Identifying overwintering location and natal origin for Snake River fall Chinook salmon

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Report of research by

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Contract W68SBV02356307

March 2012

EXECUTIVE SUMMARY

The management of Snake River fall Chinook is hindered by our lack of understanding of migratory patterns of juveniles, particularly "reservoir-type" fish that overwinter in freshwater before outmigrating. In 2011, we began the first year of study in a multi-year effort to determine the migratory patterns of juvenile Snake River fall Chinook based on otolith microchemistry and microstructure. Our first year of the study involved analyzing samples that were collected in previous years and collecting new samples that will be analyzed in 2012.

Our first step in this effort was to begin assessing variability in the water chemistry in major spawning tributaries and at sites along the mainstem Snake River. Our initial analysis focused on $^{87}Sr/^{86}Sr$ ratios. We conducted nonparametric tests to lump samples into major groups. This allowed segregation by $^{87}Sr/^{86}Sr$ ratio of the following four regional groups: Upper Snake River, Lower Snake River, Clearwater/Salmon Rivers, and Tucannon/Grande Ronde/Imnaha River. Further analyses using a greater number of samples and additional elements will help to further discriminate these regions. In 2011, we augmented our collection of water samples by collecting 27 additional samples from throughout the region.

We used the classifications derived from the water samples to assign returning adults (natural origin fish collected at Lyons Ferry Hatchery) to natal area, rearing area, and overwintering site (for yearling ocean entrants) based on isotopic ratios from specific regions of the otolith. The vast majority of individuals were assigned to natal sites in the upper Snake, lower Snake, or Clearwater/Salmon groups, with very few fish assigned to the Tucannon/Grande Ronde site. When fish were assigned to rearing area, most fish were assigned to either lower Snake or Clearwater/Salmon. Of the fish that overwintered, the vast majority of them were assigned to the lower Snake River. Assigned locations were validating by blind analysis of otoliths from juvenile fish of known origin, and these validation samples demonstrated that the method was quite successful.

In addition to we used an established relationship between otolith size and fish length to back-calculate growth trajectories for juveniles collected at Lower Granite Dam. We compared growth trajectories of fish collected during 1993 and 1994 with those of fish collected at the dam during 2007 and 2009. Growth patterns did not differ substantially between fish collected in the early 1990s and those collected more recently.

In 2011, we augmented our samples collection for future analyses by collecting additional otoliths from the following of sources: Seven hundred-twenty-two adult fall Chinook from Lyons Ferry Hatchery; Thirty juveniles from Lyons Ferry (15) and Nez Perce Tribal Hatchery (15); Eighteen juveniles sampled in beach seines in the Snake and Grande Ronde Rivers; Forty-six adult carcasses on the Clearwater collected by Nez Perce Fisheries; Approximately 50 juveniles collected at Lower Granite Dam in the sort-by-code system.

CONTENTS

INTRODUCTION

Anthropogenic disturbances have caused shifts in the life history of Snake River fall Chinook salmon. Construction of the Hells Canyon complex in the 1950s blocked the majority of historical spawning sites, and the eight dams downstream from current spawning sites have altered the hydrological regime in the migratory corridor of this species. Prior to these disturbances, these fish predominantly displayed a typical ocean-type life history (Healey 1991) in which adults spawn in fall, fry emerge the following spring, and juvenile fish migrate seaward during late spring and summer to enter seawater as subyearlings (Mains and Smith 1964, Williams et al. 2008). However, a proportion of the present population suspends its migration in Lower Granite Reservoir. Connor et al. (2005) described this behavior for juvenile Snake River fall Chinook salmon, which they termed as a "reservoir-type" life history. Fish that adopt the reservoir-type life history suspend the seaward migration, overwinter in reservoirs, and resume migration as yearlings the following spring. The significance of this finding in terms of management is that although reservoir-type fall Chinook salmon contribute approxiamtely half of the returning population of spawners (Williams et al. 2008), most mitigation actions are directed at ocean-type juveniles.

The mechanisms behind this observed shift in life history are not clear. However temperature in the rearing stream may affect timing of the juvenile Snake River Fall Chinook migration (Connor et al. 2002). It is also possible that dam-related environmental changes have altered the selective pressures experienced by migrating juvenile fall Chinook, thus selecting for a different juvenile strategy in portions of the population (Williams et al. 2008). Temperatures in the lower Clearwater River are several degrees lower during high growth periods of juvenile Fall Chinook relative to similar rivers in the basin due to the cold outflows from Dworshak reservoir, and predictably these fish migrate later and exhibit an increased propensity to overwinter (Arnsberg and Kellar 2007).

The life-history complexity of Snake River fall Chinook salmon has hindered efforts to manage this ESU. For example, the existence of an overwintering behavior in a portion of the population has complicated our ability to estimate survival through the hydropower system (Arnsberg et al. 2010). Many yearling migrants move downstream in the fall/winter, after detection systems at dams for fish tagged with a passive integrated transponder (PIT) tag have been disabled. Thus we have limited information on migratory patterns of these fish. Because of this uncertainty, major modeling efforts, such as COMPASS modeling and life-cycle modeling of the Interior Columbia Technical Recovery Team, were not able to model the population dynamics of Snake River fall Chinook.

In addition, the question of whether or not Snake River fall Chinook benefit from transportation is unresolved. Until we have a better understanding of this life-history

complexity, particularly the habitat usage of overwintering juveniles, it will be difficult to efficiently manage the entire ESU. Effective management of reservoir-type fish will require an understanding of the details of their life history, including what proportion of juveniles exhibit this strategy, where these juveniles overwinter, when they re-initiate downstream migration, and the extent of estuarine residence time.

Relating migration strategy to growth and environmental change requires the ability to understand fish movements on a meaningful scale. This would be difficult and expensive over a geographic area as large as the Snake River using traditional mark-recapture techniques. Otolith microchemistry offers a resource-efficient method of analyzing the movements of individual fish at a finer geographic scale than is possible with current tagging technology. Analyses of otolith microchemistry can yield information on key details of fish life history, such as population origin (Barnett-Johnson et al. 2005), residence times in particular habitats, and timing of migration (Kennedy et al. 2002).

Accordingly, we have identified the following objectives:

I. Determine the migratory patterns of reservoir-type yearling migrants
II. Assign adult fish to natal origin and life-history type
III. Determine juvenile growth rates across habitats and seasons
IV. Identify isotopic signatures for specific reaches in the Columbia Basin

STUDY SITE

The Snake River is the largest tributary to the Columbia River and drains an area of 280,000km^2 over six states in the Pacific Northwest. The Snake originates in Wyoming and flows 1,670 km to its confluence with the Columbia River in Eastern Washington State, with the majority of its drainage in the state of Idaho (Figure 1). This river flows through a region of diverse geologic features, with each major tributary stream crossing terrain of large variation in mafic and felsic geology (Figure 1). Therefore, it is likely that differences exist in geochemical signatures among streams. Land use varies across the basin as well, ranging from pristine wilderness to areas of heavy agricultural and urban impact.

