Snake River Fall Chinook Salmon Life History Investigations

BPA Project # 2002-032-00

Report covers work performed under BPA contract #(s) 75127, 46273 REL 12, 76356, 72875

Report was completed under BPA contract #(s) 75127, 46273 REL 12, 72875

1/1/2017 - 12/31/2017

John M. Erhardt, Rulon J. Hemingway,
and Kenneth F. Tiffan
U.S. Geological Survey
Western Fisheries Research Center
5501A Cook-Underwood Rd.
Cook, WA 98605

Paul Chittaro
National Oceanic and Atmospheric Administration
Seattle, Washington

Brian Kennedy and Jens Hegg
University of Idaho

Report Created March 2018

This report was funded by the Bonneville Power Administration (BPA), U.S. Department of Energy, as part of BPA's program to protect, mitigate, and enhance fish and wildlife affected by the development and operation of hydroelectric facilities on the Columbia River and its tributaries. The views in this report are the author's and do not necessarily represent the views of BPA. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table of Contents

Table of Contents ii

Executive Summary iii

Chapter One:

Smallmouth bass predation on subyearling fall Chinook salmon in Lower Granite Reservoir, 2016–2017 1

Chapter Two:

What did you say about my mother? The complexities of maternally derived chemical signatures in otoliths. 30

Chapter Three:

Reconstructing the early life history of a migratory species 64

Executive Summary

The following report is divided into three chapters each of which describes work conducted different project cooperators. It is important to note that some work summarizes data collected in only one or two years and should be considered preliminary and interpreted with caution.

Chapter One describes smallmouth predation on subyearling fall Chinook salmon in Lower Granite Reservoir in 2016–2017. Smallmouth bass abundance increased seasonally in shoreline habitats and highest in the lower reach of the reservoir. Abundance ranged from 26,462 to 47,592 in 2017 and from 37,358 to 61,934 in 2016. Bass abundance was highest in "natural" habitat in 2017 and fish were generally larger in habitat classified as "suitable" for subyearlings. Subyearlings were present in all habitat types sampled but their abundance was 2–4 times lower in the lower reach of the reservoir. Sand rollers—a common prey of smallmouth bass—were present in greatest numbers in "suitable" and "natural" habitat in the upper and middle reservoir reaches, but few were observed in the lower reservoir. Bass consumption of subyearlings was much lower in 2017 than in 2016, but consumption of sand rollers was similar between years. In 2017, a total of 50,611 subyearlings were consumed by smallmouth bass compared to 261,704 fish in 2016. In 2017, a total of 225,408 sand rollers were consumed by bass compared to 297,317 fish in 2016. The high flows and turbidity likely explain the lower predation losses observed in 2017.

Chapter Two describes the link between maternal migration to early juvenile life-history through maternal chemistry recorded in otoliths for Snake River fall Chinook salmon. Despite the wide use of maternal signatures to infer anadromy, the duration and dynamics of maternal otolith signatures are not well understood. Shifts in the elemental ratios and strontium isotope ($^{87}Sr/^{86}Sr$) chemistry in otoliths from juvenile Chinook salmon (*Oncorhynchus tshawytscha*) correlate with the timing of hatch and emergence respectively, indicating a chemical marker of these ontological stages. Additionally, analysis of maternal signatures show that maternally derived $^{87}Sr/^{86}Sr$ may be influenced by equilibration of the mother to freshwater, and in some cases the $^{87}Sr/^{86}Sr$ signatures of the eggs can shift significantly after being laid. These results provide guidance in separating maternal and juvenile signatures as researchers increasingly target early juvenile otolith chemistry. These results also caution against the use of $^{87}Sr/^{86}Sr$ alone as a marker of anadromy in populations with significant inland migrations.

Chapter Three describes the use of otolith microchemistry to infer the timing and location of different life history events in juvenile fall Chinook salmon. Otoliths extracted from 125 adults in 2011 indicated that 61 were of wild origin and 63 were of hatchery origin. Most of these fish originated and reared in lower Snake River. Of 122 adults analyzed, 80% of the wild fish and 72% of the hatchery fish exhibited a yearling life-history strategy and most overwintered in the lower Snake River. Fish with a yearling strategy were larger at Snake River egress and ocean entry than fish with a subyearling strategy. An analysis of the importance of different

variables to growth and size at Snake River egress and ocean entry failed to identify any one model that outperformed all other models tested.

CHAPTER ONE

Smallmouth bass predation on subyearling fall Chinook salmon in Lower Granite Reservoir, 2016–2017

John M. Erhardt, Kenneth F. Tiffan, R.J. Hemingway, Brad K. Bickford, and Tobyn N. Rhodes

U.S. Geological Survey
Western Fisheries Research Center
Columbia River Research Laboratory
5501A Cook-Underwood Rd.
Cook, Washington 98605

Introduction

Predation by nonnative fishes is one factor that has been implicated in the decline of juvenile salmonids in the Pacific Northwest. Impoundment of much of the Snake and Columbia Rivers has altered food webs and created habitat favorable for species such as smallmouth bass *Micropterus dolomieu*. Smallmouth bass are common throughout the Columbia River basin and have become the most abundant predator in lower Snake River reservoirs (Zimmerman and Parker 1995). This is a concern for Snake River fall Chinook salmon *Oncorhynchus tshawytscha* (hereafter, subyearlings) that may be particularly vulnerable due to their relatively small size and because their main-stem rearing habitats often overlap or are in close proximity to habitats used by smallmouth bass (Curet 1993; Tabor et al. 1993).

Concern over juvenile salmon predation spawned a number of large-scale studies to quantify its effect in the late 1980s, 1990s, and early 2000s (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Fritts and Pearsons 2004; Naughton et al. 2004). Smallmouth bass predation represented 9% of total salmon consumption by predatory fishes in John Day Reservoir, Columbia River, from 1983 through 1986 (Rieman et al. 1991). In transitional habitat between the Hanford Reach of the Columbia River and McNary Reservoir, juvenile salmon (presumably subyearlings) were found in 65% of smallmouth bass (>200 mm) stomachs and comprised 59% of the diet by weight (Tabor et al. 1993). Within Lower Granite Reservoir on the Snake River, Naughton et al. (2004) showed that monthly consumption (based on weight) ranged from 5% in the upper reaches of the reservoir to 11% in the forebay. However, studies in the Snake River were conducted soon after Endangered Species Act (ESA) listing of Snake River fall Chinook salmon (NMFS 1992). During this time, fall Chinook salmon abundance was at an historic low, which may explain why consumption rates were relatively low compared to those from studies conducted in the Columbia and Yakima Rivers where abundance was higher (e.g., Tabor et al. 1993; Fritts and Pearsons 2004).

We speculate that predation on subyearlings by smallmouth bass in the Snake River may have increased in recent years for several reasons. Since their ESA listing, recovery measures implemented for Snake River fall Chinook salmon have resulted in a large increase in the juvenile population (Connor et al. 2013). Considering that subyearlings probably now make up a larger portion of the forage fish population, it is plausible they should make up a larger portion of smallmouth bass diets. Second, migrating subyearlings delay downstream movement in the transition zones of the Clearwater River and Snake River for varying lengths of time (Tiffan et al. 2010), which increases their exposure and vulnerability to predators. Spatial overlap in locations of smallmouth bass and subyearlings that died during migration provides support for this (Tiffan et al. 2010). Finally, the later outmigration of subyearlings from the Clearwater River results in their presence in Lower Granite Reservoir during the warmest summer months when predation rates of smallmouth bass should be highest.

In 2016 and 2017, we focused our smallmouth bass predation efforts in Lower Granite Reservoir downstream of the transition zones and the confluence area where we worked during 2012–2015. This report primarily covers results from 2017 but some results from 2016 are also included for comparison. Similar to past years, our first objective was to quantify smallmouth bass consumption rates of subyearlings, determine bass abundance, and describe bass diets. In addition, Tiffan et al. (2016a) posited that predation risk to subyearlings may be higher in shoreline habitats that are more suitable for smallmouth bass and lower in shoreline habitats that are more suitable for subyearlings. To test this hypothesis, our second objective was to examine the relationship between smallmouth bass predation and subyearling habitat suitability. Our final objective was to combine estimates of consumption with smallmouth bass abundance to derive estimates of total Chinook salmon losses to smallmouth bass for 2016 and 2017.

Methods

Study Area

We conducted our study during April–June 2017 in Lower Granite Reservoir on the Snake River. Lower Granite Reservoir is the first impoundment encountered by juvenile salmonids emigrating from the Snake and Clearwater Rivers. From 2012 to 2015, smallmouth bass predation research was focused on the upper end of the reservoir where the river transitions from a free-flowing to impounded state. This study area covered the remaining 42 inundated river kilometers (rkms) of reservoir not studied previously; extending from the CON reach (rkm 215) described in Erhardt et al. (2017a) to Lower Granite Dam (rkm 173; Figure 1). We divided the reservoir into three equal reaches: lower (rkm 173–187), middle (rkm 187–201), and upper (rkm 201–215). This was done because smallmouth bass abundance and consumption can vary spatially (Beamesderfer and Rieman 1991; Petersen 1994), and the amount of subyearling habitat decreases with increasing proximity to the dam (Tiffan et al. 2016a).

Sampling methods

We used a stratified random design to plan our sampling of smallmouth bass in three different shoreline habitats types based on their suitability to subyearlings as identified by Tiffan et al. (2016a). We refer to the first habitat type as “suitable”, which comprised naturally occurring shorelines where the probability of subyearling presence was ≥0.5 based on the logistic regression model developed by Tiffan et al. (2016a). We used this probability cut-off point to define suitable rearing habitat for subyearlings. We refer to the second habitat type as “natural”,

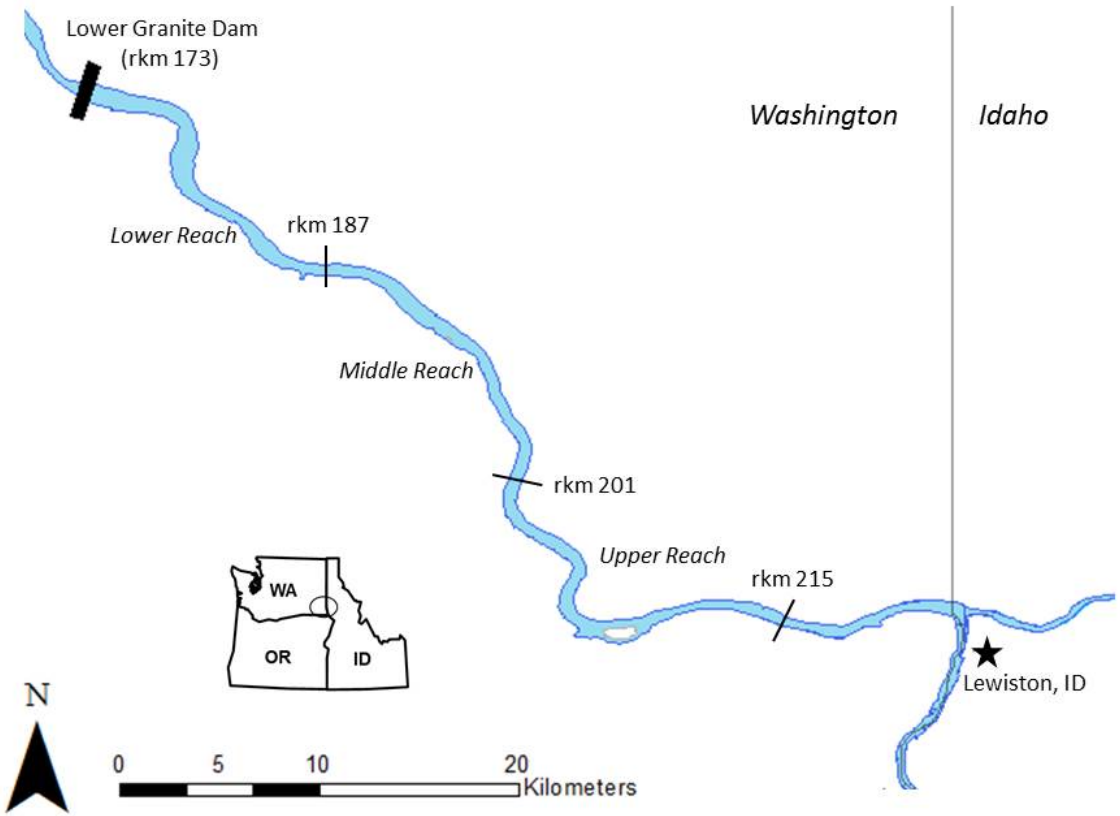

Figure 1. Lower Granite Reservoir on the Snake River and the three reaches that were sampled to evaluate Smallmouth bass predation on subyearling fall Chinook salmon in 2016–2017.

which also comprised naturally occurring shorelines. This habitat generally had steep lateral bed slopes and large talus substrate that made it unsuitable as subyearling rearing habitat because it's associated probability was <0.5. The remainder of shorelines in our study area comprised "riprap", which was also categorized as unsuitable for subyearling rearing based on the findings of Garland et al. (2002). Next, we used a geographic information system (GIS; ArcGIS®, Redlands, CA, USA) to characterize the shoreline by habitat type and calculate distances (m) for all continuous habitat patches. All habitat patches >200 m were divided into equal-sized transects (# transects = shoreline patch length divided by 200 m). For each reach and sampling interval, we randomly selected 16 transects (that were not sampled during 2016) without replacement from the pool of 100–200-m transects using proportional allocation methods based on habitat type (Scheaffer et al. 1996). No transects were established in habitat patches that were <100 m (Table 1).

Nighttime electrofishing was conducted biweekly from the last week of April until water temperatures exceeded our ESA permit restriction of 18°C for electrofishing (late June). Electrofishing output was 400 V DC with 60 pulses per second at 2–4 amps. As each transect was sampled, all stunned Smallmouth Bass ≥150 mm total length (TL) were netted and placed in an aerated live well. We also estimated the number of subyearlings and sand rollers *Percopsis transmontana*—two of the most common prey of smallmouth bass (Erhardt et al. 2017a)—that were present in each transect. After completing each transect, we collected stomach contents of smallmouth bass using a modified nonlethal lavage (Seaburg 1957) that removed 99.8% of diet items (Erhardt et al. 2014). The lavage instrument consisted of a ¼" diameter tube connected to a common garden spray nozzle that supplied filtered river water via a wash-down pump installed on the boat. Stomach contents were collected in a 425-µm sieve and preserved in 90% ethanol. All smallmouth bass collected along randomly chosen transects throughout the study were tagged with unique anchor tags for mark-recapture abundance estimation as described below.

Smallmouth bass abundance

Absolute abundance of smallmouth bass ≥150mm was estimated using catchability models derived from relationships between electrofishing CPUE (bass/m of shoreline) and mark-recapture estimates for each habitat type. Catchability models were developed for riprap and suitable shoreline habitats in the upper reservoir, just above our study area, by Erhardt et al. (2017a) during 2014–2015. We supplemented their data with mark-recapture data collected in our study. This allowed us to focus more of our effort in natural habitat where no relationship had been derived. We collected mark-recapture data in two ways. First, for transects where smallmouth bass were marked and released as part of our biweekly sampling, we resampled them 1–2 nights after marking. Second, we sampled additional transects during weeks between

Table 1. Sampling effort expended to collect smallmouth bass for gut analysis in different shoreline habitats in Lower Granite Reservoir during 2017. Sampling occurred during the weeks of April 24, May 8, May 22, June 5, and June 19. Total percent of habitat sampled including 2016 is shown in parenthesis.

Reach	Habitat	Total habitat (m)	Percent sampled	# 100–200-m transects sampled				
				Apr 24	May 8	May 22	Jun 5	Jun 19
Upper	Suitable	20,172	40.6 (77.4)	8	9	11	10	8
Upper	Natural	5,756	31.8 (70.2)	3	2	2	1	3
Upper	Riprap	11,595	38.6 (75.0)	5	5	3	5	5
Middle	Suitable	7,855	37.2 (72.0)	4	4	4	3	3
Middle	Natural	9,366	43.8 (77.8)	6	5	5	6	6
Middle	Riprap	13,224	47.4 (87.0)	7	6	7	7	7
Lower	Suitable	7,888	49.3 (71.9)	5	5	4	5	5
Lower	Natural	12,037	37.9 (75.0)	5	5	6	6	5
Lower	Riprap	12,480	40.5 (76.8)	5	6	6	5	6

standard diet sampling weeks. These transects were randomly chosen from the pool of transects not sampled during the biweekly diet sampling.

Abundance for each mark-recapture event was calculated with the Chapman estimator of the Petersen index (Seber 1982) and converted to absolute density (fish/m) based on the transect shoreline distance. We assumed no differences in catchability between reaches or years. Linear catchability models for each habitat type were derived by regressing absolute density on CPUE. Because the absolute density data had associated error (Rogers et al. 2003; Hansen et al. 2000), we calculated the slope and intercept for each model using Monte Carlo simulations. We first used the absolute abundance estimates and standard deviations from the mark-recapture models to simulate 1,000 normally distributed random values of possible abundances for each event.

These random variables were then used with the corresponding CPUE data to generate 1,000 ordinary least-squares regressions to derive slopes and intercepts. Next, we empirically determined the median and 95% CIs of the parameter estimates by examining the distribution of the estimates. Finally, the derived regressions were used to estimate smallmouth bass abundance and 95% CI's for each transect. We calculated the mean abundance by habitat in each reach during each sampling interval and then expanded the estimates by the total distance of each shoreline habitat in each reach to estimate total abundance as well as the number of bass/rkm.

Dietary analysis

Laboratory methods followed the published protocol reported in Erhardt et al. (2017a) and were consistent with our methods used in 2016 (Erhardt et al. 2017b). In brief, we took wet weights (± 0.001 g) of all bass diet items (identified to the lowest practical taxon) and identified prey fish to species using diagnostic bones (i.e., dentary, cleithrum, opercle; Parrish et al. 2006) when necessary. Size measurements (FL and original weight) of consumed prey fish were measured or back-calculated using regressions from various morphological measurements (Hansel et al. 1988, Vigg et al. 1991, Parrish et al. 2006, Erhardt et al. 2014). We summarized the predominant diet items (percent by weight) of smallmouth bass by sampling interval, habitat, and reach. We also examined the length-frequency distribution of Chinook salmon that were consumed by bass and we identified subyearlings as being <120 mm FL based on our previous work with subyearlings.

Consumption rate and loss

We calculated the consumption rate, *C* (number of Chinook salmon/smallmouth bass/day), in a series of steps similar to Fritts and Pearsons (2004). First, we calculated the original weight of each prey fish at ingestion for each bass by using length-weight regressions (Vigg et al. 1991; Parrish et al. 2006) with the back-calculated length at ingestion described above. These were summed with other diet items (if present) to derive a meal weight (*MW*) for each individual bass (Vigg et al. 1991). We accounted for a 21.3% weight loss (Shields and Carlson 1996) associated with preservation in ethanol for all diet items used in the calculation. Next, we input *MW* into an evacuation rate model of smallmouth bass digestion of salmonids developed by Rogers and Burley (1991) and modified by Fritts and Pearsons (2004) that predicts time (in hours) to 90% evacuation (E_{90}):

$$ET_{90} = (24.542)(MW^{0.29}e^{-0.15T}W^{-0.23})(24),$$

where W is bass weight (g; measured or estimated), and T is temperature. We used the mean daily temperature that was collected from data loggers from each bank near the center of each reach. Finally, we calculated C for each individual bass using the equation presented by Ward et al. (1995):

$$C = n(24/ET_{90}),$$

where n is the number of Chinook salmon found in the bass gut. C was averaged for each transect for all bass examined, including bass with empty stomachs (e.g., $C = 0.000$). Next, we calculated the mean consumption rate for individual habitat types in each reach during each sampling interval. These estimates were multiplied by the corresponding smallmouth bass abundance to determine the daily loss of Chinook salmon to predation. Total loss was then calculated by extrapolating the daily loss by the number of days between sampling intervals (14 d). We applied the abundance regressions and calculated loss for data collected in 2016 and reported in Erhardt et al. (2017b). We also calculated all consumption and loss of sand rollers using the same methods.

Results

Smallmouth bass abundance

Abundance of smallmouth bass ≥150 mm increased throughout the spring. The catchability models showed linear increases in absolute density (smallmouth bass/m) with increasing electrofishing CPUE (smallmouth bass captured/m) for all three habitats (Figure 2). Absolute density, derived from these models, was generally highest in the lower reach (peak density = 774 fish/km of shoreline) and more similar between the middle (peak density = 429 fish/km of shoreline) and upper (peak density = 393 fish/km of shoreline) reaches (Figure 3). Applying the regressions to our 2016 data showed similar results but slightly higher overall bass abundance, especially in the lower reach. Total reservoir-wide abundance of smallmouth bass, after extrapolating the habitat data, ranged from 26,462 to 47,592 during 2017 and from 37,358 to 61,934 during 2016.

Absolute densities of smallmouth bass varied across habitats within each reach (Figure 3). In the upper and middle reaches, densities were generally higher in suitable habitat (albeit only in a few instances), followed by natural habitat, and lowest in riprap habitat. In the lower reach, densities were also highest in suitable habitat, and generally higher in riprap habitat than in natural habitat. The largest percentage of the reservoir-wide smallmouth bass abundance was estimated in suitable habitat (40 to 53% in 2017; 37 to 45% in 2016). Riprap habitat generally

accounted for only a slightly higher amount (26 to 30% in 2017; 25 to 40% in 2016) than natural habitat (22 to 30% in 2017; 21 to 27% in 2016).

Similar to 2016, the size distribution of smallmouth bass were represented by higher proportions of smaller individuals (>200mmTL) in non-suitable habitats (i.e., natural and riprap; Figure 4). This was the case for all sampling intervals except the final sampling event during mid-June. Similar to the trends in abundance, the proportion of smaller individuals increased throughout the spring, which we attribute to fish recruiting to the 150-mm size cutoff and more, smaller fish moving into littoral areas from deeper overwintering habitats (Figure 4).

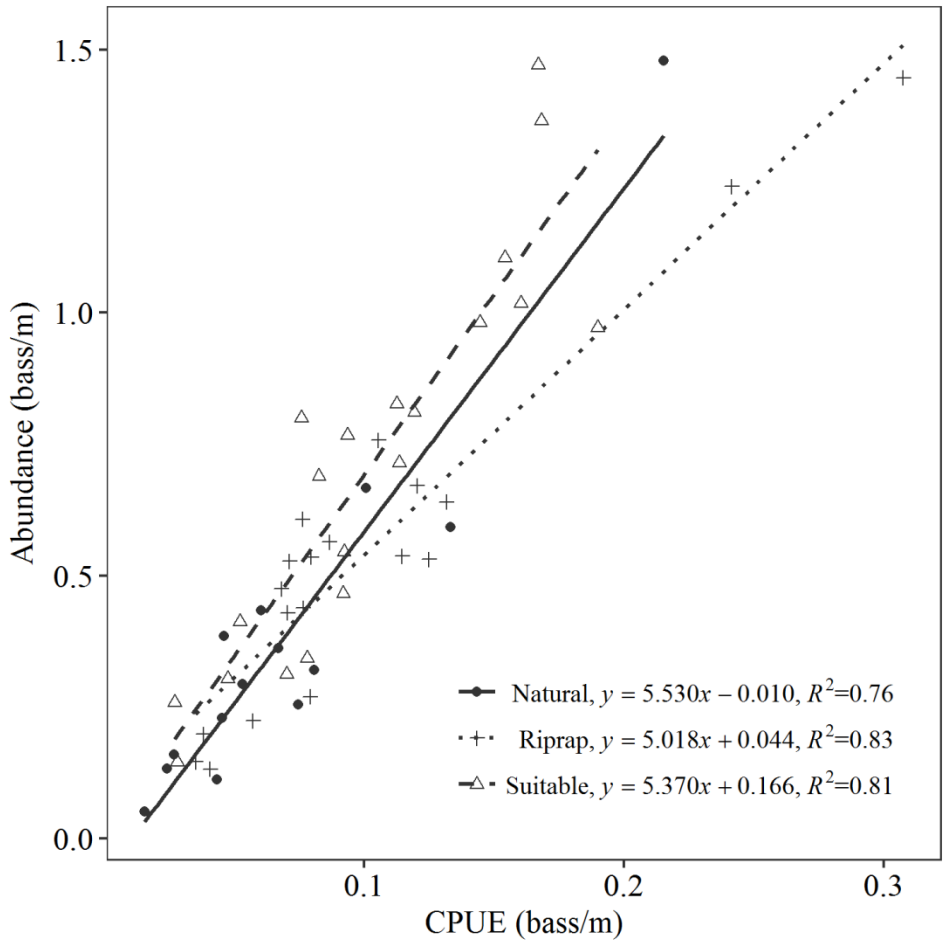

Figure 2. The relationship between electrofishing catch per unit of effort (CPUE= bass/m of shoreline) of smallmouth bass ≥150 mm TL and abundance (bass/m of shoreline) estimated from mark-recapture models in the Snake River.

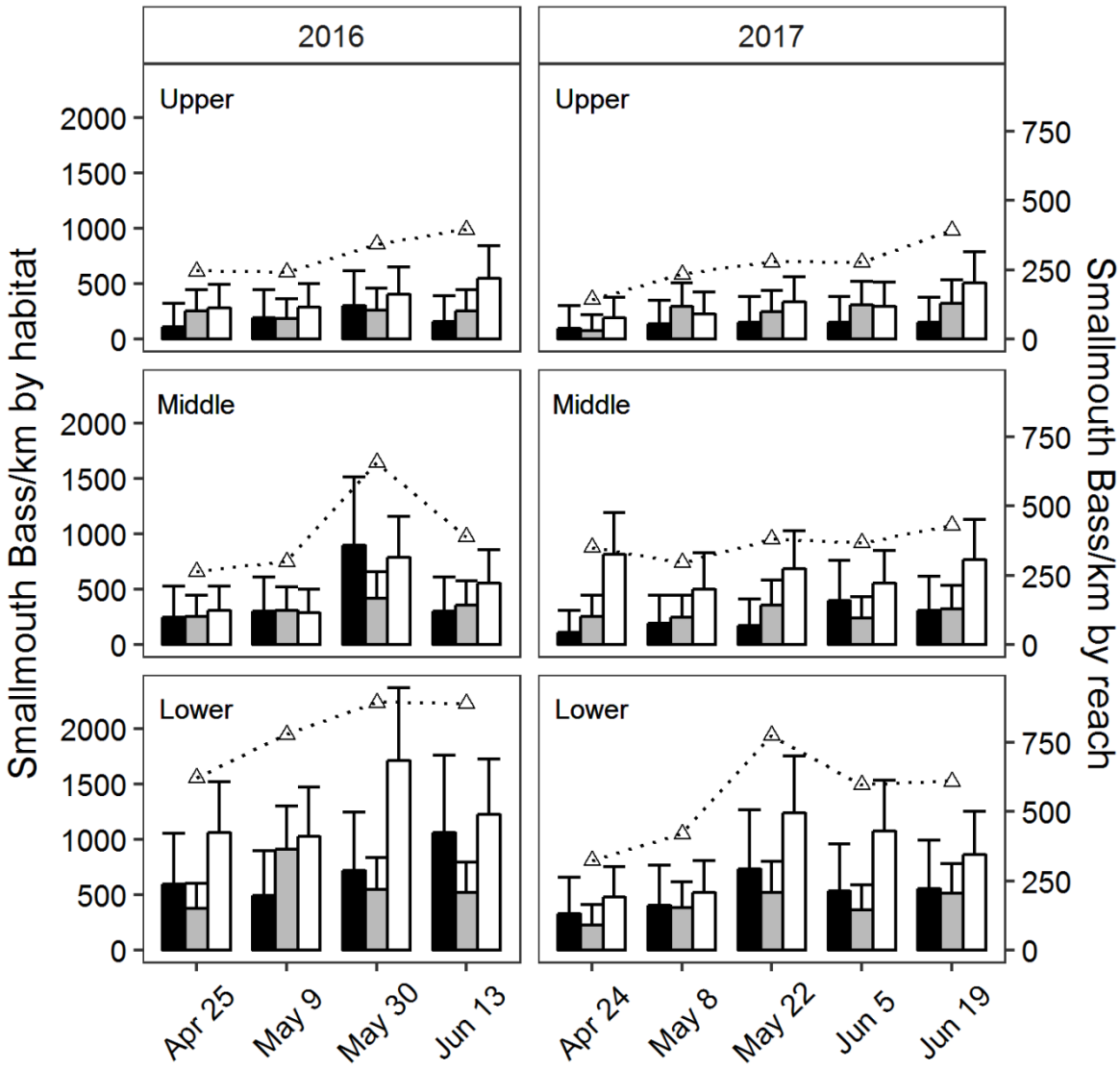

Figure 3. Absolute density (fish/km of shoreline; left axis) of smallmouth bass in three reaches (Upper, Middle, and Lower) of Lower Granite Reservoir estimated from catchability models. Black bars represent "natural" habitat, gray bars represent "riprap" habitat, and white bars represent "suitable" habitat. Error bars were estimated with Montel Carlo simulations using the percentile method. Also shown is the absolute density of smallmouth bass on a reach basis (triangles and dotted lines; right axis) after adjusting for the habitat allocation.

