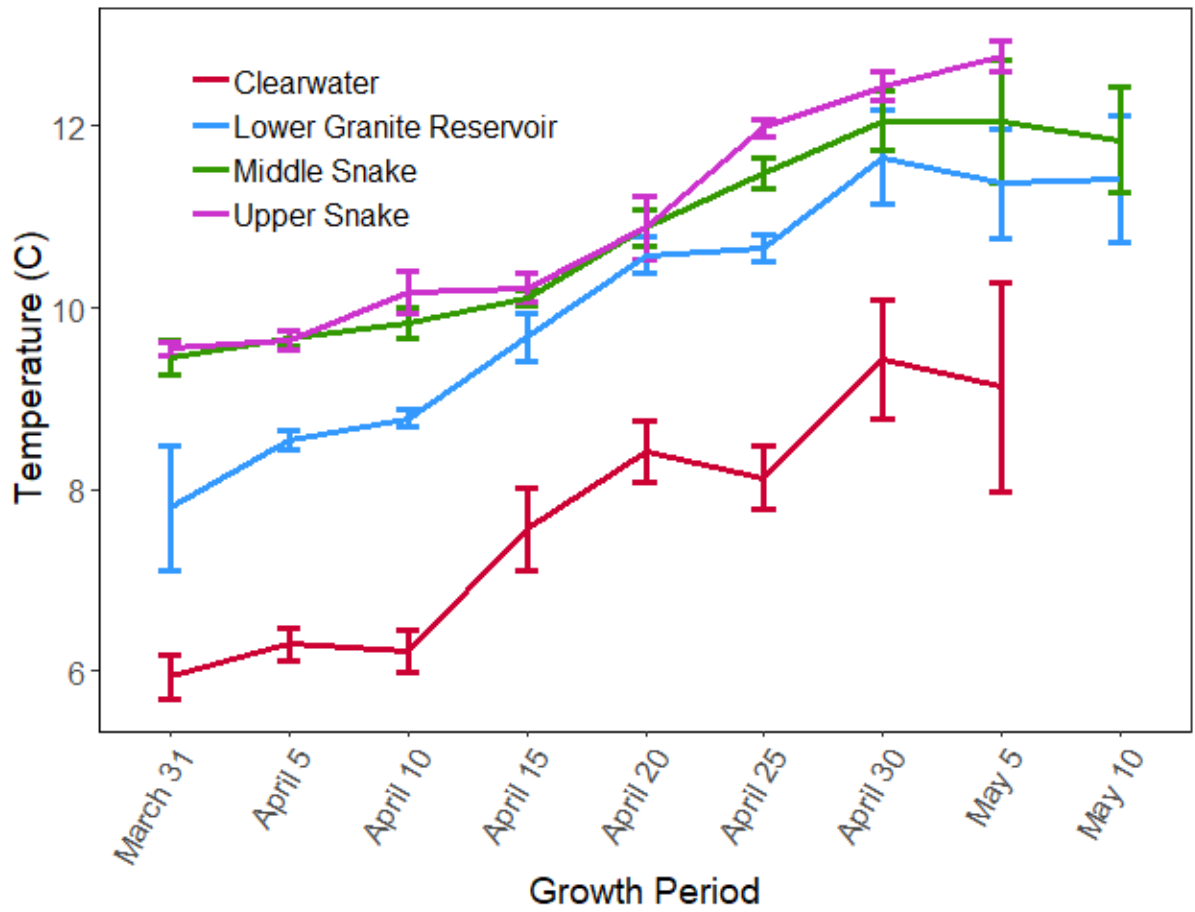
Our results also build on previous research which has demonstrated the importance of population level differences in habitat resources such as prey community and temperature for understanding juvenile salmonid growth. However, growth differences diminished over the course of the study, despite persistent habitat differences between sites. These results suggest a need to incorporate alternative drivers of early growth such as heritability of growth rates and maternally-conferred growth advantages when evaluating early growth within a population. Waples et al. (2017) demonstrated some evidence of heritability of growth rates within Chinook Salmon, and future research that included a genetic component could parse differential early growth across a multiple generations and their relationship to migration strategy.

Finally, our study demonstrated that anthropogenic alterations to river courses can have unpredictable impacts to the rearing habitat of juvenile salmonids, with unknown outcomes for migration strategy diversity. For populations outside of the Snake River where some use of reservoir habitat is necessary for downstream travel, juvenile salmon may come to rely on these altered habitats over time. Population-level diversity of migratory pathways is known to mitigate population decline during unpredictable environmental shifts, so maintaining a diversity of migratory strategies within salmon populations is crucial for

population persistence (Schindler et al. 2010). For fish inhabiting impounded river systems, this may require identifying important altered habitats that have taken the place of historic rearing habitats. Throughout their range, juvenile Chinook salmon navigate impounded rivers and feed within novel food webs, and conservation of multiple life history strategies may require identifying the role played by these temporally varying novel habitats.



**Figure 1.1.** Map of the Snake River basin indicating dams on the Snake River and Columbia River. Sampling sites included Lower Granite Reservoir (1), middle (2) and upper Snake River (3), and a section below the confluence with the North Fork Clearwater on the mainstem Clearwater (4).



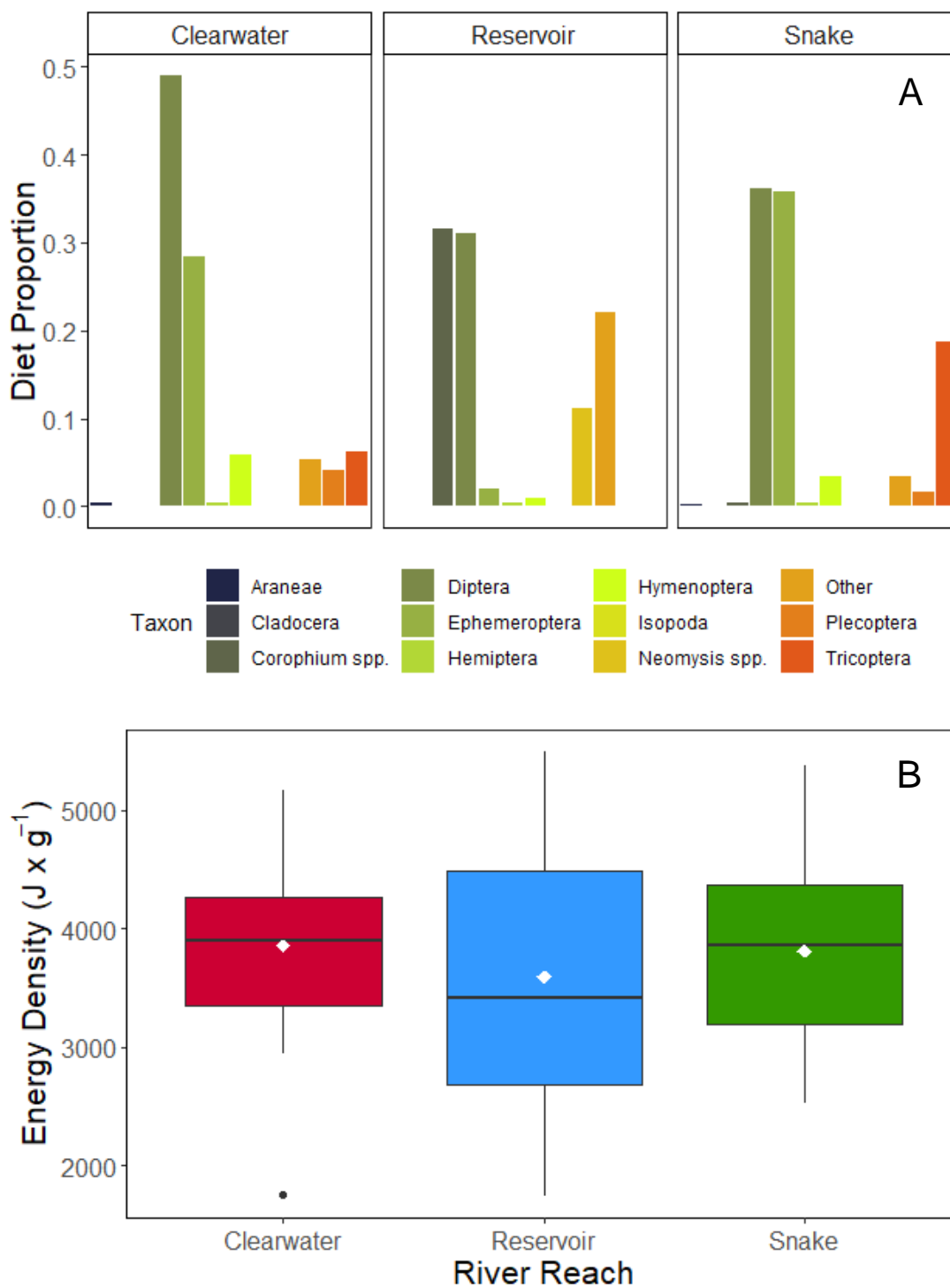
**Figure 1.2.** Mean water temperature (°C) over five day intervals for the upper and middle Snake, Clearwater, and reservoir reaches varied between 3.9°C and 13°C over the course of the study. Whiskers show standard deviations.