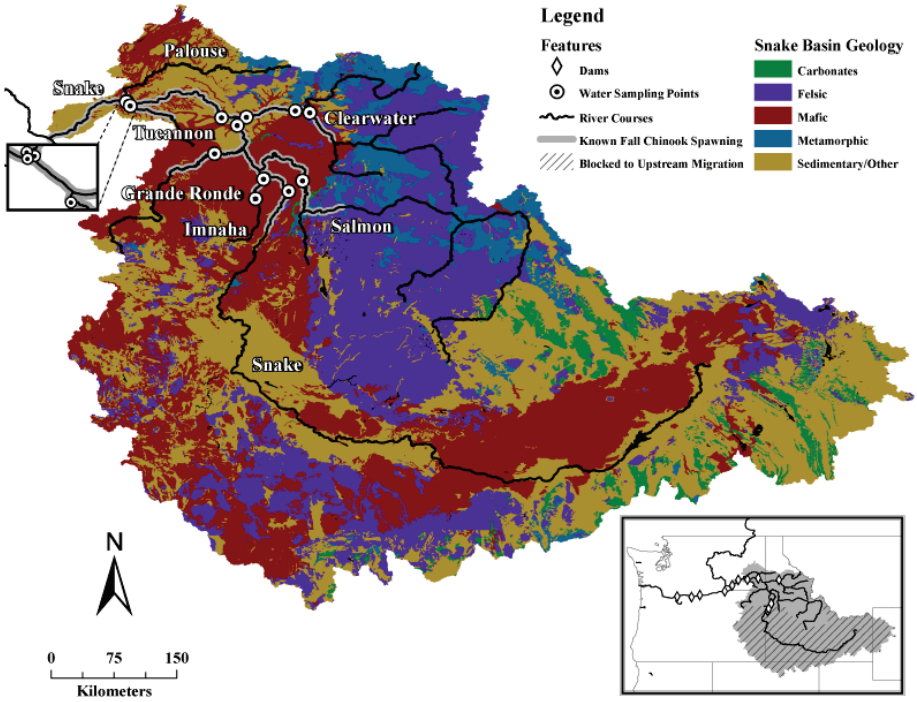

Figure 1. Map of the Snake River basin showing the majority of fall Chinook salmon spawning and location of water sample sites. Inset shows location of dams. Lithology of the watershed shows rock type categories with strong impacts on $^{87/86}Sr$ due to their isotopic chemistry. Rock types were classified by origin in the mantle (Mafic) and crust (Felsic). Metamorphic rocks of known protolith were grouped by protolith. Metamorphic rocks of unknown protolith were classified to Metamorphic category. All other rock types were classified as Sedimentary/Other. Geologic data from Preliminary Integrated Geologic Maps of the Western and Central States (Ludington et al. 2005, Stoeser et al. 2006).

Fall Chinook adult salmon runs have been affected by the placement of dams within the Snake River basin. Upstream access to 80% of historic spawning grounds were blocked by construction of the Hells Canyon dam complex in the middle Snake River in 1959 (Waples et al. 1991) (Figure 1). Below Hell's Canyon, four dams impound the river from Ice Harbor Dam near its confluence with the Columbia to the port of Lewiston, ID. Dworshak Dam, an impassable dam on the North Fork of the Clearwater River, blocks salmon migration and supplies cold, hypolimnetic water that cools the lower portion of the Clearwater River.

Outflows from Dworshak Reservoir are managed during late summer to aid the fall juvenile Chinook migration by creating cool refugia in otherwise warm downstream reservoirs (Connor et al. 2003a). Based upon aerial redd surveys, it is estimated that the majority of current fall Chinook salmon spawning occurs in two locations: the Hells Canyon reach of the Snake River (usually divided into two reaches, above and below the confluence with the Salmon river) and the Clearwater River. Smaller runs occur in the Lower Snake, Salmon, Grande Ronde, Tucannon and Imnaha Rivers (Garcia et al. 2007).

WATER CHEMICAL ANALYSIS

Methods

To quantify spatial variation of $^{87}Sr/^{86}Sr$ ratios within the Snake River basin, water samples were taken from major spawning tributaries and at sites along the mainstem Snake River (Figure 1). Sampling sites were determined based on locations of significant fall Chinook spawning activity, with some changes to account for the addition of impounded sections of the Lower Snake River. The Upper Snake River was defined as the free-flowing reach from Asotin, WA (just upstream of the confluence with the Clearwater river) to Hells Canyon Dam. The Lower Snake River was defined as the impounded reach from below Asotin to the river mouth.

Samples were collected from each site during spring, summer, and fall 2008, with duplicate fall samples collected in 2009 using established methods (Kennedy et al. 2000) (Table 1). All samples were analyzed for $^{87}Sr/^{86}Sr$ ratios using a Finnigan MAT 262 Multi-Collector Thermal Ionization Mass Spectrometer (TIMS).

Water sample sites were grouped based on statistical similarity in $^{87}Sr/^{86}Sr$ ratios. Grouping was determined using the non-parametric Kruskall-Wallis rank sum test (Hollander and Wolfe 1973) with post-hoc non-parametric multiple comparisons tests ($\alpha = 0.05$). Non-parametric tests were used due to the differences in variance between river groups, which violated the assumptions of ANOVA. Multiple comparisons were completed using results of Behrens-Fischer multiple comparisons tests (Munzel and Hothorn 2001) using the 'npmc' package for R (http://cran.es.r-project.org/src/contrib/Archive/npmc/). Successive Kruskall-Wallis tests were performed, with water sample data aggregated into river groups until multiple comparisons showed all groups to be significantly different ($\alpha = 0.05$).

Table 1. Summary of $^{87}Sr/^{86}Sr$ in water sampled in the Snake River basin 2008-2009. Error is expressed as ± 2 SE from the mean, based upon 150-200 TIMS ratios. Sample data showed spatial variation in $^{87}Sr/^{86}Sr$ among groups (i.e., tributaries and major reaches); however, samples within each group did not differ significantly (Kruskall-Wallis, post-hoc Behrens Fisher $\alpha = 0.05$). Shading indicates different locatoins within groups. At sample sites in the Clearwater and Salmon River group, $^{87}Sr/^{86}Sr$ maintained temporal stability across seasons.

$^{87}Sr/^{86}Sr$ by isotopic signature group				
Site name, and map number	Sampling period	$^{87}Sr/^{86}Sr$ ± (SE × 10^{-5})	Site average	River group average
Upper Snake River (USK)				
1. Upper Snake (Pittsburg Landing)	Fall 2008	0.708585 ±12	0.708685 ±12	0.708685 ±12
	Spring 2009	0.708704 ±10		
	Summer 2009	0.708810 ±12		
	Fall 2009	0.708639 ±12		
Clearwater and Salmon River				
2. Salmon River	Fall 2008	0.713765 ±14	0.713318 ±14	0.713308 ±14
	Spring 2009	0.712534 ±12		
	Summer 2009	0.712928 ±14		
	Fall 2009	0.713682 ±16		
	Fall 2009[a]	0.713682 ±16		
3. Lower Clearwater (Below North Fork)	Summer 2009	0.714726 ±14	0.713809 ±14	
	Fall 2009	0.713782 ±14		
4. Lower Clearwater (Lapwai Creek)	Fall 2008	0.713338 ±14		
	Spring 2009	0.712713 ±12		
	Summer 2009	0.714723 ±16		
	Fall 2009	0.713570 ±12		
5. Upper Clearwater (Orofino)	Fall 2008	0.712266 ±14	0.712292 ±13	
	Summer 2009	0.712315 ±14		
	Fall 2009	0.712294 ±12		
Lower Snake River (LSK)				
6. Lower Snake (Lewiston)	Fall 2008	0.709651 ±12	0.709677 ±12	0.709699 ±12
	Fall 2009	0.709703 ±12		
7. Lower Snake (Chief Timothy)	Fall 2008	0.709746 ±14	0.709781 ±12	
	Spring 2009	0.709655 ±10		
	Summer 2009	0.709874 ±12		
	Fall 2009	0.709849 ±12		
8. Lyons Ferry Hatchery	Fall 2008	0.709659 ±14	0.709659 ±14	

Table 1. Continued.

Isotopic signature group, site name, and map number	Sampling period	$^{87}Sr/^{86}Sr$	Site average	River group average
Lower Snake River (continued)				
9. Lower Snake (Lyons Ferry)	Fall 2008	0.709701 ±12	0.709576 ±12	
	Fall 2009	0.709450 ±12		
10. Palouse[b]	Fall 2008	0.709684 ±12	0.709225 ±12	0.709225 ±12
	Spring 2009	0.708836 ±10		
	Summer 2009	0.709023 ±14		
	Fall 2009	0.709357 ±12		
Tucannon, Grande Ronde, and Imnaha River (TGI)				
11. Grand Ronde	Fall 2008	0.706588 ±12	0.706488 ±15	0.70681 ±13
	Summer 2009	0.706300 ±20		
	Fall 2009	0.706575 ±12		
12. Imnaha (Cow Creek)	Fall 2009	0.707136 ±10	0.707204 ±12	
	Fall 2009 [a]	0.707137 ±14		
13. Imnaha (Imnaha, OR)	Fall 2009	0.707340 ±12		
14. Tucannon	Fall 2008	0.706845 ±12	0.706756 ±14	
	Spring 2009	0.706565 ±12		
	Summer 2009	0.706782 ±16		
	Fall 2009	0.706833 ±14		

[a] Indicates duplicate TIMS analysis.