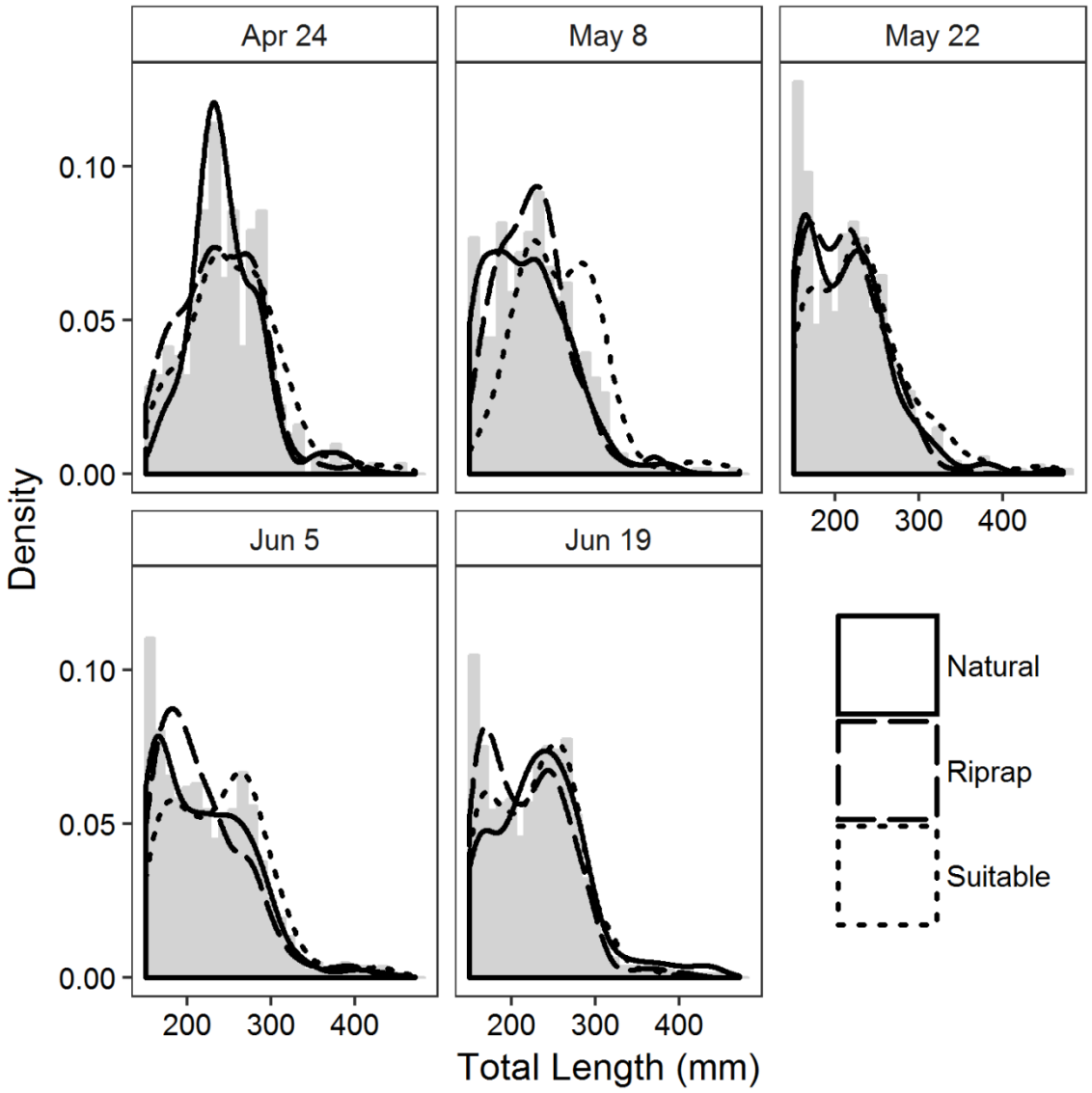

Figure 4. Size distribution of smallmouth bass ≥150 mm TL in Lower Granite Reservoir. Histogram is all data pooled and density plots are for bass in three shoreline habitat types: "natural", "riprap", and "suitable".

Prey abundance

Throughout the study, subyearlings were present in 72% of the transects classified as suitable habitat, 71% of the transects classified as natural habitat, and 71% of the habitat classified as riprap transects sampled (Table 2). In the upper and middle reaches, the catch of subyearlings in suitable habitat (means, 18–25 fish/100m) was similar to the catch in natural (means, 14–28 fish/100 m) and riprap habitat (means, 10–25 fish/100 m; Figure 5, Table 2). In the lower reach, subyearling catch was also similar across habitats (means, 6–7 fish/100 m), but about 2–4 times lower than in the other reaches. The maximum numbers of subyearlings observed in suitable habitat were 133 fish/100 m in the upper reach, 140 fish/100 m in the middle reach, and 22 fish/100 m in the lower reach (Table 2). The maximum numbers of subyearlings in natural (261fish/100 m) and riprap (7 fish/197 m) habitats were observed in the middle reach.

Sand rollers were present in 67% of transects classified as suitable habitat, 69% of transects classified as natural habitat, and 52% of transects classified as riprap (Table 2). The mean catch of sand rollers in the upper reach was highest in natural habitat (76 fish/100 m), followed by suitable habitat (40 fish/100 m) and riprap (23 fish/100 m; Figure 5, Table 2). In the middle reach, sand roller catch was substantially higher in suitable (105 fish/100 m) and natural (41 fish/100 m) habitat than in riprap (3 fish/100 m). Few sand rollers were observed in any habitat in the lower reach. The maximum numbers of sand rollers observed was 669 fish/100 m in suitable habitat in the middle reach (Table 2).

Diet

Smallmouth bass ate mainly fish and crustaceans, and the percentages in their diets varied by reach, habitat type, and sampling week (Figure 6). Length-frequency data suggested that most Chinook salmon consumed were subyearlings (Figure 7). The percentages of subyearlings in bass diets were highest during late April in suitable habitat of all three reaches (38–66%) and in riprap habitats in the upper and middle reaches (64–78; Figure 6). The only other time period where subyearlings constituted a significant portion of diet by weight was during early May in natural (28%) and suitable (28%) habitats of the lower reach. Subyearlings constituted a small portion of diet (<10%) in all remaining time intervals.

Sand rollers were most prominent in the diets of smallmouth bass in the upper reach during most time intervals (Figure 6). Generally, sand rollers were not prevalent (>25%) in the diets of bass in the middle and lower reaches with the exception of bass sampled in natural (61%) and suitable (37%) habitat in the middle reach during early May. Sand rollers only composed up to 11% of the diet by weight in suitable habitat in the lower reach during early May. The most prominent diet items in the middle and lower reach (and by weight overall) were crustaceans, which largely comprised signal crayfish (by weight) and the opossum shrimp *Neomysis mercedis* (by count). Other prey fish were only found to represent a significant portion of bass diets on a few occasions, mainly in late April. Other prey fish consumed were

Table 2. Summary of catch of subyearling fall Chinook salmon and sand rollers by reach and habitat type in Lower Granite Reservoir, 2017.

		Subyearlings				Sand rollers			
Reach	Habitat	Number of transects with 0 catch	Number of transects with >0 catch	Catch (mean±SD, fish/100 m)	Catch (range, fish/100 m)	Number of transects with 0 catch	Number of transects with >0 catch	Catch (mean±SD, fish/100 m)	Catch (range, fish/100 m)
Upper	Suitable	10	36	25±36	1–133	8	38	40±67	1–294
	Natural	5	6	14±24	1–63	2	9	76±154	1–449
	Riprap	8	15	10±12	1–39	3	20	23±26	1–112
Middle	Suitable	7	22	18±29	2–140	8	21	105±183	1–669
	Natural	4	30	28±59	1–261	7	27	41±69	1–282
	Riprap	8	31	25±40	1–197	15	24	3±4	1–14
Lower	Suitable	11	13	6±7	1–22	17	7	4±3	1–10
	Natural	14	21	6±3	1–13	16	19	4±4	1–15
	Riprap	11	20	7±7	1–24	27	4	1±0	1

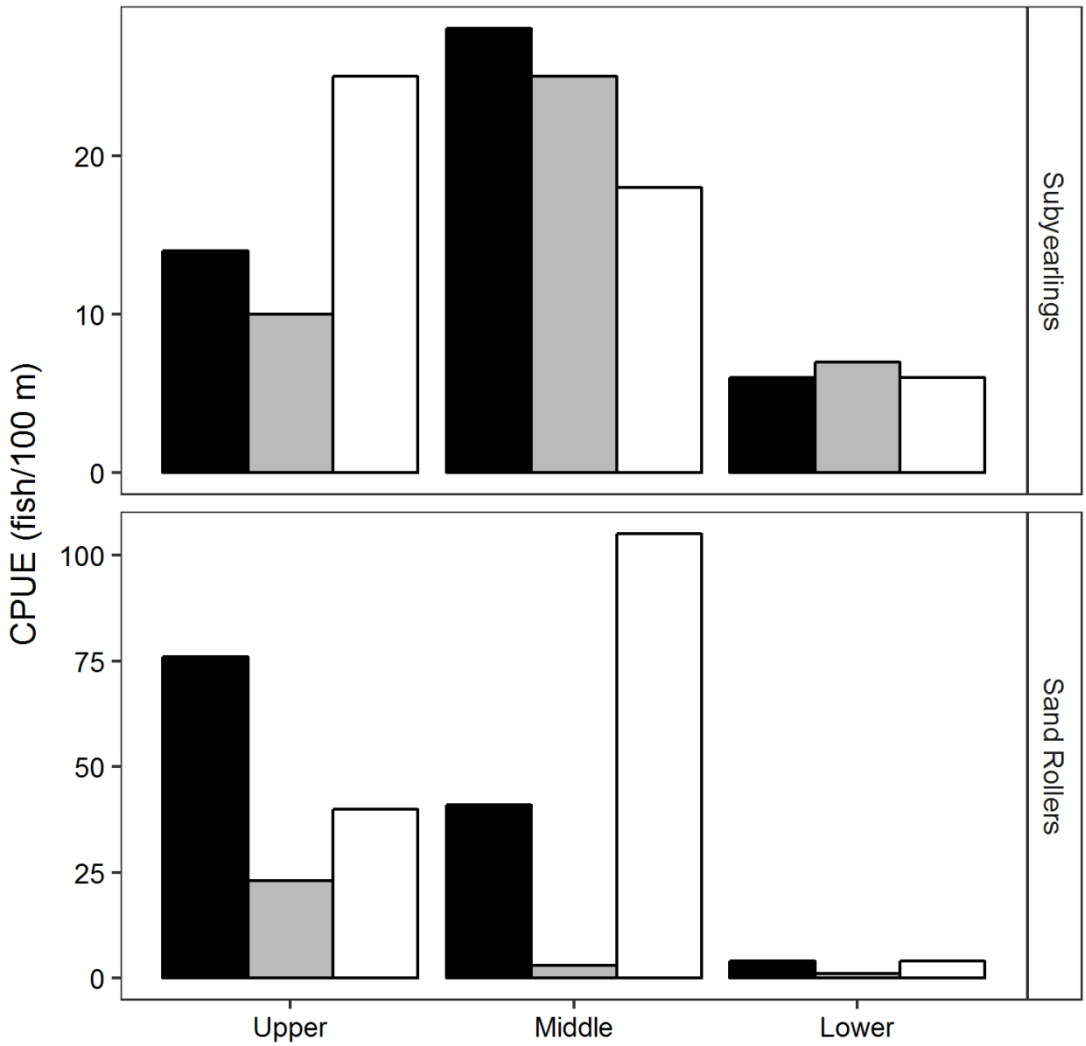

Figure 5. Mean CPUEs of subyearling Chinook salmon (top panel) and sand rollers (bottom panel) in electrofishing transects that contained fish in different reaches in Lower Granite Reservoir, 2017. Black bars represent "natural" habitat, gray bars represent "riprap" habitat, and white bars represent "suitable" habitat.

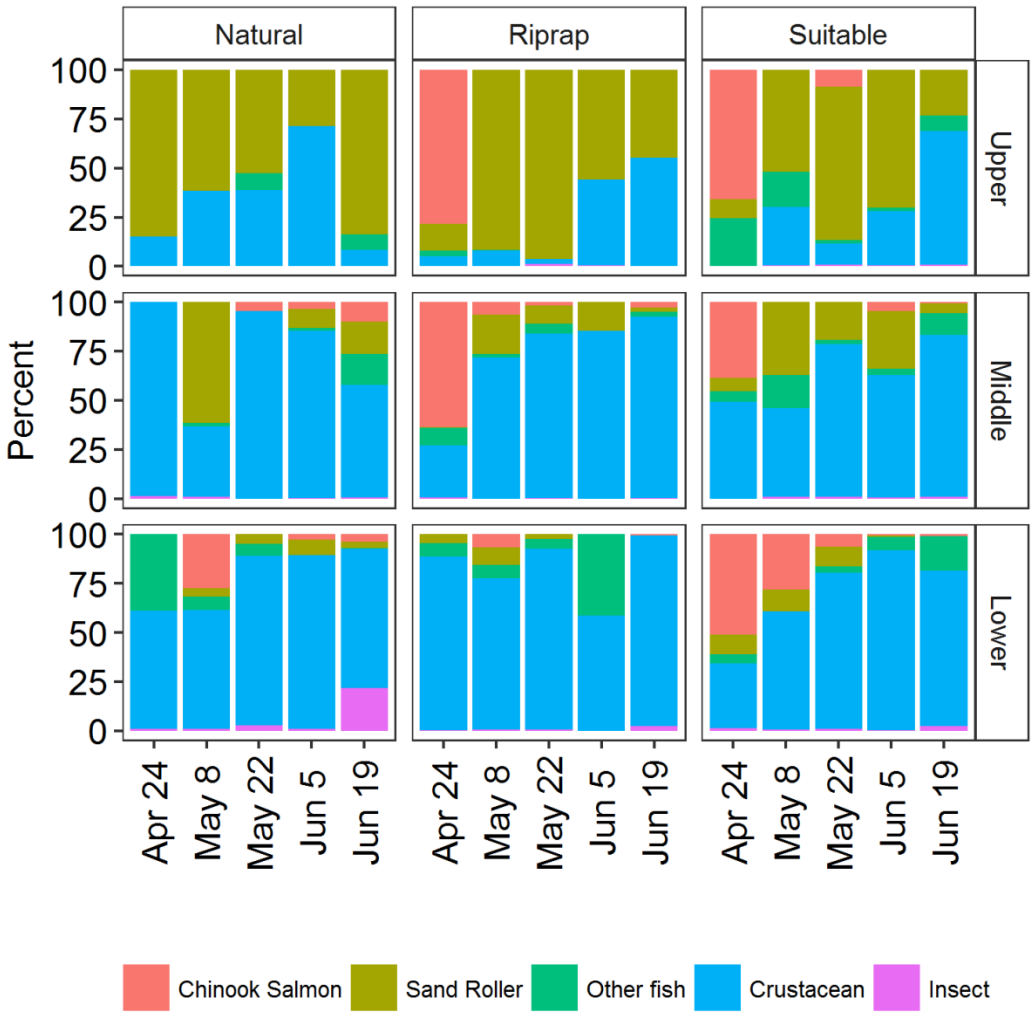

Figure 6. Percent diet by weight of smallmouth bass ≥150 mm TL from three reaches (Upper, Middle, Lower) and three habitats (Natural, Riprap, Suitable) in Lower Granite Reservoir.

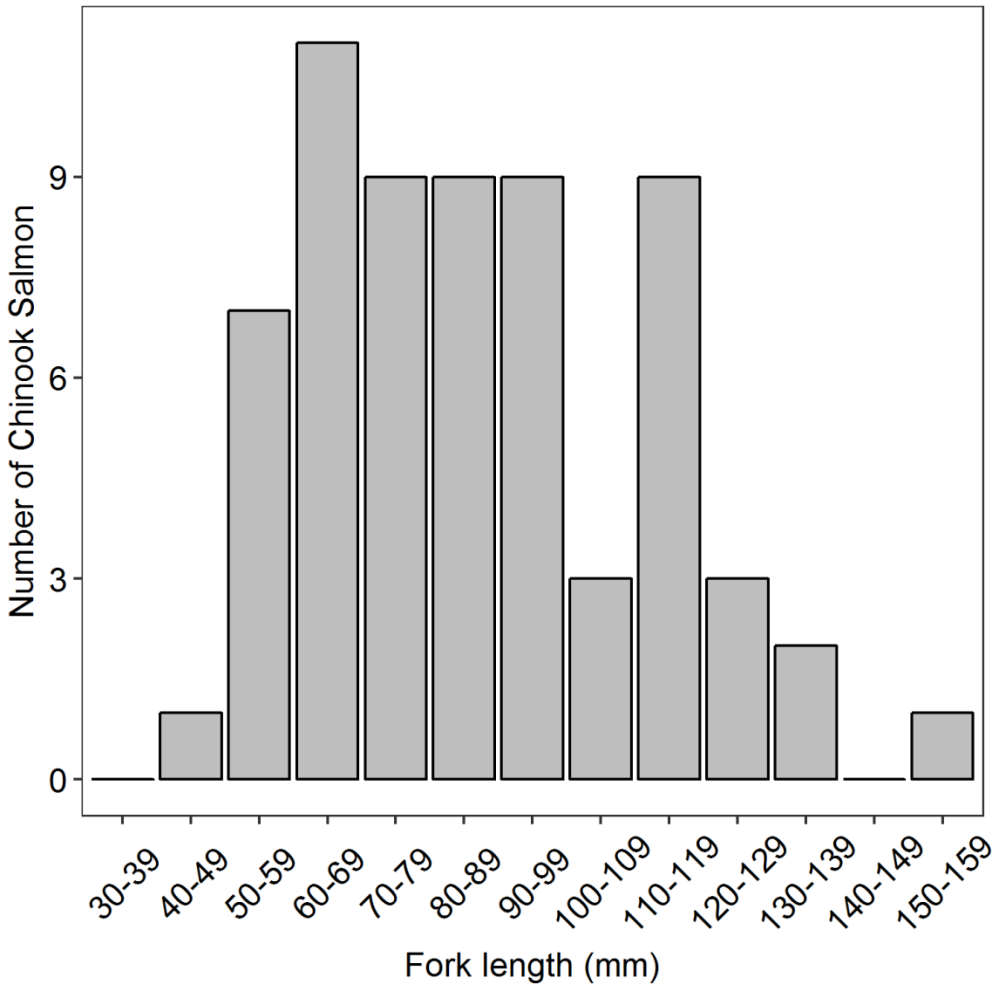

Figure 7. Length-frequency distribution of Chinook salmon consumed by smallmouth bass in Lower Granite Reservoir during 2017.

smallmouth bass (*n*=11), mountain whitefish *Prosopium williamsoni* (*n*=6), pumpkinseed *Lepomis gibbosus* (*n*=4), black crappie *Pomoxis nigromaculatus* (*n*=4), largemouth bass *Micropterus salmoides* (*n*=4), sucker spp. (*n*=4), sculpin spp. (*n*=3), bluegill *Lepomis macrochirus* (*n*=4), peamouth *Mylocheilus caurinus* (*n*=2), and steelhead *Oncorhynchus mykiss* (*n*=2).

Consumption

Smallmouth bass consumption (*C*) of subyearlings was much lower in 2017 than in 2016 (Figure 8). Peak consumption occurred in the upper reach during late April in riprap (C = 0.202) and suitable (C = 0.147) habitats. The only other time subyearlings were consumed in the upper reach was during mid-May (C = 0.034). In the middle reach, consumption was also highest in riprap habitat during late April (C = 0.112); however, subyearlings were consumed during all other time intervals but to a lesser extent (range: 0.009– 0.062). Subyearlings were also consumed during all time intervals and to a lesser extent in the lower reach (range: 0.003–0.070).

Smallmouth bass consumption (*C*) of sand rollers in 2017 was similar to 2016. Consumption was highest in upper reach during all weeks and habitats, and ranged from 0.062 to 0.399 fish/bass/d (Figure 9). Bass consumption of sand rollers decreased from the upper to lower reservoir and generally increased seasonally within each reach. In the middle reach, consumption ranged from 0.004 to 0.194 fish/bass/d. Consumption of sand rollers was comparatively low in the lower reach in all habitats and weeks and never exceeded 0.040 fish/bass/d.

Total Predation Loss

We estimated a total of 312,315 Chinook salmon were consumed during our 2-year study in Lower Granite Reservoir. There were large annual differences, however, as loss in 2016 was about five times higher than in 2017 (Table 3). We estimated a total of 261,704 Chinook salmon were consumed in 2016, with a majority (44%) being consumed in the lower reach. Across reaches, a majority of the loss occurred in natural habitat (42%) followed by suitable habitat (34%). In terms of habitat and reach, the highest loss occurred in natural habitat in the lower reach (26%). During 2017, we only estimated 50,611subyearlings were lost but a majority of the loss (41%) also came from the lower reach. Within the lower reach, a majority of the loss occurred in suitable habitat (56%).

We estimated a total of 522,725 sand rollers were consumed during our 2-year study in Lower Granite Reservoir. We estimated a total of 297,317 sand rollers were consumed in 2016, with a majority (57%) being consumed in the upper reach (Table 4). Across habitats, a majority of the loss occurred in suitable habitat (67%). Estimates were similar during 2017, where a

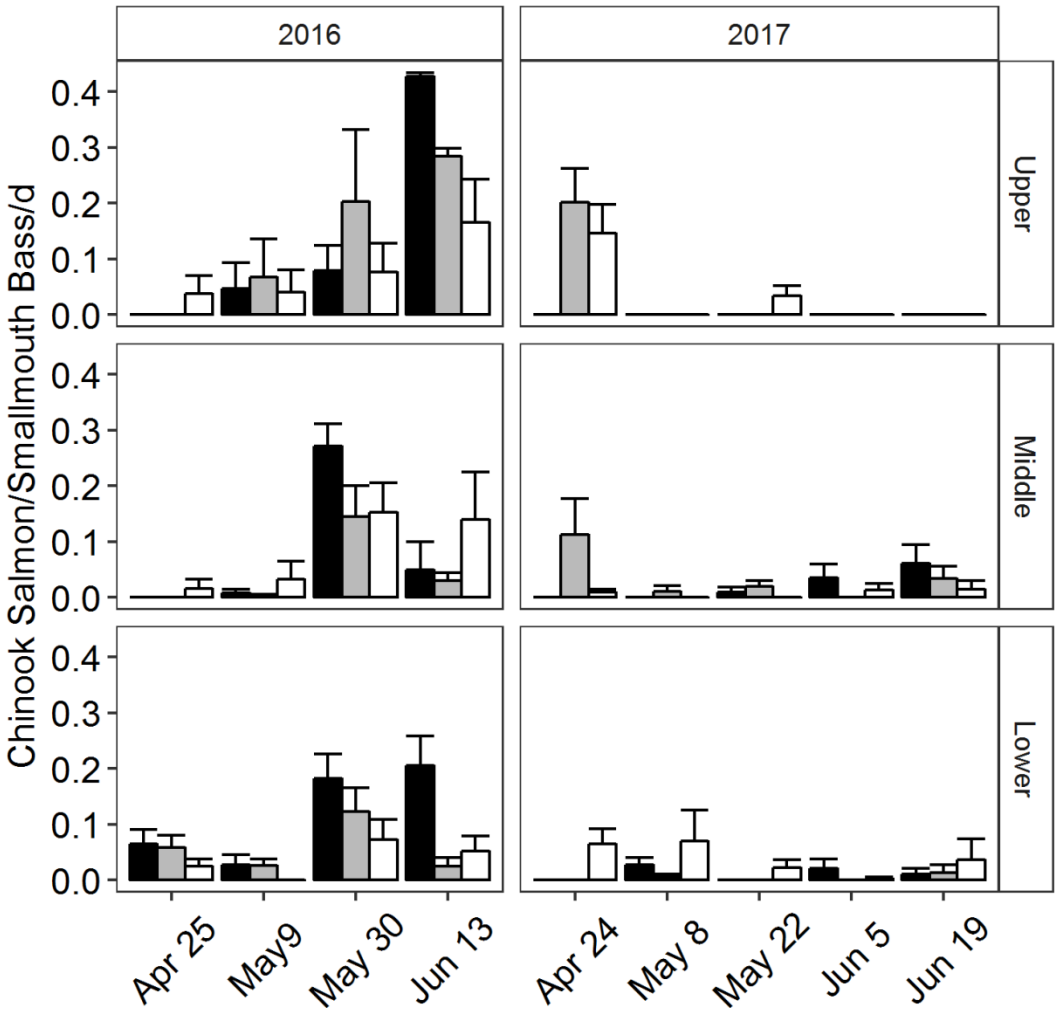

Figure 8. Mean+SE consumption rate (Chinook salmon/smallmouth bass/d) of Chinook salmon by smallmouth bass ≥150mm TL in three reaches (Upper, Middle, Lower) of Lower Granite Reservoir. Black bars represent "natural" habitat, gray bars represent "riprap" habitat, and white bars represent "suitable" habitat.

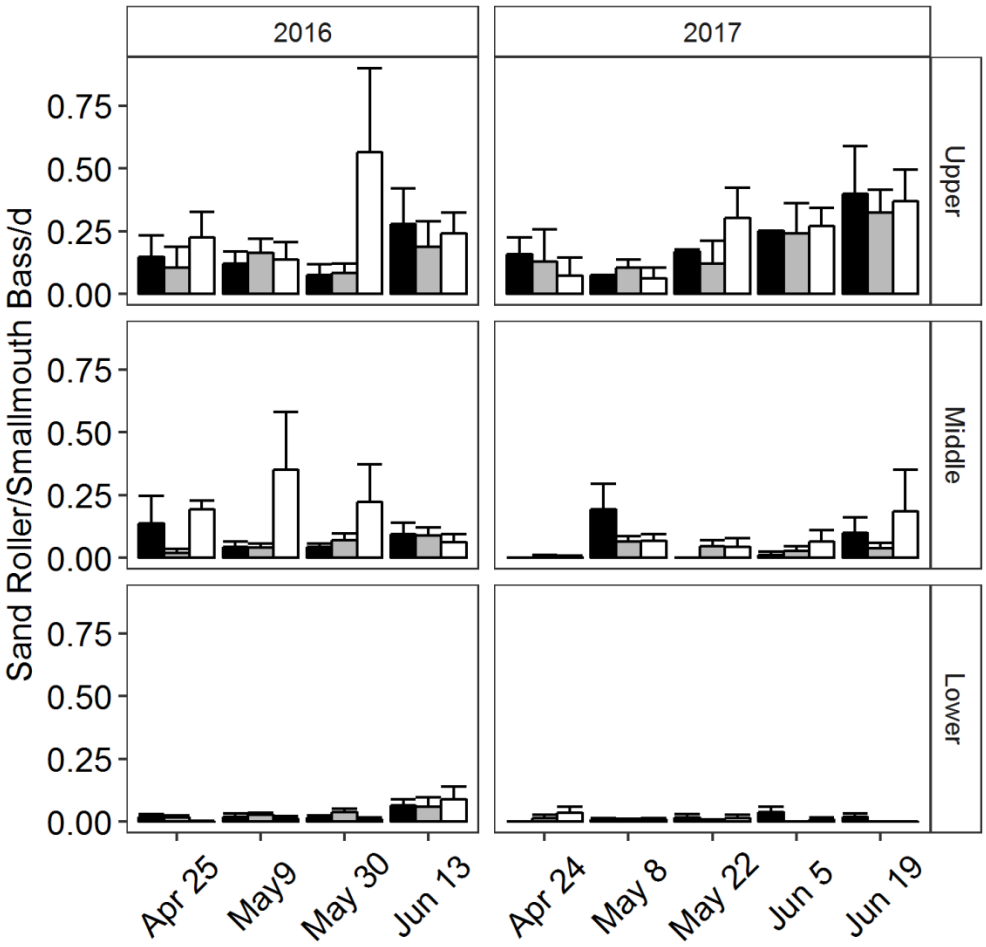

Figure 9. Mean+SE consumption rate (sand roller/smallmouth bass/d) of sand rollers by smallmouth bass ≥150mm TL in three reaches (Upper, Middle, Lower) of Lower Granite Reservoir. Black bars represent "natural" habitat, gray bars represent "riprap" habitat, and white bars represent "suitable" habitat.

Table 3. Total number of Chinook salmon consumed by smallmouth bass ≥150mm TL in three reaches and three shoreline habitat types of Lower Granite Reservoir during the springs of 2016 and 2017.

Reach	Habitat			Total
	Suitable	Natural	Riprap	
		2017		
Upper	11,219	0	2,483	13,702
Middle	2,842	4,507	8,925	16,274
Lower	14,306	4,683	1,646	20,635
Total	28,367	9,190	13,054	50,611
		2016		
Upper	42,367	8,285	23,174	73,826
Middle	23,796	34,303	13,352	71,451
Lower	23,764	68,544	24,118	116,426
Total	89,927	111,132	60,645	261,704

Table 4. Total number of sand rollers consumed by smallmouth bass ≥150mm TL in three reaches and three shoreline habitat types of Lower Granite Reservoir during the springs of 2016 and 2017.

Reach	Habitat			Total
	Suitable	Natural	Riprap	
		2017		
Upper	111,808	12,052	40,395	164,255
Middle	26,999	9,512	9,832	46,343
Lower	5,349	8,119	1,342	14,810
Total	144,155	29,683	51,569	225,408
		2016		
Upper	136,594	9,376	22,859	168,828
Middle	46,071	15,784	15,815	77,670
Lower	15,764	18,328	16,727	50,819
Total	198,428	43,488	55,401	297,317

majority (73%) of the loss of 225,408 sand rollers also occurred in the upper reach. Across habitats, a majority of the loss in 2017 also occurred in suitable habitat (64%).

Discussion

Subyearling losses to smallmouth bass predation were substantially lower in 2017 than in 2016. This can be largely explained by the lower consumption rates estimated in 2017, as well as lower bass abundance. We believe the lower consumption rate was a result of substantially higher water discharge and turbidity in 2017 compared to 2016 (Figure 10). High turbidity levels can reduce smallmouth bass foraging success (Sweka and Hartman 2003; Carter et al. 2010) and make it easier of Chinook salmon to avoid predators (Gregory 1993). Interestingly, there did not seem to be a large difference in the consumption of sand rollers between the years. Sand rollers, which have re-emerged in the upper reaches of Lower Granite Reservoir (Tiffan et al. 2017), may be easy prey for smallmouth bass regardless of turbidity or water velocity. In addition, the proportion of crayfish in bass diets was higher in 2017, suggesting that they may be more easily captured than more mobile prey fish in turbid water. In general, bass had lower meal weights in 2017, which could also reflect lower foraging success in turbid water. With two years of data collected from a relatively low water year (2016) and a high water year (2017), further sampling at other levels of discharge and turbidities would be beneficial.