**Table 1.1.** Collection data for otolith and diet samples by river location and study date.

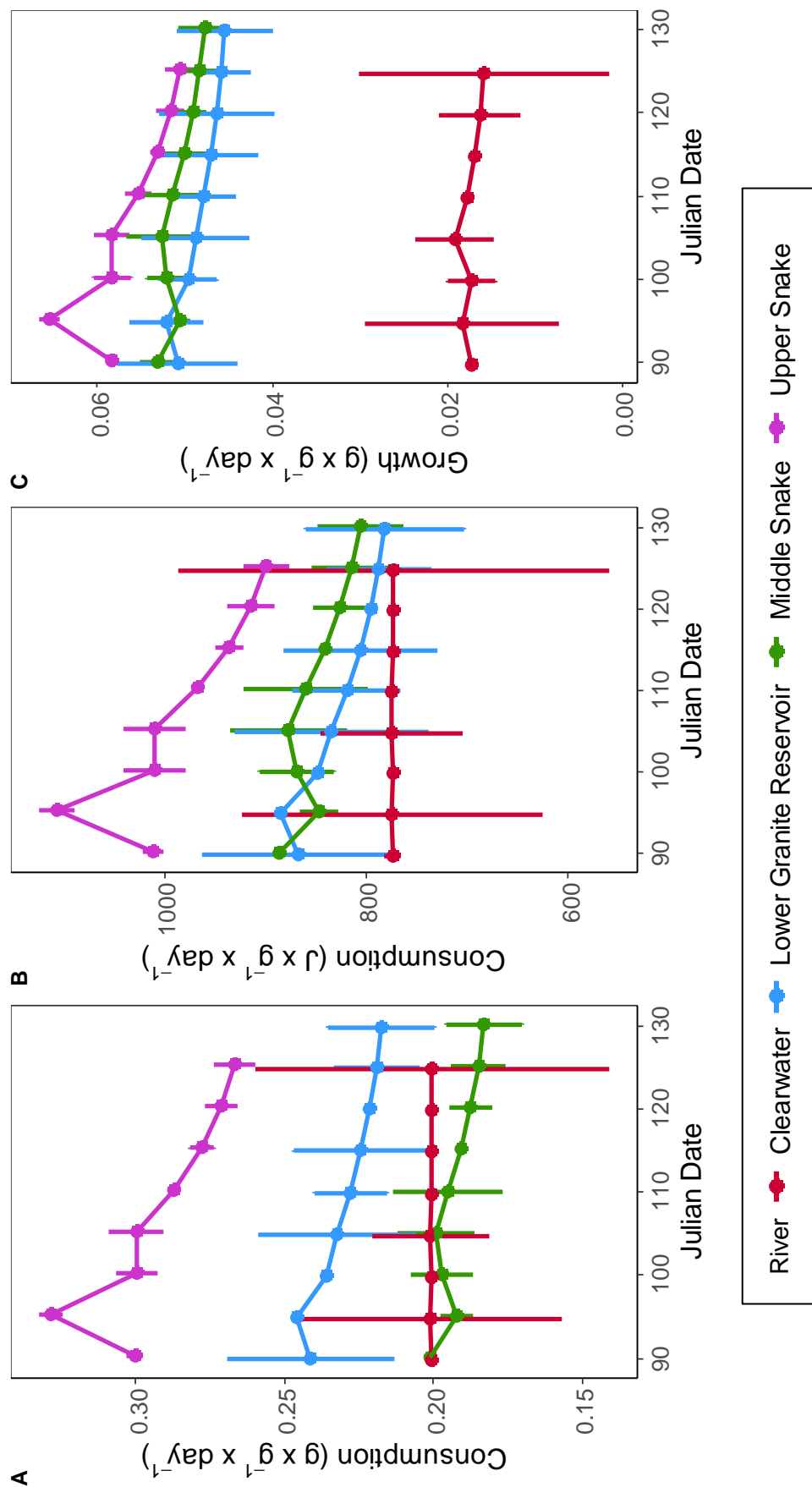
Rearing Location	Study dates	Mean daily water temperature (°C) (st dev)	Sample size for otolith analysis	Sample size for diet analysis	Mean daily otolith increment width (µm) (st dev)	Mean Capture Fork Length (mm) (st dev)
Lower Granite Reservoir	3/31/2017-5/10/2017	7.9 (1.32)	35	40	3.38 (0.92)	61.94 (7.68)
Upper Snake R.	3/31/2017-5/5/2017	10.32 (1.32)	12	20	4.06 (0.97)	73.00 (8.74)
Middle Snake R.	3/31/2017-5/10/2017	11.31 (0.91)	12	15	3.75 (1.14)	72.76 (11.76)
Clearwater R.	3/31/2017-5/5/2017	11.49 (1.09)	7	30	3.14 (0.97)	51.75 (10.01)

**Table 1.2.** Candidate generalized least squares models evaluating how somatic growth and consumption relate to date, temperature and location in the Snake River basin.

Model	Consumption (J/g/d)			Consumption (g/g/d)			Growth g/g/d		
	AICc	$\Delta$ AICc	AIC Wt	AICc	$\Delta$ AICc	AIC Wt	AICc	$\Delta$ AICc	AIC Wt
Null Model	5294.060	345.6862	0.00	-1325.71	1080.71	0.00	-2769.486	875.2976	0.00
River	5060.519	112.1450	0.00	-2290.40	116.02	0.00	-3537.964	106.8201	0.00
Julian Date	5161.397	213.0239	0.00	-2082.48	323.94	0.00	-3293.487	0.0000	0.00
River + Julian Date	4973.393	25.0199	0.00	-2375.01	31.41	0.00	-3623.199	351.2967	0.00
River + Julian Date + Interaction	4948.373	0.00	1	-2406.42	0.00	1	-3644.784	0.00	1



**Figure 1.3.** (A) Mean diet composition of juvenile fall Chinook salmon by river. (B) Mean diet energy density by river, white diamonds indicate group mean.



**Figure 1.4.** Standardized five-day consumption in grams (A), consumption in Joules (B), and growth in grams (C) for Snake River fall Chinook salmon rearing in the four river reaches of the study. Model predicted growth and consumption were standardized by the average fish size (1.7 g) across study sites to be directly comparable.



## CHAPTER 2

### Spatial Variation in Natal River Rearing and Downstream Movement in Snake River Fall Chinook Salmon

#### Abstract

Chinook salmon, (*Oncorhynchus tshawytscha*), demonstrate high diversity in early life history strategies primarily relating to age at migration, habitat use during migration, and the timing of ocean entry. In the Snake River population of fall Chinook salmon juveniles historically migrated as age -0 before their first winter, but in recent years an overwintering age -1 migration strategy, has emerged. This strategy appears to be spatially distributed throughout rearing areas with a greater proportion of age -1 migrants originating in the Clearwater River than the Snake and overwintering in downstream reservoirs. To understand relative growth in natal and downstream habitats before freshwater exit, we used otolith microchemistry and microstructure analysis to determine what percentage of the population migrate as age -1 juveniles and determine how natal river rearing relates to migration age. Fish that originate in the Clearwater River migrate at age -1 more often than at age -0, while fish originating in the Snake migrate more often at age -0. Natal origin was related to differential habitat use, with Clearwater natal group fish performing 48% of their freshwater growth in their natal river relative to 40% for Snake River fish. These differences were associated with different mean size (fork length) at natal river exit and at ocean entry. Additionally, age -1 migrants from both rivers did a greater proportion of freshwater growth in downstream reservoir habitat than age -0 migrants, but the proportion of growth varied by natal group. Our findings confirm previous research that determined that downstream reservoirs are important rearing habitat for Snake River fall Chinook salmon of both life

history types and suggests that reservoir use may be driven by different mechanisms depending on natal group origin.