[b] The Palouse River was excluded from final LDFA analysis.

In 2011, we augmented our collection of water samples for an expanded water chemical analysis in upcoming study years. We collected 27 additional samples in 2011 from the following locations:

Spring: Eight samples (2 time points) from the Salmon and Clearwater Rivers to characterize variation in $^{87}Sr/^{86}Sr$ during spring.

Summer: Seven samples from across spawning and rearing sites, including from Heller Bar, to increase resolution in the Snake River below its confluence with the Salmon River.

Fall: Twelve samples at base flow to characterize $^{87}Sr/^{86}Sr$ across spawning and rearing sites.

Results

Among water samples from major reaches of the Snake River Basin, $^{87}Sr/^{86}Sr$ signatures varied substantially (Table 1, Figure 2a) with significant differences between reaches (Kruskall-Wallis, chi-square = 104.6, $P \leq 0.001$). Pairwise comparison tests indicated four major groups of distinguishable reaches in the basin based on isotopic signature. These groups were combined into a reduced model for the purpose of fish classification, and all comparisons were significant in this reduced model (Behrens-Fisher, $P = <0.001$; Table 1). The four major isotopic signature groups were:

USK Upper Snake River

CWS Clearwater and Salmon Rivers

LSK Lyons Ferry Hatchery and Lower Snake River (from Salmon River confluence to Columbia River confluence

TGI Tucannon, Grande Ronde, and Imnaha Rivers

The $^{87}Sr/^{86}Sr$ values of water samples from these four isotopic signature groups were used as a training set to create a linear discriminant function analysis (LDFA) for subsequent classification with fish. In these subsequent classifications, cross-validation was used to estimate the true classification error rate, with prior probability of group membership assumed equal. The cross-validation error rate for this model was 0%, and the LDFA was subsequently used to classify fish to location at discrete juvenile life history stages.

We expected $^{87}Sr/^{86}Sr$ signatures to remain relatively stable over time, as reported in past studies of otolith microchemistry (Bain and Bacon 1994, Kennedy et al. 2000). However, the Clearwater and Salmon Rivers showed high seasonal variation (Table 1). In both rivers, $^{87}Sr/^{86}Sr$ values generally decreased during spring and increased during summer and fall, with the exception of the Lower Clearwater, which had a high summer value. The relatively high signature for the Lower Clearwater during summer was likely due to large releases of water from Dworshak Dam on the North Fork Clearwater River (Connor et al. 2003a). However, the sample from the upper Clearwater reach (4 miles upstream from the Clearwater confluence with the North Fork Clearwater) was above the area influenced by possible dam effects. Samples from this site maintained a steady signature throughout the seasons with very little variation (Table 1). While Dworshak Dam likely affects the Sr chemistry of the Lower Clearwater River during summer, other seasonal variation in both the Clearwater River and the Salmon River (which is undammed) may be due to spatial variation in snowmelt patterns, the effect of seasonal saturation of soils with different weathering rates or isotopic signatures, or the effect of snow trapped windblown dust (Clow et al. 1997).

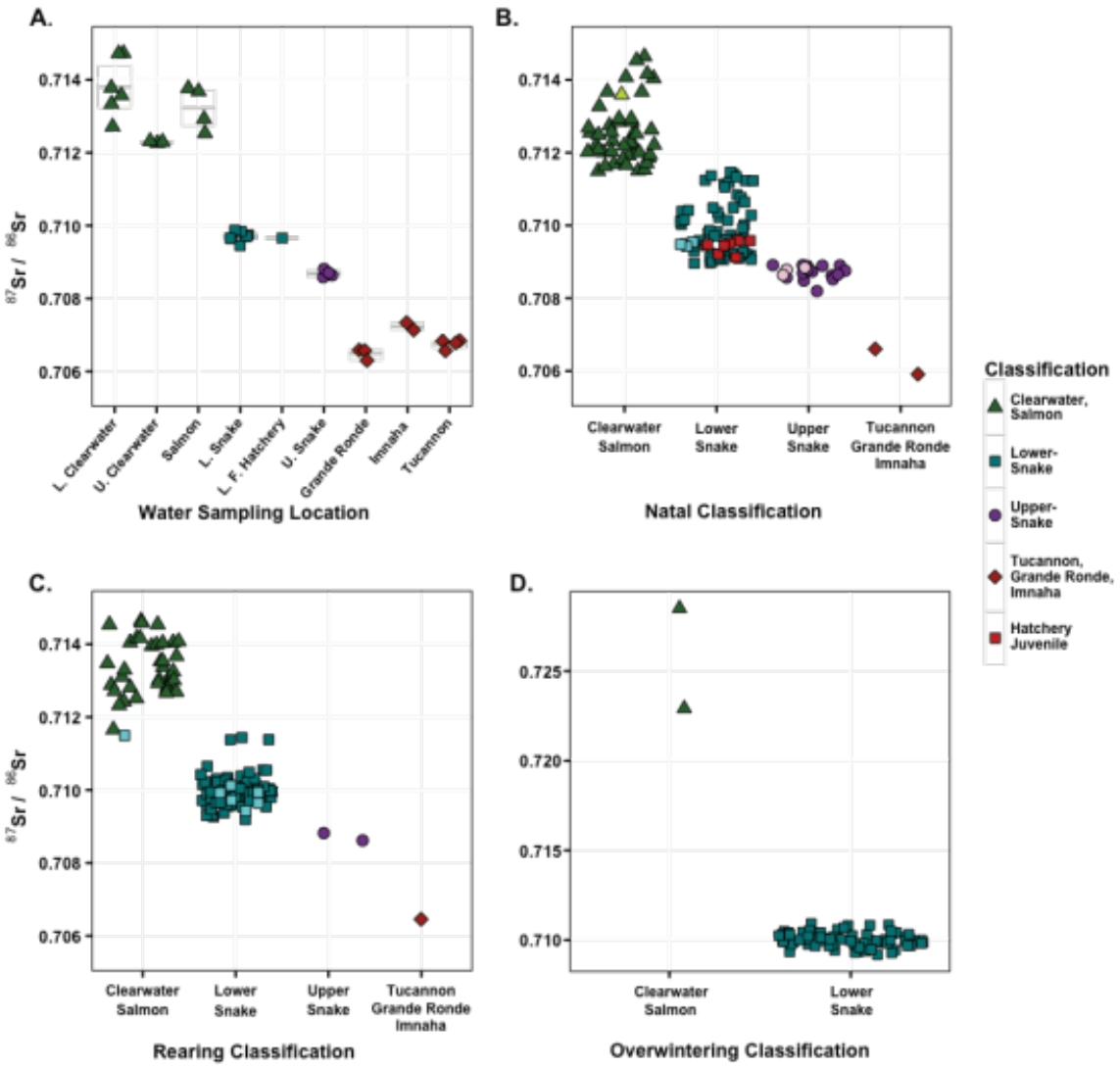

Figure 2. Plots of $^{87}Sr/^{86}Sr$ ratios classified by river group, with misclassified fish denoted by color/shape that does not match that of the classification group. **A)** Statistically significant differences among water samples by river group. Wide variation in the Clearwater-Salmon group was driven largely by seasonal variation in $^{87}Sr/^{86}Sr$ signature. **B)** Natal origin classification based on linear discriminant function analyses (LDFA) of otolith chemical composition for 120 wild adult and 14 juvenile of known origin. Light colors indicate juvenile fish of known origin. **C)** Rearing location classification based on LDFA of otolith chemistry for 120 wild adults and 14 juveniles of known origin. Note distinct clusters by source-river group and that 6 of the 7 samples of known origin (indicated by light color) were correctly classified. **D)** Overwintering location classification based on LDFA for 74 wild adults, indicating the majority of these fish overwintered as juveniles in Lower Snake River reservoirs. Note two points with much higher signatures (change in Y-axis scale); these represent fish that likely overwintered in the Columbia River system, outside our study area.