The spatial and temporal variability in smallmouth bass and prey densities illustrate the complexities associated with assessing the impacts of predation on Chinook salmon in Lower Granite Reservoir. Stratifying by habitat based on subyearling rearing habitat 'suitability' allowed us to increase the precision of our estimates and identify different areas of predation vulnerability (i.e., high bass abundances) and areas of high consumption and loss. We found a significant number of Chinook salmon (312,315 fish) were lost in our 42-km reservoir study area to predation during the 2-year study, but there was large annual variation in the estimates (2016= 6,231 Chinook Salmon/rkm, 2017= 1,205 Chinook Salmon/rkm). We integrated the results of Erhardt et al. (2017a) with our data from 2016 and 2017 to identify the magnitude of predation losses along the spatial continuum within the reservoir. Predation losses increased from the transitional habitats above the Clearwater River (~3,512 fish/rkm; SRTZ reach from Erhardt et al. [2017a]) to the transitional confluence of the Clearwater River (~8,426 fish/rkm; CON reach from Erhardt et al. [2017a]), decreased in the upper reservoir areas that are composed mainly of suitable habitat (~3,126 fish/rkm), remained relatively stable in mid-reservoir areas that are more dominated by riprap shorelines (~3,133 fish/rkm), then increased again in the lower reservoir (~4,895 fish/rkm) habitats which are mainly unsuitable natural and riprap. This pattern supports the hypotheses that the CON reach in the Erhardt et al. (2017a) study is a predation bottleneck,

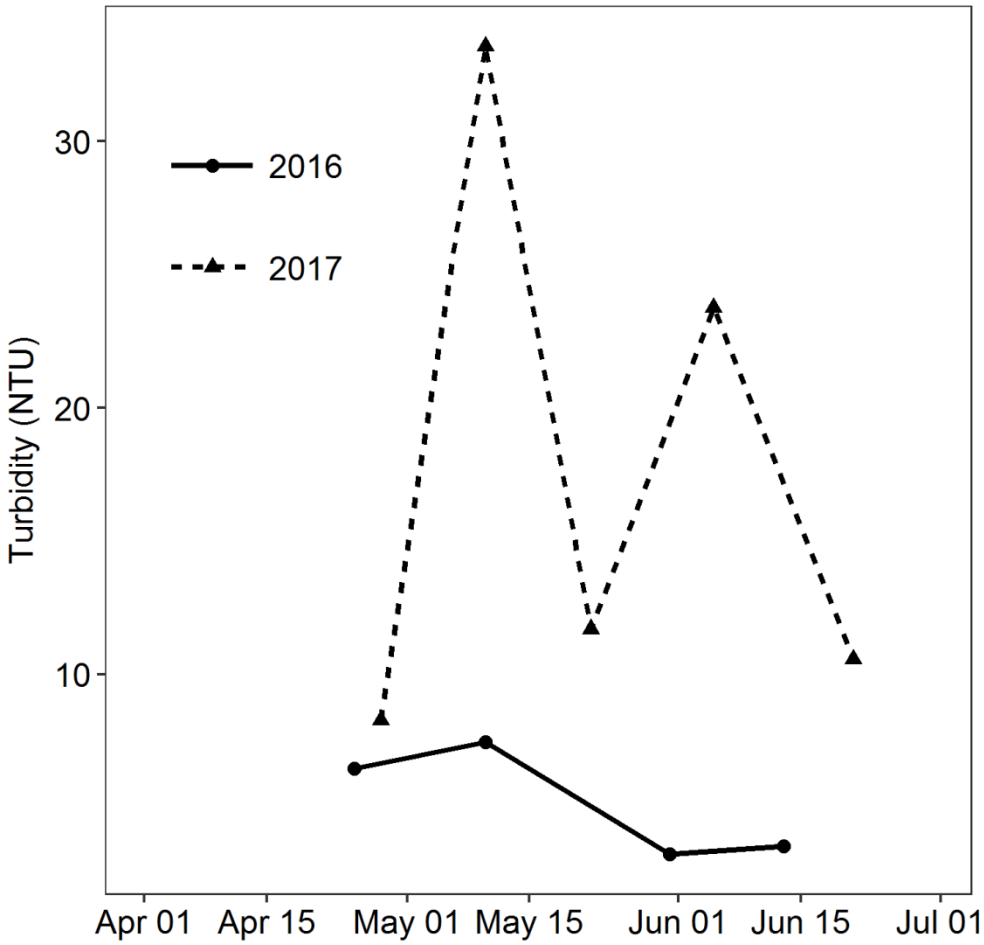

Figure 10. Mean turbidity (NTU) from smallmouth bass sampling locations in Lower Granite Reservoir.

and that consumption of subyearlings may be associated with habitat-related predation vulnerability.

The downstream pattern in total loss of Chinook salmon correlates with the distribution of smallmouth bass throughout the reservoir. Synthesizing our abundance data using methods similar to those for estimating loss along with those of Erhardt et al. (2017a) depicts a similar pattern. Mean spring bass abundance increased from the SRTZ (3,512 bass/rkm) to the CON (8,426 bass/rkm), decreased in the upper reservoir (3,126 bass/rkm), stayed relatively stable in the middle reservoir (3,133 bass/rkm), and then increased in the lower reservoir (4,895 bass/rkm). Erhardt et al. (2017a) reported slightly lower bass abundance in the upper reservoir compared to a similar study by Naughton et al. (2004) conducted during the 1990's. We found that bass abundance has increased near the dam since the Naughton et al. (2004) study. In that study, they estimated 1,294 smallmouth bass ≥175mm TL were in the 6-rkm forebay (or 216 bass/rkm). By comparison, we extrapolated our lower reach absolute density estimates of similar-sized bass to the 6-rkm forebay resulting in 9,631 bass (1,605 bass/rkm), which is a 7.4-fold increase in bass abundance since the 1990's. Our mean total bass abundance in the reservoir equated to 872 bass/rkm (after removing the portion of 150–174 mm bass), which is also higher than that reported by Anglea (1997; 395 bass/rkm) for their 53-rkm study area that included the CON reach.

The variation in smallmouth bass abundance by reach that we observed may be related to the type and availability of habitat preferred by bass. The lower reach of the reservoir contained more riprap and natural habitat, which was characterized by steeper lateral bed slopes and larger substrates (Tiffan et al. 2016a) that smallmouth bass prefer (Munther 1970; Todd and Rabeni 1989). This may explain their greater abundance in that part of the reservoir. In contrast, the upper reach contains the most shallow-water habitat and fine substrates and may explain the lower bass abundance there (Tiffan et al. 2016a).

Habitat differences within the reservoir may explain some of the patterns we observed in smallmouth bass consumption and loss of subyearlings during 2016; however, during 2017 patterns were difficult to discern given the drastically lower estimates of consumption. High velocities and turbidities may have influenced habitat preference and influenced our ability to successfully estimate prey abundance. This was especially evident in the upper reaches where consumption was very low and highly variable. During 2017, a majority of the loss (28%) occurred in suitable habitat of the lower reach. Habitat suitable for subyearling rearing is much reduced in the middle and lower reaches compared to the upper reservoir (Tiffan et al. 2016a). This is because these reaches lack the shallow-water habitat with low lateral bed slopes that subyearlings prefer (Tiffan et al. 2006); however, smallmouth bass also use this type of habitat for spawning. The general lack of suitable habitat that bass use for spawning coupled with greater bass abundance in the lower reservoir may explain the higher predation loss of subyearlings in that part of the reservoir where both prey and predators were concentrated.

Conversely, subyearlings may have suffered less predation in suitable habitat in the upper reach because there was more habitat area to use and fewer bass.

The proportions of hatchery- and natural-origin subyearlings consumed by, and available to, smallmouth bass during sampling probably varied between the two years which could also explain annual differences in loss estimates and subyearling abundance. Smallmouth bass may increase their consumption of subyearlings directly following hatchery releases, as was documented in the lower free-flowing sections of Hells Canyon (Connor et al. 2017). Our sampling in late April and early May occurred before the release of hatchery subyearlings from upriver release sites. Thus, the subyearlings consumed during those sampling weeks were likely of natural origin. By late May, over 2 million hatchery subyearlings had been released above our study area and many of the consumed fish were probably of hatchery origin, although natural-origin fish were likely consumed as well. Future research may allow us to partition consumed subyearlings into hatchery and natural origin with greater certainty.

Sand rollers were prominent in smallmouth bass diets in the upper reach of our study area. The greater bass consumption of sand rollers in the upper reach of the reservoir may be related to their greater abundance there as they use shallow habitats for spawning (Tiffan et al. 2017). We also found a greater diversity and higher percentages of other prey fish (mostly centrarchids) in smallmouth bass diets in our study area compared to upriver transitional habitats. As hypothesized by Tiffan et al. (2016b), nonsalmonid prey fish may be helping to relieve predation pressure on subyearlings fall Chinook salmon in Lower Granite Reservoir.

References

Anglea, S. M. 1997. Food habits, abundance, and salmonid fish consumption of smallmouth bass and distribution of crayfish in Lower Granite Reservoir, Idaho-Washington. Master's thesis. University of Idaho, Moscow.

Beamesderfer, R. C., and B. E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:439–447.

Bruton, M. N. 1985. The effects of suspensoids on fish. Hydrobiologia 125:221–241.

Carter, M. W., D. E. Shoup, J. M. Deters, and D. H. Wahl. 2010. Effects of turbidity and cover on prey selectivity of adult smallmouth bass. Transactions of the American Fisheries Society 139:353–361.

Connor, W. P., K. F. Tiffan, J. M. Plumb, and C. M. Moffitt. 2013. Evidence for density-dependent changes in growth, downstream movement, and size of Chinook salmon subyearlings in a large-river landscape. Transactions of the American Fisheries Society 142:1453–1468.

Connor, W. P., F. L. Mullins, K. F. Tiffan, J. M. Plumb, R. W. Perry, J. M. Erhardt, R. J. Heminway, B. K. Bickford, and T. N. Rhodes. 2017. Research, Monitoring, and Evaluation of Emerging Issues and Measures to Recover the Snake River Fall Chinook Salmon ESU. 2016 Annual Report to Bonneville Power. Project 199102900, Portland, Oregon

Curet, T. S. 1993. Habitat use, food habits and the influence of predation on subyearling Chinook Salmon in Lower Granite and Little Goose reservoirs, Washington. Master's thesis. University of Idaho, Moscow.

Erhardt, J. M., S. J. St. John, B. K. Bickford, T. N. Rhodes, and K. F. Tiffan. 2014. Smallmouth bass predation on juvenile fall Chinook salmon in Lower Granite Reservoir on the Snake River. Pages 27–60 *in* K. F. Tiffan , W. P. Connor, B. J. Bellgraph, and P. M. Chittaro, editors. Snake River Fall Chinook Salmon Life History Investigations. 2012 Annual Report to the Bonneville Power Administration, Project 2002-032-00, Portland, Oregon.

Erhardt, J. M., K. F. Tiffan, and W. P. Connor. 2017a. Juvenile Chinook salmon mortality in a Snake River Reservoir: smallmouth bass predation revisited. Transactions of the American Fisheries Society. DOI:10.1002/tafs.10026.

Erhardt, J. M., B. K. Bickford, R. J. Hemingway, T. N. Rhodes, and K. F. Tiffan. 2017b. Snake River Fall Chinook Salmon Life History Investigation. 2016. Annual Report to the Bonneville Power Administration, Project 200203200, Portland, Oregon.

Fritts, A.L., and T.N. Pearsons. 2004. Smallmouth bass predation on hatchery and wild salmonids in the Yakima River, Washington. Transactions of the American Fisheries Society 133:880–895.

Garland, R.D., K.F. Tiffan, D.W. Rondorf, and L.O. Clark. 2002. Comparison of subyearling fall Chinook salmon's use of riprap revetments and unaltered habitats in Lake Wallula of the Columbia River. North American Journal of Fisheries Management 22:583–589.

Gregory, R. S. 1993. Effects of turbidity on the predator avoidance behavior of juvenile Chinook salmon (*Oncorhynchus tschawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 50:241–246.

Hansel, H.C., S.D. Duke, P.T. Lofy, and G.A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of American Fisheries Society 117:55–62.

Hansen, M. J., T. D. Beard Jr., and S. W. Hewett. 2000. Catch rates and catchability of walleyes in angling and spearing fisheries in northern Wisconsin lakes. North American Journal of Fisheries Management 20:109–118.

Munther, G.L. 1970. Movement and distribution of smallmouth bass in the middle Snake River. Transactions of the American Fisheries Society 99: 44–53.

NMFS (National Marine Fisheries Service). 1992. Threatened status for Snake River spring/summer Chinook salmon, threatened status for Snake River fall Chinook salmon. Federal Register 57:78(22 April 1992):14,653–14,663.

Naughton, G.P., D.H. Bennett, and K.B. Newman. 2004. Predation on juvenile salmonids by smallmouth bass in the Lower Granite Reservoir system, Snake River. North American Journal of Fisheries Management 24:534–544.

Parrish, J. K., K. Haapa-aho, W. Walker, M. Stratton, J. Walsh, and H. Ziel. 2006. Small-bodied and juvenile fishes of the mid-Columbia region including keys to diagnostic otoliths and cranial bones. University of Washington, Seattle.

Petersen J.H. 1994. Importance of spatial pattern in estimating predation on juvenile salmonids in the Columbia River. Transactions of the American Fisheries Society 123:924–930.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Predergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:405–420.

Rieman, B.E., R.C. Beamsderfer, S. Vigg, and T.P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448–458.

Rogers, J.B., and C.C. Burley. 1991. A sigmoid model to predict gastric evacuation rates of smallmouth bass (*Micropterus dolomieu*) fed juvenile salmon. Canadian Journal of Fisheries and Aquatic Sciences 48:933–937.

Rogers, M. W., M. J. Hansen, and T. D. Beard Jr. 2003. Catchability of walleye to fyke netting and electrofishing in norther Wisconsin lakes. North American Journal of Fisheries Management 23:1193–1206.

Scheaffer, R. L., W. Mendenhall III, and R. L. Ott. 1996. Elementary survey sampling. 5th edition. Duxbury Press, Belmont California.

Seaburg, K.G. 1957. A stomach sampler for live fish. The Progressive Fish Culturist 19:137–139.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Edward Arnold, London.

Shields, P.A., and S.R. Carlson. 1996. Effects of formalin and alcohol preservation of lengths and weights of juvenile sockeye salmon. Alaska Fishery Research Bulletin 3(2):81–93.

Sweka, J. A., and K. J. Hartman. 2003. Reduction of reactive distance and foraging success in smallmouth bass, *Micropterus dolomieu*, exposed to elevated turbidity levels. Environmental Biology of Fishes 67:341–347.

Tabor, R.A., R.S. Shively, and T.P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. North American Journal of Fisheries Management 13:831–838.

Tiffan, K.F., L.O. Clark, R.D. Garland, and D.W. Rondorf. 2006. Variables influencing the presence of subyearling fall Chinook salmon in shoreline habitats of the Hanford Reach, Columbia River. North American Journal of Fisheries Management 26:351–360.

Tiffan, K. F., T. J. Kock, C. A. Haskell, W. P. Connor, and R. K. Steinhorst. 2009. Water velocity, turbulence, and migration rate of subyearling fall Chinook salmon in the free-flowing and impounded Snake River. Transactions of the American Fisheries Society 138:373–384

Tiffan, K.F., W.P. Connor, B.J. Bellgraph, and R.A. Buchanan, editors. 2010. Snake River fall Chinook salmon life history investigation. 2009. Annual Report to the Bonneville Power Administration, Project 200203200, Portland, Oregon.

Tiffan, K.F., J.R. Hatten, and D.A. Trachtenbarg. 2016a. Assessing juvenile salmon rearing habitat and associated predation risk in a lower Snake River Reservoir. River Research and Applications 32:1030–1038.

Tiffan, K.F., W.P. Connor, P. Chittaro, and B. Kennedy. 2016b. Snake River Fall Chinook Salmon Life History Investigations. 2014-15 Annual Report to the Bonneville Power Administration, Project 200203200, Portland, Oregon.

Tiffan, K. F., J. M. Erhardt, T. N. Rhodes, and R. J. Heminway. 2017. Ecology of the sand roller (*Percopsis transmontana*) in a lower Snake River Reservoir, Washington. Northwestern Naturalist 98:203–214

Todd, B.L., and C.F. Rabeni. 1989. Movement and habitat use by stream-dwelling smallmouth bass. Transactions of the American Fisheries Society 118:229–242.

Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternate prey fish by northern squawfish, walleyes, Smallmouth Bass, and channel catfish in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:421–438.

Ward, D. L., J.H. Petersen, and J.L. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. Transactions of the American Fisheries Society 124:321–334.

Zimmerman, M.P., and R.M. Parker. 1995. Relative density and distribution of Smallmouth Bass, Channel Catfish, and Walleye in the lower Columbia and Snake rivers. Northwest Science 69:19–28.

CHAPTER TWO

What did you say about my mother? The complexities of maternally derived chemical signatures in otoliths

Jens C. Hegg and Brian P. Kennedy

University of Idaho
Department of Fish and Wildlife Resources
975 West 6th Street
Moscow, ID 93844

and

Paul M. Chittaro

National Oceanic and Atmospheric Administration
Northwest Fisheries Science Center
2725 Montlake Boulevard East
Seattle, WA 98112

Introduction

In many fish species migration is a facultative strategy, often encompassing various degrees of partial migration (Tsukamoto and Arai 2001, Secor and Kerr 2009, Chapman et al. 2011, Brodersen et al. 2014). Even within species and populations that are generally considered to be obligately migratory, the timing of migratory movements can be quite diverse (Isaak et al. 2003, Burke 2004, Hegg et al. 2015a). In many cases life-history characteristics such as growth rate and propensity to migrate are heritable, and understanding their expression in the context of fitness necessitates linking parent and progeny (Stewart et al. 2006, Thériault et al. 2007, Liberoff et al. 2014, 2015, Waples et al. 2017). Further, maternal effects and conditions early in life can have large effects on adoption of particular strategies by individual fish (Taylor 1990, Morinville and Rasmussen 2003). However, it can be difficult without genetic parentage information to link the life-history of the mother to her progeny. Further, understanding behavior and the effects of environment on juvenile fish can be difficult in fish too small to apply electronic tags.

Otoliths provide a window into the link between mothers and progeny, as well as detailed juvenile information. An inner ear structure of bony fish, otoliths grow in size with the addition of daily layers of calcium carbonate (Campana and Thorrold 2001). These layers incorporate elements and isotopes that occasionally substitute into the calcium carbonate structure. Many of these elements and isotopes are recorded in proportion to the water the fish inhabits, creating a temporal and spatial record throughout its life (Kennedy et al. 1997, Thorrold et al. 1998, Campana 2005). Numerous studies have reported the presence of a maternal chemical signature in the core of otoliths using various chemical proxies, allowing researchers to infer some aspects of maternal location, spawning migration, and anadromy from their progeny (Kalish 1990, Volk et al. 2000, Miller and Kent 2009, Shippentower et al. 2011, Courter et al. 2013, Liberoff et al. 2015). At the same time, otoliths provide information on juvenile natal location, movement, growth and condition in the layers just outside the zone of maternal influence near the otolith core (Thorrold et al. 1998, Walther and Thorrold 2010, Hamann and Kennedy 2012, Hegg et al. 2013a, Schaffler et al. 2014, Shrimpton et al. 2014, Turner et al. 2015).

Despite the amount of available research using these adjacent areas of the otolith, Veinott et al. (2014) highlight variability in some core signatures and a lack of conclusive agreement on the markers of maternal signature and its duration. Further, some assumptions of maternal chemical incorporation and duration in the otolith core are untested (Elsdon et al. 2008). Limburg et al. (2001) note that a lack of understanding of the duration of maternal signatures may affect their interpretation of Baltic sea trout that lack a freshwater phase. It is also unknown whether the maternal transition is related to underlying ontological changes in maturing fish which might provide further information on juvenile development. As the number of studies utilizing otolith chemistry to infer detailed juvenile movement patterns increase in frequency it is

important to determine how to distinguish maternally-derived, versus environmentally-derived, chemical signatures of juvenile fish.

The maternal signature is retained in the otolith because the egg is provisioned using nutrients derived from the mother. The larva obtains all of its nutrients from the yolk sac until it commences feeding, which occurs shortly after hatching, at which point the larva begins significant chemical exchange with the surrounding water (Hayes et al. 1946). Therefore, as the otoliths develop prior to hatching, its isotopic signature should reflect that of the mother (Kalish 1990, Waite et al. 2008). If the mother has migrated from a location with a different chemical signature her eggs will retain a chemical signature related to her past location, attenuated by the degree to which her body chemistry has equilibrated with the chemistry of the spawning stream (Volk et al. 2000, Bacon et al. 2004). This has also been demonstrated as a marking technique, by exposing mothers to known isotopic signatures prior to spawning (Thorrold et al. 2006, Woodcock et al. 2013, De Braux et al. 2014). This maternally derived chemical information recorded in the otolith can then be used to infer information about the maternal provenance or behavior.

The use of maternally-derived chemical signatures that allow for the identification of marine influence in fish been repeatedly demonstrated (Kalish 1990, Miller and Kent 2009, Liberoff et al. 2015). In most freshwater systems the concentration of strontium (Sr) is much lower than that of the ocean, providing a large and predictable shift in Sr/Ca in dissolved ions that is conserved between anadromous and resident fish (Kraus and Secor 2004, Brown and Severin 2009). However, examples exist showing that in some systems Sr/Ca is a poor indicator of ocean residence (Kraus and Secor 2004), that expected patterns of chemical signatures of ocean residence can be population specific (Hamer et al. 2015), and that Sr/Ca ratios change in relation to the time females spend in freshwater and the difficulty of the migration (Donohoe et al. 2008).

It has also been demonstrated that maternal signatures are conserved in otolith $^{87}Sr/^{86}Sr$ signatures (Barnett-Johnson et al. 2008, Miller and Kent 2009, Hegg et al. 2013a). In contrast to Sr/Ca, however, the relationship between maternal $^{87}Sr/^{86}Sr$ values and juveniles is less well quantified. The assumption in anadromous species has been that $^{87}Sr/^{86}Sr$ maternal signatures follow the same mechanism as Sr/Ca, reflecting the global marine value of 0.70918 due to maternal investment in the yolk material (Courter et al. 2013). Several studies, however, have shown that migratory distance and migratory difficulty may influence the maternal $^{87}Sr/^{86}Sr$ signature (Volk et al. 2000, Bacon et al. 2004, Miller and Kent 2009). As more studies use $^{87}Sr/^{86}Sr$ as a marker of maternal anadromy (Courter et al. 2013, Hodge et al. 2016), it is necessary to understand the dynamics of maternal chemistry in the otolith core, as well as the migratory conditions under which the assumptions of maternal chemical influence hold.

Based upon a review of the otolith literature, the factors controlling the duration of the maternal signature have been largely unexplored. Many studies mention the need to avoid mistaking the period of maternal influence with the period of natal origin, or vice-versa (Barnett-Johnson et al. 2008, 2010, Donohoe et al. 2008, Hegg et al. 2013a). However, determining the end of maternal chemical influence on the otolith has often been determined subjectively, often based on associations with microstructural checks, without a clear understanding of the link between microstructure and chemistry (Barnett-Johnson et al. 2008, Hegg et al. 2013a). Most studies of the microchemistry of the otolith core have focused on markers of the otolith primordium, rather than the extent of maternally derived influence, using various microchemical ratios to calcium including barium (Ba/Ca), magnesium (Mg/Ca), and manganese (Mn/Ca) (Ruttenberg 2005, Macdonald et al. 2008).

Late season spawning Chinook salmon (*Oncorhynchus tshawytscha*) in the Snake River of Idaho provide an ideal population for examining the presence and duration of the maternal otolith signature. Females in this population are entirely anadromous and individuals migrate long distances (500-1000 kms) inland to spawn over a narrowly defined period in October and November (Garcia et al. 2005). Prior work has characterized the isotopic variation across spawning areas in the basin, indicating that juvenile signatures are significantly different between spawning areas and that $^{87}Sr/^{86}Sr$ and Sr concentration in freshwater habitats are significantly different from the marine signature (Hegg et al. 2013a). These factors provide both a range of freshwater strontium concentrations to interpret otolith signatures, as well as the migration distance required to explore the degree to which maternal marine signature varies from the global marine signature with inland migration.

This study used individual otolith transects from a collection of known-origin, juvenile fall Chinook salmon from both wild and hatchery sources to quantify the duration and stability of maternal signatures in otoliths. This work also investigates the variability in these signatures that may be due to the equilibration of mothers to river-specific chemical signatures prior to spawning, as well as changes in the microchemistry of the egg after deposition in the redd. Given the inland location of the population we hypothesized that maternal $^{87}Sr/^{86}Sr$ signatures would reflect some degree of freshwater influence. We used a multi-tracer approach, including ratios of Sr/Ca, Ba/Ca, Mn/Ca, and Mg/Ca as well as $^{87}Sr/^{86}Sr$ to examine the presence and duration of the maternal signature on the otolith. Further, we explored whether changes in each tracer were simultaneous, and thus indicative of a single event, or if individual tracers may signal different ontological time-points in the early life of fish. First, using the suite of chemical signatures we determine the presence and duration of a maternal marine signature in individual juvenile otoliths. Given the variability we quantify in maternal signatures, we then measure the spatial and temporal variability of maternal signatures across the study area.

Methods

Study System

Fall Chinook salmon in the Snake River are listed as threatened under the Endangered Species Act (Good et al. 2005). The population inhabits low-elevation, mainstem habitats of the Snake River and its tributaries. The majority of spawning occurs in the free flowing Snake River between Asotin, Washington and Hells Canyon dam and in the Clearwater River (Garcia et al. 2008). The main spawning areas in the Snake River are classified as "Upper", above the confluence with the Salmon River, and "Lower", in the free-flowing section below the Salmon River confluence to Asotin, WA. The watersheds of the basin are geologically heterogeneous with enough distinction to provide significant differences in water $^{87}Sr/^{86}Sr$ ratios between the major spawning reaches that can be used to classify fish to their natal location (Hegg et al. 2013a, 2013b). Adult salmon migrate a minimum of 750 km to the main spawning areas in the Snake and Clearwater Rivers above the town of Lewiston, ID. The watershed is heavily influenced by hydropower with eight downstream dams, four on the Columbia River and four on the Snake River, creating slow moving reservoir habitat downstream of Lewiston, ID.

The population is notable for a recent shift from a historically ubiquitous sub-yearling strategy, whereby individuals migrated shortly after emergence, toward a later, yearling strategy in response to anthropogenic changes to the river system (Connor et al. 2005, Williams et al. 2008). Studies have indicated that this change in juvenile life-history is likely heritable and under active selection in response to reservoirs and hydropower regulation that provide cool water opportunities during summer that did not exist historically (Williams et al. 2008, Waples et al. 2017). A separate study seeks to quantify the spatially explicit outmigration behaviors (Hegg et al. In prep). However, to accurately assess early life-history behaviors using chemical proxies in otoliths, it is essential to determine the degree of maternal influences on the early chemistry of juvenile fish.

Background Water Sample Collection

Water samples were collected from 2008 through 2016 throughout the spawning range of Snake River Fall Chinook salmon to characterize the spatial and temporal variation in strontium isotopic chemistry within the basin (Figure 1). Samples were collected during base-flow periods in late summer and fall in all years to capture the most representative signature of water and rock interactions within each river. Starting in 2009, as resources permitted, samples were taken seasonally. Sampling began in the spring as soon as flows were safe to sample and included summer, and fall seasons to characterize the stability of the signatures. Additionally, in 2010,

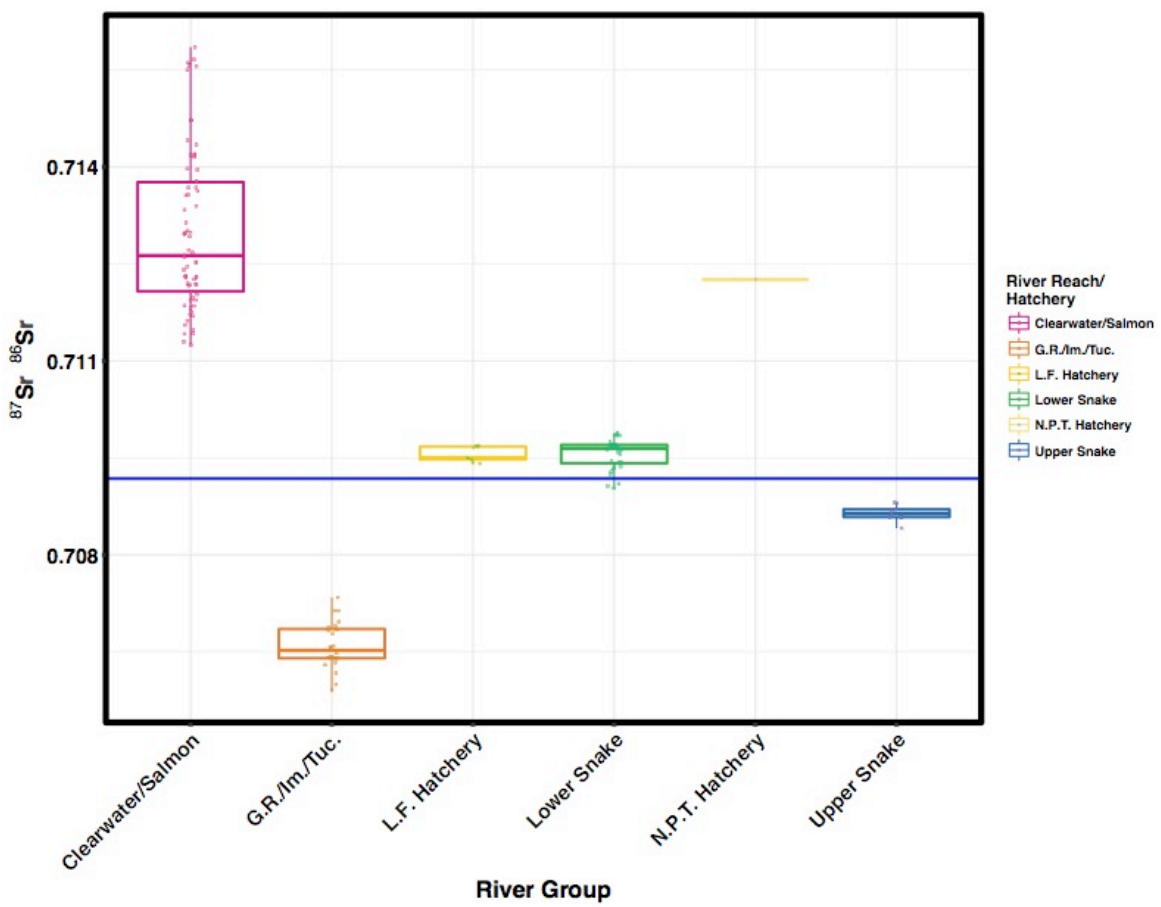

Figure 1. Water $^{87}Sr/^{86}Sr$ chemistry of the study area. Water samples of $^{87}Sr/^{86}Sr$ within the range of Fall Chinook salmon in the Snake River basin show distinct grouping between major river groups in the basin. Lyons Ferry Hatchery is located on the Lower Snake River. The Nez Perce Tribal Hatchery is located on the Clearwater River. Water within this hatchery is mixed from two sources, low $^{87}Sr/^{86}Sr$ well water and water from the Clearwater River, depending on water conditions. Thus, care should be taken in interpreting a single sample.

samples were taken in the Clearwater and Salmon Rivers at three periods encompassing the peak of the hydrograph to characterize seasonal variation observed in prior studies (Hegg et al. 2015b)

Samples were collected in acid cleaned 125ml HDPE bottles according to established protocol (Kennedy et al. 2000). Samples were analyzed for $^{87}Sr/^{86}Sr$ isotope ratios on a Finnigan MAT 262 Multi-Collector thermal ionization mass spectrometer (TIMS) as well as a Isotopix Phoenix TIMS. Throughout the research period, replicate analysis of the National Institute of Standards and Technology standard reference material (SRM-987) was used to determine the analytical error. The Finnegan MAT 262 yielded mean $^{87}Sr/^{86}Sr$ of 0.710231 (2SD = 0.000032, n=16), the Isotopix Phoenix yielded a mean $^{87}Sr/^{86}Sr$ of 0.710244 (2SD = 0.000009, n=89).