## **Introduction**

The response of animal populations to environmental regime changes can be mediated by the existing diversity of life history strategies in a given population. Within a population, several life history strategies may be continually successful and persistent (Reimers 1971; Schroeder et al. 2015). Multiple strategies arise in species which experience unpredictable environmental conditions and habitat heterogeneity, and endure because of stochastic environmental conditions which favor varying strategies over time (Hilborn et al. 2003; Crozier and Zabel 2006). The sum of these strategies can be thought of as a “portfolio” of distinct life history pathways (Moore et al. 2010). This “portfolio effect” has been demonstrated to increase population viability by spreading the “risk” of unfavorable conditions across segments of the population (Schindler et al. 2010; Greene et al. 2010).

Life history diversity is particularly notable in anadromous species of fish. Born in fresh water, these species migrate to the ocean where they perform most of their lifetime growth before returning to freshwater to reproduce (Quinn 2018). At the species level, timing of seaward migration and age and season of adult return to freshwater may vary between populations relative to localized habitat conditions (Healey 1991; Quinn 2018). Direct effects such as growth limitations caused by water temperature (Thorpe et al. 1989; Metcalfe and Thorpe 1990) or indirect effects like competition for prey resources can both contribute to habitat use and migration timing (Bradford and Taylor 1997; Roni et al. 2012). The impact of anthropogenic habitat alterations and shifting climate regimes may also interact with life history strategies by altering the quality of available habitat, affecting the phenology of prey

resources (Crozier et al. 2008; Scheuerell et al. 2009), and altering or shifting hydrologic regimes (Beechie et al. 2006).

Juvenile migration strategies comprise a major component of salmonid life history diversity and have been observed to vary between populations of Chinook salmon (*Oncorhynchus tshawytscha*) relative to landscape-level differences in water temperature regimes and distance to the saltwater (Taylor 1990). Chinook salmon also demonstrate high diversity in early life history strategies within populations, primarily relating to age at migration, habitat use during migration, and time to ocean entry (Bourret et al. 2016). This diversity results from individuals navigating a series of threshold transitions, a progression which is driven by the combined effects of heritable life history traits and plastic responses to environmental variation (Stearns 1976; Hilborn et al. 2003; Crozier and Hutchings 2014). Within a single population, plastic life history strategies may not result in genetic divergence but rather coexist in varying proportions (Dodson et al. 2013). For example, studies of Chinook salmon populations in several Oregon rivers have demonstrated up to six persistent juvenile life history strategies (Reimers 1971; Schroeder et al. 2015).

The fall-run population of Chinook salmon in the Snake River and Clearwater River have been intensively monitored since listing under the Endangered Species Act in 1992 (Good et al. 2005). Since the beginning of this monitoring effort, a novel juvenile migration strategy has been observed (Connor et al. 2005). At the time of listing under the ESA, it was assumed that the population expressed exclusively the “subyearling” strategy of migrating as age-0 juveniles. However, in the period between 1995-2003 Conner et al. (2005) documented an emergent “yearling” strategy in the population where individuals that delayed migration their first year overwintered before beginning downstream migration the following spring.

This strategy seems to be increasing in prevalence, and to be spatially distributed in the basin. Most yearling migrants originate in the Clearwater River, a major tributary to the Snake River, and overwinter in habitats downstream of the confluence of the two rivers (Hegg et al. 2013a). The yearling strategy may result from both increased growth opportunity in reservoir habitat (Connor et al. 2005; Tiffan et al. 2014), and elongated migration time caused by the hydropower operations on the river (Tiffan et al. 2012)

Understanding the causes of these divergent life-histories requires both wide spatial resolution and detailed temporal information. Traditional tagging methods rely on stationary receiver networks or logistically challenging mobile telemetry, and often result in samples that are limited by frequency of observation or sample size. Instead, we employed otolith chemical and structural analysis to understand variation in habitats experienced by fish during early growth. Evaluating strontium isotopes stored in otoliths have become a standard method for identifying habitat use and movement pathways in migratory fish (Kennedy et al. 1997; Barnett-Johnson et al. 2008). Otoliths are mineral structures used by fish in hearing and orientation, and grow in direct proportion to somatic growth and overall length (Campana 1990). Otoliths are formed through daily accretion of calcium carbonate in a protein matrix and are commonly used in isotope tracer studies because, unlike bone or scales, they are not resorbed over the lifetime of the fish (Campana 1999). The calcium carbonate layers incorporate chemistry relative to water geochemistry, which in turn is directly related to the bedrock geology of the basin (Kennedy et al. 2000; Hegg et al. 2013b). In a basin where the spatial distribution of strontium isotope chemistry is understood, specific regions of otolith structure may be matched to discrete movements and periods of growth within the life history of a fish as long as basin geo-chemistry is sufficiently distinct between sub-basins (Kennedy

et al. 2002; Miller et al. 2011). Previous research in the Snake River basin has confirmed that sufficient spatial variation in water chemistry exists to discriminate fish origin based on major river tributaries (Hegg et al. 2013b). Additionally, researchers have been successful in use discriminant function analyses to classify adult otoliths to their river of origin based on water chemistry from the major tributaries. These assignments were confirmed using reference otoliths from juvenile salmon collected in the major spawning areas (Hegg et al. 2013a). Building from this previous research, we can combine isotope tracers with microstructural analysis of juvenile growth present in adult otoliths to identify early movements, habitat use, and relative growth in each identified habitat.

In this study we used otolith microchemistry and microstructural analysis to understand the diversity of life history strategies in juvenile fall Chinook salmon from the Snake and Clearwater rivers. Knowing that fish originating in the Clearwater River tend to migrate more often as yearlings than fish originating in the Snake River, we first sought to confirm what proportion of fish from each river performed the yearling strategy. To assess how life history strategy interacted with habitat, we evaluated whether absolute growth in natal versus downstream habitat was related to river of origin and life history type. The results of our research indicate differential natal river use between Clearwater and Snake River origin fish and confirm our previous understanding of the distribution of the yearling life history strategy. Additionally, these findings provide insight into the importance of rearing habitat in the lower Clearwater River.

## Methods

### Study Area

This study focused on the population of fall Chinook salmon that spawns between Lower Granite Dam and Hells Canyon Dam on the Snake River. Fall Chinook salmon also spawn in several major tributaries of the Snake River, most notably the Clearwater, the Grande Ronde, the Imnaha, and the Tucannon. Historically, the majority of fall-run population occurred above the location of Hells Canyon Dam in the Snake River (Groves and Chandler 1999) (Figure 2.1), but spawning has shifted into the lower reaches of the Snake River and the Clearwater River since the completion of the Hells Canyon Dam Complex in 1963 (Connor et al. 2002). The mainstem Clearwater River is un-impounded, but spawning does not extend far beyond the confluence with the North Fork Clearwater in Orofino, Idaho . The North Fork Clearwater is impounded by Dworshak dam 1.9 miles upstream of the confluence and cold water releases from Dworshak reservoir are used for summer temperature control in downstream habitats (Connor et al. 1998).

### Water Chemistry

To classify the juvenile growth regions from adult otoliths, we developed water chemistry baselines for the major tributaries in the basin. Water samples were collected between 2012 –2016 in standardized sampling areas of the spawning range of Snake River fall Chinook salmon (Figure 2.1). These water samples were added to the existing database of water chemistry from previous research conducted by Hegg et al. (2013a) between 2009-2011. Sample sites were visited in late summer or early fall during river base flow so as to capture the best signal of bedrock geology in water samples.

Water samples were collected in acid washed 125 mL high density polyethylene bottles according to established methods (Kennedy et al. 2000). Samples were analyzed for  $^{87}\text{Sr}/^{86}\text{Sr}$  MAT 262 Multi-Collector thermal ionization mass spectrometer (TIMS) or Isotopix Phoenix TIMS. Replicate analysis of the National Institute of Standards and Technology standard reference material (SRM-987) was used throughout the course of the study to determine analytical error for both machines. The Finnegan MAT 262 yielded mean  $^{87}\text{Sr}/^{86}\text{Sr}$  values of 0.710231 (2SE = 0.000008, n=16), the IsotopX Phoenix yielded a mean  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope ratio of 0.710244 (2SE = 0.000001, n=89) (Hegg et al. 2018).