RESOLUTION OF OTOLITH ISOTOPIC SIGNATURE

Methods

Otolith Sample Collection

During 2011, our analyses of otolith microstructure and microchemistry were based on otoliths collected in previous years. However, we augmented our samples collection for future analyses by collecting additional otoliths from the following of sources:

1) Seven hundred-twenty-two adult fall Chinook from Lyons Ferry Hatchery. All were unmarked and unclipped, and thus presumably of natural origin. Eight had been previously tagged (PIT).
2) Thirty juveniles from Lyons Ferry (15) and Nez Perce Tribal Hatchery (15).
3) Eighteen juveniles sampled in beach seines in the Snake and Grande Ronde Rivers
4) Forty-six adult carcasses on the Clearwater collected by Nez Perce Fisheries
5) Approximately 50 juveniles collected at Lower Granite Dam in the sort-by-code system

Of the fish collected in 2011, 112 adult and 4 juvenile samples have been analyzed for $^{87}Sr/^{86}Sr$ and trace elements at Washington State University (WSU). These samples will be used in future analyses. Isotopic analysis of $^{87}Sr/^{86}Sr$ detailed below is based upon otoliths from the 2006-2008 sampling period (Table 2). Growth analysis was performed on juvenile fish from 1993 (10 fish), 1994 (10 fish), 2007 (15 fish), and 2009 (7 fish). Future work will incorporate data from additional sampling years.

Adult Samples—Left sagittal otoliths were collected over 3 years (2006-2008) from returning adult fall Chinook salmon that were potentially of wild origin (based upon a lack of marks or tags). Otoliths were collected during spawning operations at Lyons Ferry Fish Hatchery, WA, and prepared for growth and microchemical analysis using established methods (Secor et al. 1991). Analyses were performed on the dorsal side of the otolith in the region perpendicular to the sulcus (Figure 2). This area was chosen because it contained the most repeatable and clear growth rings. Scale samples were taken for all fish at the time of otolith removal and analyzed by Washington State Dept of Fish and Wildlife to confirm hatchery or wild origin, age, and yearling or subyearling migration strategy.

Juvenile Samples—Otoliths were collected from seven juvenile fish that had been PIT tagged at three known locations within the basin (1 Clearwater, 3 Lower Snake, 3 Upper Snake). These samples were collected at Lower Granite Dam and used to validate classifications of natal origin based on otolith chemical analyses. The capture location at Lower Granite dam also provided a known chemical signature for these fish corresponding to the time of their

rearing/juvenile migration. In addition, otoliths from nine yearling juveniles from the 2008 brood year at Lyons Ferry Hatchery were analyzed for natal origin and included in the validation sample for natal origin classification.

To examine growth of juveniles, we sampled the otoliths of fall Chinook salmon juveniles captured at Lower Granite Dam on the Snake River in 1993, 1994, 2007, and 2008. These fish had been PIT tagged at various locations upstream and subsequently diverted using the separation-by-code facility at Lower Granite dam. Fork lengths had been recorded at the time of capture, which occurred from June to August. The 1993 and 1994 samples were archived by the U.S. Geological Survey and stored in resin (Otoliths provided by K. Tiffan, USGS, Cook, WA). A total of 61 fish were included in the fish length/otolith radius relationships, with fish selected to represent the range of fork lengths in the sample.

We removed the left sagittal otolith from each individual, removed adhering tissue, and stored dry. Otoliths were then mounted to a microscope slide with Crystal Bond (http://www.crystalbond.com/), and each was polished on both sides in a sagittal plane, using slurries (grit sizes of 1 and 5 alumina micropolish) and a grinding wheel with Buehler 1500 and micro-polishing pads. Polishing ceased when the core of the otolith was exposed and daily increments were visible under a light microscope.

Resolution of Otolith Isotopic Patterns

Otoliths were analyzed for $^{87}Sr/^{86}Sr$ ratio at each life history time point. Isotopic ratio was analyzed at the GeoAnalytical Lab of Washington State University using a Finnigan Neptune (Thermo Scientific) multi-collector inductively coupled plasma mass spectrometer coupled with a New Wave UP-213 laser ablation sampling system (LA-MC-ICPMS). A marine shell standard was used to evaluate measurement error and was assumed to be in equilibrium with the global marine value of $^{87}Sr/^{86}Sr$ (0.70918). The average marine shell value over the length of the study was 0.709214 ±0.000010 (1 SE). A correction factor was calculated for each analysis day based upon the average deviation of the shell standard from the marine value, and otolith $^{87}Sr/^{86}Sr$ values were adjusted accordingly.

Two methods were combined to recover the isotopic patterns in otoliths (Figure 3). First, a transect was analyzed from the otolith's edge to its core at 90° from the sulcus on the dorsal side. If clear rings were not present in that region, the analysis was shifted to the nearest location with more distinct rings. The laser was set to ablate the sample at a constant speed (30 μm/second, 40-μm laser spot size, 0.262-second integration time). This scan recorded changes in $^{87}Sr/^{86}Sr$ ratio across the otolith with excellent temporal resolution but lower precision (±0.00028, 2 SE).

To capture a more precise $^{87}Sr/^{86}Sr$ ratio for each life stage, transect ablations were followed by ring analyses. Ring analysis ablated a curved path along individual rings of the otolith at points of stable signature within its natal, rearing, and overwintering sections (10 µm/second, 30-µm laser spot size, 0.262 integration time, 100 integrations). This method provided very precise measures of isotopic chemistry (±0.00012, 2 SE) at specific life history stages. In cases where a more precise scan was not completed, signatures were determined using the transect scan. This was done by calculating the mean of the corrected $^{87}Sr/^{86}Sr$ integration points within a region of stable $^{87}Sr/^{86}Sr$ corresponding to the life stage being analyzed.

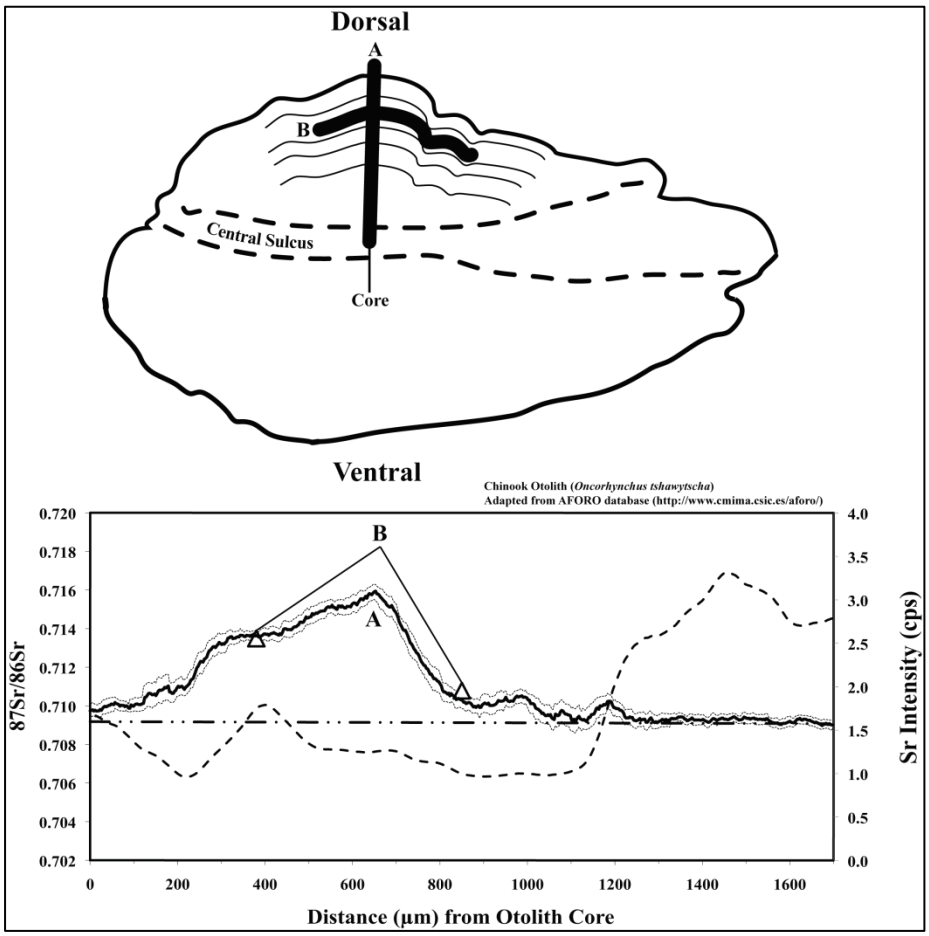

Figure 3. Upper panel shows drawing of otolith dorsal section where laser ablation transects (A) were at 90° to the sulcus and extended from the otolith core to rim. Ablation paths along rings (B) were used for more precise estimates of time-specific signatures. Chart below shows error for A (fine dotted lines) and B expressed as ±2 SE (fine dotted lines). Error bars for B are much smaller than the marker. Strontium intensity (dotted dashed line) and convergence to the global marine signature (dashed line) were used to determine ocean entry.