Fish and Otolith Collection

Wild juvenile fish (n=430) were captured using beach seines from spawning areas between the Snake and Clearwater Rivers as part of seasonal population surveys between April and August in years spanning 2007 to 2014 (Connor et al. 1998). Some of these fish (n=111) were PIT tagged, released, and recaptured at fish passage facilities at Lower Granite Dam on the Snake River during their downstream out-migration, providing two known locations for these fish (tagging site and recapture site). Juvenile fish were also collected from the two hatcheries that produce Fall Chinook in the Snake River basin. Hatchery fish were collected from Lyons Ferry Hatchery in 2009 and 2011 (n=28), and from Nez Perce Tribal Hatchery in 2011 and 2012 (n=35).

Fish samples were kept frozen until otoliths could be removed through dissection. Otoliths were stored dry in polypropylene microcentrifuge tubes. Otoliths were then mounted on the sagittal plane on petrographic microscope slides using Crystalbond adhesive and ground by hand on fine grit Micromesh aluminum oxide sandpaper to reveal the otolith primordium and daily otolith increments. (Secor et al. 1992, Hegg et al. 2013a).

Otolith Microchemical Analysis

Otoliths were analyzed for $^{87}Sr/^{86}Sr$ using a Finnigan Neptune (ThermoScientific) multi-collector inductively coupled plasma mass spectrometer coupled with a New Wave UP-213 laser ablation sampling system (LA-MC-ICP-MS). Analysis for trace element composition was conducted using an Element 2 (ThermoScientific) ICP-MS attached to the same laser ablation system. For each analysis method otoliths were analyzed using a transect moving from the edge of the otolith to the core. This transect was positioned approximately 90° from the sulcus on the dorsal side of the otolith to capture the area containing the clearest succession of rings from the edge to the core. The laser was set to ablate at a constant speed. For $^{87}Sr/^{86}Sr$ ratios the LA-MC-ICP-MS system was set to 10μm/second scan speed, 40μm laser spot size, and 0.262 second

integration time. For trace element analysis, the laser was set to scan at 10μ/second, 30μm laser spot size, and a 1 second sampling time in the ICP-MS method. Samples were run using a dry flow of helium (He) through the sample chamber was approximately 0.8L/minute, which combined with .6L/min argon (Ar) before entering the plasma. Oxide formation rates were <1% Th/ThO_2. The trace element analysis included the elements calcium (^{43}Ca), strontium (^{86}Sr), barium (^{138}Ba), Magnesium (^{25}Mg), and Manganese (^{55}Mn).

Strontium ratio data was corrected based on the global marine signature for each analysis day using a marine shell standard (mean $^{87}Sr/^{86}Sr$ = 0.709186, SD = 0.000077, n=535). Error across individual otoliths varies based on fish location and is best assessed on stable regions. The maternal period between the otolith core and 150μm is relatively stable across all otoliths. In our study the standard deviation of the $^{87}Sr/^{86}Sr$ signature in the maternal region averaged across all otoliths was 0.00095 (SD = 0.00063, n = 279).

Elemental counts were corrected to the SRM 610 standard (Jochum et al. 2011). Correction was done using a ten second, within-run blank during which gas was flowing over the sample but the laser was not ablating. Blank counts were then subtracted from the measured concentration of SRM 610 for each element. All measurements were normalized to known CaO in SRM-6to 10 and aragonite, to account for variations in laser ablation efficiency. A three standards were run for every 10-20 samples, and an average of the correction factor for these standards was used to correct those samples. Limits of detection (LOD) for each element were calculated as 3 X SD from the mean of all sample blanks during otolith analysis runs in which our samples were a part (n = 859). Detector problems affected approximately 15% of the sample blanks. The LOD for all samples are included in parentheses. Expressed as a ratio of elements to calcium, detection limits were; Sr/Ca 0.0059 (0.029) $mm \cdot mol^{-1}$, Ba/Ca 0.00036 (0.023) $mm \cdot mol^{-1}$, Mn/Ca 0.011 (0.031) $mm \cdot mol^{-1}$, and Mg/Ca 0.003 (0.022) $mm \cdot mol^{-1}$. A suitable solid standard with a similar matrix was not available to report accuracy and precision of elemental analyses.

The edges of the otolith were identified within the data using a CUSUM algorithm on Sr and Ca counts, then confirmed visually. Extraneous data was trimmed beyond the edge of the otolith before reversing the sequence to form a data transect from the core to the edge. The distance of each data point from the core, in microns, was calculated using the scan speed and integration/sampling time of the laser and ICP-MS software.

Statistical Analysis

Water chemistry and otolith data were aggregated into chemically distinguishable reaches as detailed by Hegg et al. (2013a) with the inclusion of two groups for hatchery signatures. One chemically distinguishable river group is made up of the Clearwater and Salmon Rivers (CWS). A second group is the Lower Snake River (LSK), which extends downstream from the

confluence of the Snake and Salmon Rivers downstream to Asotin. A third group is the Upper Snake River (USK) consisting of the Snake River upstream of the confluence with the Salmon River to Hells Canyon Dam. Finally, the Grande Ronde, Imnaha, and Tucannon Rivers, comprise the fourth river group. Each of these rivers, flowing from the south, runs over the Columbia River basalts, a geological formation of flood basalts (referred to as CRB). Finally, Lyons Ferry Hatchery (LFH) and Nez Perce Tribal Hatchery (NPTH) made up two separate groupings. Hatchery fish were analyzed separately despite the inability to distinguish these groups using $^{87}Sr/^{86}Sr$ in the past (Hegg et al. 2013a). This was done with the hope that multi-tracer data would help to distinguish these groups, and because we expected early juvenile or maternal microchemistry might differ from wild fish.

Duration of Maternal Signature

Otolith transects were analyzed graphically to determine the location of a change between maternally derived and post-hatch chemistry. Large, rapid, changes in element/calcium ratio in the early otolith allowed for statistical confirmation of the location of chemical change. To confirm the identified location on the otolith did, in fact, represent a significant change in elemental signature, the mean signature from 100μm of otolith growth before the identified change was compared to the mean signature 100μm after, for all fish within each river group. This comparison was done using a two-sided, paired t-test assuming unequal variance ($\alpha = 0.05$) with Bonferroni correction for multiple comparisons. The chemical tracers that showed the most significant change across river groups were then used to develop a multivariate change-point algorithm to determine the otolith location of the maternal/natal change for individual fish.

The maternal/natal transition in $^{87}Sr/^{86}Sr$ was less distinct and involved a gradual slope during the maternal period (See Variation in Maternal Signature section below), transitioning to a second slope during an extended equilibration period. We used a segmented regression approach to test for the presence of a transition in slope near 150μm, the point at which we determined a transition graphically. We used the {segmented} package for R which uses a likelihood maximization approach to determine the optimal breakpoints in a linear model (Muggeo 2003, 2008). We applied this algorithm to the segment of each otolith $^{87}Sr/^{86}Sr$ transect between 50μm and 250μm from the otolith core, encompass a range around the expected transition. The model fit was limited to a single breakpoint and each maximization was limited to a maximum of 200 iterations. If the model failed to converge it was assumed that the data did not contain a breakpoint and was instead best described by a simple linear model. Breakpoint analysis was only conducted for those river groups whose river signature was different from the expected maternal signature (somewhere between the global marine average and the Lower Snake River), since these were the only signatures likely to exhibit a sharp enough shift to test. Therefore, fish from Lyons Ferry Hatchery and the Lower Snake River were not tested. Breakpoint analysis was run on data smoothed with a centered, 20-point moving average. To

ensure that smoothing did not affect results, breakpoint analysis was run across a range of smoothness from the raw data to 20-point smoothing at increments of 5-points.

We also tested two change-point methods for their ability to identify the location of the maternal/natal chemical transition for individual otolith elemental ratios. Both were applied to the data between 150μm and 350μm from the core of each otolith. The first 150μm was excluded so as to avoid the known peak in Mn/Ca near the core (Brophy et al. 2004, Ruttenberg 2005), while covering the location on the otolith where the presumed maternal/natal change occurs. The first change-point method tested was the multivariate {ecp} package for R, which used the three most significant elemental tracers from the paired t-test above (James and Matteson 2014). Additionally, we applied a univariate change-point algorithm from the {changepoint} package for R (Killick and Eckley 2013). This univariate approach used only the most significant chemical tracer from the prior paired t-test. The univariate change-point algorithm was applied using the "AMOC" (At Most One Change-point) procedure and an asymptotic penalty, for changes in both mean and variance.

Variation in Maternal Signature

To determine the degree to which maternal signatures vary we fit a linear model to the maternal $^{87}Sr/^{86}Sr$ signatures of all known juvenile fish and the known average $^{87}Sr/^{86}Sr$ of the river in which they were captured. Under the null hypothesis that all fish maintain an ocean signature we would expect the slope of this regression to be zero, with an intercept of 0.70918, the global ocean signature. A significant slope other than zero, with an intercept other than 0.70918 would indicate that maternal signatures vary with maternal equilibration to the spawning stream.

Stability of Maternal Signature

During the course of analysis, we noted that the mean $^{87}Sr/^{86}Sr$ in the early otolith (<150μm from the otolith core) of the CWS and NPTH groups appeared to differ. This was striking because contributing mothers of both groups inhabit similar water chemistries from the Clearwater River prior to spawning. Further, we noted that otolith chemistry during this early period appeared to change during development in both groups, with opposite slopes. Chemistry this early in the otolith is likely to reflect chemistry in the egg (Boyd et al. 2010), a period whose rate of chemical change has not been well studied and which some authors claim to be a closed system chemically and isotopically (Volk et al. 2000, Elsdon et al. 2008). To test for differences between these groups we tested the mean $^{87}Sr/^{86}Sr$ ratio between the CWS and NPTH groups using a two-sample t-test. To test for isotopic change within the egg during this isotopically "closed" period we also fit a linear model to the aggregate maternal data in each group to determine the presence and magnitude of change in the maternal signal.

To support our findings, we calculated expected changes in the $^{87}Sr/^{86}Sr$ ratios of the egg under seven scenarios of maternal equilibration and spawning water chemistry (Table 1). In these scenarios, we tested four different maternal equilibration chemistries; mothers equilibrated to the ocean, the Lower Snake River, the Clearwater River (as measured during Oct. & Nov.), and the observed signature at the otolith core (0μm) for known NPTH juveniles taken from the linear model above. For each of these maternal equilibration scenarios the change in $^{87}Sr/^{86}Sr$ was calculated assuming eggs were laid into Clearwater River water, or into water similar to the well water used at NPTH. As a proxy for NPTH well water we used the signature for the Potlatch River, a nearby river which is representative of the low $^{87}Sr/^{86}Sr$ basalt signature of the area.

The signature observed in the core of NPTH otoliths represents an "intermediate" signature between the Lower Snake and the Clearwater Rivers, an indication that mothers may not be fully equilibrated to the Clearwater River signature at spawning. This "intermediate" signature provided a direct test of whether the changes we observed in the otoliths were supported by our calculations.

Calculations were based on two-component isotope mixing models including both concentration and isotope ratio differences (Faure and Mensing 2004 p. 350, equation 16.11). We calculated the expected change in $^{87}Sr/^{86}Sr$ during the first 80 hours after fertilization, when the egg takes on the majority of its external water (Loeffler and Løvtrup 1970). We then calculated the further change in $^{87}Sr/^{86}Sr$ due to the small amount of water exchange during the period from fertilization to hatch (0.33% of egg volume per day) as estimated by Loeffler and Løvtrup (1970). Calculations were based on values available from the literature. We used egg Sr concentration data for wild and hatchery steelhead from Kalish (1990), average egg volume in Atlantic salmon from Rombaugh and Garside (1982), and changes in Atlantic salmon egg volume over time from Leoffler and Løvtrup (1970). We assumed the number of days to hatch to be 73, the average for the Clearwater River in 2013 (Bill Arnsberg, Nez Perce Tribal Fisheries, pers. comm.).

Results

Duration of Maternal Signature

Graphical analysis of otoliths by known natal location indicated that changes occurred at consistent locations on the otolith for elemental ratios and $^{87}Sr/^{86}Sr$, regardless of river group. However, elemental ratios and $^{87}Sr/^{86}Sr$ did not change simultaneously. Instead $^{87}Sr/^{86}Sr$ exhibited changes at different locations on the otolith than elemental ratios.

Table 1. Calculated change in $^{87}Sr/^{86}Sr$ in eggs between laying and hatch. The change in $^{87}Sr/^{86}Sr$ signature was calculated for six different scenarios of maternal equilibration and laying location. In the table strontium concentrations increase from top to bottom, and decrease from left to right. The largest changes within the egg were calculated for scenarios with low maternal concentration and high concentration in the surrounding water (grey outline). This indicates that concentration likely controls the change in strontium ratio of the egg. Calculations were based on sampled water chemistry and values from the literature. Strontium concentration in fish tissue was taken from Kalish et al. (1990), measured in ocean and freshwater reared steelhead. Changes were calculated for the first 80 hours, when the egg takes in the majority of external water, as well as the remaining 73 days of maturation (the average estimated days to hatch for Clearwater River juveniles in 2013). The furthest right-hand column represents the signature observed at the core of known NPTH juveniles, equilibrating to a signature similar to the well-water used to rear NPTH eggs.

Mother's signature (starting signature of egg)

High Concentration → ***Low Concentration***

Ocean	**Lower Snake**	**Clearwater**	**Observed signature of NPTH fish at 0μm**
$^{87}Sr/^{86}Sr$ = 0.70918 Sr ppm = 4.73	$^{87}Sr/^{86}Sr$ = 0.70956 Sr ppm = 0.88	$^{87}Sr/^{86}Sr$ = 0.71321 Sr ppm = 0.88	$^{87}Sr/^{86}Sr$ = 0.70981 Sr ppm = 0.88

Signature of Surrounding Water (Low Conc. ← → High Conc.)				
Potlatch (similar to NPTH well water) $^{87}Sr/^{86}Sr$ = 0.70891 Sr ppm = 0.15	First 80h = 0.00000 To hatch = 0.00001 **Total Δ = 0.00001**	First 80h = -0.00003 To hatch =-0.00003 **Total Δ = 0.00006**	First 80h = -0.0002 To hatch = -0.0002 **Total Δ = -0.00040**	First 80h = -0.00086 To hatch = -0.00005 **Total Δ = -0.00091**
Clearwater River $^{87}Sr/^{86}Sr$ = 0.71321 Sr ppm = 0.03	First 80h = 0.00001 To hatch = 0.00001 **Total Δ = 0.00002**	First 80h = 0.00003 To hatch = 0.00004 **Total Δ = 0.00007**	N/A	First 80h = 0.00004 To hatch = 0.00003 **Total Δ = 0.00007**

Strontium ratio appeared to exhibit an inflection point ~150μm from the otoliths core. This was particularly noticeable in the signatures from the Clearwater, Grand Ronde, and NPTH river groups. Breakpoints within each river group were approximately normally distributed, with no group violating the assumption of normality ($p > 0.4$ for all groups, $\alpha = 0.05$) using the Shapiro-Wilkes normality test (Razali and Wah 2011). The mean breakpoint within the Clearwater River was located at 151μm (SD = 22μm). Mean breakpoints for the Grande Ronde were 150μm (SD = 20μm). For NPTH the mean breakpoint was 148μm (SD=24μm). The median breakpoint for the Upper Snake river group was 145μm (SD=24.9). Both the NPTH and USK groups exhibited a second, smaller, group of breakpoints near 200μm as data smoothness decreased. The mean breakpoint for all groups remained within 15μm across all smoothing profiles, though the results became increasingly abnormally distributed as data smoothness decreased. The median breakpoint remained relatively stable across groups regardless of smoothing, with the exception of NPTH and the Upper Snake river groups whose median increased to 180μm and 185μm respectively on the raw data.

Elemental ratios, particularly Mn/Ca and Ba/Ca, showed a marked change beginning at 225μm from the otolith core (Figure 2). These changes were less pronounced in fish from the hatchery. Comparison of the 100μm segments on either side of 225μm using two-sided, paired t-tests assuming unequal variance ($\alpha = 0.05$) with Bonferroni correction showed that Mn/Ca was highly significant for all groups, while Ba/Ca was significant for all river groups except hatchery fish from LFH (Figure 3). Sr/Ca ratios were significantly different only for the USK and LSK groups and LFH. Mg/Ca ratios showed no significant differences. Mn/Ca ratios were at or below LOD in many samples during this period, however, the consistent pattern of increasing Mn/Ca after 225μm indicates this increase is likely biological despite low concentrations of Mn.

Multivariate change-point analysis on Mn/Ca and Ba/Ca ratios using the {ecp} package did not provide consistent determination of the location of chemical change in individual otoliths. Similarly, univariate change-point analysis on Mn/Ca using the {changepoint} package resulted in inconsistent determination of the maternal/natal chemical shift at the individual level. Using a value of 225μm appeared to describe the location of the maternal/natal transition as well or better than change-point analysis. Individual variation in the magnitude of the chemical change, as well as data noise, was likely to blame for the difficulty in determining logical change-points at the individual level.

Plots of $^{87}Sr/^{86}Sr$ for each non-hatchery river group showed changes in the signature at approximately 150μm from the otolith core, as much as 100μm earlier than the location of chemical changes in the elemental ratios (Figure 4). Following the initial change in $^{87}Sr/^{86}Sr$ ratio after ~150μm the signature then began moving toward a second stable period near ~250-300μm. The signature for LFH was consistent throughout the life of the fish, with no distinct changes.

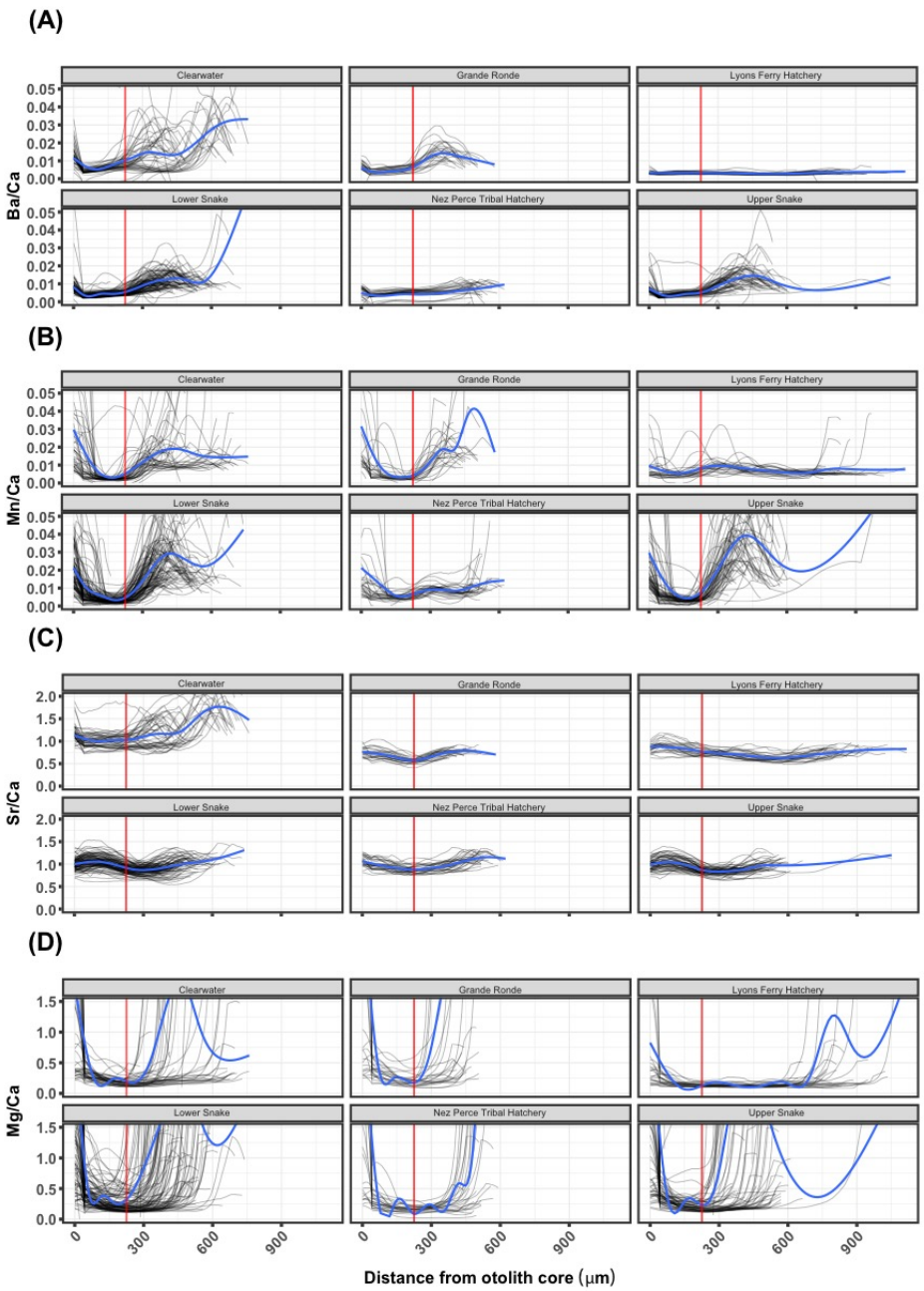

Figure 2. Element to calcium ratios for juvenile fish from known locations. Plots of individual element to calcium ratios (mm•mol^{-1}), plotted by river and hatchery grouping, show a shift in chemistry beginning at ~225μm from the otolith core (red line). This shift is most apparent in Ba/Ca (A) and Mn/Ca (B), and less apparent in Sr/Ca (C) and Mg/Ca (D). Plots are smoothed with a 10-point moving average and exclude high values on the y-axis to maintain detail of the maternal/juvenile transition. Blue lines represent the smoothed average of all individual transects using a generalized additive model.

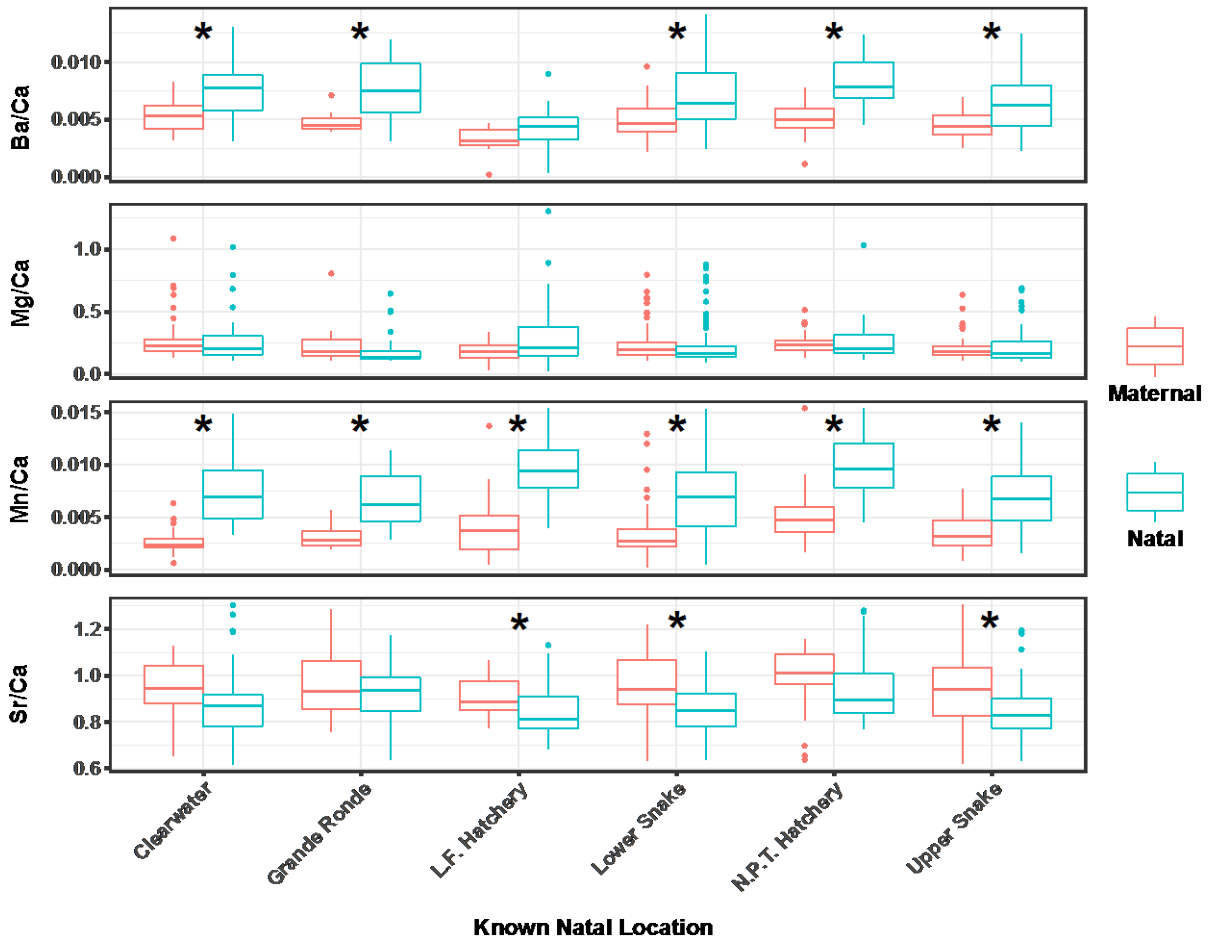

Figure 3. Differences in elemental ratios of maternal vs juvenile periods. Boxplots show the difference in elemental ratios 100µm before and after the 225µm otolith radius. Asterisks indicate cases in which maternal signatures (red) were significantly different than natal signatures (blue) based on paired t-tests with Bonferroni correction for multiple comparisons.

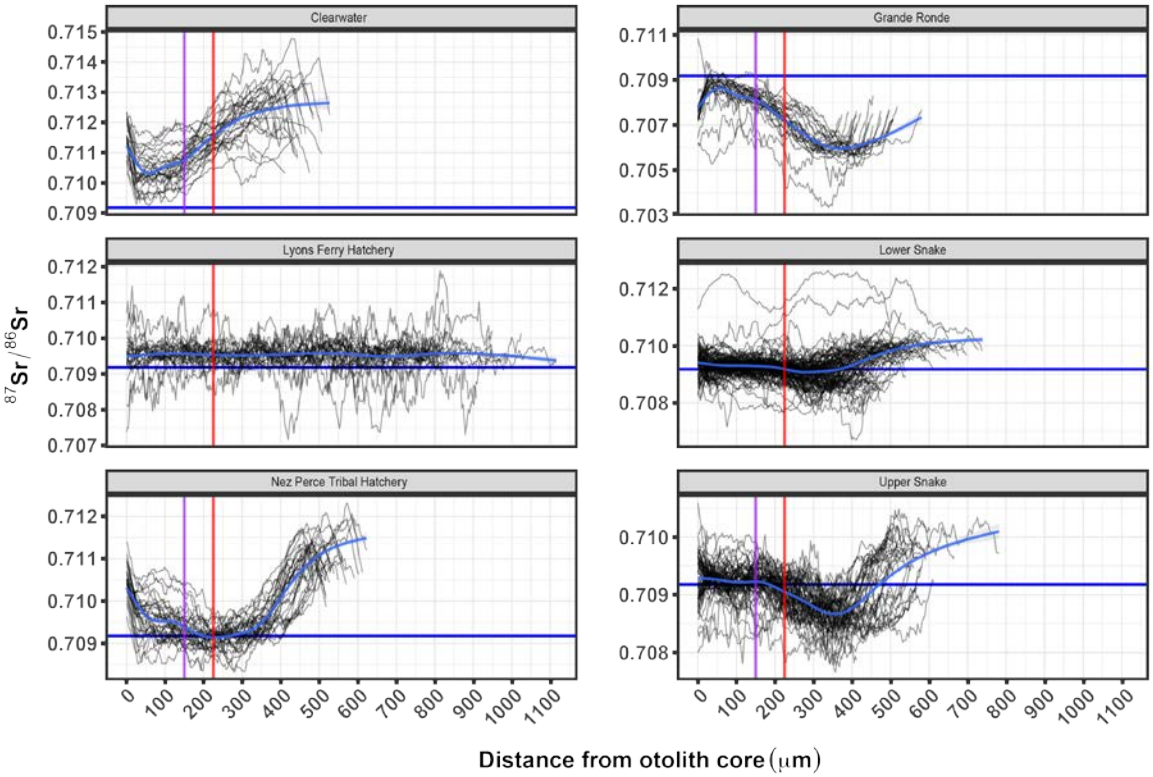

Figure 4. Strontium isotope ratios ($^{87}Sr/^{86}Sr$) of individual fish from known locations. Plots of individual $^{87}Sr/^{86}Sr$ transects show a relatively stable period from the core of the otolith to ~150μm from the otoliths core (purple vertical line). This region was not apparent in the Lyons Ferry and Lower Snake river groups, presumably due to the similarity in signature between maternal and natal water. After this point transects slowly equilibrate toward the expected $^{87}Sr/^{86}Sr$ value for their river group. Strontium ratio does not seem to change at 225μm (red vertical line) where elemental ratios show a change, indicating that $^{87}Sr/^{86}Sr$ may be recording a different ontological change within the developing fish. Fish from NPTH equilibrate toward an unknown well-water signature before moving upwards to signature reflecting the Clearwater River as river water is mixed with the hatchery well-water late in the season. Some late-season juveniles were removed from the Clearwater River plot for clarity (n=21) because their transects followed a pattern of movement that suggested hatchery origin and acclimation in unknown water sources. The global marine signature, 0.70918, is noted for reference (horizontal blue line).