#### Otolith Collection and Preparation

Left saggital otoliths were collected from spawning fall Chinook salmon between 2006-2013. Fish were collected at the Lower Granite Dam adult passage facility before being transported to Lyon's Ferry Hatchery (Washington Department of Fish and Wildlife/ Fish and Wildlife Service) to supplement returning broodstock (Milks and Oakerman 2014). We removed both saggital otoliths from Fall Chinook salmon which were identified as unmarked and untagged (having no hatchery fin clips or coded wire tag), and therefore presumed to be of natural origin. Length and sex were recorded for each fish and scale samples taken by WDFW staff to determine age. Extracted otoliths were stored in polypropelene microcenterfuge slides until being mounted on petrographic slides using thermoplastic cement. Otoliths were mounted dorsal side up and polished using a lapping wheel with 2400 and 6000 regular Micro-mesh™ cushioned abrasive sanding paper to reveal otolith microstructure (Campana 1999; Hegg et al. 2013a).

Otoliths from wild juvenile fall Chinook from the Snake River basin were used as a validation for our classification method. Wild juvenile fish were collected by beach seine on

spawning grounds and PIT tagged before being recaptured downstream at the Lower Granite Dam fish passage facility (N=111). Recaptured fish were sacrificed and kept frozen before until otoliths were removed. Juvenile otoliths were stored and prepared following the same procedure as adult otoliths.

#### Otolith Chemistry Analysis

All otolith Sr87/Sr86 data was collected at the Washington State University GeoAnalytical Laboratory using a Finnigan Neptune (ThermoScientific) multicollector inductively coupled plasma mass spectrometer (IC-PMS) using a New Wave UP-213 laser ablation system.

A marine shell standard was used to determine measurement error and was measured between every 5-10 samples over the course of the study (mean  $^{87}\text{Sr}/^{86}\text{Sr} = 0.709186$ , standard deviation = 0.000077, n=535). Daily measurement error corrections were performed based on marine shell measurements (Hegg et al. 2013a).

A single laser ablation pass was performed on each otolith, starting at the outer edge and terminating at the otolith core, positioned 90° relative to the sulcus (Figure 2.2). Laser ablation was performed at a constant speed of 10 microns/second with a 30 micron spot size and a 0.262 second integration time.

#### Otolith Microstructure Analysis

Otolith radius is known to increase proportionally to length over the lifetime of a fish (Campana 1990). We used the quadratic relationship with an unconstrained intercept developed for fall Chinook salmon by Zabel et al. (2010) to estimate fish fork lengths (FL) used in the study (Equation 1).



$$L = -17.4 + 0.20 * O + 0.000029 * O^2 \quad (1)$$

In this equation  $O$  is the otolith radius ( $\mu\text{m}$ ) measured along the microchemistry laser ablation transect,  $L$  is fork length (mm), and the intercept is not biologically constrained.

### Data Analysis

All otoliths used in this study were previously analyzed for natal origin in Hegg et al. (in prep). Those determined by Hegg et al. (in prep) to be of wild origin were analyzed for rearing and movement behaviors.

We performed all statistical analyses in R statistical software version 3.5.1 (The R Project for Statistical Computing). We determined natal habitat locations using a linear discriminant function analysis trained with the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio from water samples collected at known spawning and rearing locations (Figure 2.1). These locations were the Snake River, the lower Clearwater River (below the confluence with the North Fork Clearwater River), Lower Granite Reservoir (above Lower Granite Dam and downstream of the Snake River-Clearwater River confluence), and the combined Grande Ronde, Imnaha, and Tucannon. This final group of rivers are combined because bedrock strontium does not vary sufficiently between them to discriminate between rivers. We used the leave-one-out cross validation method to validate water chemistry correct assignments, then used known-origin juveniles as the "test" set (Table 2.1). We had a misclassification rate 6.013% using the "test" set of juveniles and a correct assignment rate of 90.29% using leave one out cross validation of water chemistry samples.

To determine natal location, we averaged the strontium isotope ratio values from the transect region between 250—300  $\mu\text{m}$  from the otolith core. This region is considered the first stable signature of Sr isotope values attributable to the chemistry of natal habitat rather than

that of a maternal contribution (Hegg 2018). Average strontium isotope ratio from this region was then classified using the linear discriminant function described above.

Subsequent rearing habitat locations were determined by classifying each observation along the strontium transect until entry into salt water, as determined by  $^{87}\text{Sr}/^{86}\text{Sr}$  reaching the global marine ocean average strontium value of 0.70918 (Miller et al. 2011). Habitat use subsequent to natal location was constrained to downstream movements (once a fish was identified in a downstream habitat it could not occupy an upstream habitat later on in the transect) and movements were classified as the first observation of a new habitat assignment (Walsworth et al. 2015). Oscillating regions of habitat assignments were assigned entirely to the downstream habitat once said habitat was identified (Walsworth et al. 2015). Due to few water samples in the lower Snake River, we did not have sufficient data to discriminate distinct river sections beyond Lower Granite Dam. As a result, fish assigned to Lower Granite Reservoir as their natal location were assigned Lower Granite Reservoir as their only classification until ocean entry. These fish were excluded from the growth natal/downstream comparison portion of the study. Finally, water  $^{87}\text{Sr}/^{86}\text{Sr}$  values between the upper region of the Clearwater River was confounded with downstream Columbia River  $^{87}\text{Sr}/^{86}\text{Sr}$  values (Miller et al. 2011, Hegg et al. 2013a; Table 2.2). Many fish displayed late Clearwater assignments after large sections of Reservoir assignments. These Clearwater assignments were likely sections of lower Columbia River growth and were grouped into the Reservoir habitat assignment that preceded them, per the requirement of downstream only movement (Figure 2.3). Strontium isotope ratio values from all otoliths were smoothed using a 3-cell moving average to diminish machine-induced variability prior to habitat assignment.

We determined migration life history (yearling vs. subyearling) using the method described in Hegg et al (2013a). Strontium isotope ratios were analyzed from 250–800  $\mu\text{m}$ . Fish in which a saltwater signal was identified before 800 $\mu\text{m}$  were considered subyearling migrants, while fish that did not display a freshwater signal until at or beyond 800 $\mu\text{m}$  were considered yearling migrants. This maximum is based on previous research which determined this otolith size exceeds the average size of subyearling otoliths when they exit the Lower Granite Reservoir, determined by the otolith size to fish length relationship (Zabel et al. 2010).

## **Results**

### Water Chemistry

As previously determined by Hegg et al. (2013a),  $^{87}\text{Sr}/^{86}\text{Sr}$  varied significantly throughout the study area (Table 2.2, Figure 2.4). Pairwise comparisons found all habitat location classes were significantly different from one another ( $p < 0.05$ ). Riverine strontium isotope ratios in the Columbia River beyond the confluence with the Snake were confounded with upstream Clearwater River strontium isotope ratios, however these sections of growth were distinguishable from upstream sections by the intermediate Snake River observations (Table 2.2).

### Natal Habitat

Of the 290 fish analyzed in our study, 162 were classified to the Clearwater River, 112 were classified to the Snake River, 141 were classified to Lower Granite Reservoir, and 16 were classified to the Grande Ronde/Imnaha/Tucannon River group. Because so few fish were identified as originating in the Grande Ronde/Imnaha/Tucannon River group, the following

results will focus primarily on Snake River and Clearwater River originating fish. We found that fish originating in the Clearwater River performed 48% of freshwater growth in their natal river, those originating in the Snake River performed 40% of freshwater growth in their natal river, and fish originating in the Grande Ronde/Imnaha/Tucannon complex spent 52% of growth in their natal tributary (Table 2.3). In the Clearwater River this natal rearing accounted for an average natal exit size of  $84.0 \pm 36.1$  mm FL and in the Snake River this corresponded to  $51.0 \pm 11.2$  mm FL (Figure 2.6a).

### Reservoir Habitat

Fish originating in the Clearwater, Snake, and Grande Ronde/Imnaha/Tucannon Rivers grew in length similarly once they exited their natal river (Tukey's Honestly Significant Difference  $p > 0.05$ ). Fall Chinook salmon that originated in the Clearwater River grew an average of  $132 \pm 56.2$  mm FL in downstream habitat while fish from the Snake River grew  $126 \pm 50.6$  mm FL in downstream habitat. Fish originating in the Snake River and Grande Ronde/Imnaha/Tucannon group exited freshwater at smaller sizes overall than did fish originating in the Clearwater River (Figure 2.6b).