Life-Stage Determination

We examined three signatures corresponding to the location of fish during juvenile migration using the juvenile section of each adult otolith: natal origin, rearing, and overwintering. The first stable signature, located beyond 110 μm but within 250 μm of the otolith core on the dorsal side, was considered to be the signature of natal origin. If no stable signature was detected in this region, the first peak or valley in $^{87}Sr/^{86}Sr$ was used as the natal signature. The range of 110-250 μm was used in order to most closely approximate the natal location while ensuring that the otolith portion selected would reflect a microchemical signature that was outside the area of maternal influence and that had accumulated prior to any downstream movement (rearing habitat). These distances corresponded to hatch checks and downstream migration initiation in previous studies of fall Chinook (Barnett-Johnson et al. 2005, Zabel and Chittaro 2011).

Rearing signature was considered to be the first stable, freshwater signature located 250-800 μm from the core. An overwintering signature was considered the first stable signature or peak beyond 800 μm from the otolith core. This distance was based on previous calculations of otolith size at length for fall Chinook juveniles (Zabel et al. 2010). These calculations indicated that a distance of 800 μm from the otolith core reflected a size that was larger than expected for a juvenile migrant fish passing Lower Granite dam in October (when juvenile bypass systems are down, and captures of yearling and subyearling migrants have ended). These results were checked against scale analysis to confirm similarity in determination of yearling life history (78% similarity, see Table 2). Any fish exhibiting a freshwater signature beyond 800 μm from the otolith core was considered a yearling fish for subsequent analysis.

Table 2. Summary statistics of adult fall Chinook captured between 2006 and 2008 at Lower Granite Dam and sampled as a part of hatchery spawning operations at Lyons Ferry Hatchery.. All fish were first determined to be yearling or sub-yearling based on scale analysis. The percentage of agreement between otoliths and scale analysis is listed below.

Year	Sample Size	Mean Age	% Female	% Yearling Female	% Yearling	% Otolith/Scale Agree
2006	15	4.3	100	67	67	87
2007	38	3.7	42	63	66	80
2008	67	4.0	72	60	57	75
Overall	**120**	**4.0**	**66**	**62**	**62**	**78**

Data Analysis: Discriminant Function Classification

Adult fish were classified to natal, rearing, and overwintering locations using linear discriminate function analysis (LDFA) with equal prior probability and jackknife re-sampling. For all water sample sites within the basin $^{87}Sr/^{86}Sr$ signatures were pooled into distinguishable groups based on the non-parametric multiple comparisons described in the *Water Chemistry* section above. These groups were used as the training set to develop the LDFA. Overwintering was determined using otolith ocean entry signature (>800 μm = yearling). Otoliths from juveniles of known origin were included in the classification to provide validation of our ability to correctly classify fish.

We tested the hypothesis that expression of the yearling juvenile life history is non-randomly distributed within the basin using Fisher's exact test (Routledge 2005). We compared the proportion of yearling fish originating from each isotopic classification river group to the proportion of yearlings from pooled river groups within the basin, to determine if statistically significant differences in yearling proportion exist between spawning areas ($\alpha = 0.05$).

Results

Natal Origin Classification

We classified all adult otoliths (n = 120), as well as known origin juveniles (n = 14), to natal origin based on $^{87}Sr/^{86}Sr$ signatures recovered from the natal section of these otoliths (100-250μm) using the previously developed LDFA model (Table 2). The lower Snake River (LSK) isotopic group claimed the largest share of natal fish (58 fish, 48%), followed by the Clearwater/Salmon CWS (44 fish, 37%) and upper Snake River groups (USK, 16 fish, 13%). The Tucannon, Grande Ronde, and Imnaha River group (TGI) had the smallest share of natal fish (2 fish, 2%). Classification was successful for 100% of the juveniles with known origin (Figure 2).

To compare the proportion of yearling life history between natal locations, the percentage of yearling fish (ocean entry >800 μm from otoliths core) was calculated for each group from the LDFA (Table 2). Clearwater/Salmon River group contained the largest percentage of yearling fish (77%, 74% female), while the respective lower and upper Snake River groups consisted of 62 and 13% yearling fish (55 and 37% female). Lastly, the Tucannon/Grande Ronde/Imnaha River group was made up of 50% yearling fish (100% female); however, the sample size for this group was small (2 fish).

The proportion of yearling fish in the Clearwater/Salmon group was significantly higher than the pooled proportion in the rest of the basin (Fishers exact test, $P = 0.01$, $\alpha = 0.05$). In contrast the USK group contained a significantly lower proportion of yearling fish than the rest

of the basin using the same test (P >0.001, α = 0.05). The lower Snake and Tucannon/Grande Ronde/Imnaha group did not show significant differences; however, the latter had a small sample size and thus statistical power was insufficient to draw a conclusion.

Table 3. Results of the LDFA used to classify adult fish to their natal, rearing, and overwintering river group based upon $^{87/86}Sr$ ratio. River groupings were determined from water chemistry (see Table 1). Juvenile validation samples consisted of juvenile fish of known origin (wild = 7, hatchery = 9) and were used to test the classification; shaded cells indicate correct classifications of these fish.

Isotopic signature group	Sample size n (%)	Subyearling	Yearling n (%)	Juvenile validation samples	Female (%)	Yearling female (%)
			Natal location			
Tucannon/Grande Ronde/Imnaha	2 (2)	1	1 (50)	0	100	100
Clearwater and Salmon	44 (37)	10	34 (77)[b]	1	71	74
Lyons Ferry/ Lower Snake	58 (48)	22	36 (62)	10	55	58
Upper Snake	16 (13)	12	2 (13)[a, b]	3	37	100
Total	120	45	71 (61)	14		
			Rearing location			
Tucannon/Grande Ronde/Imnaha	1 (1)	1	0	0	0	0
Clearwater and Salmon	37 (31)	9	28 (76)	1	61	61
Lyons Ferry/ Lower Snake	78 (66)	33	45 (58)[a]	6	65	71
Upper Snake	2 (2)	2	0	0	-	-
Total	120	45	73 (62)	7		
			Overwintering location			
Tucannon/Grande Ronde/Imnaha	0	-	-	-	-	-
Clearwater and Salmon	2 (3)	-	-	-	50	-
Lyons Ferry/ Lower Snake	72 (97)	-	-	-	68	-
Upper Snake	0	-	-	-	-	-
Total	74					

[a] Yearling signatures for two fish were unrecoverable and were excluded from yearling analysis.

[b] Yearling proportion was significantly different from the rest of the basin (Fishers exact test, $\alpha = 0.05$)

Rearing Location Classification

All adult otoliths (n = 120) and all otoliths from juveniles of known origin (n = 7), were classified to rearing location based on $^{87}Sr/^{86}Sr$ signature in the rearing section of their otolith (250-800 µm from core) using the LDFA model (Table 2). We classified 78 fish (66%) as having reared in habitats of the Lower Snake River (LSK) group, 37 (31%) as having reared in habitats of the Clearwater and Salmon River group (CWS), and 2 and 1 fish (2 and 1%) as having reared in habitats of the Upper Snake River and Tucannon, Grande Ronde, and Imnaha River groups, respectively (USK and TGI).