Fish from NPTH began at a signature near 0.7096, before a sudden transition to a signature near 0.70918 around 150μm, before beginning near 300μm to move toward a signature near 0.7110 toward the end of their life.

Variation in Maternal Signatures

The regression of maternal signatures to the signatures of the rivers in which juveniles were captured resulted in a significant linear model ($p<0.00001$, $\alpha=0.05$) with the form,

$$Maternal\ ^{87}Sr/^{86}Sr\ =\ 0.2673 * Maternal\ ^{87}Sr/^{86}Sr +\ 0.5197$$

Both the slope and intercept terms were highly significant ($p<0.00001$, $\alpha=0.05$), providing support for the alternate hypothesis that maternal signatures are different from the ocean signature, and significantly influenced by the signature of the natal river. This effect is apparent in the histogram of maternal signatures expressed in our study, with Clearwater and Grande Ronde juveniles exhibiting maternal signatures that trend in the direction of their natal river from the global marine average (Figure 5).

Stability of Maternal Signatures

Despite mothers experiencing similar $^{87}Sr/^{86}Sr$ regimes, the maternal signatures of CWS and NPTH juveniles were significantly different prior to 150μm in a two-sample t-test ($p<0.00001$). CWS juveniles had a mean maternal $^{87}Sr/^{86}Sr$ signature of 0.7104, while NPTH juveniles had a mean maternal $^{87}Sr/^{86}Sr$ signature of 0.7096 (Figure 6A).

Maternal signatures in both groups also showed significant, but opposing, slopes and intercept values when a linear model was applied to the maternal data in each group, indicating changes in chemistry within the egg (Figure 6B). The linear model fit to Clearwater River juveniles returned an intercept of $^{87}Sr/^{86}Sr = 0.7101$ ($p=<0.00001$, $\alpha=0.05$) and a slope of .00000314 microns ($p=0.0016$, $\alpha=0.05$). Variability in the data was high ($R^2 = .0115$). Juveniles from NPTH were fit to a linear model with an intercept of $^{87}Sr/^{86}Sr = 0.7098$ ($p=<0.00001$, $\alpha=0.05$) and a slope of -0.00000236 microns ($p=0.0025$, $\alpha=0.05$). Variability in the NPTH juvenile data was also high ($R^2 = 0.0102$).

Our calculation of the expected change in egg maternal signatures indicated that $^{87}Sr/^{86}Sr$ can exhibit changes nearing 0.0001 between the time eggs are laid and when they hatch in some cases (Table 1). The degree of change was driven largely by concentration differences, with mothers equilibrated to the high concentration of the ocean showing little change. The largest

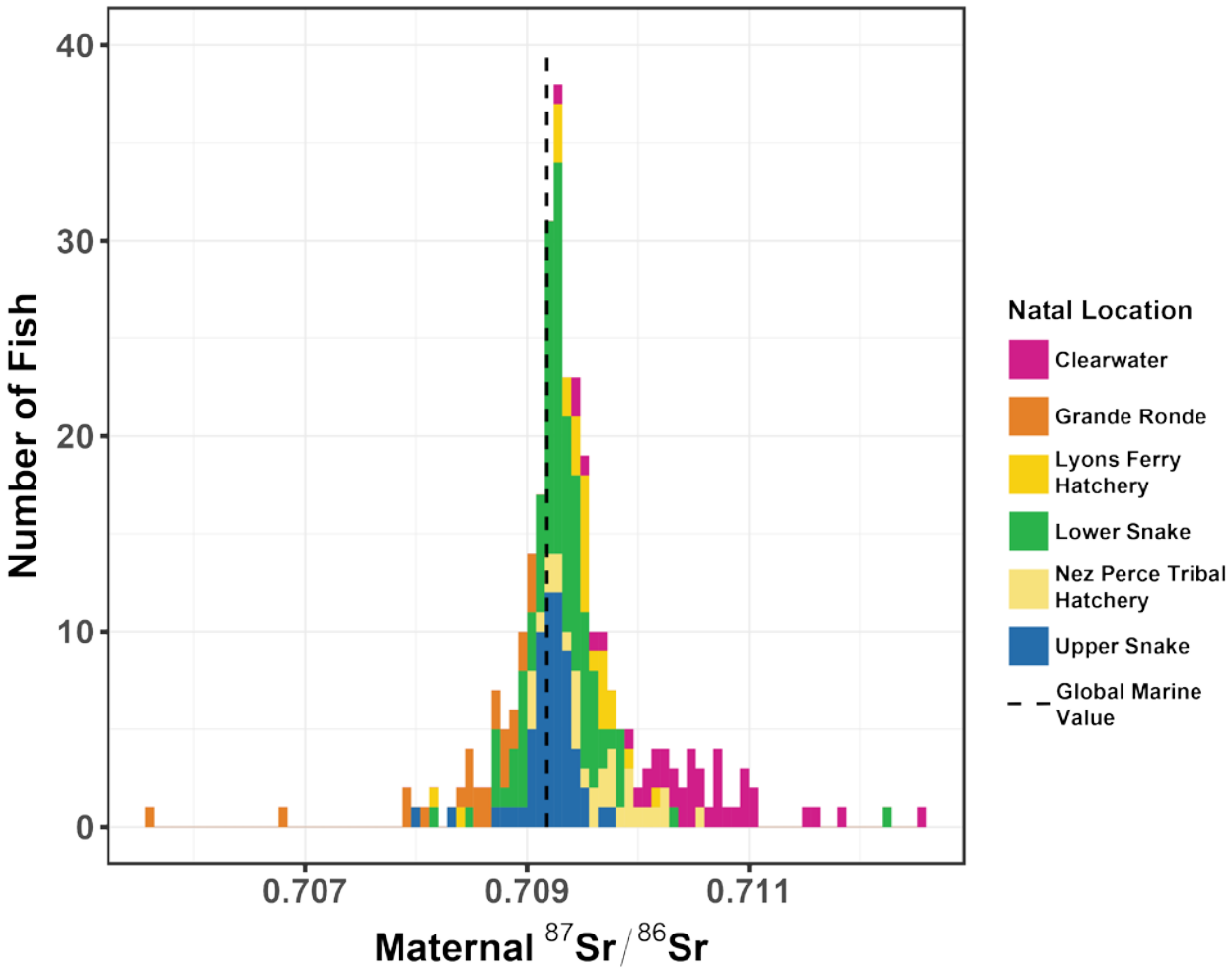

Figure 5. Variation in maternal $^{87}Sr/^{86}Sr$ signature. Maternal $^{87}Sr/^{86}Sr$ signatures of known origin juvenile fish vary significantly from the global marine value of 0.70918 (dotted line). Individual fish are colored by their known location, showing that maternal signatures vary in the direction of the water chemistry of the natal stream of the fish (Figure 1). Means for each group are; Clearwater (0.71050), Grande Ronde (0.70845), Lyons Ferry Hatchery (0.70946), Lower Snake (0.70931), Nez Perce Tribal Hatchery (0.70964), Upper Snake (0.70920).

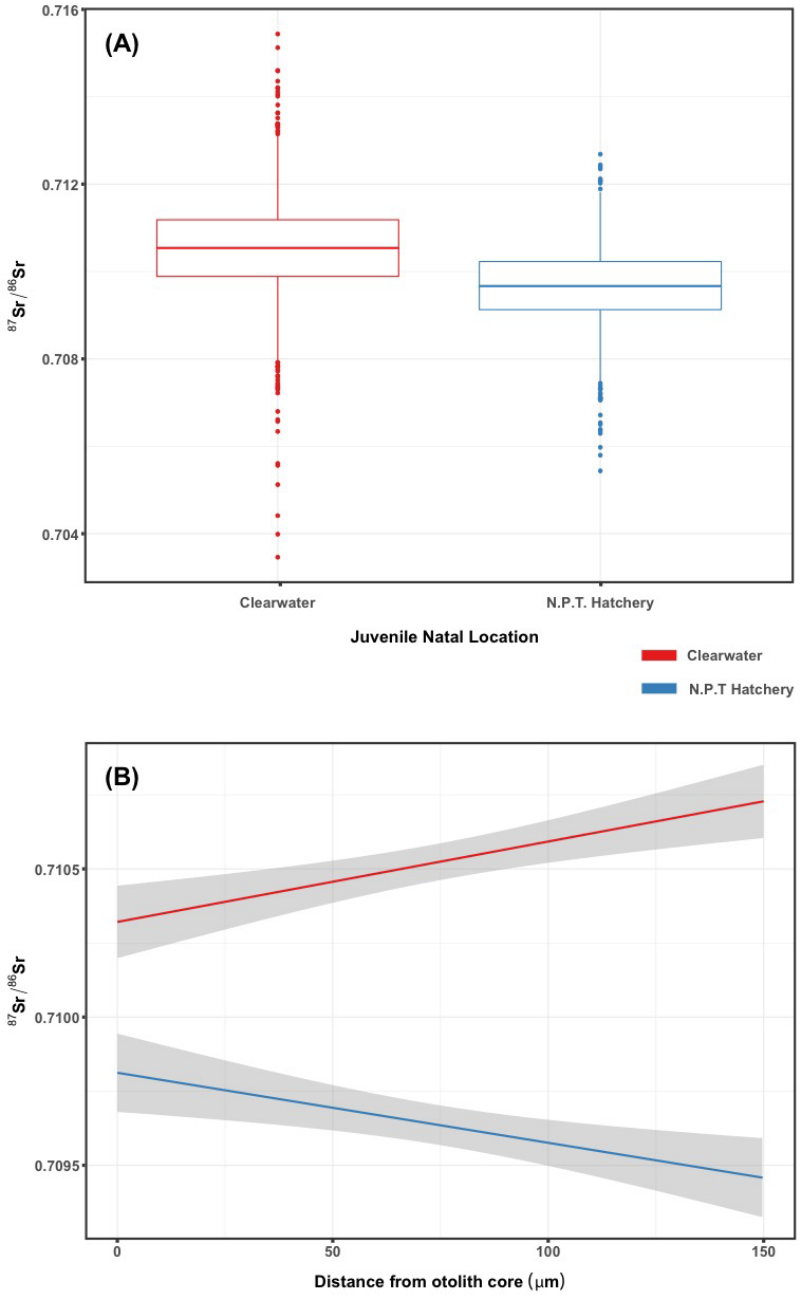

Figure 6. Mean maternal signatures of hatchery and natural origin Clearwater juveniles. Despite NPTH adults being exposed to the same, or more, time in Clearwater River water, their progeny exhibit significantly lower $^{87}Sr/^{86}Sr$ maternal signatures (A) than juveniles spawned naturally in the Clearwater River (T-test, $p<0.0001$). Eggs at NPTH are reared in well-water, not Clearwater River water. Further, the maternal signatures of juveniles from each location exhibit significant slopes in the direction of the signature of their natal water sources, indicating equilibration of the egg signature before hatch (B). Dark blue lines represent the slope of the aggregate data, while grey shading represents confidence intervals for each regression.

change in $^{87}Sr/^{86}Sr$ signature (0.00094) was seen for mothers equilibrated to the "intermediate" signature observed in NPTH fish, with eggs laid into NPTH well-water. This change, interestingly, is very similar to the significant difference (0.0009) between the mean $^{87}Sr/^{86}Sr$ maternal signatures of the Clearwater and NPTH groups above (Figure 6A). In this case, the egg changed its $^{87}Sr/^{86}Sr$ ratio by 0.00005 in the direction of the ambient water between initial swelling and hatch, supporting our observation of a slope in maternal signatures in Clearwater and NPTH juveniles (Figure 6B). In all cases approximately half of the $^{87}Sr/^{86}Sr$ ratio change occurred in the first 80 hours after hatch, with the subsequent change occurring slowly during the period after hatch, further supporting the observation of a slope in $^{87}Sr/^{86}Sr$ signature prior to 150μm in the otolith.

Discussion

Connecting maternal migratory behavior with the behavior and ecology of their progeny can reveal important details in the ecology of a population. In the case of fish, the maternally derived chemistry stored in the core of otoliths provides important clues about the behavior of mothers. This maternally derived chemistry has been particularly effective as a signature to identify ocean residence for partially migratory salmonid populations (Kalish 1990, Volk et al. 2000, Miller and Kent 2009, Shippentower et al. 2011, Liberoff et al. 2015). Recent work has extended this tool, using $^{87}Sr/^{86}Sr$ ratio to infer the degree of anadromy in multiple inland populations of steelhead (Courter et al. 2013). Additional studies have cited a period of maternal influence near the core of the otolith, however the duration and chemical makeup of this maternal signature is unclear (Barnett-Johnson et al. 2008, Miller et al. 2011, Hegg et al. 2015b).

While the use of maternal Sr/Ca signature as a marker of anadromy has been validated (Kalish 1990, Zimmerman 2005), very little information is available regarding the duration of this maternal signature. Several elemental tracers have been proposed as markers of the otolith core, including Ba/Ca and Mn/Ca, but the origin of these elevated elemental ratios may have more to do with juvenile ontogeny and formation of the core itself than maternal behavior (Brophy et al. 2004, Ruttenberg 2005). Whether these elemental systems change in concert with a single developmental stage, or whether there are asynchronous patterns of chemical changes during development has not been tested.

The hatching of juvenile fish, or alternately the moment of first exogenous feeding, is usually cited as the ontological event that precipitates a change between maternal and natal chemical signatures. The assumption made in most studies is articulated by Volk et al. (2000); that the egg makes up a closed system reflecting the chemistry of the mother during the time at which the eggs are sufficiently developed to close to outside chemical influence. Under this assumption, the juvenile otolith only begins to equilibrate to the external chemistry of the river

after hatching when it begins to interact directly with the external environment. Some authors have extended the assumption to conclude that the equilibration of $^{87}Sr/^{86}Sr$ must be correlated to the first exogenous feeding (Barnett-Johnson et al. 2008).

Duration of the Maternal Signature

Our data indicate that Mn/Ca and Ba/Ca, and to a lesser degree Sr/Ca, appear to mark a sharp transition in the otolith chemistry of juvenile fish at 225μm from the otolith core (Figure 2). The simultaneous changes in these elements argue for an underlying ontological change in the juvenile; however it is unclear whether this signals hatch, the onset of exogenous feeding, or another physiological or external driver. There is considerable individual variation in the magnitude and location of this change, however, making individual determination difficult and indicating that individual conditions may play a large role in this chemical change.

The results of our $^{87}Sr/^{86}Sr$ analysis show that in contrast to elemental signatures, $^{87}Sr/^{86}Sr$ ratios appear to change near 150μm from the otolith core, with a more gradual change in signature than that seen for elemental ratios (Figure 3). At this point the signature moves steadily toward the signature of the natal river, reaching a stable plateau between ~250μm and ~300μm depending on the population. This change in signature is especially visible in juveniles from the CWS and CRB groups, natal locations whose $^{87}Sr/^{86}Sr$ values are farthest removed from the global marine signature and therefore might be expected to exhibit the fastest change toward equilibrium.

The difference in the timing of change between elemental and $^{87}Sr/^{86}Sr$ isotopic ratios was interesting. Strontium ratios in our study began to change at 150μm, ~75μm earlier than do elemental signatures (225μm). This distance corresponds to roughly 12 - 19 days, based on the range of known Chinook growth rates in the basin (Zabel et al. 2010). Further, experimental results indicate that otolith radius at emergence varies from 173μm to 259μm (Paul Chittaro, unpublished data). It is reasonable, based on this difference in timing, to assume that the shift in elemental ratios and $^{87}Sr/^{86}Sr$ are synchronized with different ontogenetic changes in the juvenile fish.

Since hatching represents the first time the egg is capable of a large degree of ion exchange with the surrounding water, the change in $^{87}Sr/^{86}Sr$ ratio at ~150μm likely represents hatching. Strontium and calcium uptake in juvenile fish begins to climb steadily after hatching, and experimental results indicate that it is possible to isotopically mark non-feeding salmonid fry using water spiked with ^{84}Sr (Hayes et al. 1946, Yamada and Mulligan 1987, De Braux et al. 2014). Further, between 30 and 83% of strontium is incorporated into the otolith from the surrounding water, enough to begin changing the $^{87}Sr/^{86}Sr$ signature once the fish begins

exchanging ions directly with the surrounding water through its gills and endothelium (Hayes et al. 1946, Walther and Thorrold 2006).

Previous research indicates that the onset of exogenous feeding could be accompanied by a change in elemental ratios. Experimental evidence indicates that the rate of strontium intake increases to an even faster rate following first-feeding (Yamada and Mulligan 1987), and that magnesium concentration also increases 12-15 days after juveniles hatch (Hayes et al. 1946). The physiological changes that accompany the onset of exogenous feeding could change the regulation of these elements in relation to calcium within the fish's tissues, as well as changes related to the intake of food sources with differing concentrations of elements as compared to that of the yolk sac. The microchemical change also broadly correlates with a first-feeding microstructural check at 235-240μm determined by Barnett-Johnson (2007) in Chinook salmon from California's Central Valley.

Taken together our data suggest that both elemental ratios and $^{87}Sr/^{86}Sr$ ratios provide information on maternally derived chemical influence on the otolith. However, the change from maternal to natal chemistry in $^{87}Sr/^{86}Sr$ and elemental data appears to correspond to different ontological stages. Changes in $^{87}Sr/^{86}Sr$ ratio appear to correspond to the hatching of the larval fish ~150μm, with equilibration continuing until sometime at, or soon after, the onset of exogenous feeding. Elemental ratios of manganese, barium, and strontium appear to reflect the onset of exogenous feeding at ~225μm with a more sudden shift to some equilibrium. While the equilibration of $^{87}Sr/^{86}Sr$ seems to coincide with the change in elemental data, we have no evidence to indicate that this is necessarily causal.

Variation in Maternal Signature

Although Sr/Ca in the core of the otolith can be used to determine maternal anadromy, long inland migrations may attenuate the ocean-derived maternal signature, resulting in variation in the maternal signature. Rieman et al. (1994) showed that Sr/Ca was an incomplete predictor of resident and anadromous maternal behavior in juveniles from a population of *O. nerka* in Idaho, 900km from the ocean. Bacon et al. (2004) found that inland populations in the Pacific Northwest had attenuated or nonexistent Sr/Ca and $^{87}Sr/^{86}Sr$ maternal signatures and Donohoe et al. (2008) showed that a metric of migratory difficulty could explain attenuation of the maternal signature.

This attenuation of maternal signature indicates that mothers who spend significant time in freshwater equilibrate to some degree to the freshwater chemistry along their migratory path and in the natal stream. This equilibration should also be reflected in maternally derived $^{87}Sr/^{86}Sr$ ratios. Our results show that maternal $^{87}Sr/^{86}Sr$ signatures of juvenile Snake River fall Chinook

salmon do vary significantly from the global marine value (Figure 5). As might be expected, the maternal signatures vary in the direction of the water chemistry of the natal stream, indicating a large degree of maternal equilibration not just to the mainstem river in which they reside for most of their upstream migration but to the spawning tributary itself. This is especially evident in fish captured from the Clearwater and Grande Ronde Rivers, spawning reaches whose $^{87}Sr/^{86}Sr$ signatures deviate considerably from the global marine signature, making these changes more apparent. This variation in maternal $^{87}Sr/^{86}Sr$ signatures indicates that for inland populations, maternal $^{87}Sr/^{86}Sr$ ratio does not correlate perfectly to marine residence of the mother.

This result, it seems, would argue that care should be taken in using $^{87}Sr/^{86}Sr$ as a marker of maternal anadromy. However, Courter et al. (2013) used $^{87}Sr/^{86}Sr$ to infer the production of anadromous juveniles in resident rainbow trout in the Yakima River, another inland system in the Columbia River basin with similar inland migration distances. Their success may indicate some degree of species or life-history specific retention of ocean signatures in spawning female salmon. However, without an understanding of these hypothetical species or life-history specific mechanisms, our results indicate caution in interpreting maternal $^{87}Sr/^{86}Sr$ signatures from the otoliths of populations with significant migration distances. This is particularly the case given that our results indicate that the $^{87}Sr/^{86}Sr$ signature of the egg can vary from that of the mother, and that the maternal signature may not be stable in all cases.

Stability of Maternal $^{87}Sr/^{86}Sr$ Signature

The apparent differences, and significant slope of change, in the maternal $^{87}Sr/^{86}Sr$ ratio of fish from the Clearwater River and NPTH groups challenge the assumption made in many studies that the egg is a closed system, reflecting only the chemical signature of the mother. Spawning females used as broodstock at NPTH are captured at Lower Granite dam and make up a random subsample of the run (Milks and Oakerman 2016). They are then transported to the NPTH complex where they are housed in Clearwater River water until they are spawned (Bill Arnsberg, Nez Perce Tribal Fisheries, pers. comm.). Adults who spawn naturally in the Clearwater River move upstream past Lower Granite dam, through the remainder of the Snake River and into the Clearwater River, spawning at a similar time. Thus, adults taken for broodstock at NPTH ultimately spend as much, or perhaps more, time exposed to Clearwater River water as adults who spawn naturally in the river. Despite the similar duration of time mothers are exposed to high $^{87}Sr/^{86}Sr$ Clearwater River water, the mean maternal signature of NPTH juveniles is significantly lower than that of juveniles originating in the Clearwater River (Figure 6A).

Because adult spawners experience similar water chemistries before spawning in both groups, the discrepancy in their progeny's maternal signature is best explained by changes in the

isotopic signature of the egg after spawning. The eggs of the two groups of fish do experience different water chemistries between spawning and hatch, providing a mechanism for the observed difference in maternal $^{87}Sr/^{86}Sr$ if the egg takes up Sr from the surrounding water.

While NPTH adults are kept in Clearwater River water before spawning, spawned eggs are reared in a different water source. This water is a mix of water from the Clearwater River itself and a well drawing from an aquifer below the river which changes through the year. As the river level rises in the spring, the proportion of Clearwater River water increases (Bill Arnsberg, Nez Perce Tribal Fisheries, pers. comm.). The Potlatch River and Lapwai Creek, both nearby low-elevation streams influenced by the same basalt sources as the aquifer from which well water is taken, exhibit signatures of 0.7089 and 0.7068 respectively (Hegg, unpublished data). The mixing of low $^{87}Sr/^{86}Sr$ ratio water influenced by the Columbia River basalts, and the higher $^{87}Sr/^{86}Sr$ water from the Clearwater River which is influenced by older metamorphic rocks upstream, creates the characteristic movement from low $^{87}Sr/^{86}Sr$ ratio early in NPTH otoliths to higher $^{87}Sr/^{86}Sr$ signatures more reflective of the Clearwater River as fish age (Figure 3). Therefore, it is possible that the differing signatures of the water in which eggs at NPTH and in the Clearwater River incubate is responsible for the difference we observed in their maternal signatures.

The idea that the maternal signature of eggs might change seems to be in conflict with the idea that the egg is a closed system (Volk et al. 2000). It is also in contrast to several studies showing that the Sr/Ca chemistry of eggs does not change (Waite et al. 2008, Gabrielsson et al. 2012), and that Sr/Ca signatures are inherited from mothers directly (Kalish 1990, Rieman et al. 1994). However, it should be kept in mind that these studies have been conducted in fish with relatively short spawning runs, whose strontium and calcium concentrations are relatively high compared to the freshwater signatures into which their eggs are laid. Isotope ratio mixing is highly dependent on the concentration of the sources being mixed (Faure and Mensing 2004). Therefore, it would require a relatively large amount of fresh water introduction into the egg to change either Sr/Ca or $^{87}Sr/^{86}Sr$ if the ocean-acquired maternal contribution is significantly elevated.

Salmon eggs do take in as much as 12-15% of their volume in water during the first hours after being laid, and external calcium is required during the process of water hardening, indicating that strontium would also be absorbed in proportion to its concentration in the water (Potts and Rudy 1969, Finn 2007). Further, the egg does not actively osmoregulate and continues to take on water at an approximate rate of $1/300^{th}$ of its mass per day (Loeffler and Løvtrup 1970). Recent research has shown that eggs can be successfully tagged using isotopes of strontium and barium during this initial uptake of water (De Braux et al. 2014, Warren-Myers et al. 2015). Thus, changes to the $^{87}Sr/^{86}Sr$ signature is possible in the hours after eggs are laid, and before the otolith is formed, creating a difference between the maternal signature of the juvenile

otolith and the true maternal signature of its mother at the time the egg was laid. Further, under certain combinations of water and egg chemistry, the slow water exchange during development could create changes in the $^{87}Sr/^{86}Sr$ signature during the period between water-hardening and hatch, much as we observed in NPTH and Clearwater River juveniles.

Our calculations make clear that spawning females must equilibrate substantially to the concentration of freshwater before the $^{87}Sr/^{86}Sr$ signature of the egg could be changed by influx of freshwater (Table 1). The high concentration of Sr in ocean-equilibrated fish effectively buffers changes in $^{87}Sr/^{86}Sr$. But, for females that have substantially equilibrated to freshwater, our calculations show that the $^{87}Sr/^{86}Sr$ signature of the egg can change up to 0.00086 within the first 80 hours after being laid, and as much as 0.00091 by the time of hatch.

The largest calculated change between the mothers' signature and the signature of the egg at hatch was in the case testing NPTH equilibrated maternal signatures, with eggs laid into NPTH well water. In this case the signature changed significantly, and, it should be noted that this change is very close to the value of 0.0009 that we observed between the CWS and NPTH groups, an indication that our calculations are accurately representing the observed shift in $^{87}Sr/^{86}Sr$ for these fish.

Further, our data provide evidence that the signature of the egg can change significantly even after the initial hours of water-hardening. This is shown by the significant slopes of $^{87}Sr/^{86}Sr$ ratio during the maternal period in CWS and NPTH juveniles. Despite large amounts of individual variation, CWS and NPTH maternal signatures show highly significant slopes moving in the direction equilibration to the ambient water, a positive slope in CWS fish and a negative slope in NPTH juveniles (Figure 6B). This is further supported by our calculations showing that a change in $^{87}Sr/^{86}Sr$ ratio in the fourth digit, well within the analytical precision, could be expected in each case.

Conclusions

Maternally derived chemical signatures in fish otoliths, and Sr/Ca in particular, have been instrumental in connecting maternal anadromy to the life-history of their progeny. More recently researchers have begun to infer anadromy from maternally derived $^{87}Sr/^{86}Sr$ signatures as well. At the same time researchers are examine ever more detailed early movement and life-stages of juvenile fish. As more inferences are made from otoliths about the maternal and early juvenile periods it is increasingly important to know when the maternal signature end and juvenile signature begins to avoid including erroneous chemical data that could bias results. Despite this need, there has been little understanding of when the influence of maternally derived chemistry ends on the otolith. Our study indicates that both elemental and $^{87}Sr/^{86}Sr$ ratios mark ontogenetic

changes within larval fish. Further, these signals can be used to determine the end of maternal influence, and the beginning of signatures derived from the water of the natal location. However, our results show that $^{87}Sr/^{86}Sr$ and elemental data are asynchronous, and likely signal two different ontogenetic changes in the developing fish. We believe it is likely that changes in $^{87}Sr/^{86}Sr$ signal hatching, while elemental signatures of Mn/Ca and Ba/Ca likely signal the onset of exogenous feeding. Further, our results indicate that as female spawners equilibrate toward freshwater concentrations, the $^{87}Sr/^{86}Sr$ signature of their eggs may shift after they are laid, and in some cases significant changes can occur. Thus, eggs may not directly reflect the maternal signature, complicating the use of $^{87}Sr/^{86}Sr$ as a method for determining maternal anadromy in inland populations with significant migrations. Further work is needed to verify the duration and stability of maternal signatures under varying elemental concentrations and signatures, and the relationship of elemental signatures to early ontological changes in larval fish.

References

Bacon, C.R., Weber, P.K., Larsen, K.A., Reisenbichler, R., Fitzpatrick, J.A., and Wooden, J.L. 2004. Migration and rearing histories of chinook salmon (Oncorhynchus tshawytscha) determined by ion microprobe Sr isotope and Sr/Ca transects of otoliths. Can. J. Fish. Aquat. Sci. 61(12): 2425–2439.

Barnett-Johnson, R., Grimes, C.B., Royer, C.F., and Donohoe, C.J. 2007. Identifying the contribution of wild and hatchery Chinook salmon (Oncorhynchus tshawytscha) to the ocean fishery using otolith microstructure as natural tags. Can. J. Fish. Aquat. Sci. 64(12): 1683–1692. NRC Research Press Ottawa, Canada. doi:10.1139/f07-129.

Barnett-Johnson, R., Pearson, T.E., Ramos, F.C., Grimes, C.B., and MacFarlane, R.B. 2008. Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. Limnol. Oceanogr. 53(4): 1633–1642.

Barnett-Johnson, R., Teel, D.J., and Casillas, E. 2010. Genetic and otolith isotopic markers identify salmon populations in the Columbia River at broad and fine geographic scales. Environ. Biol. fishes 89(3): 533–546.

Boyd, J.W., Oldenburg, E.W., McMichael, G.A., Dell, M., and Schadt, T. 2010. Color photographic index of fall Chinook salmon embryonic development and accumulated thermal units. PLoS One 5(7): e11877. Academic Press. doi:10.1371/journal.pone.0011877.