### Life History Strategy

The occurrence of the yearling life history strategy was similar between hatch years but varied significantly by river of origin (two-way ANOVA  $p < 0.05$ ). The vast majority of fish originating in the Clearwater River overwintered to exit freshwater as yearling migrants. This pattern was consistent between hatch years (Figure 2.7) and yearlings comprised in total 143 or 88% of the migrants over the hatch years examined. Snake River fish migrated less

often as yearlings, however it was still the most common strategy, with yearlings comprising a total of 57 individuals or 51% of the migrants across hatch years.

The proportion of growth (FL) performed by fish in their natal tributaries differed by life history strategy (Fisher's Exact Test). Fish that migrated as subyearlings from the Clearwater River tended to grow more in natal habitat than fish that migrated as yearlings from the Clearwater River. Fish originating in the Snake River showed a similar pattern with subyearlings increasing more in length in natal habitat than yearling migrants. However, overall subyearlings originating in the Snake River gained less length in their natal river than fish originating in the Clearwater (Figure 2.5).

## **Discussion**

For migratory species, the phenology of environmental cues often dictates the particular windows of timing for the initiation and completion of migratory stages within a population (Dingle and Drake 2007). A coordinated migration in which all members of the population experience similar habitat quality may occur when these environmental cues are synchronized across the population (Bauer et al. 2016). If population fragmentation or habitat changes elongates or shifts the timing window for migration cues, a population can develop spatial variation in migration stage transitions (e.g. Both and Marvelde 2007; White et al. 2010).

Migratory life history diversity in Chinook salmon can include several stages of downstream movement and growth which are not adequately described in terms of migration age (Bourret et al. 2016). In this study we sought to identify rearing strategy composition of fall Chinook salmon originating in the major spawning areas of the Snake River, where both

subyearling and yearling migration strategies exist. Our results demonstrate that the amount of growth in natal habitat varies spatially within the Snake River population of fall Chinook salmon. We found that Clearwater-origin fish performed 48% of their growth in natal habitats, while Snake River fish performed only 40% of freshwater growth in natal habitats. More significantly, while proportion of natal habitat rearing did not vary largely by river of origin, absolute size at natal exit differed between rivers with Clearwater River origin fish exiting natal habitat at an average of 84 mm as opposed to Snake River origin fish which exited natal habitat at 51 mm. Finally, we found that subyearling migrants did a greater proportion of freshwater growth in their natal habitat than did yearling migrants, and that this pattern was consistent across natal groups.

The disparity in natal habitat growth between Clearwater River and Snake River juvenile Chinook salmon is the most striking finding of this study because it contradicts previous research that found that Clearwater-origin fish grew more slowly but to the same size as Snake River fish before moving out of natal habitat (Connor et al. 2002). Previous research has observed slower growth of fall Chinook salmon to parr size (> 45 mm fork length) in the Clearwater River relative to the Snake River spawning area, a difference attributed to water temperature regimes that favor faster growth in the Snake River (Connor et al. 2002). However, this is the first study in which differential natal exit size has been identified. Relative to fish originating in the Snake, which would have migrated at a smaller size historically due to early growth advantage and the need to avoid high summer water temperatures, Clearwater-rearing fish do not experience warm spring water temperatures that advance early growth or high summer water temperatures that make summer rearing in their natal river stressful (Groves and Chandler 1999; Connor et al. 2002). Taken together, these

results suggest that natal rearing in the Clearwater river is more advantageous than previously understood.

A great deal of research in the Snake River basin has focused on movement and growth of the varied life history types within the lower Snake River reservoirs (e.g. Connor et al 2005; Tiffan and Connor 2012; Tiffan et al. 2012; Connor et al. 2013). All fish originating in the Snake and Clearwater Rivers must migrate through the downstream reservoir habitat while making their seaward migration, and this study confirms previous research that identified the reservoirs on the Snake River as potentially important rearing habitats for the successfully returning adults in addition to serving as migration corridors (Connor et al. 2005, 2013; Hegg et al. 2013a). Yet when Clearwater River fish enter the reservoir, they have already grown to a much larger size, and/or are experiencing the reservoir habitat later, than fish originating in the Snake River. Clearwater origin fish must still grow substantially to reach migration size since they are still smaller than average subyearling migrants (Connor et al. 2005), and most fish from the Clearwater do overwinter rather than migrating their first year. However, our findings also suggest that reservoir habitat plays a less important role in the rearing of fish originating in the Clearwater River relative to those originating in the Snake River.

Previous research has demonstrated that size during early ocean residence (Tomaro et al. 2012; Weitkamp et al. 2015) is important for Chinook salmon growth and survival. Because size at ocean entry is related to age at ocean entry, juvenile Chinook salmon migration strategies are often thought of in terms of age and timing of migration (Taylor 1990; Moran et al. 2013). However, in describing migration strategy in terms of age, we have historically struggled to identify the full diversity of behaviors and strategies present in a

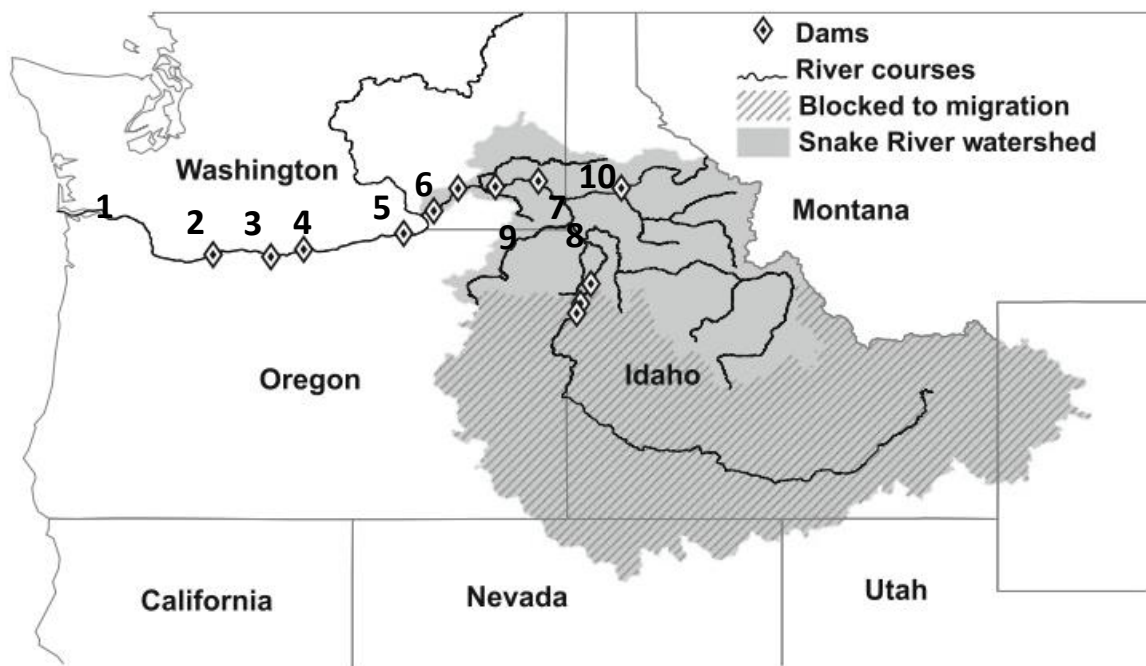
given population (Bourret et al. 2016). Advances in tagging infrastructure and otolith chemistry have revealed that diverse strategies exist within age classes and that both subyearling and yearling migrants can exploit a variety of habitats for different periods of time (e.g. Bourret et al. 2014; Schroeder et al. 2015; Phillis et al. 2018). Our study provides evidence of an additional aspect of life history diversity previously unrecognized in the Snake River population of Chinook salmon, namely differential natal river growth. It is unclear how the growth differences observed in this study affected survival and reproductive outcomes for fall Chinook salmon since we relied on data from fish that survived to spawn, however future research could consider these differences when evaluating population resilience.

The availability of reservoir rearing habitat has allowed for the diversification and short-term persistence of migration strategies in the Snake River fall Chinook salmon (Connor et al. 2005). The results of this study build on previous research that determined the increased prevalence of an alternative rearing strategy, but also demonstrate that the downstream overwintering strategy manifests differently across the population. With the increasing impact of climate change, salmon populations will be subject to unpredictable and shifting environmental regimes. This makes the identification and preservation of populations with life history traits that could buffer these populations against regime shifts increasingly important to future conservation efforts (Crozier and Zabel 2006). Any study that focuses on only the surviving adults in the population may fail to recognize the sources or mechanisms of survival at earlier stages. In the study, we have identified the likely migratory strategies for several subpopulations and demonstrate, for example, that surviving adults have by and large used reservoirs for a large portion of their freshwater rearing. Further research could identify



the survival consequences and population impacts of selective mortality across the population based upon varied reservoir use.