To compare proportions of fish with a yearling life history between rearing locations, we defined yearling fish as those with an ocean-entry signature on the otolith that was located more than 800 µm from the otolith core. The percentage of these yearling fish was then calculated for each group from the LDFA (Table 3).

Proportions of yearling ocean entrants varied considerably between rearing groups. Of fish classified to have reared in the Lower Snake group and Clearwater/Salmon group, 58 and 76% were yearling ocean entrants (71 and 61% female). In contrast, none of the fish classified as having reared in Upper Snake and Tucannon/Grande Ronde/Imnaha groups had entered the ocean as yearlings.

Classification of rearing location was successful for six of the seven samples from juveniles of known origin (Figure 3C); one fish was misclassified to the Clearwater/Salmon River group, possibly as a result of rearing within areas assigned to this group either before tagging or between tagging and recapture at Lower Granite Dam.

Overwintering Location

All adult yearlings (n = 74) were classified to overwintering location (Figure 2) based upon the $^{87}Sr/^{86}Sr$ signature in the overwintering portion of their otoliths (portion >800 µm from core; Table 3). Specifically, 72 fish (97%) were classified as having overwintered in areas of the Lower Snake River group, while 2 fish (3%) were classified as overwintering in areas of the Clearwater/Salmon River group (these groups consisted of 68% and 50% female fish, respectively). No adult fish was classified to have overwintered in habits of either the Tucannon/Grande Ronde/Imnaha or Upper Snake River group.

JUVENILE GROWTH ANALYSIS

Methods

Study fish for back-calculation of growth trajectories were juvenile fall Chinook that were captured by beach seine, PIT-tagged, and subsequently recaptured in the separation-by-code facilities at Lower Granite Dam. We estimated growth trajectories for a total of 42 individuals from seine samples taken in 1993 (10 fish), 1994 (10 fish), 2007 (15 fish), and 2009 (7 fish).

Polished otoliths were photographed using a digital camera (Cybernetics[1]) mounted on a compound microscope (Zeiss; set at 20× magnification). Using Image Pro software (MediaCybernetics), we measured total otolith radius (distance from otolith core to margin) on the ventral side along a transect perpendicular to the longitudinal axis. This transect was selected for its reliable clarity.

When possible, we also identified the hatch check of each otolith, which was distinguishable by a dark band and secondary primordium (Zhang et al. 1995), and which corresponded to the transition from embryo to fry.

Next, we measured the distance from the primordium to the hatch check along a transect perpendicular to the longest axis, as above. Finally, to standardize samples in terms of seasonal growth, we measured otolith increments (in microns) over a variable period (28-84 d) to ensure that all periods of growth trajectory would begin on 15 May comparison purposes.

To back-calculate growth trajectories from these increments, we used the methods presented in Zabel et al. (2010). Specifically, we applied the quadratic relationship with a biological intercept to the relationship between fork length (mm) and otolith length (μm):

$$FL_i = \beta_0 + \beta_1 \cdot OL_i + \beta_1 \cdot OL_i^{\,2} + \varepsilon_i$$

where FL_i was fork length of the i th individual, OL_i was its otolith length, β_0 and β_1 were coefficients, and ε_i was a residual that is distributed normally (Figure 4). The fitted relationship was constrained to pass through a "biological intercept," defined as fish length and otolith length at the time of hatching. This intercept is represented by the solid point in Figure 4. We obtained this point by taking the average otolith length at the hatch check (110.4 μm), and using fish length at hatching from previous studies of ocean-type Chinook (Beacham and Murray 1990, Healey 2001). Zabel et al. (2010) reported that this method could accurately estimate growth

[1] Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

trajectories for Snake River fall Chinook.

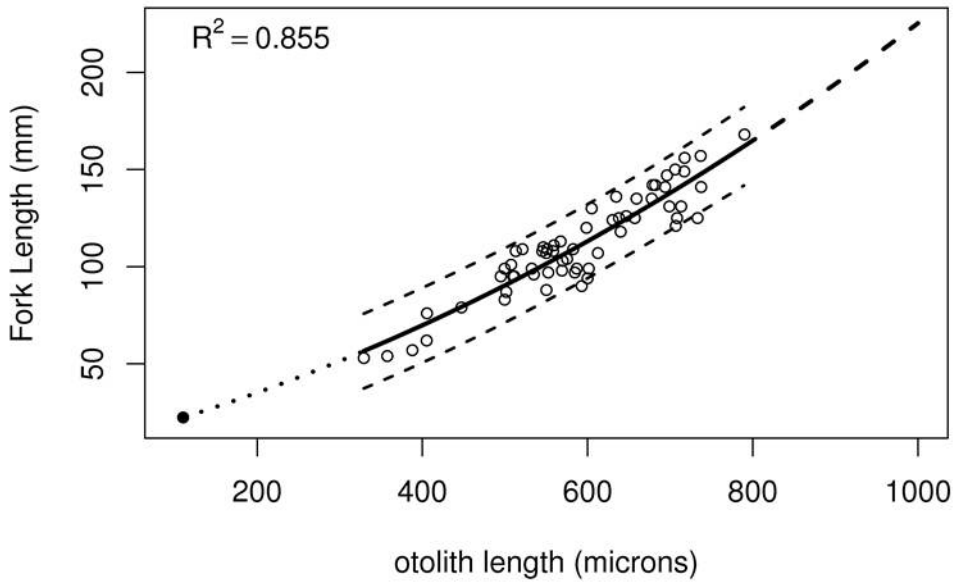

Figure 4. Relationship between fork length (mm) and otolith length (microns). Open points represent individual fish and the solid line is the best fit relationship through the points while being constrained to pass through the biological intercept (solid point). The dashed lines represent the 95% prediction intervals.

Once we obtained this relationship, we back-calculated growth trajectories of individual fish based on the methods detailed in Zabel et al. (2010). We back-calculated daily growth for recently collected fish (2007 and 2009) and archived otoliths (1993 and 1994). To smooth day-to-day variation, we used average fish size and growth over 5-d periods.

Results

Back-calculated growth trajectories showed that juveniles grew approximately 1 mm/d. Juvenile fish growth did not appear to vary considerably between the early period (1993 and 1994) and the recent period (2007 and 2009) (Figure 5). We plan to analyze these growth patterns in a more rigorous manner in the future. Nonetheless, fish from the early period clearly arrived at Lower Granite Dam later in the season and at a larger size than those from the recent period (Figure 5).