De Braux, E., Warren-Myers, F., Dempster, T., Fjelldal, P.G., Hansen, T., and Swearer, S.E. 2014. Osmotic induction improves batch marking of larval fish otoliths with enriched stable isotopes. ICES J. Mar. Sci. 71(9): 2530–2538. doi:10.1093/icesjms/fsu091.

Brodersen, J., Chapman, B.B., Nilsson, P.A., Skov, C., Hansson, L.A., and Brönmark, C. 2014. Fixed and flexible: coexistence of obligate and facultative migratory strategies in a freshwater fish. PLoS One 9(3): e90294. Public Library of Science. doi:10.1371/journal.pone.0090294.

Brophy, D., Jeffries, T.E., and Danilowicz, B.S. 2004. Elevated manganese concentrations at the cores of clupeid otoliths : possible environmental , physiological , or structural origins. Mar. Biol. 144: 779–786. doi:10.1007/s00227-003-1240-3.

Brown, R.J., and Severin, K.P. 2009. Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish. Can. J. Fish. Aquat. Sci. 66(10): 1790–1808. doi:10.1139/F09-112.

Burke, J.L. 2004. Life histories of juvenile Chinook salmon in the Columbia River estuary: 1916 to the present. Oregon State University.

Campana, S.E. 2005. Otolith science entering the 21st century. Mar. Freshw. Res. 56(5): 485–496.

Campana, S.E., and Thorrold, S.R. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Can. J. Fish. Aquat. Sci. 58(1): 30–38.

Chapman, B.B., Brönmark, C., Nilsson, J.Å., and Hansson, L.A. 2011. The ecology and evolution of partial migration. Oikos 120(12): 1764–1775. Blackwell Publishing Ltd.

doi:10.1111/j.1600-0706.2011.20131.x.

Connor, W., Burge, H., and Bennett, D. 1998. Detection of PIT-tagged subyearling Chinook salmon at a Snake River dam: implications for summer flow augmentation. North Am. J. … 18(Figure 1): 530–536. Taylor & Francis Group. doi:10.1577/1548-8675(1998)018<0530:DOPTSC>2.0.CO;2.

Connor, W.P., Sneva, J.G., Tiffan, K.F., Steinhorst, R.K., and Ross, D. 2005. Two alternative juvenile life history types for fall Chinook salmon in the Snake River basin. Trans. Am. Fish. Soc. 134(2): 291–304.

Courter, I.I., Child, D.B., Hobbs, J.A., Garrison, T.M., Glessner, J.J.G., Duery, S., and Fraser, D. 2013. Resident rainbow trout produce anadromous offspring in a large interior watershed. Can. J. Fish. Aquat. Sci. 70(5): 701–710. NRC Research Press. doi:10.1139/cjfas-2012-0457.

Donohoe, C.J., Adams, P.B., and Royer, C.F. 2008. Influence of water chemistry and migratory distance on ability to distinguish progeny of sympatric resident and anadromous rainbow trout (Oncorhynchus mykiss). Can. J. Fish. Aquat. Sci. 1075(65): 1060–1075. doi:10.1139/F08-029.

Elsdon, T.S., Wells, B.K., Campana, S.E., Gillanders, B.M., Jones, C.M., Limburg, K.E., Secor, D.H., Thorrold, S.R., Walther, B.D., and Barnes, H.R. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. In Oceanography and Marine Biology: an annual review, vol 46. pp. 297–330. doi:10.1201/9781420065756.ch7.

Faure, G., and Mensing, T.M. 2004. Isotopes: principles and applications. John Wiley & Sons Inc.

Finn, R.N. 2007. The physiology and toxicology of salmonid eggs and larvae in relation to water quality criteria. Aquat. Toxicol. 81(166): 337–354. doi:10.1016/j.aquatox.2006.12.021.

Gabrielsson, R.M., Kim, J., Reid, M.R., Stirling, C.H., Numata, M., and Closs, G.P. 2012. Does the trace element composition of brown trout Salmo trutta eggs remain unchanged in spawning redds? J. Fish Biol. 81(6): 1871–1879. Blackwell Publishing Ltd. doi:10.1111/j.1095-8649.2012.03396.x.

Garcia, A.P., Bradbury, S., Arnsberg, B.D., and Groves, P.A. 2008. Fall Chinook salmon spawning ground surveys in the Snake River basin upriver of Lower Granite Dam, 2007 Annual Report. Available from http://www.osti.gov/bridge/servlets/purl/962477-V6etxJ/.

Garcia, A.P., Bradbury, S., Arnsberg, B.D., Rocklage, S.J., and Groves, P.A. 2005. Fall Chinook salmon spawning ground surveys in the Snake River basin upriver of Lower Granite Dam, 2004. 2004 Annu. Rep. to Bonnev. Power Adm. Proj.: 3.

Good, T.P., Waples, R.S., and Adams, P. 2005. Updated status of federally listed ESU's of West Coast salmon and steelhead. In NOAA Technical Memorandum NMFS-NWFSC-66. Edited byU.S.D. of Commerce. NOAA.

Hamann, E.J., and Kennedy, B.P. 2012. Juvenile dispersal affects straying behaviors of adults in a migratory population. Ecology 93(4): 733–740.

Hamer, P., Henderson, A., Hutchison, M., Kemp, J., Green, C., and Feutry, P. 2015. Atypical correlation of otolith strontium:calcium and barium:calcium across a marine-freshwater life history transition of a diadromous fish. Mar. Freshw. Res. 66(5): 411–419. doi:10.1071/MF14001.

Hayes, F.R., Darcy, D.A., and Sullivan, C.M. 1946. Changes in the Inorganic Contituents of Developing Salmon Eggs. J. Biol. Chem. 163: 621–632. Available from http://www.jbc.org/content/163/3/621.short.

Hegg, J.C., Giarrizzo, T., and Kennedy, B.P. 2015a. Diverse Early Life-History Strategies in Migratory Amazonian Catfish: implications for Conservation and Management. PLoS One 10(7). doi:10.1371/journal.pone.0129697.

Hegg, J.C., Giarrizzo, T., and Kennedy, B.P. 2015b. Diverse Early Life-History Strategies in Migratory Amazonian Catfish: Implications for Conservation and Management. bioRxiv (in-review, PloS One) pre-print: 1–37. doi:http://dx.doi.org/10.1101/018671.

Hegg, J.C., Kennedy, B.P., Chittaro, P.M., and Zabel, R.W. 2013a. Spatial structuring of an evolving life-history strategy under altered environmental conditions. Oecologia 172(4): 1017–1029. Springer-Verlag. doi:10.1007/s00442-012-2564-9.

Hegg, J.C., Kennedy, B.P., and Fremier, A.K. 2013b. Predicting strontium isotope variation and fish location with bedrock geology: understanding the effects of geologic heterogeneity. Chem. Geol. 360–361: 89–98. doi:10.1016/j.chemgeo.2013.10.010.

Hodge, B.W., Wilzback, M.A., Duffy, W.G., Quinones, R.M., and Hobbs, J.A. 2016. Life history diversity in Klamath River steelhead. Trans. Am. Fish. Soc. 145(2): 227–238. Taylor & Francis. doi:10.1080/00028487.2015.1111257.

Isaak, D.J., Thurow, R.F., Rieman, B.E., and Dunham, J.B. 2003. Temporal variation in synchrony among Chinook salmon (Oncorhynchus tshawytscha) redd counts from a wilderness area in central Idaho. Can. J. Fish. Aquat. Sci. 60(7): 840–848.

James, N.A., and Matteson, D.S. 2014. ecp: An R Package for Nonparametric Multiple Change Point Analysis of Multivariate Data. JSS J. Stat. Softw. 62(7). Available from http://www.jstatsoft.org/ [accessed 4 April 2017].

Jochum, K.P., Weis, U., Stoll, B., Kuzmin, D., Yang, Q., Raczek, I., Jacob, D.E., Stracke, A., Birbaum, K., Frick, D.A., Günther, D., and Enzweiler, J. 2011. Determination of reference values for NIST SRM 610-617 glasses following ISO guidelines. Geostand. Geoanalytical Res. 35(4): 397–429. Blackwell Publishing Ltd. doi:10.1111/j.1751-908X.2011.00120.x.

Kalish, J.M. 1990. Use of Otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull. 88(4): 657–666. Available from http://fishbull.noaa.gov/884/kalish.pdf [accessed 22 March 2017].

Kennedy, B.P., Blum, J.D., Folt, C.L., and Nislow, K.H. 2000. Using natural strontium isotopic signatures as fish markers: methodology and application. Can. J. Fish. Aquat. Sci. 57(11): 2280–2292.

Kennedy, B.P., Folt, C.L., Blum, J.D., and Chamberlain, C.P. 1997. Natural isotope markers in salmon. Nature 387(6635): 766–767.

Killick, R., and Eckley, I.A. 2013. Changepoint: An R Package for changepoint analysis. R Packag. version 0.6, URL http//CRAN.R-project.org/package=changepoint: 1–15. Available from http://www.lancs.ac.uk/~killick/Pub/KillickEckley2011.pdf.

Kraus, R.T., and Secor, D.H. 2004. Incorporation of strontium into otoliths of an estuarine fish. J. Exp. Mar. Bio. Ecol. 302(1): 85–106. doi:10.1016/j.jembe.2003.10.004.

Liberoff, A.L., Miller, J.A., Riva-Rossi, C.M., Hidalgo, F.J., Fogel, M.L., Pascual, M.A., and Tierney, K. 2014. Transgenerational effects of anadromy on juvenile growth traits in an introduced population of rainbow trout (Oncorhynchus mykiss). Can. J. Fish. Aquat. Sci. 71(November 2013): 398–407. NRC Research Press. doi:10.1139/cjfas-2013-0466.

Liberoff, A.L., Quiroga, A.P., Riva-Rossi, C.M., Miller, J.A., and Pascual, M.A. 2015. Influence of maternal habitat choice, environment and spatial distribution of juveniles on their propensity for anadromy in a partially anadromous population of rainbow trout (Oncorhynchus mykiss). Ecol. Freshw. Fish 24(3): 424–434. doi:10.1111/eff.12157.

Limburg, K.E., Landergren, P., Westin, L., Elfman, M., and Kristiansson, P. 2001. Flexible modes of anadromy in Baltic sea trout: making the most of marginal spawning streams. J. Fish Biol. 59(3): 682–695. Blackwell Publishing Ltd. doi:10.1006/jfbi.2001.1681.

Loeffler, C.A., and Løvtrup, S. 1970. Water Balance in the Salmon Egg. J. Exp. Biol. 52: 291–298. Available from http://jeb.biologists.org/content/52/2/291.article-info.

Macdonald, J.I., Shelley, J.M.G., and Crook, D. a. 2008. A Method for improving the estimation of natal chemical signatures in otoliths. Trans. Am. Fish. Soc. 137(6): 1674–1682. doi:10.1577/T07-249.1.

Milks, D., and Oakerman, A. 2016. Lyons Ferry Hatchery evaluation fall Chinook salmon annual report: 2014. Olympia, WA. Available from https://www.fws.gov/lsnakecomplan/Reports/WDFW/Eval/2014 Annual FCH Report FINAL.pdf [accessed 8 April 2017].

Miller, J.A., Butler, V.L., Simenstad, C.A., Backus, D.H., Kent, A.J.R., and Gillanders, B. 2011. Life history variation in upper Columbia River Chinook salmon (Oncorhynchus tshawytscha): a comparison using modern and~ 500-year-old archaeological otoliths. Can. J. Fish. Aquat. Sci. 68(4): 603–617.

Miller, J.A., and Kent, A.J.R. 2009. The determination of maternal run time in juvenile Chinook salmon (Oncorhynchus tshawytscha) based on Sr/Ca and 87Sr/86Sr within otolith cores. Fish. Res. 95(2–3): 373–378. doi:10.1016/j.fishres.2008.09.030.

Morinville, G.R., and Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (Salvelinus fontinalis). Can. J. Fish. Aquat. Sci. 60(4): 401–410. NRC Research Press Ottawa, Canada. doi:10.1139/f03-036.

Muggeo, V.M.R. 2003. Estimating regression models with unknown break-points. Stat. Med. Stat. Med 22: 3055–3071. doi:10.1002/sim.1545.

Muggeo, V.M.R. 2008. segmented: an R package to fit regression models with broken-line relationships. R News 8(1): 20–25.

Potts, W.T.W., and Rudy, P.P. 1969. Water Balance in the Eggs of the Atlantic Salmon Salmo

Salar. J. Exp. Biol 50: 223–337. Available from http://ida.lib.uidaho.edu:4254/content/jexbio/50/1/223.full.pdf [accessed 23 March 2017].

Razali, N.M., and Wah, Y.B. 2011. Power comparisons of Shapiro-Wilk, Kolmogorov-Smirnov, Lilliefors and Anderson-Darling tests. J. Stat. Model. Anal. 2(1): 21–33. Available from https://www.nrc.gov/docs/ML1714/ML17143A100.pdf [accessed 16 March 2018].

Rieman, B.E., Myers, D.L., and Nielsen, R.L. 1994. Use of otolith microchemistry to discriminate Oncorhynchus nerka of resident and anadromous origin. Can. J. Fish. Aquat. Sci. 51(1): 68–77. NRC Research Press Ottawa, Canada. doi:10.1139/f94-009.

Rombough, P.J., and Garside, E.T. 1982. Cadmium toxicity and accumulation in eggs and alevins of atlantic salmon Salmo salar. Can. J. Zool. 60: 2006–2014. Available from http://www.nrcresearchpress.com/doi/pdf/10.1139/z82-258.

Ruttenberg, B.I. et al. 2005. Elevated evels of trace elements in cores of otoliths and their potential for use as natural tags. Mar. Ecol. Prog. Ser. 297: 273–281. doi:10.3354/meps297273.

Schaffler, J.J., Miller, T.J., and Jones, C.M. 2014. Spatial and temporal variation in otolith chemistry of juvenile Atlantic menhaden in the Chesapeake Bay. Trans. Am. Fish. Soc. 143(4): 1061–1071. doi:doi:10.1080/00028487.2014.889748.

Secor, D.H., Dean, J.M., and Laban, E.H. 1992. Otolith removal and preparation for microstructural analysis. In Otolith Microstructure Examination and Analysis, Canadian S. Edited by S.E. Campana and D.K. Stevenson. Ottawa. pp. 19–57. Available from http://www.dfo-mpo.gc.ca/Library/141734.pdf [accessed 23 January 2018].

Secor, D.H., and Kerr, L.A. 2009. Lexicon of life cycle diversity in diadromous and other fishes. Challenges diadromous fishes a Dyn. Glob. Environ. Am. Fish. Soc. Symp. 69 69: 537–556. Available from http://secor.cbl.umces.edu/ctv/Secor&Kerr_AFS.Symp_2009.pdf [accessed 31 July 2017].

Shippentower, G.E., Schreck, C.B., and Heppell, S.A. 2011. Who’s your momma? Recognizing maternal origin of juvenile steelhead using injections of strontium chloride to create transgenerational marks. Trans. Am. Fish. Soc. 140(5): 1330–1339. Taylor & Francis Group. doi:10.1080/00028487.2011.620488.

Shrimpton, J.M., Warren, K.D., Todd, N.L., McRae, C.J., Glova, G.J., Telmer, K.H., and Clarke, a D. 2014. Freshwater movement patterns by juvenile Pacific salmon Oncorhynchus spp. before they migrate to the ocean: Oh the places you’ll go! J. Fish Biol. 85(4): 987–1004. doi:10.1111/jfb.12468.

Stewart, D.C., Middlemas, S.J., and Youngson, a. F. 2006. Population structuring in Atlantic salmon (Salmo salar): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. Ecol. Freshw. Fish 15(4): 552–558. doi:10.1111/j.1600-0633.2006.00197.x.

Taylor, E.B.B. 1990. Environmental correlates of life-history variation in juvenile chinook salmon, Oncorhynchus tshawytscha (Walbaum). J. Fish Biol. 37(1): 1–17. doi:10.1111/j.1095-8649.1990.tb05922.x.

Thériault, V., Garant, D., Bernatchez, L., and Dodson, J.J. 2007. Heritability of life-history tactics and genetic correlation with body size in a natural population of brook charr (Salvelinus fontinalis). J. Evol. Biol. 20(6): 2266–2277. Blackwell Publishing Ltd. doi:10.1111/j.1420-9101.2007.01417.x.

Thorrold, S.R., Jones, C.M., Campana, S.E., McLaren, J.W., and Lam, J.W.H. 1998. Trace element signatures in otoliths record natal river of juvenile American shad (Alosa sapidissima). Limnol. Oceanogr.: 1826–1835.

Thorrold, S.R., Jones, G.P., Planes, S., and Hare, J.A. 2006. Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. Can. J. Fish. Aquat. Sci. 63(6): 1193–1197. NRC Research Press Ottawa, Canada. doi:10.1139/f06-048.

Tsukamoto, K., and Arai, T. 2001. Facultative catadromy of the eel Anguilla japonica between freshwater and seawater habitats. Mar. Ecol. Prog. Ser. 220: 265–276. doi:10.3354/meps220265.

Turner, S.M., Limburg, K.E., and Palkovacs, E.P. 2015. Can different combinations of natural tags identify river herring natal origin at different levels of stock structure ? Can. J. Fish. Aquat. Sci. 72(February): 845–854. doi:10.1139/cjfas-2014-0403.

Veinott, G., Westley, P.A.H., Purchase, C.F., and Warner, L. 2014. Experimental evidence simultaneously confirms and contests assumptions implicit to otolith microchemistry research. Can. J. Fish. Aquat. Sci. 71(3): 356. NRC Research Press. doi:doi: 10.1139/cjfas-2013-0224.

Volk, E.C., Blakley, A., Schroder, S.L., and Kuehner, S.M. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: using otolith core chemistry to distinguish maternal associations with sea and freshwaters. Fish. Res. 46(1–3): 251–266.

Waite, E.M., Closs, G.P., Kim, J., Barry, B., Markwitz, A., and Fitzpatrick, R. 2008. The strontium content of roe collected from spawning brown trout Salmo trutta L. reflects recent otolith microchemistry. J. Fish Biol. 72(7): 1847–1854. Blackwell Publishing Ltd. doi:10.1111/j.1095-8649.2008.01842.x.

Walther, B.D., and Thorrold, S.R. 2006. Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. Mar. Ecol. Prog. Ser. 311: 125–130. doi:10.3354/meps311125.

Walther, B.D., and Thorrold, S.R. 2010. Limited diversity in natal origins of immature anadromous fish during ocean residency. Can. J. Fish. Aquat. Sci. 67(10): 1699–1707. doi:10.1139/F10-086.

Waples, R.S., Elz, A., Arnsberg, B.D., Faulkner, J.R., Hard, J.J., Timmins-Schiffman, E., and Park, L.K. 2017. Human-mediated evolution in a threatened species? Juvenile life-history changes in Snake River salmon. Evol. Appl. (February). doi:10.1111/eva.12468.

Warren-Myers, F., Dempster, T., Fjelldal, P.G., Hansen, T., and Swearer, S.E. 2015. Immersion during egg swelling results in rapid uptake of stable isotope markers in salmonid otoliths. Can. J. Fish. Aquat. Sci. 72(5): 722–727. doi:10.1139/cjfas-2014-0390.

Williams, J.G., Zabel, R.W., Waples, R.S., Hutchings, J.A., and Connor, W.P. 2008. Potential

for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. Evol. Appl. 1(2): 271–285.

Woodcock, S.H., Grieshaber, C.A., and Walther, B.D. 2013. Dietary transfer of enriched stable isotopes to mark otoliths, fin rays, and scales. Can. J. Fish. Aquat. Sci. 70(1): 1–4. NRC Research Press. doi:10.1139/cjfas-2012-0389.

Yamada, S.B., and Mulligan, T.J. 1987. Marking nonfeeding salmonid fry with dissolved strontium. Can. J. Fish. Aquat. Sci. 44(8): 1502–1506. NRC Research Press Ottawa, Canada . doi:10.1139/f87-180.

Zabel, R., Haught, K., and Chittaro, P. 2010. Variability in fish size/otolith radius relationships among populations of Chinook salmon. Environ. Biol. fishes 89(3): 267–278. Springer Netherlands. doi:10.1007/s10641-010-9678-x.

Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Can. J. Fish. Aquat. Sci. 62(1): 88–97. CSIRO PUBLISHING. doi:10.1139/f04-182.

CHAPTER THREE

Reconstructing the early life history of a migratory species

Paul M. Chittaro, Richard W. Zabel, Laurie Weitkamp, Lyndal Johnson,
and Cynthia Bucher

National Oceanic and Atmospheric Administration
Northwest Fisheries Science Center
2725 Montlake Boulevard East
Seattle, WA 98112

and

Jens C. Hegg and Brian P. Kennedy

University of Idaho
Department of Fish and Wildlife Resources
975 West 6th Street
Moscow, ID 93844

Introduction

Many species take part in annual or seasonal migrations that are thought to optimize fitness (Baker 1978) and which are prompted by food and/or reproductive requirements (Ronce et al. 2001, Lascelles et al. 2014). Ultimately, optimizing fitness involves tradeoffs between growth and survival (e.g., Gross 1987). However, due to anthropogenic disturbances that disrupt habitat quality, quantity, and connectivity (Lotze et al. 2006, Halpern et al. 2008), migratory species are being adversely affected as the habitats they rely on for all or part of their life are lost or disturbed (Martin et al. 2007, Robinson et al. 2009, Fukushima et al. 2014). Disturbances to habitat can lead to phenotypic changes that are presumably guided by selection (Williams et al. 2008).

Fall Chinook salmon in the Snake River Basin (a tributary of the Columbia River in the U.S. Pacific northwest) have lost about 90% of their historic spawning habitat with the creation of the Hell's Canyon Dam complex in the 1960's (Ruckelshaus et al. 2002) (Figure 1). Due to dramatic declines in its abundance, Snake River fall Chinook salmon was listed as threatened under the Endangered Species Act, ESA (Pacific Fisheries Management Council 2014). Unfortunately, several factors continue to limit its recovery including migration through eight dams (Mathur et al. 1996, Singer et al. 2013), dam-altered hydrology and water temperature (Steel and Lange 2007, Geist et al. 2010, Harnish et al. 2014), predation from invasive species (Kuehne and Olden 2012), reduced availability and quality of rearing (Tiffan et al. 2006, Tiffan et al. 2014) and spawning habitat (Chapman et al. 1986, Geist et al. 2008, Hatten et al. 2009), harvest levels, and hatchery practices (Ruckelshaus et al. 2002).

Notable in this population is the presence of a relatively novel juvenile outmigration strategy for which little is understood (Connor et al. 2002, Williams et al. 2008). Historically, the Snake River fall Chinook salmon consisted predominantly of a subyearling outmigration strategy whereby juveniles migrate to the ocean a few months after their spring emergence (i.e., first feeding)(Connor et al. 2002, Williams et al. 2008). Over the last two decades a yearling outmigration strategy has been reported in which juveniles are thought to remain in freshwater for an extended period (i.e., overwinter) prior to migrating to the ocean the following spring (Connor et al. 2005). Because migration timing has significant effects on the degree to which individuals overlap in space and time with vital resources (Stearns 1992, Crozier et al. 2008, Scheuerell et al. 2009), which in turn can impact population recovery, it is important that we identify the rivers and migration strategies that contribute individuals to the adult population.

Here we examine the early life history of Snake River Chinook salmon by examining their otoliths, which are calcified structures used for balance. The chemical and structural analysis of a fish's hard parts, particularly scales and otoliths, make them a useful tool for acquiring information about an individual's movement and performance (Campana 1999). During the life

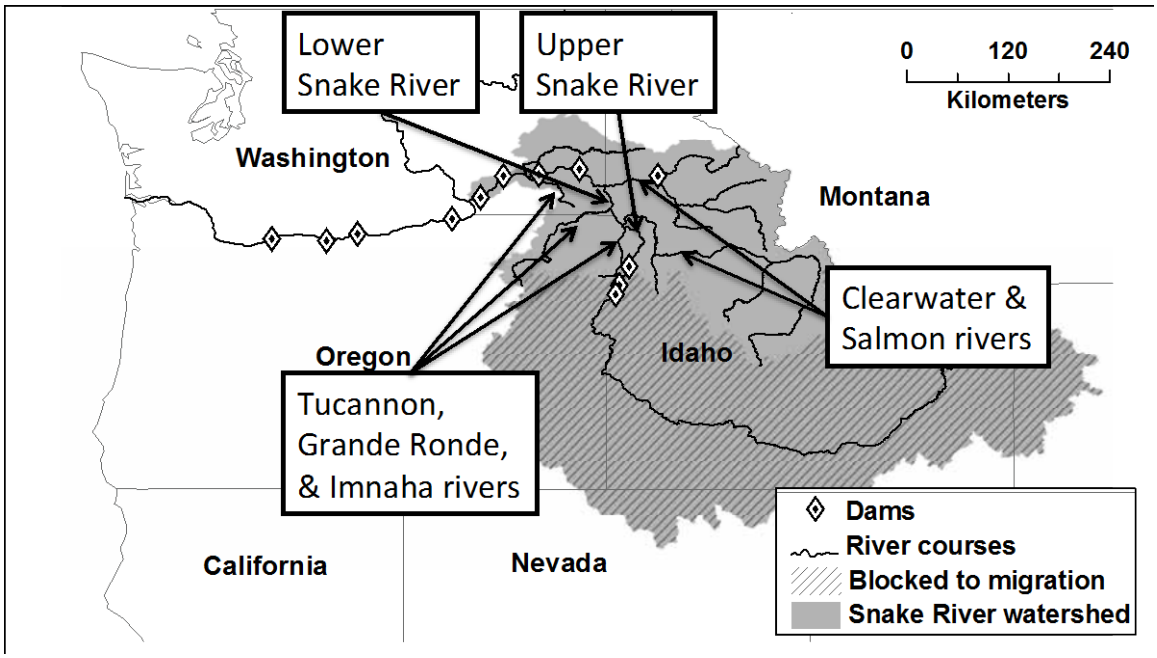

Figure 1. Map of the Snake River watershed showing location of dams and area blocked to spawning of fall Chinook salmon (*Oncorhynchus tshawytscha*). Four river spawning locations were identified to have unique 87Sr/86Sr values (Hegg et al. 2013a): lower Snake River, upper Snake River, Clearwater and Salmon rivers, and Tucannon, Grande Ronde, and Imnaha rivers.

of a fish its otoliths grow continually by the deposition of layers of calcium carbonate and protein, and these layers form visible increments that can be used to determine age (Jones 1992, Stevenson and Campana 1992). This age information together with body size-age relationships means that body size and somatic growth can be estimated for earlier points in an individual's life (Casselman 1987). Further, as otolith layers form, ions are deposited onto the otolith's growing surface often at concentrations that reflect those in the environment (Bath et al. 2000), and therefore all individuals, regardless of size and age, are naturally tagged with environmentally derived ions. The combined information provided by otolith structure and chemistry allow retrospective determination of age-, size-, and location-specific chemical signatures that can be used to assess habitat use, somatic growth, and movement (Kennedy et al. 2002, Elsdon et al. 2008, Walther and Thorrold 2010).

In this study, we used otolith chemistry and structure as a means to investigate early life history movement and performance of Snake River fall Chinook salmon. This population is an ideal study species because they have predictable spawning times and locations allowing adults to be readily collected, and an early life history in which they occupy chemically distinct freshwater, estuarine, and ocean habitats, which can facilitate otolith-derived reconstruction of their movement and habitat use (Hegg et al. 2013b). The purpose of our project was three-fold. First, we wanted to identify where returning adults originated and reared, and which juvenile outmigration strategy they exhibited (subyearling vs. yearling). Second, using somatic growth as an indicator of performance, we sought to determine whether performance varied with respect to natal origin, rearing location, and migration strategy. Lastly, we used a generalized linear modeling (glm) approach to investigate the extent to which growth and size at Snake River egress and ocean entry were explained by a suite of independent variables. Results from this study are intended to help inform recovery planning for Snake River fall Chinook salmon including future habitat restoration and conservation efforts in the Snake River Basin and Columbia River.

Methods

Study species

Spawning of Snake River fall Chinook salmon occurs primarily in gravel beds of Snake and Clearwater rivers (Zabel et al. 2010) with peak spawning occurring in November (Connor et al. 2002, Harnish et al. 2014). Individuals hatch and remain in the interstitial spaces of the gravel until their yolk-sac is depleted, after which they leave the gravel and become free-swimming juveniles (referred to as emergence)(Quinn 2005). Juveniles that successfully migrate downstream will spend 1-4 years in the ocean before returning to the Columbia River estuary and migrating upriver to spawn in freshwater.

Fish collection and otolith preparation

Returning adult fall Chinook salmon (n=125; 830mm average fork length; 72mm standard deviation) were randomly subsampled from spawning operations at Lyons Ferry Hatchery, Washington, November 2011. These sampled adults lacked an internal or external artificial tag, such as an acoustic or radio tag, and had an intact adipose fin (injecting/attaching tags and fin clipping are procedures used in hatcheries to identify hatchery produced individuals). However, not all hatchery produced fish are tagged and/or clipped, and therefore these fish were initially presumed to be wild produced.

Juvenile fall Chinook salmon (n=21; 90mm average fork length; 17mm standard deviation) were collected during the summer of 2011 at Lower Granite Dam and used to evaluate the accuracy of our classification of adults to rearing location (see *Classification of adults and juveniles to natal and rearing locations*). This test of classification accuracy was possible because rearing location was known for these juveniles. Specifically, these juveniles were previously implanted with passive integrated transponder tags (PIT tags) upriver of Lower Granite Dam (located on the lower portion of the Snake River).

We measured the fork length (mm) of each fish, removed their sagittal otoliths, and placed these otoliths into dry storage. Left sagittal otoliths were mounted on glass microscope slides using thermoplastic cement (Crystal Bond[1], http://www.crystalbond.com). Each otolith (juveniles and adults) was polished on both sides in a sagittal plane using slurries (600-grit silicon carbide, 5.0 alumina oxide, and 1.0 micropolish; http://www.buehler.com) and a grinding wheel with Buehler© 1500 micropolishing pads. Polishing ceased when the core was visible. We photographed polished otoliths using a digital camera (Leica DFC450) mounted on a compound microscope (Zeiss©). Age for each adult was provided by Lyons Ferry Hatchery, and was based on scale analysis of three scales taken dorsal to the lateral line and posterior to the dorsal fin (Milks et al. 2013).