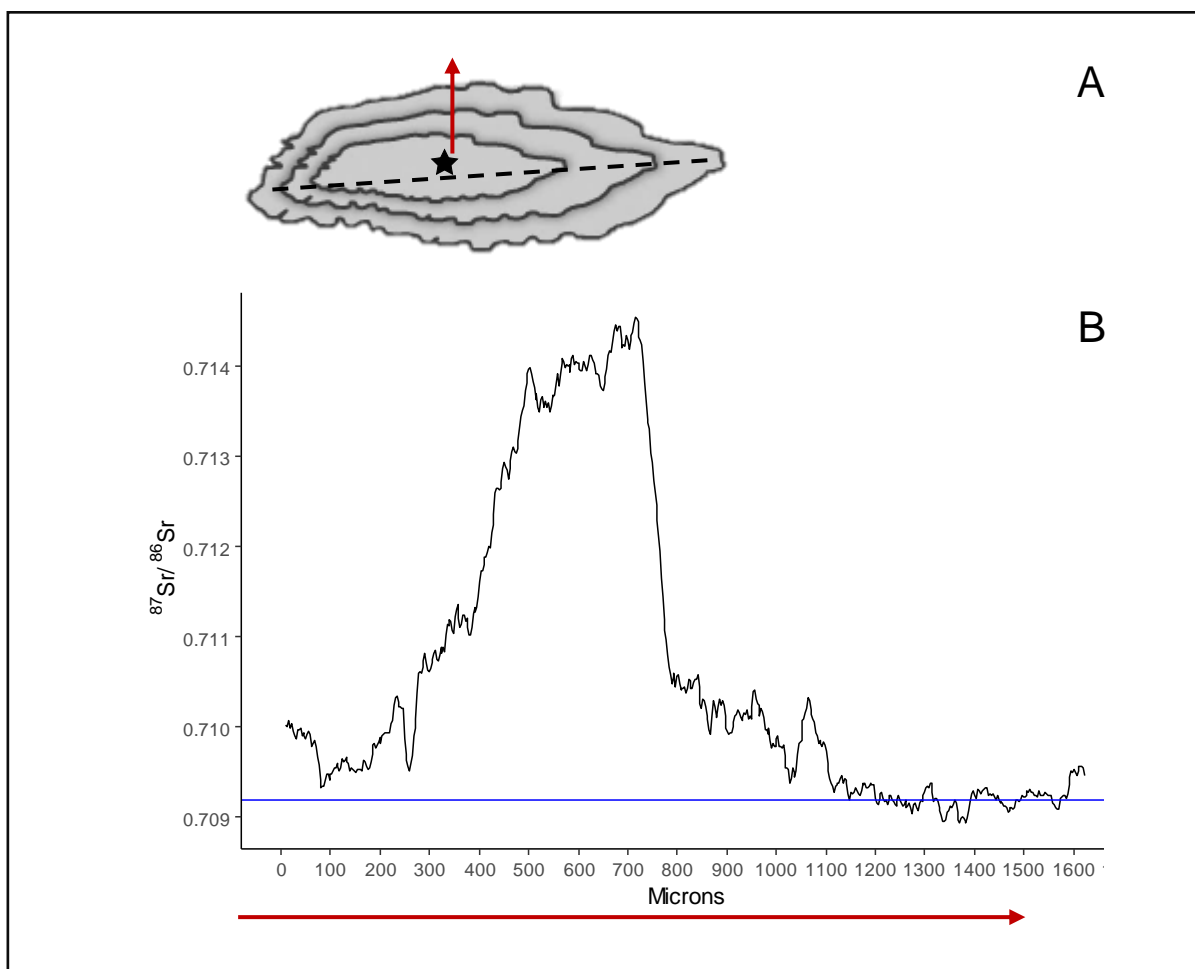
Given the increasing impact of climate change and the ubiquity of anthropogenic changes to large river systems (Nilsson et al. 2005; Parmesan 2006), it is likely that shifts in migration phenology will continue across the range of salmonid species (Crozier et al. 2008). In instances where entire populations or evolutionarily significant units of species come to rely on novel habitat, subsequent changes to those habitats could have large scale implications for the persistence of threatened species. Therefore, understanding the selective consequences of these life history changes is important in instances where populations come to rely on human-mediated habitats.



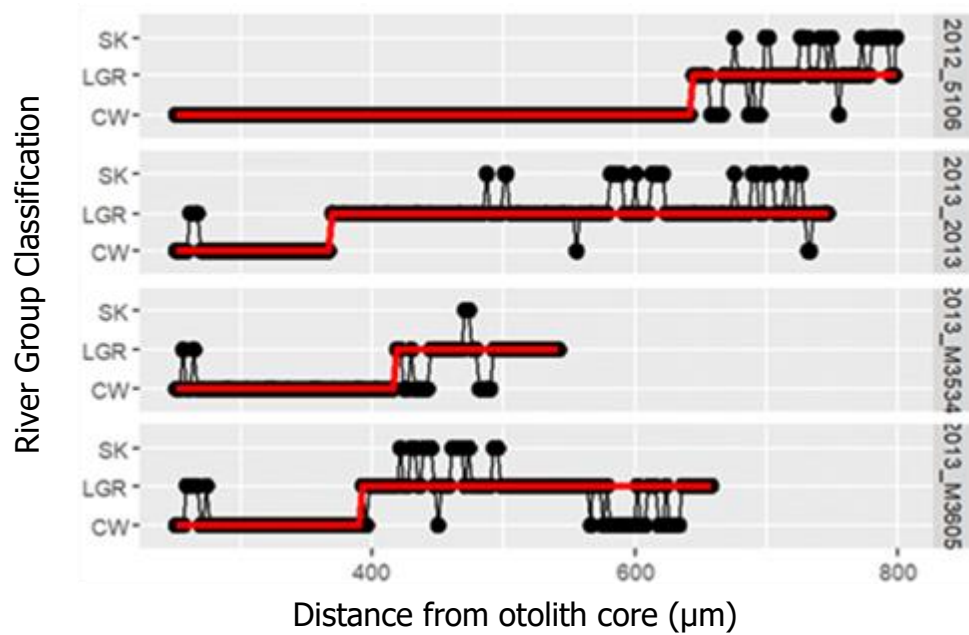
**Figure 2.1.** The Snake river basin, Idaho, USA is shown with the current available habitat of the Snake river Fall Chinook and the drainage area blocked to migration by dams or natural barriers. The majority of fall Chinook spawning extends from Lower Granite Dam to Hells Canyon Dam on the Snake river, and in the lower reaches of the Clearwater river. Numbered locations refer to water chemistry sampling locations: 1= Columbia River mainstem, below confluence with Willamette, 2=Columbia River mainstem, below Bonneville Dam, 3= Columbia River mainstem, below Dalles Dam, 4=Columbia River mainstem, below John Day Dam, 5= Columbia River mainstem, below McNary Dam, 6=Snake River, above confluence with Columbia River, 7= Snake River mainstem, above Lower Granite Dam, 8=Snake River mainstem, above confluence with Clearwater River, 9=Grande Ronde/Imnaha/ Tuccannon, 10=Clearwater River group. Water samples used in this study were collected in areas 7-10.

**Table 2.1.** Juvenile fall Chinook capture data for reference otoliths used in discriminate function test set. Capture length sample sizes (n) are listed to the right of the vertical bar for otolith samples where length data was available.