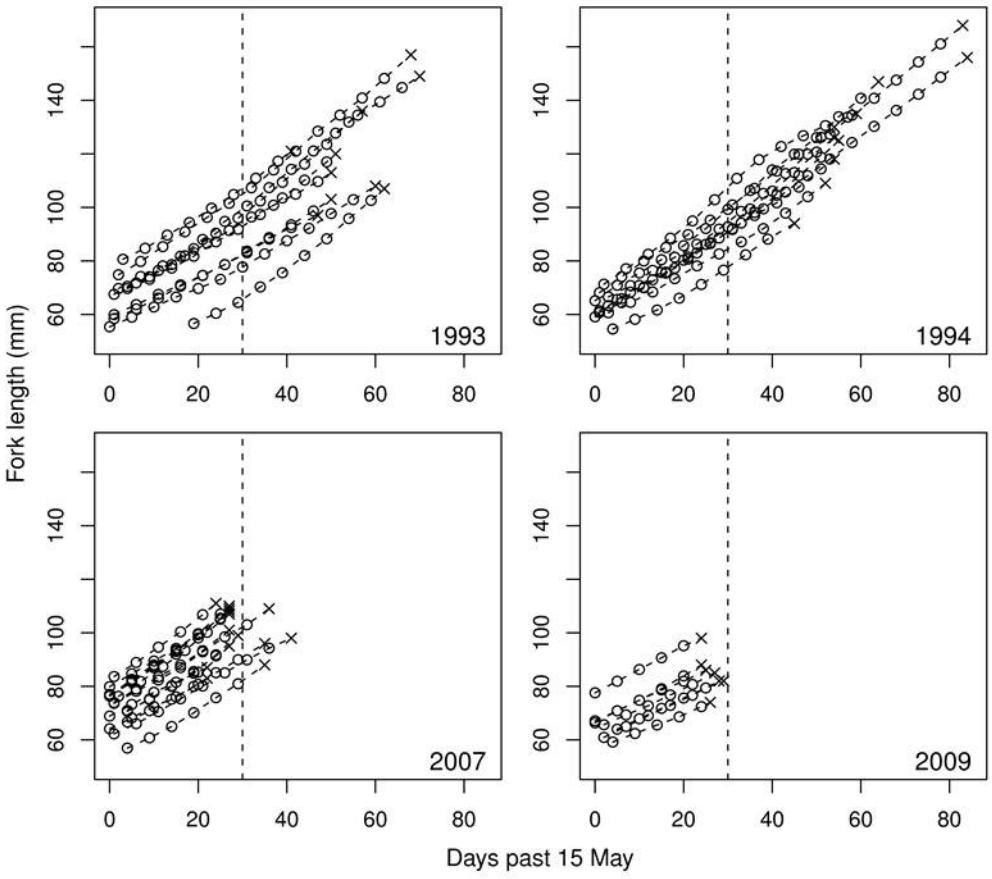

Figure 5. Estimated growth trajectories for individual fall Chinook collected at Lower Granite Dam during the 80 days following 15 May in 1993 and 1994 vs. 2007 and 2009. Each cross (×) represents the day fish passed Lower Granite Dam, and open circles (○) represent length averaged over a 5-d period.

DISCUSSION

Our data suggest a definite spatial structure in the distribution of life history strategies employed by our study population. Historically, Snake River fall Chinook likely exhibited low diversity in juvenile migration strategies, with juveniles migrating primarily as subyearlings. Our data confirm more recent findings from studies (Connor et al. 2002, Connor et al. 2005) showing that the current population is made up of both yearling and subyearling juvenile migrants. These data also provide the first direct evidence that a majority of yearling fish overwinter in the Snake River, with a small fraction potentially moving downstream to the Columbia River.

Aggregation of watersheds and rivers into groups with similar $^{87}Sr/^{86}Sr$ signatures introduced a potential loss in the spatial resolution with which locations could be determined based on otolith microchemistry. However, our results indicated that the majority of distinct population groups within the basin were distinguishable using this method. Aerial redd surveys have indicated that the majority of fall Chinook salmon spawning occurs in the Upper Snake and Lower Clearwater River (Garcia et al. 2007). Our classifications of fish origin based on isotopic similarity between otolith and aggregate water samples (LDFA) agreed with this finding and identified major spawning locations in the Upper Snake, Lower Snake, and Lower Clearwater Rivers. This finding supports our conclusion that the level of spatial resolution obtained using these aggregations was sufficient to capture the ecologically important populations.

Within the Lower Snake River group, our grouping of spawning habitats below the Salmon/Snake River confluence with those from Lower Snake River reservoirs could potentially obscure the downstream movement of fish that hatched below the Salmon River. The Salmon River contributed less than 1% to the total production for the Clearwater and Salmon River group. Similarly low production levels for the Tucannon, Grande Ronde and Imnaha River group resulted in poor representation from these sites in our sampled population. However, these groupings captured the majority of important spawning locations in the basin and thus did not detract from our overall conclusions.

The fact that a large percentage of fish were classified to the Lower Snake River group presented some ambiguity in interpreting location of natal origin for these fish. The isotopic signature of this group includes an imprint from both Snake River reservoirs and free-flowing reaches of the Snake River (below its confluence with the Salmon River). As a result, the location of spawning was not well defined chemically. Although some Snake River fall Chinook spawn in the tailraces of dams, it is likely that the majority of fish classified to the Lower Snake River group had been spawned in the free-flowing section of the Snake River (between Asotin, WA, and the confluence of the Snake and Salmon River).

As juveniles move downstream to rear, the distinction between the free-flowing Snake River and the reservoirs becomes more important. Our results indicated that fish from the Clearwater River moved downstream to rear in the Lower Snake River. Therefore, these fish must have been rearing in Snake River reservoirs, since no free-flowing reach exists below the confluence of the Snake and Clearwater River.

Juveniles originating in the Upper or Lower Snake River could potentially rear in either the free-flowing or reservoir habitats of the Lower Snake River and be classified to the same Lower Snake River group (LSK). Beach-seine sampling has shown that juveniles follow a period of passive downstream migration in Lower Granite reservoir during the rearing phase (Connor et al. 2003b). Thus, we would expect that during the rearing phase, the majority of fish bearing an LSK signature would in fact be located within the reservoir system.

Overwintering Location

Proportions of yearling ocean entrants varied considerably between rearing groups. However, of fish classified as having reared in the respective Lower Snake and Clearwater/Salmon groups, 58 and 76% were yearling ocean entrants. These results indicate that among Snake River fall Chinook juveniles that enter the ocean as yearlings, the majority overwinter in lower Snake River reservoirs. Connor et al. (2005) assumed overwintering location to be Lower Granite Reservoir on the Lower Snake River; however, the location of overwintering habitat had not been confirmed.

We classified two fish to the Clearwater and Salmon River (CWS) group for overwintering location. Interestingly, these two fish had $^{87}Sr/^{86}Sr$ ratios significantly higher than those of any fish measured in our study (Figure 3D). The isotopic signatures of these fish were most similar to those of fish from the Columbia River (Barnett-Johnson et al. 2010, Miller et al. 2011), indicating that they likely overwintered in the Columbia River below its confluence with the Snake. Yearling juveniles that move downstream to the Columbia River for overwinter rearing could be counted as subyearlings in passage data collected at Snake River dams.

Spatial Distribution of Migration Strategy

These results strengthen the case for a link between temperature in the natal stream and expression of the yearling migration strategy. As the range of Snake River Chinook has decreased, the importance of relatively cooler spawning habitat in the Clearwater River has increased (Waples et al. 1991). Managed outflows from Dworshak Reservoir are used to further cool the lower reaches of the Clearwater River and the Snake River during key summer migration periods. These flows provide thermal refugia in downstream reservoirs to increase smolt survival (Connor et al. 2003a). Previous studies have linked cooler temperatures and later hatch dates in the Clearwater River to a shift toward later juvenile migration and increased abundance of yearling fish (Connor et al. 2002). Given that temperature can be a significant determinant of juvenile growth and survival in salmon (McCullough 1999, Connor et al. 2003a), these anthropogenic effects have the potential to create selective pressures toward change in juvenile migration timing.

Among study fish classed by natal origin to the Upper Snake River group 13% were yearling ocean entrants. In comparison, 77% of fish classed by origin to the Clearwater and Salmon River group had entered the ocean as yearlings (Table 3). The average spring temperature of the Clearwater River is 9°C, significantly lower than that of the Snake River (11.8°C; (Connor et al. 2002). This confirms previous studies that indicated large numbers of yearlings originating in the Clearwater River (Connor et al. 2005).

Furthermore, our data on rearing location show that fish from the Clearwater River remain in the Clearwater until later in the year and move to rearing areas in the Lower Snake River later than other spawning groups (Figure 3). Whether this is a result of later emergence, slower growth, or differences in life history expression is unknown, but supports the observations of Connor et al. (2002) that early emergence, temperature or growth opportunity seem to play a part in determining yearling behavior.

Whether this apparent increase in juvenile life history diversity is an example of individual plasticity or adaptive evolution depends upon whether the yearling life history is evolutionarily advantageous. Selection for a yearling life history strategy would require differential survival between the two life history strategies. Because our study was limited to otoliths from returning adult fish, direct estimation of differential survival cannot be calculated. Still, we would expect the representation of yearlings returning to spawn would be greater if a higher probability of survival exists for this population.

We found that 62% of returning adult fish had followed a yearling juvenile life history (Table 3), a high percentage considering the Clearwater provides only 36% of the total juvenile production for the Snake River basin (Garcia et al. 2007). Connor et al. (2005) also noted that a

large percentage of returning adults (41%) had followed a yearling life history. While this is not proof of increased survival among yearling fish, it adds to the circumstantial evidence of selection for the yearling life history.