Otolith Microstructure

To reconstruct the juvenile size at Snake River egress and ocean entry from adult otoliths we used a quadratic relationship between fork length and otolith radius that was developed for Snake River fall Chinook salmon (Zabel et al. 2010). To use this relationship to estimate size at Snake River egress and ocean entry we needed the otolith radius at Snake River egress and ocean entry. First, we determined the location on the otolith of Snake River egress and ocean entry using otolith microchemistry (see below). Then we measured otolith radius to Snake River egress

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

and ocean entry as the distance from the otolith core to the location on the otolith of Snake River egress and ocean entry, respectively, along a transect perpendicular to the longitudinal axis on the dorsal side of the otolith. Along this same transect we also measured the otolith radius to the outside margin of the first annual mark (Murray 1994). We used the otolith radius to the first annual mark to classify individuals to a migration strategy (see below). Otolith radius was measured from digital photographs using Image Pro software (version 7.0; MediaCybernetics©).

Otolith Microchemistry

To reconstruct where adults resided as juveniles we used the chemistry of their otoliths. Polished otoliths from adults and juveniles were analyzed for $^{87}Sr/^{86}Sr$ at the GeoAnalytical Lab at Washington State University (Pullman, WA), using a Finnigan Neptune (ThermoScientific) multi-collector inductively coupled plasma mass spectrometer with helium as the carrier gas. The mass spectrometer was coupled with a New Wave UP-213 laser ablation sampling system (frequency of 20Hz, 40µm spot size) (LA-MC-ICPMS). Using an automated microscope stage, the laser beam moved at a speed of 10µm/s and ablated the polished otolith along a transect from the otolith edge to its core (the transect was perpendicular to the longitudinal axis on the dorsal side of the otolith). This edge-to-core scan line on the otolith corresponds to the entire life of the fish (Figure 2a).

Data acquisition of the LA-MC-ICPMS lasted 250s, 14s of which were designated for instrument calibration and gas background counts prior to the start of each ablation. To evaluate measurement error, we analyzed a marine shell standard that was assumed to be in equilibrium with the global marine value of $^{87}Sr/^{86}Sr$ (0.70918) (Faure and Mensing 2004). The marine shell standard was analyzed 3-4 times every 15-20 otolith samples. During the course of this study the average $^{87}Sr/^{86}Sr$ ratio for the marine shell was 0.709197 (SD =0.000036, n=21). Values of otolith $^{87}Sr/^{86}Sr$ ratio were adjusted daily using a correction factor calculated each analysis day from the average deviation of the shell standard to the marine value (Hegg et al. 2013a).

It was necessary to estimate the origin (i.e., hatchery or wild) of our adult samples before proceeding with analyses. In a separate study, wild and hatchery produced adults were differentiated based on unique $^{87}Sr/^{86}Sr$ ratio and trace element ratios (25Mg:43Ca, 55Mn:43Ca, 66Zn:43Ca, 86Sr:43Ca, 138Ba:43Ca, and 208Pb:43Ca) in hatcheries releasing Snake River fall Chinook salmon (Heggs pers com). We applied this technique to the 125 adults of this study and we incorporated this hatchery-wild classification into our analyses of early life history residence, size, and growth. We measured trace elemental ratios using a Finnigan Element2 high resolution ICP–MS (with helium as the carrier gas), coupled with the New Wave laser ablation system (New Wave UP-213) at the GeoAnalytical Facility of Washington State University.

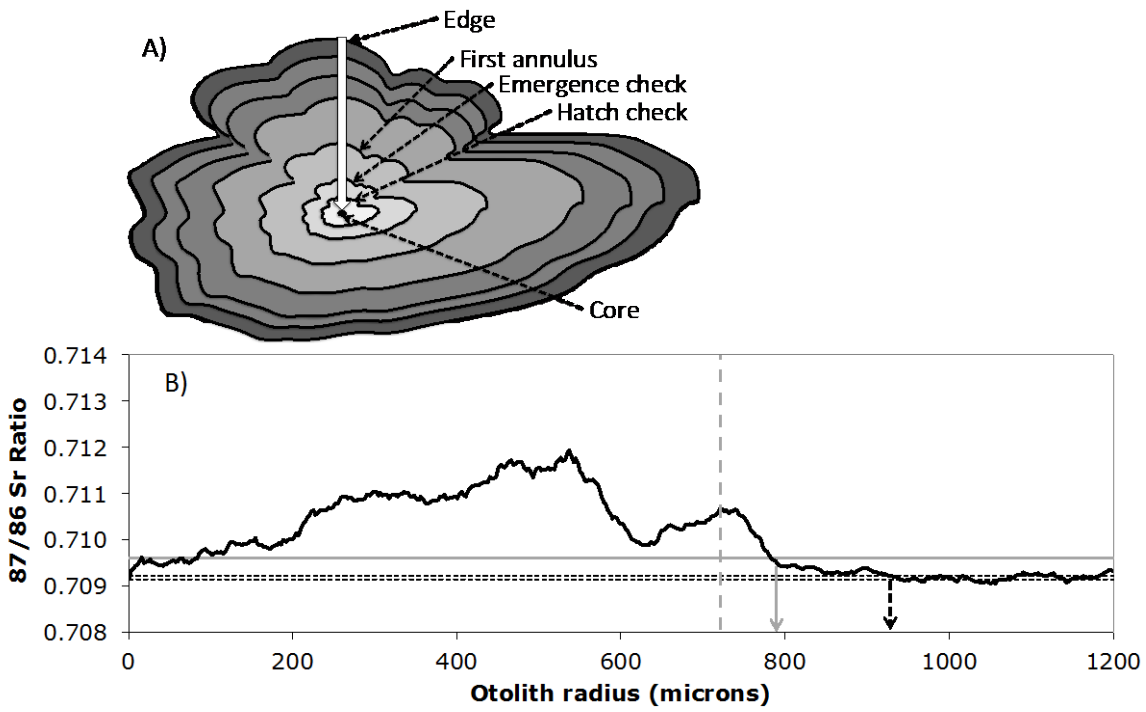

Figure 2. A) Illustration of an adult otolith showing hatch, emergence, and first annulus marks and the path of laser ablation (white arrow). B) Representation showing how changes in $^{87}Sr/^{86}Sr$ ratio of an adult Chinook salmon otolith were used to identify the otolith radius at Snake River egress and ocean entry, and whether the fish exhibited the yearling or subyearling migration strategy. Laser ablation inductively coupled plasma mass spectrometry from otolith edge to core was used to produce a time series of $^{87}Sr/^{86}Sr$ ratio (black line). We used visual inspection of the $^{87}Sr/^{86}Sr$ ratio to determine the otolith radius when an individual exited Snake River (Snake River is indicated by the grey line at 0.70960; the grey arrow corresponds to Snake River egress). We used the merging of $^{87}Sr/^{86}Sr$ ratio onto the range of 0.70914-0.70922 (represented as two dashed black lines), which is centered on the global marine signature of 0.70918, to identify the otolith radius when an individual entered the ocean (indicated by a black arrow). Lastly, we determined migration strategy by comparing otolith radius at first annulus to otolith radius at ocean entry. If otolith radius to the first annulus (indicated as the vertical dashed grey line) is less than otolith radius at ocean entry, then the fish is categorized as exhibiting the yearling migration strategy, otherwise the fish is categorized as exhibiting the subyearling strategy.

One of our goals was to reconstruct where each adult was during three early life history stages: natal, rearing, and overwintering. To reconstruct the natal, rearing, and overwintering locations we targeted three portions within the juvenile section of adult otoliths. Similar to Hegg et al. (2013a) the $^{87}Sr/^{86}Sr$ ratio associated with the natal stage was defined as the first stable ratio between 110µm and 250µm from the otolith core. If no stable ratio was detected, the first peak or valley in $^{87}Sr/^{86}Sr$ ratio was used as the natal signature. This range (i.e., 110–250µm) was used to avoid a maternal influence and the onset of downstream migration (Hegg et al. 2013a) since previous observations indicated emergence of fall Chinook salmon at an average otolith radius of 256µm (standard deviation 32µm, n=45) . The rearing $^{87}Sr/^{86}Sr$ ratio was determined by targeting a portion of otolith between a radius of 250µm and 500µm from the core, while the overwintering $^{87}Sr/^{86}Sr$ ratio was quantified by focusing on a portion of otolith between 500µm and the radius from the core corresponding to when a fish exited the Snake River. These rearing and overwintering portions of each otolith were based on findings from our study of otolith radius at Snake River egress. Specifically, most of our sampled adults (~60%) showed evidence of egress from Snake River (i.e., $^{87}Sr/^{86}Sr$ ratio fell below 0.70960 since the upper and lower Snake River have a $^{87}Sr/^{86}Sr$ ratio of 0.709651 and 0.709746, respectively) between a radius of 500µm and 800µm. Therefore, we targeted a rearing $^{87}Sr/^{86}Sr$ ratio to be between 250µm and 500µm and an overwintering $^{87}Sr/^{86}Sr$ ratio beyond 500µm.

Because rearing location was known for juveniles collected at Lower Granite Dam, we quantified the $^{87}Sr/^{86}Sr$ ratio associated with rearing location so as to evaluate our classification accuracy (see below). To determine the rearing $^{87}Sr/^{86}Sr$ ratio for otoliths from juveniles we used the same procedure for determining the rearing ratio for otoliths from adults; we targeted the portion of otolith between a radius of 250µm and 500µm from the core.

Classification of adults and juveniles to natal and rearing locations

Results from Hegg et al. (2013a) indicated that $^{87}Sr/^{86}Sr$ ratio for water samples (taken across seasons and years) were significantly different among four major spawning locations. These four chemically unique locations were 1) Clearwater and Salmon rivers, 2) lower Snake River, 3) upper Snake River, and 4) Tucannon, Grande Ronde, and Imnaha rivers (see Table 1 and Figure 3 in Hegg et al. 2013a). The upper Snake River was defined as the section of Snake River downstream of Hells Canyon Dams and upstream of the confluence between Snake and Salmon rivers, while the lower Snake River was the section that is downstream of the confluence between the Snake and Salmon rivers and upstream of the reservoir created by dams near the confluence between the Snake and Clearwater rivers (Figure 1).

Because there is a strong positive correlation between $^{87}Sr/^{86}Sr$ ratio in otoliths and water (Kennedy et al. 1997) we used the $^{87}Sr/^{86}Sr$ ratio in water to represent the chemical signatures for each of the four locations (taken from Hegg et al. 2013a) to which we classified the natal, rearing

and overwintering (see Classification of migration strategy and overwintering location) signatures from adult fish, respectively. Specifically, we ran a linear discriminant function analysis (LDFA) that used the $^{87}Sr/^{86}Sr$ ratio from water samples as a training dataset. The resultant LDFA equation was used to classify adults to their natal location (i.e., location from which they hatched) and rearing location (i.e., a location they resided after the onset of downstream migration), and juveniles to their rearing location. Each of these three classifications was performed with equal prior probability and leave-one-out cross validation. The purpose of classifying juveniles to their rearing location was to evaluate the ability of the LDFA to correctly classify juveniles when rearing location was known: of the 21 juveniles collected at Lower Granite Dam in 2011, 19 and 2 of these fish reared in the lower and upper Snake River, respectively.

Identifying migration strategy and overwintering location

For each adult, we assigned a migration strategy (i.e., yearling or subyearling) using a combination of otolith radius to the first annual mark and otolith radius at ocean entry (Figure 2b). A fish was categorized as exhibiting a subyearling strategy if it was in the ocean before its first annulus formed. Alternatively, if the otolith radius to the first annual mark was less than or equal to the otolith radius at ocean entry then the fish was designated as exhibiting a yearling strategy. Otolith radius corresponding to ocean entry was measured at the convergence of $^{87}Sr/^{86}Sr$ ratio, from the edge-to-core scan, onto the range of 0.70914-0.70922, which is centered on the global marine signature of 0.70918 (Figure 2b).

For those individuals that we categorized as exhibiting the yearling migration strategy we also determined where they overwintered. Our assessment of overwintering location used the same statistical approach (i.e., LDFA with equal prior probability and leave-one-out cross validation) outlined for the classification of adults to natal and rearing locations.

Body size and growth

To estimate fork length at Snake River egress and ocean entry from adult otoliths we first determined where on each otolith these two points in time occurred by using data of $^{87}Sr/^{86}Sr$ ratio from the otolith edge-to-core scans. As previously mentioned, otolith radius at ocean entry was measured at the point on the edge-to-core scan where the $^{87}Sr/^{86}Sr$ ratio converged with the range of 0.70914-0.70922, which is centered on the global marine signature of 0.70918 (Figure 2b). In contrast, otolith radius at Snake River egress was measured at the point on the edge-to-core scan where $^{87}Sr/^{86}Sr$ ratio was between 0.70960 (upper and lower Snake River have a $^{87}Sr/^{86}Sr$ ratio of 0.709651 and 0.709746, respectively) and 0.70922 (the upper bound used to identify ocean entry). Next, we input these values of otolith radius at Snake River egress and ocean entry into the quadratic relationship between fork length and otolith radius developed for

Snake River fall Chinook salmon (Zabel et al. 2010) and calculated fork length at Snake River egress and ocean entry. From these estimates of fork length, we then calculated the amount of somatic growth (mm) each fish experienced during the interval of time between Snake River egress and ocean entry (i.e., fork length at ocean entry subtracted from fork length at Snake River egress). Finally, we used ANOVA to evaluate whether fork length and growth varied significantly among fish classified to different natal, rearing, and overwintering locations, migration strategies, and hatchery or wild produced.

We used a generalized linear modeling (glm) approach to investigate the extent to which body size (i.e., fork length at Snake River egress and ocean entry) and growth of juvenile Chinook salmon was explained by a suite of six independent variables: hatch year, natal and rearing location, sex, migration strategy, and hatchery or wild produced. We ran 63 models (including a null model with no effects) representing all possible combinations of the aforementioned dataset of six variables. All model parameters were estimated by maximizing the likelihood function.

To compare models, we calculated four values for each model: Akaike's Information Criterion (AIC), delta AIC, relative likelihood, and AIC weight. Smaller AIC values indicate "better" models and when comparing two models we calculated the difference in AIC values (delta AIC) (Akaike 1973, Burnham and Anderson 2002). A delta AIC of less than 2 indicates little difference between competing models; a delta AIC of 2–10 indicates moderate support for a difference between the models, and a delta AIC of greater than 10 indicates strong support (Burnham and Anderson 2002). Relative likelihood represents the likelihood of a model given the data, whereas AIC weight is the discrete probability of each model (Burnham and Anderson 2002). The best model was defined as having a delta AIC of 0.00, although preference was given to the simplest model if two or more models had a delta AIC of less than 2.

Results

Classification of adults and juveniles to natal and rearing locations

Of our 125 adults, 61 and 63 were classified as wild and hatchery produced, respectively, and 1 individual was not classified. Results of the natal classification of the wild adult fall Chinook salmon among four locations indicated that 74% of these individuals originated from lower Snake River, 21% from upper Snake River and the remaining 5% from Clearwater and Salmon rivers (Table 1). Regarding hatchery adult fall Chinook salmon, 89% originated from lower Snake River and 11% from upper Snake River (Table 1). The accuracy of assignment for the LDFA classifications based on jack-knife resampling was 80% and 72% for wild and hatchery fish, respectively, indicating a high level of classification accuracy.

Table 1. Results of the four LDFA used to classify adult fall Chinook salmon (n=125) to their natal, rearing, and overwintering location, and juvenile fall Chinook salmon (n=21) to their rearing location. The number (and percent) of wild and hatchery fish that were classified to each natal, rearing, and overwintering location is indicated, as is the respective number (and percent) of individuals that exhibited the yearling migration strategy.

	Wild fish		Hatchery fish	
Classification type and area	Number of fish (%)	Yearling (%)	Number of fish (%)	Yearling (%)
Natal				
Tucannon, Grande Ronde, Imnaha	0 (0)	0 (0)	0 (0)	0 (0)
Clearwater, Salmon	3 (5)	2 (66)	0 (0)	0 (0)
Lower Snake	45 (74)	38 (84)	56 (89)	39 (69)
Upper Snake	13 (21)	8 (62)	7 (11)	5 (71)
Total sample size	61	48 (80*)	63	44 (70*)
Rearing				
Tucannon, Grande Ronde, Imnaha	2 (3)	0 (0)	0 (0)	0 (0)
Clearwater, Salmon	14 (22)	11 (79)	0 (0)	0 (0)
Lower Snake	30 (50)	24 (80)	59 (94)	41 (69)
Upper Snake	15 (25)	13 (87)	4 (6)	3 (75)
Total sample size	61	48 (80*)	63	44 (72*)
Overwintering				
Tucannon, Grande Ronde, Imnaha	2 (4)		0 (0)	
Clearwater, Salmon	7 (15)		2 (4)	
Lower Snake	38 (79)		40 (92)	
Upper Snake	1 (2)		2 (4)	
Total sample size	48		44	
PIT-tagged juveniles from known rearing locations	Number of fish (%)	Classification to rearing location (%)		
Lower Snake	19 (90)	18 (86)		
Upper Snake	2 (10)	3 (14)		
Total sample size	21			

* Migration strategy was not determined for one wild and two hatchery fish.

Our rearing classification of wild adults among the four locations indicated that 50% reared in lower Snake River, 25% in upper Snake River, 22% in Clearwater and Salmon rivers, and 3% in Tucannon, Grand Ronde, and Imnaha rivers (Table 1). In terms of hatchery adults, our rearing classification among the four locations indicated that 94% reared in lower Snake River and 6% in upper Snake River (Table 1). The accuracy of assignment for the LDFA classifications of wild and hatchery fish based on jack-knife resampling was 90% and 80%, respectively, indicating a high level of classification accuracy. The test of the LDFA classification accuracy, which used rearing signatures from otoliths of collected juveniles for which rearing location was known, indicated that all but one individual out of 21 (4%) were correctly classified (Table 1).

Identifying migration strategy and overwintering locations

Of 122 wild and hatchery adults, the majority (80% and 72%) were categorized as exhibiting a yearling strategy. Three individuals were not assigned a strategy because their otolith annual mark could not be visually identified. Our overwintering classification of adults among the four locations indicated that the majority of wild adults (79%) overwintered in lower Snake River (92% of the hatchery adults), 15% in Clearwater and Salmon rivers (4% of the hatchery adults), 2% in upper Snake River (4% of the hatchery adults), and 4% in Tucannon, Grand Ronde, and Imnaha rivers (Table 1). Almost half (44%) of our wild yearlings were assigned to lower Snake River as their natal, rearing, and overwintering location. The accuracy of our overwintering assignment for the LDFA classifications based on jack-knife resampling was 87% and 85% for wild and hatchery fish, respectively.

Body size and growth

Our back-calculated estimates of fork length at Snake River egress showed that 40% of wild adults that exhibited the yearling strategy overlapped with those that exhibited the subyearling strategy, while 35% of individuals overlapped in size at ocean entry. Specifically, estimates of fork length at Snake River egress ranged from 116-167mm and 124-298mm for wild subyearlings and yearlings, respectively, while fork length at ocean entry ranged from 128-189mm and 140-323mm for wild subyearlings and yearlings, respectively (Figure 3a and b). For hatchery fish, estimates of fork length at Snake River egress ranged from 106-170mm and 124-316mm for subyearlings and yearlings, respectively, while fork length at ocean entry ranged from 114-184mm and 129-323mm for subyearlings and yearlings, respectively.

ANOVA results indicated that wild yearlings had a significantly larger fork length than wild subyearlings, by an average of 53mm and 62mm, at Snake River egress ($F_{1,58}$=14.5, $p<0.001$; inset of Figure 3a) and ocean entry ($F_{1,58}$=15.9, $p<0.001$; inset of Figure 3b), respectively. In terms of hatchery fish, ANOVA results indicated that yearlings had a

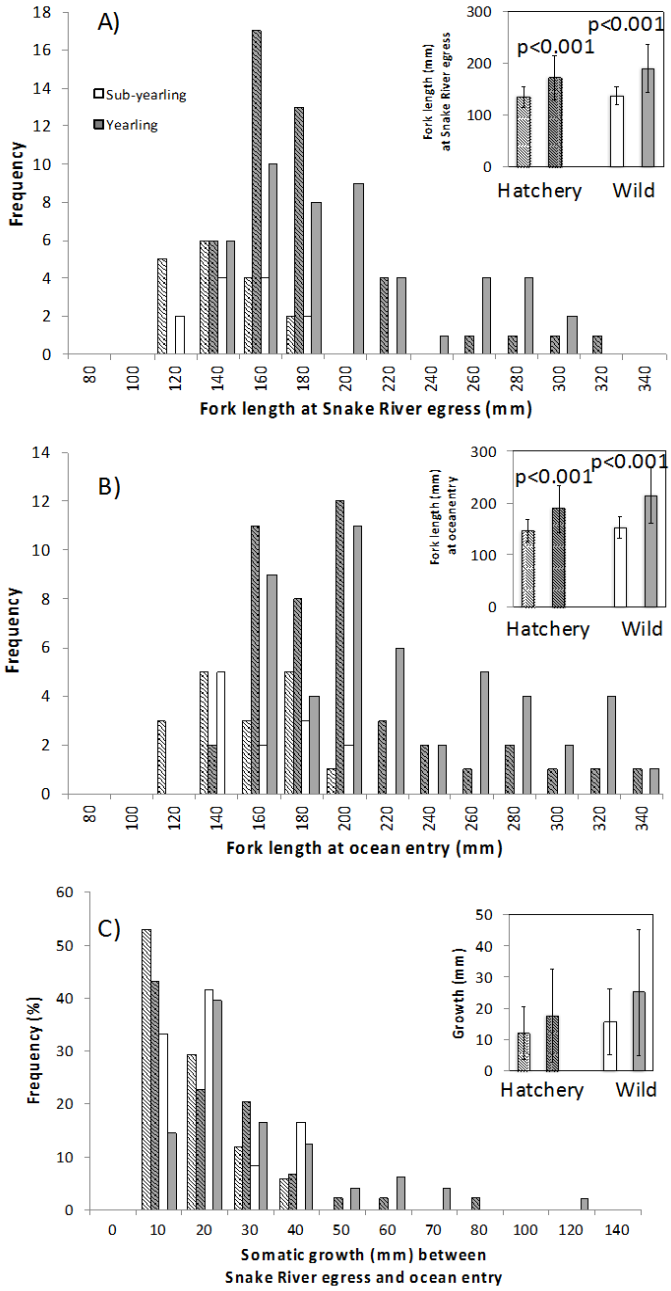

Figure 3. Frequency distributions of otolith derived back-calculated estimates of fall Chinook salmon fork length at A) Snake River egress and B) ocean entry. Plot C) is the percent frequency distribution of somatic growth (mm) that was accumulated between Snake River egress and ocean entry. Within each plot bars correspond to either yearling (grey bars) or subyearling (white bars) migration strategies and hatchery (hatched bars) or wild (solid bars) produced. Inset plots show the average (box) and standard deviation (whiskers) of hatchery and wild fish with respect to subyearling and yearling migration strategies. P-values from ANOVAs are indicated.

significantly larger fork length than subyearlings, by an average of 37mm and 42mm, at Snake River egress ($F_{1,59}$=11.2, p<0.001; inset of Figure 3a) and ocean entry ($F_{1,59}$=13.6, p<0.001; inset of Figure 3b), respectively. We also observed significantly larger fork length of yearlings at both Snake River egress and ocean entry within hatchery and wild produced fish that had a natal or rearing location in the Lower and Upper Snake River (Figure 4a-d), while the other natal and rearing locations had insufficient sample sizes (i.e., n<5) to permit statistical analyses. In terms of growth, 67% of all sampled fish exhibiting the subyearling and yearling strategies grew 10mm or more during the period of time from when they exited the Snake River and entered the ocean, and no significant differences in growth were detected between migration strategies within either hatchery or wild fish (inset Figure 3c).

Our generalized linear modeling (GLM) revealed that the same three independent variables best explained variability in both size at Snake River egress and ocean entry. Specifically, the best models consisted of migration strategy, whether a fish was hatchery or wild produced, and hatch year (Table 2). Size at Snake River egress and ocean entry were significantly greater for fish that were yearlings, wild produced, and that hatched in 2007: although of our sampled fish only four hatched in 2007, compared to 2008 and 2009 which had 103 and 17 individuals, respectively. Finally, our analysis of growth that occurred between Snake River egress and ocean entry indicated that the best model included variables of sex, migration strategy, and whether a fish was hatchery or wild produced (Table 2). According to this model, growth was significantly greater in fish that were females and wild produced, and marginally significantly greater for yearlings.

Discussion

In this study, we investigated the early life history of Snake River fall Chinook salmon from adults returning to spawn so as to better comprehend what factors influence adult abundance. Specifically, we reconstructed where adults originated, reared and overwintered, whether they exhibited a subyearling or yearling migration strategy, and how big they were as they moved to the ocean. Our results indicated that of our sampled adults the lower Snake River was important for during all three life history stages, that yearlings were the prevailing migration strategy, and that considerable overlap in body size existed between yearlings and subyearlings suggesting that spending more time in freshwater (i.e., yearlings) might not result in a larger body size. These findings provide details about the early life history of Snake River fall Chinook salmon, an understanding of which is critical to aid in their management and conservation.

Classification to natal, rearing, and overwintering locations

Current estimates of the spawner abundance for wild Snake River fall Chinook salmon is

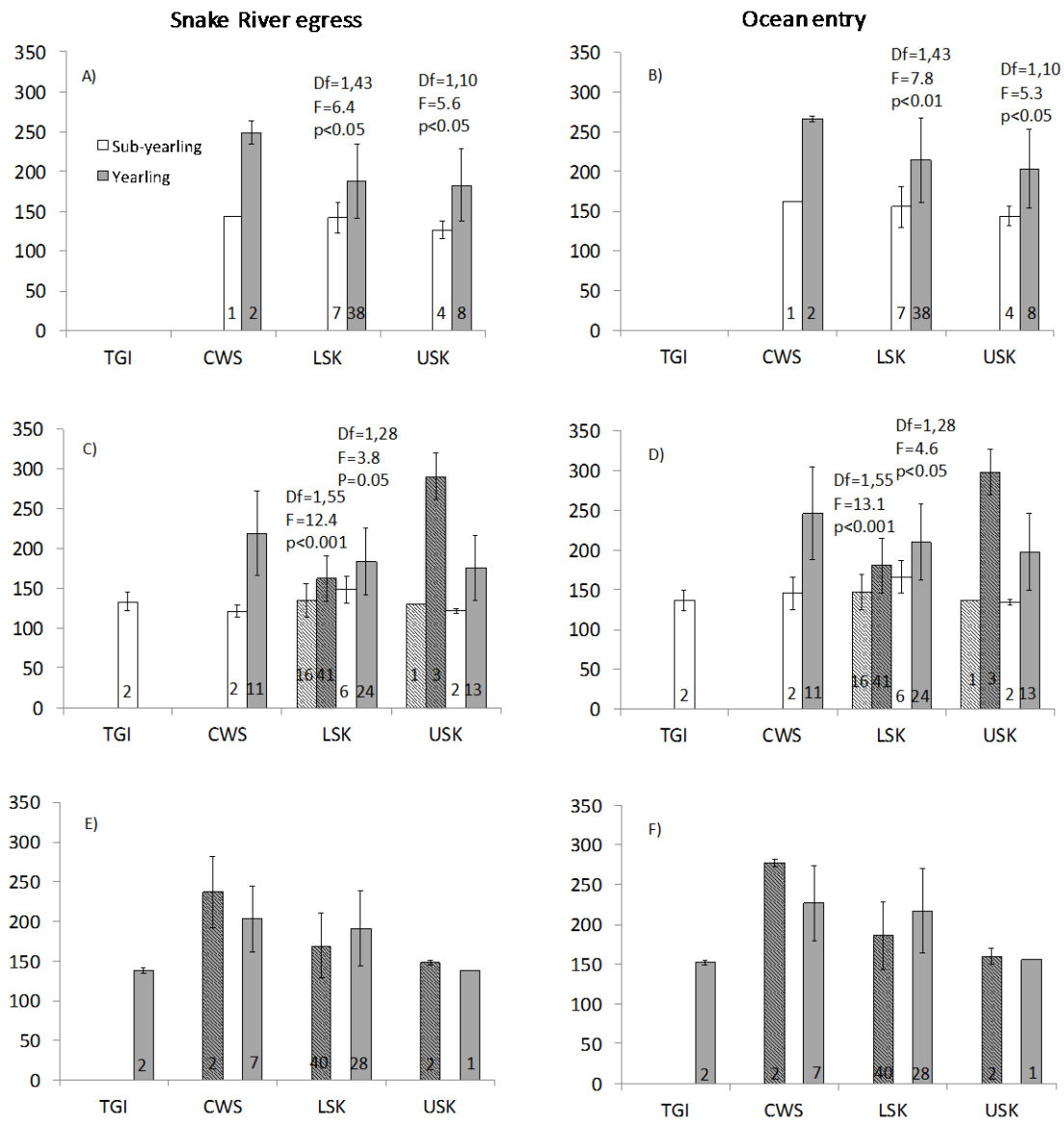

Figure 4. Estimates of fall Chinook salmon fork length (mm) with respect to natal (A and B), rearing (C and D), and overwintering (E and F) locations, and Snake River egress (A, C, and E) and ocean entry (B, D, and F). Within each plot fork length is further differentiated between individuals assigned as subyearling (white bars) or yearling (grey bars) migration strategy and between those that are hatchery or wild produced. Classifications to natal, rearing, and overwintering locations are based on analyses of $^{87}Sr/^{86}Sr$ ratio (see Methods). Significant ANOVA results from comparisons between migration strategies, within a location, are indicated with *p* values. Average (bar) and standard deviations (whiskers) are depicted, and sample sizes are indicated within bars. Location abbreviations: Tucannon, Grande Ronde, and Imnaha rivers (TGI), Clearwater and Salmon rivers (CWS), lower Snake River (LSK), and upper Snake River (USK).

Table 2. Top model results from the generalized linear modeling approach investigating the extent to which fork length (i.e., size) at Snake River egress, ocean entry, and growth varied with respect to six variables. Delta AIC is the difference between each model and the model with the lowest AIC. Relative likelihood is the likelihood of a model given the data, and AIC weight is the discrete probability of each model.