Location	Known Origin Juvenile Microchemistry						Capture Length		Otolith Radius	
	2010	2011	2012	2013	2014	n	mean (sd)	mean (sd)	(-)	
Clearwater River	3	-	-	13	-	2	75.5 (13.4)	380	(-)	
Snake River	7	5	30	6	6	10	75.1 (21.8)	393	(80.4)	
Lower Granite Reservoir	13	12	34	12	12	14	64.7 (2.46)	366	(31.9)	
Grande Ronde/Imnaha/Tucannon	4	3	6	6	6	17	66.5 (6.31)	413	(40.0)	



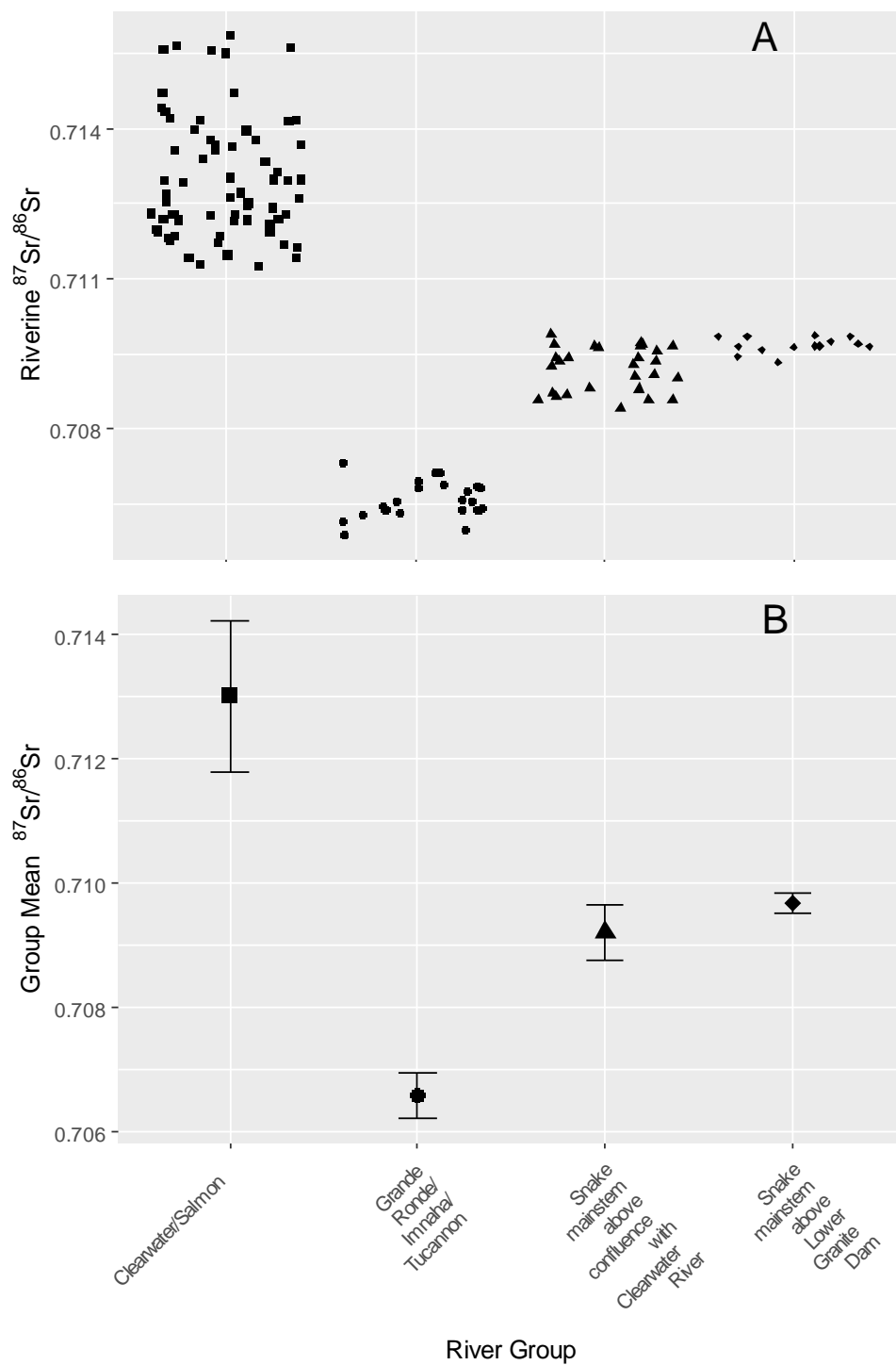
**Figure 2.2.** (A) Otolith shown ventral side up as polished. The core is labeled with a star and dashed line indicates the direction of sulcus. (B)  $^{87}\text{Sr}/^{86}\text{Sr}$  transect data beginning at core (0  $\mu\text{m}$ ) and progressing to the edge of the otolith. Red line indicates direction of laser ablation on both figures.



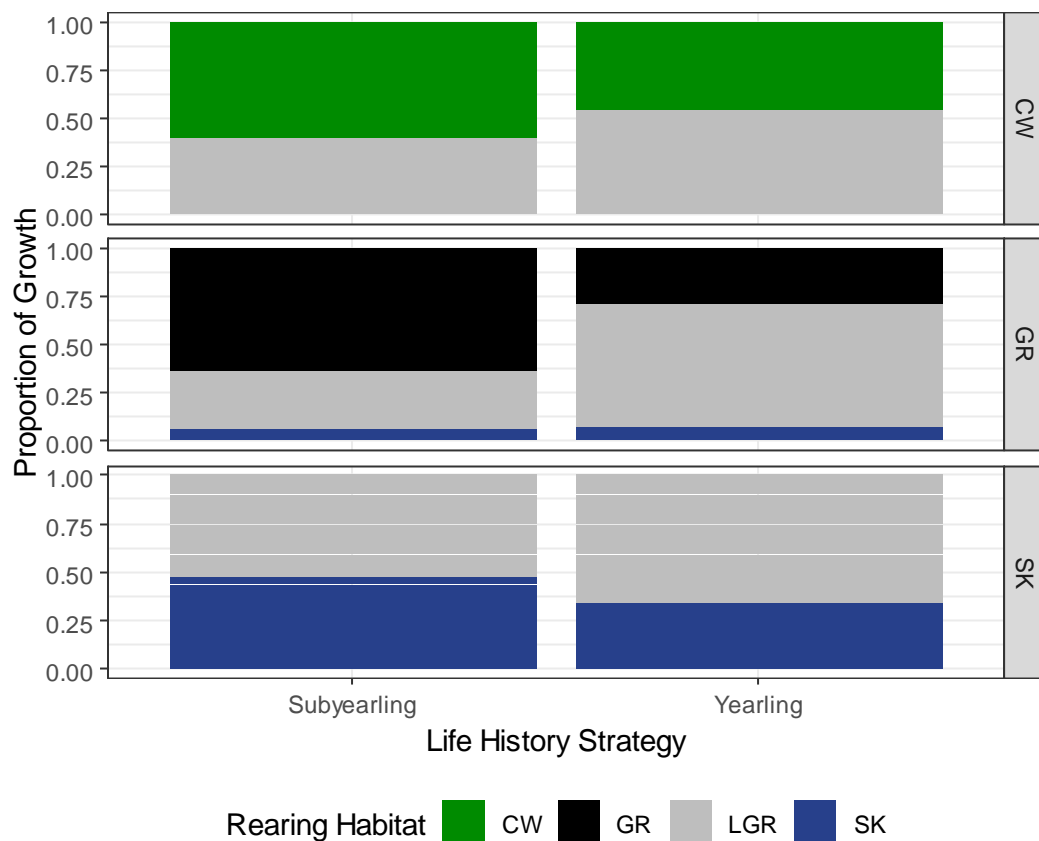
**Figure 2.3.** Example output from linear discriminant function analysis (LDF) shows river classifications as black points progressing from the otolith core to edge. “Corrected” data shown as red line where oscillating sections of classification were grouped with the dominant downstream classification. Downstream “CW” classifications in fish 2013\_M3605 (bottom pane) is an example of the LDF identifying lower Columbia river water signatures that are confounded with Clearwater river water signatures.

**Table 2.2.** Water sample locations and  $^{87}\text{Sr}/^{86}\text{Sr}$  data for Snake and Columbia river basin. Labels reference map (Fig. 1) locations.