This study shows that $^{87}Sr/^{86}Sr$ microchemistry and the temporally explicit growth of otoliths can be an important tool to examine life history expression at the level of the individual. The temporal and spatial precision of otolith studies may be improved by combining $^{87}Sr/^{86}Sr$ ratios with other elemental signatures within the otolith (Thorrold et al. 2001). By combining individual migration data from otoliths with growth and survival estimates we can begin to make specific predictions regarding the fitness advantages of observed migration strategies. Comparing the success of migration strategies under spatially heterogeneous environmental regimes may also inform our understanding of the relative contribution of evolution and phenotypic plasticity within Snake River fall Chinook salmon.

ACKNOWLEGEMENTS

Thanks to members of the CIFEES lab at University of Idaho including E. Hamann, J. Reader and S. Bourret for help in sample collection, analysis, and method development. B. Connor with U. S. Fish and Wildlife and B. Arnsberg from Nez Perce Tribal Fisheries collected juvenile samples for this study. Thanks to D. Milks, staff at Lyons Ferry Hatchery and the Washington Department of Fish and Wildlife for facilitating sample collection and providing scale analysis. Thanks to the Washington State University Geoanalytical Lab, J. Vervoort, C. Knaack, and G. Hart for the use of their equipment and help in isotopic method development. Thanks to J. Butzerin (NOAA) for excellent editing of previous versions of this report. Finally, thanks to the Army Corps of Engineers, Walla Walla for providing funding.

REFERENCES

Arnsberg, B. D. and D. S. Kellar. 2007. Nez Perce Tribal Hatchery monitoring and evaluation of fall Chinook salmon supplementation in the Clearwater River Subbasin. 2002 Annual Report to the U.S. Department of Energy, Bonneville Power Administration, Project No. 1983-350-003.

Arnsberg, B. D., D. S. Kellar, and M. A. Tuell. 2010. Nez Perce Tribal Hatchery monitoring and evaluation project; Fall Chinook salmon (*Oncorhynchus tshawytscha*) supplementation in the Clearwater River Subbasin. 2007 Annual Report to the U.S. Department of Energy, Bonneville Power Administration, Project No. 1983-350-003.

Bain, D. and J. Bacon. 1994. Strontium isotopes as indicators of mineral weathering in catchments. Catena **22**:201-214.

Barnett-Johnson, R., F. Ramos, C. Grimes, and R. MacFarlane. 2005. Validation of Sr isotopes in otoliths by laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): opening avenues in fisheries science applications. Canadian Journal of Fisheries and Aquatic Sciences **62**:2425-2430.

Barnett-Johnson, R., D. J. Teel, and E. Casillas. 2010. Genetic and otolith isotopic markers identify salmon populations in the Columbia River at broad and fine geographic scales. Environmental biology of fishes:1-14.

Beacham, T. D. and C. B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of 5 species of Pacific salmon - a comparative analysis. Transactions of the American Fisheries Society **119**:927-945.

Clow, D., M. Mast, T. Bullen, and J. Turk. 1997. Strontium 87/strontium 86 as a tracer of mineral weathering reactions and calcium sources in an alpine/subalpine watershed, Loch Vale, Colorado. Water Resources Research **33**:1335-1351.

Connor, W. P., H. Burge, J. Yearsley, and T. Bjornn. 2003a. Influence of flow and temperature on survival of wild subyearling fall Chinook salmon in the Snake River. North American Journal of Fisheries Management **23**:362-375.

Connor, W. P., H. L. Burge, R. Waitt, and T. C. Bjornn. 2002. Juvenile life history of wild fall chinook salmon in the Snake and Clearwater rivers. North American Journal of Fisheries Management **22**:703-712.

Connor, W. P., J. G. Sneva, K. F. Tiffan, R. K. Steinhorst, and D. Ross. 2005. Two alternative juvenile life history types for fall Chinook salmon in the Snake River basin. Transactions of the American Fisheries Society **134**:291-304.

Connor, W. P., R. K. Steinhorst, and H. L. Burge. 2003b. Migrational behavior and seaward movement of wild subyearling fall Chinook salmon in the Snake River. North American Journal of Fisheries Management **23**:414-430.

Garcia, A., S. Bradbury, I. Ahsahka, B. Arnsberg, I. Orofino, P. Groves, and I. Boise. 2007. Fall Chinook Salmon Spawning Ground Surveys in the Snake River Basin Upriver of Lower Granite Dam, 2007.

Healey, M. C. 1991. Life history of Chinook salmon.*in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Healey, M. C. 2001. Patterns of gametic investment by female stream- and ocean-type chinook salmon. Journal of Fish Biology **58**:1545-1556.

Hollander, M. and D. Wolfe. 1973. Nonparametric Statistical Methods. John Wiley and Sons, New York.

Kennedy, B., J. Blum, C. Folt, and K. Nislow. 2000. Using natural strontium isotopic signatures as fish markers: methodology and application. Canadian Journal of Fisheries and Aquatic Sciences **57**:2280-2292.

Kennedy, B., A. Klaue, J. Blum, C. Folt, and K. Nislow. 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. Canadian Journal of Fisheries and Aquatic Sciences **59**:925-929.

Ludington, S., B. C. Moring, R. J. Miller, K. Flynn, M. J. Hopkins, P. Stone, D. R. Bedford, and G. A. Haxel. 2005. Preliminary integrated geologic map databases for the United States -- western states: California, Nevada, Arizona, Washington, Oregon, Idaho, and Utah [version 1.3]. Pages Open-File Report OF-2005-1305. U.S. Geological Survey.

Mains, E. M. and J. M. Smith. 1964. The distribution, size, time, and current preferences of seaward migrant chinook salmon in the Columbia and Snake Rivers., Fisheries Research Papers, Washington Department of Fisheries, 2:5-43.

McCullough, D. A. 1999. A Review and Synthesis of Effects of Altherations to the Water Temperature Regime of Freshwater Life Stages of Salmonids, with Special Refence to Chinook Salmon *in* U. S. E. P. Agency, editor.

Miller, J. A., V. L. Butler, C. A. Simenstad, D. H. Backus, A. J. R. Kent, and B. Gillanders. 2011. Life history variation in upper Columbia River Chinook salmon (Oncorhynchus tshawytscha): a comparison using modern and~ 500-year-old archaeological otoliths. Canadian Journal of Fisheries and Aquatic Sciences **68**:603-617.

Munzel, U. and L. A. Hothorn. 2001. A Unified Approach to Simultaneous Rank Test Procedures in the Unbalanced One way Layout. Biometrical Journal **43**:553-569.

Routledge, R. 2005. Fisher's exact test. Wiley.

Secor, D., J. Dean, and E. Laban. 1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Institute; Belle W. Baruch Institute for Marine Biology and Coastal Research.

Stoeser, D. B., G. N. Green, L. C. Morath, W. D. Heran, A. B. Wilson, D. W. Moore, and B. S. Van Gosen. 2006. Preliminary integrated geologic map databases for the United States: central states: Montana, Wyoming, Colorado, New Mexico, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Texas, Iowa, Missouri, Arkansas, and Louisiana. U.S. Geological Survey.

Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. Science **291**:297.

Waples, R., R. Jones Jr, B. Beckman, and G. Swan. 1991. Status review for Snake River fall chinook salmon. NOAA Technical Memorandum NMFS N/NWC-201, Seattle, Washington.

Williams, J. G., R. W. Zabel, R. S. Waples, J. A. Hutchings, and W. P. Connor. 2008. Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. Evolutionary Applications **1**:271-285.

Zabel, R. and P. Chittaro. 2011. Unpublished otolith hatch check data for Snake River fall Chinook Salmon NOAA - Northwest Fisheries Science Center, Seattle, WA.

Zabel, R., K. Haught, and P. Chittaro. 2010. Variability in fish size/otolith radius relationships among populations of Chinook salmon. Environmental biology of fishes **89**:267-278.

Zhang, Z., R. J. Beamish, and B. E. Riddell. 1995. Differences in otolith microstructure between jatchery-reared and wild Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences **52**:344-352.