Model	AIC	Delta AIC	Relative likelihood	AIC weight
Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Hatch year + Rear + Sex	1231.46	0.00	1.00	0.14
Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Rear + Sex	1231.76	0.30	0.86	0.12
Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Hatch year + Natal + Sex	1237.87	0.41	0.82	0.12
Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Hatch year + Sex	1232.00	0.54	0.76	0.11
Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Hatch year + Rear	1232.01	0.55	0.76	0.11
Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Hatch year + Natal	1232.28	0.81	0.67	0.09
^ Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Hatch year	1232.36	0.90	0.64	0.09
Size at Snake River egress ~ Migration strategy + Hatchery/Wild + Rear + Natal + Sex + Hatch year	1233.16	1.70	0.43	0.06
^ Size at ocean entry ~ Migration strategy + Hatchery/Wild + Hatch year	1254.07	0.00	1.00	0.23
Size at ocean entry ~ Migration strategy + Hatchery/Wild + Hatch year + Rear	1254.43	0.36	0.84	0.20
Size at ocean entry ~ Migration strategy + Hatchery/Wild + Hatch year + Natal	1255.42	1.35	0.51	0.12
Size at ocean entry ~ Migration strategy + Hatchery/Wild + Hatch year + Sex	1255.93	1.85	0.40	0.09
^ Growth ~ Migration strategy + Hatchery/Wild + Sex	1008.19	0.00	1.00	0.64

^ Best model.

approximately 2,200 individuals (Cooney et al. 2011) with a long-term goal to achieve a population of about 14,000 individuals (Milks et al. 2013). Because of this need to expand the number of individuals returning to spawn, knowing where adults resided as juveniles is important for predicting where subsequent cohorts are likely to originate as well as where mitigation and conservation efforts could be targeted to assist population recovery. Our assessment of where adults resided as juveniles revealed that lower Snake River was an important location given that it was used as a natal, rearing, and overwintering location by most of our sampled returning adults (Table 1).

Our findings that the majority of hatchery fish were assigned lower Snake River as their natal origin is in agreement with the fact that Lyons Ferry Hatchery, the primary source of hatchery fall Chinook salmon, is located within the lower portion of the Snake River, which is reflected in its $^{87}Sr/^{86}Sr$ ratio. Although Hegg et al. (2013a) did not differentiate between hatchery and wild fish in their sample of presumed wild adults their results provide an interesting comparison to those of this study. For instance, our analysis showed that almost all of our wild adults (95%) originated from Snake River, while Hegg et al. (2013a) reported that 37% of their adults originated from Clearwater and Salmon rivers and 61% from Snake River. These estimates from Hegg et al. (2013a) are comparable to what we would expect if the representation of returning adults were proportional to river production. For instance, estimates of available spawning habitat in the Snake River watershed indicated that Clearwater and Salmon rivers, Snake River (combined upper and lower portions), and Tucannon, Grande Ronde, and Imnaha rivers accounted for 44%, 41%, and 15% of this total area, respectively (StreamNet Project 2012), while spawning surveys from 1991-1998 showed that Snake (combined upper and lower portions) and Clearwater rivers comprised 58% and 27% of the redds, respectively, with 15% found in other areas (Connor et al. 2002). Given these river-specific estimates of spawning habitat and production why did the overwhelming majority of our sampled adults that survived to return to spawn originate from lower and upper Snake River and so few from the Clearwater and Salmon rivers?

We speculate that uncharacteristically low water temperatures might be linked to the high incidence of fish that originated from Snake River. Given that a greater production of fall Chinook salmon is believed to occur in areas with relatively cool water temperatures (Connor et al. 2002) and that spring water temperatures are typically warmer in Snake River than Clearwater River (average temperatures of 11.8°C and 9.0°C, respectively, Connor et al. 2002), the cooler temperatures experienced throughout the region in 2007-2008 might have improved the natal habitat, particularly in Snake River, for developing fall Chinook salmon. From the summer of 2007 until the summer of 2008 a moderate La Nina event occurred whereby sea surface temperatures were 1-1.5°C lower than average (from monthly ERSST.v4 SST in 5°N-5°S, 120°-170°W; http://www.cpc.ncep.noaa.gov/data/indices/). During this period of time 85% of our sampled adults hatched (i.e., 4, 103, and 17 fish hatched in 2007, 2008, and 2009 respectively,

and for one fish hatch year was unknown) and these fish experienced water temperatures that were 0.6-2.2°C lower relative to other years (spanning at most from 1994-2016, http://waterdata.usgs.gov/nwis) in the Snake and Clearwater rivers. Even downriver in the lower portion of the Columbia River and estuary, average spring/summer water temperatures were cooler in 2008 (14.0°C) compared to 2007 (16.6°C) and 2009 (17.8°C) (unpublished temperature logger data). In contrast, the fish used in the study by Hegg et al. (2013a) hatched from 2002-2006, a period that was characterized by weak and moderate El Nino events (defined as 0.5-0.9°C and 1-1.5 °C warmer sea surface temperatures, respectively). The reconstruction of adults that hatched in 2002-2006 indicated that 34% fewer fish originated from Snake River (upper and lower portions) relative to our study, and during this time water temperatures in the Snake and Clearwater rivers were, on average, 0.5-2.3°C warmer than those in 2008 (http://waterdata.usgs.gov/nwis). Could a higher probability of survival for fish that originated from Snake River be a direct or indirect outcome of the lower 2008 temperatures and/or were these lower temperatures a detriment to fish from Clearwater and Salmon rivers? Although answering this question is beyond the scope of this study it emphasizes the need to understand the mechanisms involved in shaping the survival of Chinook salmon particularly as it relates to explaining annual variability in the contribution of individuals to the adult population.

Identifying migration strategy

Species recovery is often a complex process that is made more difficult because of gaps in our ecological understanding (Hutchings and Reynolds 2004, Lotze et al. 2011). When Snake River fall Chinook salmon was listed as threatened under ESA in 1992, the subyearling migration strategy was regarded as the dominant strategy, and this understanding was reflected in management plans (Council 2014). About a decade later the discovery of the yearling strategy and its relatively high occurrence (Connor et al. 2005) emphasized that rebuilding Snake River fall Chinook salmon would likely require the inclusion of both subyearling and yearling migration strategies in a management structure (Bourret et al. 2016). Given that traits, like age of maturity, have been shown to be linked to a species' ability to handle anthropogenic effects and environmental variability (Moore et al. 2014, Juan-Jordá et al. 2015) the subyearling and yearling migration strategies could represent an important buffer to changing environmental conditions, and ultimately recovery (Moran et al. 2013, Bourret et al. 2016).

In our study, 80% of the sampled wild adults exhibited the yearling strategy while Hegg et al. (2013a) and Connor et al. (2005) reported 62% and 41%, respectively. Further, 79% of adults that exhibited the yearling strategy originated from lower Snake River, which differs from earlier work that reported larger numbers of yearlings originating from Clearwater and Salmon rivers (Connor et al. 2005, Hegg et al. 2013a). As previously suggested, the cooler water temperatures in 2007-2008 may explain the predominance of fish that originated from lower Snake River, and these cooler temperatures might also favor the yearling strategy. Specifically,

Connor et al. (2002) reported that timing of emergence and migration, and the percentage of fall Chinook salmon that overwintered, were all inversely related to spring water temperature. The degree of annual variability in both the contribution of adults from natal locations and the proportion of adults exhibiting the yearling strategy highlights that more work is needed to better understand the interaction between life history traits and the environment (Kindsvater et al. 2016).

The large proportion of yearlings reported here and elsewhere suggests that their survival to adulthood is higher relative to that for subyearlings. It is possible that individuals exhibiting the yearling strategy are taking advantage of large pools of relatively still water (dam-created reservoirs) that may provide resources such as prey and shelter, which results in a fitness benefit (Connor et al. 2005). Despite these potential resource advantages this prevalence of yearlings in our sampled adults is still surprising given that dam operations that improve juvenile passage survival are in operation during the period of time when subyearlings, not yearlings, are migrating. For example, juvenile bypass facilities route fish downstream, away from the dam's powerhouse, and dam operations are modified (e.g., an increase in the release of reservoir water) to facilitate fish passage around dams (Connor et al. 2005). Contrary to the subyearling migration strategy, fish exhibiting the yearling strategy are believed to move downstream in the winter, a time when bypass systems and dam operations that improve passage survival are not in operation (Connor et al. 2005, Buchanan et al. 2009). Does our observation of a large number of fish exhibiting the yearling strategy mean that the seasonal passage improvements for subyearlings are relatively minor when compared to the advantage of overwintering in freshwater? Clearly, more work is needed to address the relationship between overwintering and survival, and the factors and processes that influence an individual to exhibit a particular migration strategy.

Body size and growth

Our analysis of body size revealed that wild and hatchery juveniles that went on to exhibit the yearling strategy were 37 to 62mm larger at Snake River egress and ocean entry than those that would exhibit the subyearling strategy (Figure 3a and b insets). This finding of larger yearling fish is not surprising if we assume that they overwintered within the Snake River watershed, in which case they would be older than their subyearling counter-parts by the time they exit the Snake River and enter the ocean. But what explains the overlap in size between migration strategies such that 40% of wild yearlings overlapped with subyearlings at Snake River egress, and 35% of individuals overlapped at ocean entry (Figure 3a and b insets)? Further, hatchery fish showed even greater overlap in size, whereby 68% of yearlings overlapped with subyearlings at Snake River egress and 52% of individuals at ocean entry (Figure 3a and b insets). How much of this size overlap is the result of resource quality and quantity (e.g., water temperature and prey) versus hatch date and time spent growing (i.e., age)? Further, does this

degree of size overlap suggest that, for many yearlings, there may not be a size-related advantage to overwintering in freshwater?

Some of the observed overlap in size between migration strategies could be explained if fish overwintered in the Columbia River downstream of its confluence with Snake River instead of within the Snake River watershed. If fish overwintered below the Snake River then they would be expected to be about the same size (and age) at Snake River egress relative to subyearlings, yet larger (and older) at ocean entry. Indeed, we observed a decrease in the number of fish (hatchery or wild) that overlap in size between Snake River egress and ocean entry, but only for a few fish (i.e., 2-7 fish). Regardless, the larger body size and the positive relationships between body size and fitness (Kingsolver and Huey 2008) and survival (Sogard 1997, Zabel and Achord 2004, Duffy and Beauchamp 2011) suggests a mechanism that explains why a substantial proportion of our returning adults exhibited the yearling strategy. In fact, higher survivals were estimated for yearlings rather than subyearlings (0.78 vs. 0.64, respectively) during the portion of their juvenile migration between Bonneville Dam, the most downstream impoundment, and the mouth of the Columbia River (McMichael et al. 2010).

For many anadromous Pacific salmon, estuarine habitats are viewed as important areas where juveniles rear and grow before completing their physiological transition to a saltwater existence (Thorpe 1994, Fresh et al. 2005, Limm and Marchetti 2009, Sagar et al. 2013). But several studies have highlighted that some salmonids spend little time in the estuary (e.g., less than 5 days) and thus little somatic growth is attributed to estuarine residency (MacFarlane and Norton 2002, MacFarlane 2010, Harnish et al. 2012, Thom et al. 2013, Hearn et al. 2014). Moreover, yearlings are thought to be less dependent on the estuarine environment than subyearlings (Thorpe 1994). Our reconstruction of somatic growth, which occurred between their exit from the Snake River to their ocean entry (a distance of approximately 500 rkm), indicated that both strategies grew similar amounts, with yearlings showing slightly more growth than subyearlings and with wild fish growing slightly more than hatchery fish (Figure 3c inset). Pooling our adults indicated a median growth of 14mm with a range from 3 to 114mm (Figure 3c). If we assume a median somatic growth rate of 0.53 mm/day (unpublished data derived from otoliths of juvenile Fall Chinook salmon in the lower portion of the Columbia River and estuary), then our adults would have resided about 26 days (ranging from 5 to 215 days) within this portion of the Columbia River.

It is important to note that our data are only from individuals that survived to adulthood, and thus may be skewed towards faster growers if there exists such selective pressure (Zabel and Williams 2002). Another caveat is that size at ocean entry might represent different geographic locations among individuals. Specifically, we calculated size at ocean entry using the otolith radius that related to when an individual entered the ocean (i.e., convergence of $^{87}Sr/^{86}Sr$ ratio from the otolith scan onto the global marine signature of 0.70918; Figure 2). But the geographic

location of the isotopic transition from brackish water to ocean water (i.e., 0.70918) will vary temporally depending on tidal height, wind driven waves, ocean currents, bathymetry, fresh water from land drainage, and precipitation (Simenstad et al. 2011). Therefore, depending on where the isotopic transition from brackish water to ocean water occurred as a fish migrated to the ocean, the otolith radius at ocean entry could represent a different geographic location among fish. Clearly, additional research is required to resolve these issues that limit the use of otoliths from surviving adults as a tool to reconstruct their estuarine residence time and growth.

According to our generalized linear modeling (GLM) approach, variability in both size at Snake River egress and ocean entry were explained by a shared suite of variables (migration strategy, whether fish were wild or hatchery produced, and hatch year) with alternative models also including the remaining independent variables of natal and rearing location and sex (Table 2). Ideally, results from the GLM approach would highlight potential mitigation actions that benefit juvenile size and growth in freshwater and estuarine habitats with the goal of improving survival to adulthood. Unfortunately, the results of this study provide little guidance for such actions given that factors identified to be strongly correlated to size and growth were factors for which managers have little control (e.g., migration strategy, hatch year, and sex) with the exception of hatchery or wild production. And overall the AIC weights were low for the GLMs, especially those investigating variability in size at Snake River egress and ocean entry, suggesting that there is considerable amount of unexplained variability.

Because most of our sampled fish were assigned to the lower Snake River as their natal, rearing, or overwintering location, low samples sizes limited our ability to statistically examine patterns of size and growth among natal, rearing and overwintering locations. That being said, wild yearlings that had a natal origin or reared in Clearwater and Salmon rivers tended to be larger than those in lower or upper Snake River (Figure 4c-d). It's possible that the observed larger size of fish classified to be from the Clearwater and Salmon rivers is related to the cooler water temperatures (average water temperature, in 2008, from 3 sites within the Clearwater River and 2 sites within the Snake River was 9.6°C and 11.1°C, respectively; http://waterdata.usgs.gov/nwis) and resultant lower metabolic demands (Brett et al. 1982) or potentially, a combination of factors such as temperature, Chinook density, and prey availability (Crozier et al. 2010, Chittaro et al. 2014).

Overall, our study highlights some interesting aspects of fall Chinook salmon early life history revealed through the use of microstructural and microchemical analyses of adult otoliths. In particular, because lower Snake River was used as a natal location by a large proportion of surviving adults, this location appears to be a critical component to population viability. However, a more thorough analysis of the contribution of fish by hatch year will likely provide a greater understanding of the importance of lower Snake River relative to the Clearwater and Salmon rivers, as well as the importance of climatic events such as La Nina and El Nino. Further,

despite fish that exhibited the yearling strategy spending more time in freshwater than subyearlings, both strategies overlapped in size. Although, given that our study focused on individuals that survived to return to spawn and that the yearling migration strategy was exhibited by most of our sampled adults, there appears to be a survival advantage for individuals that exhibit the yearling migration strategy. What does the prevalence of yearlings mean for the recovery of wild fall Chinook salmon in the Snake River basin? For example, should hatchery practices release yearlings and subyearlings to ensure adequate representation of both strategies (Connor et al. 2005) or should only subyearlings be cultured given their historical predominance? Future work is needed to better comprehend the factors and processes that influence size and growth, and ultimately survival to adulthood.

Acknowledgements

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, C. Knaack, for the use of their equipment. This work was funded by grants to R. Zabel and B. Kennedy from Bonneville Power Commission (#46273-REL-127).

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Baker, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier, New York, NY.

Bath, G. E., S. R. Thorrold, C. M. Jones, S. E. Campana, J. W. McLaren, and J. W. H. Lam. 2000. Strontium and barium uptake in aragonitic otoliths of marine fish. Geochimica et Cosmochimica Acta. 64:1705-1714.

Bourret, S. L., C. C. Caudill, and M. L. Keefer. 2016. Diversity of juvenile Chinook salmon life history pathways. Reviews in Fish Biology and Fisheries:1-29.

Brett, J. R., W. C. Clarke, and J. E. Shelbourn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon, Oncorhynchus tshawytscha. . Canadian Technical Report of Fisheries and Aquatic Sciences 1127.

Buchanan, R. A., J. R. Skalski, and G. A. McMichael. 2009. Differentiating mortality from delayed migration in subyearling fall Chinook salmon (Oncorhynchus tshawytscha). Canadian Journal of Fisheries and Aquatic Sciences 66:2243–2255.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263-297.

Casselman, J. M. 1987. Determination of age and growth. Pp. 209-242. In A.H. Weatherley and H.S. Gill. The biology of fish growth. Academic Press, London. 443 pages.

Chapman, D. W., D. E. Weitkamp, T. L. Welsh, M. B. Dell, and T. H. Schadt. 1986. Effects of River Flow on the Distribution of Chinook Salmon Redds. Transactions of the American Fisheries Society 115:537-547.

Chittaro, P. M., R. W. Zabel, K. Haught, B. L. Sanderson, and B. P. Kennedy. 2014. Spatial and temporal patterns of growth and consumption by juvenile spring/summer Chinook salmon *Oncorhynchus tshawytscha*. Environmental Biology of Fishes 97:1397–1409.

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.

Cooney, R. T., M. J. Ford, D. Bambrick, D. Berge, M. W. Chilcote, R. Clapp, B. Farman, R. Furfey, R. Graves, L. Krasnow, B. Lind, E. Murray, E. Patino, and R. Tweten. 2011. 5 year review: summary & evaluation of Snake River sockeye, Snake River spring-summer chinook, Snake River fall-run chinook, and Snake River Basin steelhead. NOAA Fisheries report. 65pg.

Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolutionary Applications 1:252-270.

Crozier, L. G., R. W. Zabel, E. E. Hockersmith, and S. Achord. 2010. Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. Journal of Animal Ecology 79:342-349.

Duffy, J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (Oncorhynchus tshawytscha) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Sciences 68:232-240.

Elsdon, T. S., B. K. Wells, S. E. Campana, B. M. Gillanders, C. M. Jones, K. E. Limburg, D. H. Secor, S. R. Thorrold, and B. D. Walther. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. Oceanography and marine biology: an annual review [Oceanogr. Mar. Biol. Annu. Rev.]. Vol. 46, pp. 297-330. 2008.

Faure, G., and T. M. Mensing. 2004. Isotopes: principles and applications. John Wiley & Sons Inc. Pp. 928.

Fresh, K. L., E. Casillas, L. L. Johnson, and D. L. Bottom. 2005. Role of the estuary in the recovery of Columbia River basin salmon and steelhead: an evaluation of the effects of selected factors on salmonid population viability. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-69, 105 p.

Fukushima, M., T. Jutagate, C. Grudpan, P. Phomikong, and S. Nohara. 2014. Potential Effects of Hydroelectric Dam Development in the Mekong River Basin on the Migration of Siamese Mud Carp (*Henicorhynchus siamensis* and *H. lobatus*) Elucidated by Otolith Microchemistry. PLoS ONE 9:e103722.

Geist, D. R., E. V. Arntzen, C. J. Murray, K. E. McGrath, Y.-J. Bott, and T. P. Hanrahan. 2008. Influence of River Level on Temperature and Hydraulic Gradients in Chum and Fall Chinook Salmon Spawning Areas Downstream of Bonneville Dam, Columbia River. North American Journal of Fisheries Management 28:30-41.

Geist, D. R., Z. Deng, R. P. Mueller, S. R. Brink, and J. A. Chandler. 2010. Survival and Growth of Juvenile Snake River Fall Chinook Salmon Exposed to Constant and Fluctuating Temperatures. Transactions of the American Fisheries Society 139:92-107.

Gross, M. R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14-25.

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P. Madin, M. T. Perry, E. R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A Global Map of Human Impact on Marine Ecosystems. Science 319:948-952.

Harnish, R. A., G. E. Johnson, G. A. McMichael, M. S. Hughes, and B. D. Ebberts. 2012. Effect of Migration Pathway on Travel Time and Survival of Acoustic-Tagged Juvenile Salmonids in the Columbia River Estuary. Transactions of the American Fisheries Society 141:507-519.

Harnish, R. A., R. Sharma, G. A. McMichael, R. B. Langshaw, and T. N. Pearsons. 2014. Effect of hydroelectric dam operations on the freshwater productivity of a Columbia River fall Chinook salmon population. Canadian Journal of Fisheries and Aquatic Sciences 71:602-615.

Hatten, J. R., K. F. Tiffan, D. R. Anglin, S. L. Haeseker, J. J. Skalicky, and H. Schaller. 2009. A Spatial Model to Assess the Effects of Hydropower Operations on Columbia River

Fall Chinook Salmon Spawning Habitat. North American Journal of Fisheries Management 29:1379-1405.
Hearn, A., E. Chapman, G. Singer, W. Brostoff, P. LaCivita, and A. P. Klimley. 2014. Movements of out-migrating late-fall run Chinook salmon (Oncorhynchus tshawytscha) smolts through the San Francisco Bay Estuary. Environmental Biology of Fishes 97:851-863.
Hegg, J., B. Kennedy, P. Chittaro, and R. Zabel. 2013a. Spatial structuring of an evolving life-history strategy under altered environmental conditions. Oecologia 172:1017-1029.
Hegg, J. C., B. P. Kennedy, and A. K. Fremier. 2013b. Predicting strontium isotope variation and fish location with bedrock geology: Understanding the effects of geologic heterogeneity. Chemical Geology 360–361:89-98.
Hutchings, J. A., and J. D. Reynolds. 2004. Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk. Bioscience [Bioscience]. Vol. 54, no. 4, pp. 297-309. Apr 2004.
Jones, C. M. 1992. Development and application of the otolith increment technique. In Otolith microstructure examination and analysis. Edited by D.K. Stevenson and S.E. Campana. Canadian special publication of fisheries and aquatic sciences 117.:1-12.
Juan-Jordá, M. J., I. Mosqueira, J. Freire, and N. K. Dulvy. 2015. Population declines of tuna and relatives depend on their speed of life. Proceedings of the Royal Society of London B: Biological Sciences 282.
Kennedy, B., C. Folt, J. Blum, and C. Chamberlain. 1997. Natural isotope markers in salmon. Nature 387:766-767.
Kennedy, B. P., A. Klaue, J. D. Blum, C. L. Folt, and K. H. Nislow. 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. Canadian Journal of Fisheries and Aquatic Sciences 59:925-929.
Kindsvater, H. K., M. Mangel, J. D. Reynolds, and N. K. Dulvy. 2016. Ten principles from evolutionary ecology essential for effective marine conservation. Ecology and Evolution:n/a-n/a.
Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness: three rules. . Evolutionary Ecology Research 10:251–268.
Kuehne, L. M., and J. D. Olden. 2012. Prey naivety in the behavioural responses of juvenile Chinook salmon (Oncorhynchus tshawytscha) to an invasive predator. Freshwater Biology 57:1126-1137.
Lascelles, B., G. Notarbartolo Di Sciara, T. Agardy, A. Cuttelod, S. Eckert, L. Glowka, E. Hoyt, F. Llewellyn, M. Louzao, V. Ridoux, and M. J. Tetley. 2014. Migratory marine species: their status, threats and conservation management needs. Aquatic Conservation: Marine and Freshwater Ecosystems 24:111-127.
Limm, M., and M. Marchetti. 2009. Juvenile Chinook salmon (Oncorhynchus tshawytscha) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. Environmental Biology of Fishes 85:141-151.
Lotze, H. K., M. Coll, A. M. Magera, C. Ward-Paige, and L. Airoldi. 2011. Recovery of marine animal populations and ecosystems. Trends in Ecology & Evolution 26:595-605.
Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. Science 312:1806-1809.

MacFarlane, R. B. 2010. Energy dynamics and growth of Chinook salmon (Oncorhynchus tshawytscha) from the Central Valley of California during the estuarine phase and first ocean year. Canadian Journal of Fisheries and Aquatic Sciences 67:1549-1565.

MacFarlane, R. B., and E. C. Norton. 2002. Physiological ecology of juvenile chinook salmon (Oncorhynchus tshawytscha) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fishery Bulletin 100:244-257.

Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris. 2007. Optimal Conservation of Migratory Species. PLoS ONE 2:e751.

Mathur, D., P. G. Heisey, E. T. Euston, J. R. Skalski, and S. Hays. 1996. Turbine passage survival estimation for chinook salmon smolts (Oncorhynchus tshawytscha) at a large dam on the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 53:542-549.

McMichael, G. A., R. A. Harnish, B. J. Bellgraph, J. A. Carter, K. D. Ham, P. S. Titzler, and S. Hughes. 2010. Survival and Migratory Behavior of Juvenile Salmonids in the Lower Columbia River Estuary in 2009. PNNL-19545, Pacific Northwest National Laboratory, Richland, Washington.

Milks, D., A. Grider, and M. Schuck. 2013. Lyons Ferry Hatchery Evaluation Fall Chinook Salmon Annual Report: 2011. Washington Department of Fish and Wildlife Fish Program. Pp139.

Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. Journal of Animal Ecology 83:1035-1046.

Moran, P., D. J. Teel, M. A. Banks, T. D. Beacham, M. R. Bellinger, S. M. Blankenship, J. R. Candy, J. C. Garza, J. E. Hess, S. R. Narum, L. W. Seeb, W. D. Templin, C. G. Wallace, and C. T. Smith. 2013. Divergent life-history races do not represent Chinook salmon coast-wide: the importance of scale in Quaternary biogeography. Canadian Journal of Fisheries and Aquatic Sciences 70:415-435.

Murray, C. B. 1994. A Method for Preparing Chinook Salmon Otoliths for Age Determination, and Evidence of Its Validity. Transactions of the American Fisheries Society 123:358-367.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout American Fisheries Society and University of Washington Press, Seattle.:378pp.

Robinson, R. A., H. Q. P. Crick, J. A. Learmonth, I. M. D. Maclean, C. D. Thomas, F. Bairlein, M. C. Forchhammer, C. M. Francis, J. A. Gill, B. J. Godley, J. Harwood, G. C. Hays, B. Huntley, A. M. Hutson, G. J. Pierce, M. M. Rehfisch, D. W. Sims, B. M. Santos, T. H. Sparks, D. A. Stroud, and M. E. Visser. 2009. Travelling through a warming world: climate change and migratory species. Endangered Species Research 7:87-99.

Ronce, O., I. Olivieri, J. Clobert, and E. Danchin. 2001. Perspectives on the Study of Dispersal Evolution. J. Clobert; E. Danchin; A.A. Dhondt; J.D. Nichols. Dispersal, Oxford University Press, pp.341-357, 2001, 0 19 850659 0.

Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: What science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33:665-706.

Sagar, J. P., A. B. Borde, L. L. Johnson, C. A. Corbett, J. L. Morace, K. H. Macneale, W. B. Temple, J. Mason, R. M. Kaufmann, V. I. Cullinan, S. A. Zimmerman, R. M. Thom, C. L. Wright, P. M. Chittaro, O. P. Olson, S. Y. Sol, D. J. Teel, G. M. Ylitalo, and N. D. Jahns. 2013. Juvenile salmon ecology in tidal freshwater wetlands of the lower columbia river and estuary: synthesis of the ecosystem monitoring program, 2005–2010. Prepared by the Lower Columbia Estuary Partnership for the Bonneville Power Administration, April, 2013, Available from the Lower Columbia Estuary Partnership, Portland, OR.

Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (Oncorhynchus spp.). Journal of Applied Ecology 46:983-990.

Simenstad, C. A., J. L. Burke, J. E. O'Connor, C. Cannon, D. W. Heatwole, M. F. Ramirez, I. R. Waite, T. D. Counihan, and K. L. Jones. 2011. Columbia River estuary ecosystem classification: concept and application. U.S. Geological Survey Open-File Report 2011-1228, 54 p.

Singer, G., A. Hearn, E. Chapman, M. Peterson, P. LaCivita, W. Brostoff, A. Bremner, and A. P. Klimley. 2013. Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss). Environmental Biology of Fishes 96:363-379.

Sogard, S. M. 1997. Size-Selective Mortality in the Juvenile Stage of Teleost Fishes: a Review. Bulletin of Marine Science 60:1129-1157.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford, U.K.

Steel, E. A., and I. A. Lange. 2007. Using wavelet analysis to detect changes in water temperature regimes at multiple scales: Effects of multi-purpose dams in the Willamette River basin. River Research and Applications 23:351-359.

Stevenson, D. K., and S. E. e. Campana. 1992. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117: 126p. .

StreamNet Project. 2012. Streamnet Generalized Fish Distribution, Fall Chinook. ftp://ftp.streamnet.org/pub/streamnet/gisdata/map_data_biological/StreamNet_FishDist_July2010.zip.

Thom, R. M., N. K. Sather, G. C. Roegner, and D. L. Bottom. 2013. Columbia Estuary Ecosystem Restoration Program. 2012 Synthesis Memorandum. Prepared by PNNL and NOAA Fisheries for the Portland District Army Corps of Engineers. Pp. 117.

Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17:76-93.

Tiffan, K. F., J. M. Erhardt, and S. J. St. John. 2014. Prey Availability, Consumption, and Quality Contribute to Variation in Growth of Subyearling Chinook Salmon Rearing in Riverine and Reservoir Habitats. Transactions of the American Fisheries Society 143:219-229.

Tiffan, K. F., R. D. Garland, and D. W. Rondorf. 2006. Predicted Changes in Subyearling Fall Chinook Salmon Rearing and Migratory Habitat under Two Drawdown Scenarios for John Day Reservoir, Columbia River. North American Journal of Fisheries Management 26:894-907.

Walther, B. D., and S. R. Thorrold. 2010. Limited diversity in natal origins of immature anadromous fish during ocean residency. Canadian Journal of Fisheries and Aquatic Sciences 67:1699-1707.

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. W., and S. Achord. 2004. Relating Size of Juveniles to Survival Within and Among Populations of Chinook Salmon. Ecology 85:795-806.

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

Zabel, R. W., and J. G. Williams. 2002. Selective Mortality in Chinook Salmon: What Is the Role of Human Disturbance? Ecological Applications 12:173-183.