Label	Location	River $^{87}\text{Sr}/^{86}\text{Sr}$	Source
1	Columbia River mainstem, below confluence with Willamette	0.7104	Bourret et al. 2014
2	Columbia River mainstem, below Bonneville Dam	0.713278	Miller et al. 2011
3	Columbia River mainstem, below Dalles Dam	0.713042	Miller et al. 2011
4	Columbia River mainstem, below John Day Dam	0.713906	Miller et al. 2011
5	Columbia River mainstem, below McNary Dam	0.713570	Miller et al. 2011
6	Snake River, above confluence with Columbia River	0.710339	Miller et al. 2011
7	Snake River mainstem, above Lower Granite Dam	0.709677	This study
8	Snake River mainstem, above confluence with Clearwater River	0.709203	This study
9	Grande Ronde/Imnaha/ Tuccannon River group	$0.70681 \pm 320$	Hegg et al. 2013a
10	Clearwater River	0.7130058	This study

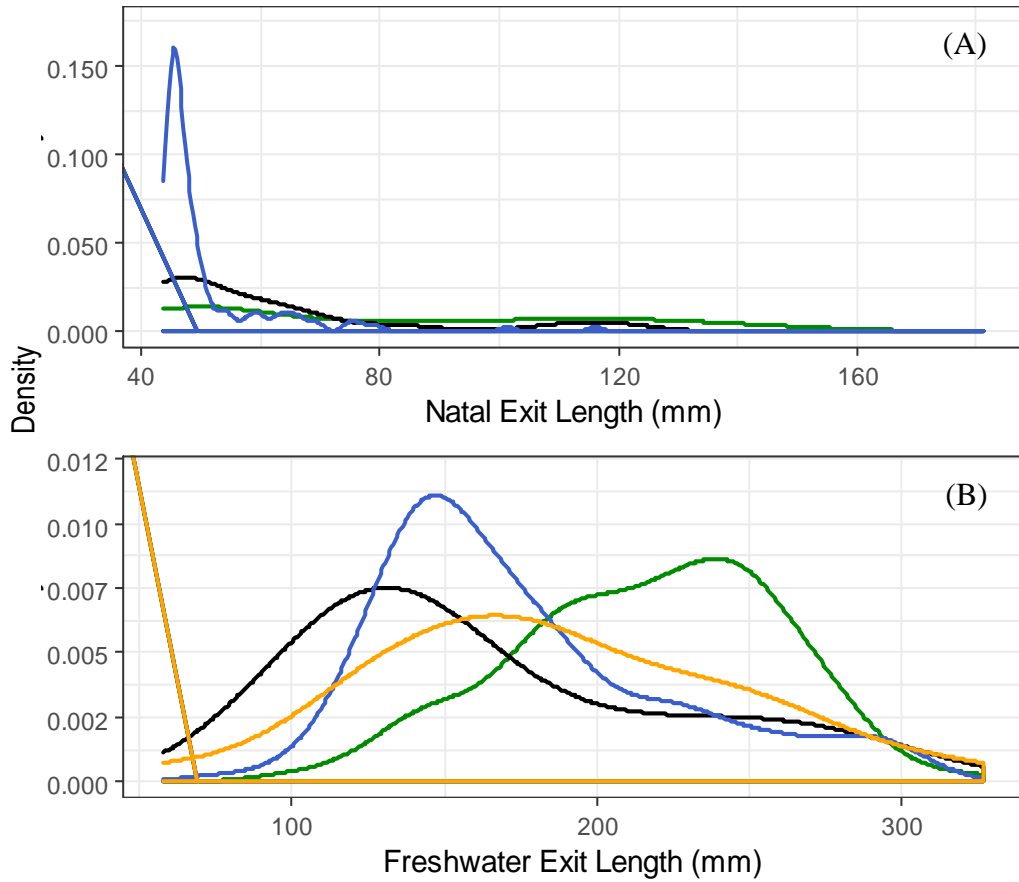


**Figure 2.4.** Water sample  $^{87}\text{Sr}/^{86}\text{Sr}$  values for the four natal reaches evaluated in this study. (A) Sample  $^{87}\text{Sr}/^{86}\text{Sr}$  values for each sampling period from 2008-2016, points jittered to prevent overlapping. (B) Natal reach group mean  $^{87}\text{Sr}/^{86}\text{Sr} \pm$  standard errors.



**Figure 2.5.** Bar plot showing proportion of rearing performed in each habitat by life history type (Yearling or Subyearling) from each rearing group (CW- Clearwater River, GR-Grande Ronde/Imnaha/Tucannon River group, LGR-Lower Granite Reservoir, SK-Snake River Group).

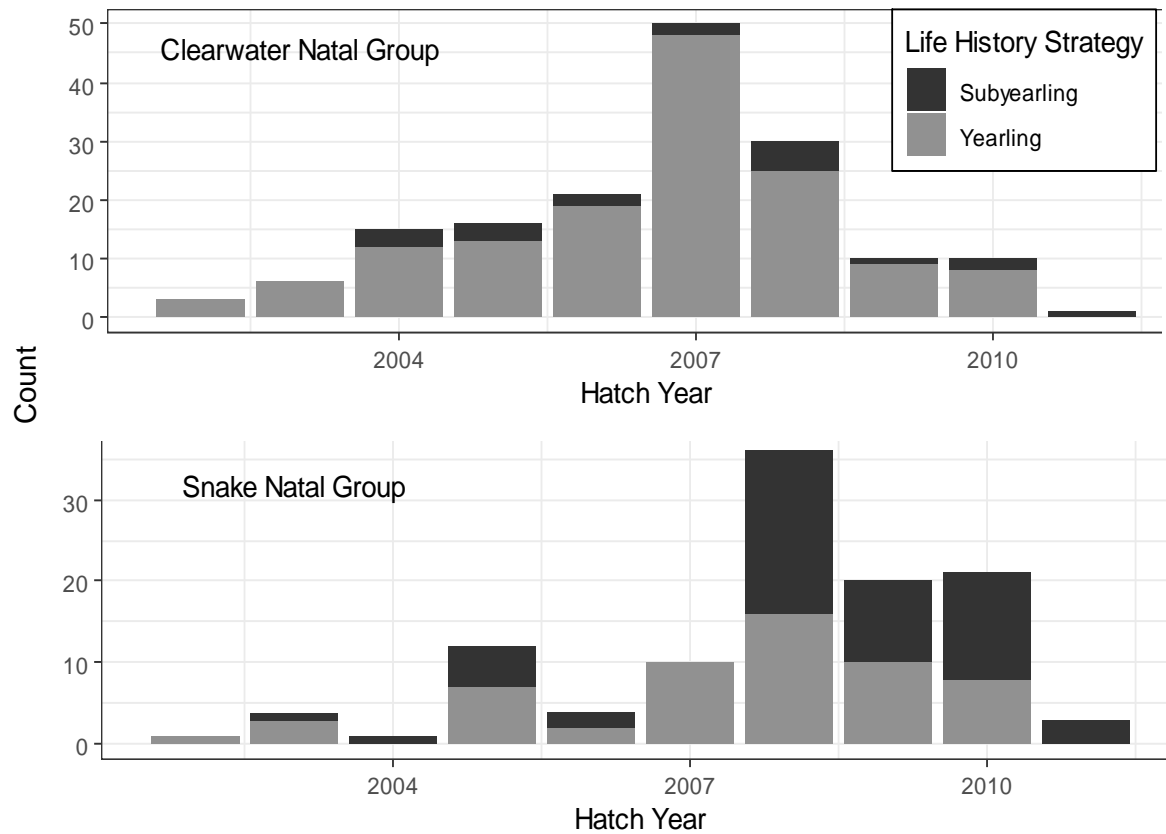




**Figure 2.6.** Fork length (mm) calculated from otolith radius length at (A) natal habitat exit and (B) Freshwater exit. Colors indicate rearing groups and are: Black= Grande Ronde/Imnaha/Tucannon, Blue=Snake river, Orange=Lower Granite Reservoir, Green= Clearwater river.

**Table 2.3.** Group mean natal and downstream growth proportions were calculated as the average of individual habitat use proportions (habitat growth:total growth) for each habitat.

Rearing Group	Mean Proportion of growth in Natal River <i>sd</i>	Mean Natal River Growth (mm) <i>sd</i>	Mean Downstream Growth (mm) <i>sd</i>	Mean Natal Exit Size (mm) <i>sd</i>	Mean Ocean Entry Size (mm) <i>sd</i>	N
Clearwater	0.480 <i>0.178</i>	49.2 <i>36.1</i>	132 <i>56.2</i>	84.0 <i>36.1</i>	216 <i>43.4</i>	162
Snake	0.403 <i>0.119</i>	16.2 <i>11.2</i>	126 <i>50.6</i>	51.0 <i>11.2</i>	177 <i>47.8</i>	112
Grande Ronde	0.527 <i>0.256</i>	27.0 <i>23.7</i>	108 <i>71.4</i>	61.8 <i>23.8</i>	176 <i>62.1</i>	16



**Figure 2.7.** Life history strategy totals for each hatch year examined. The yearling life history was the dominant strategy in the Clearwater natal group over the course of the study, but varied year to year in the Snake natal group.

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