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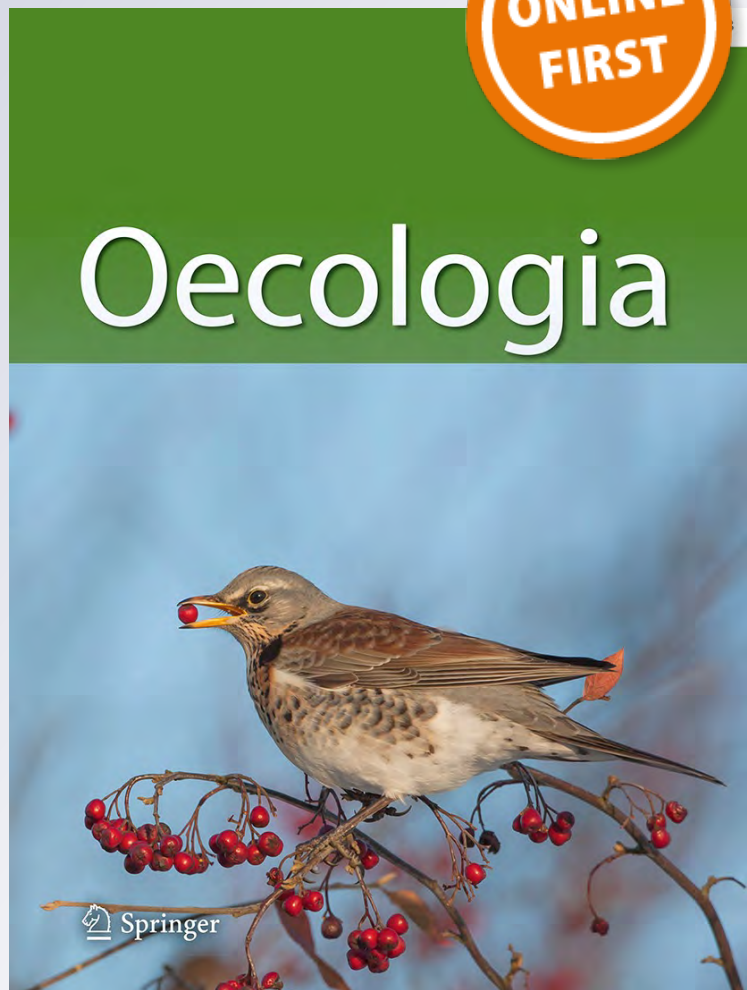
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# Spatial structuring of an evolving life-history strategy under altered environmental conditions

Jens C. Hegg · Brian P. Kennedy · Paul M. Chittaro · Richard W. Zabel

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**Abstract** Human disturbances to ecosystems have created challenges to populations worldwide, forcing them to respond phenotypically in ways that increase their fitness under current conditions. One approach to examining population responses to disturbance in species with complex life histories is to study species that exhibit spatial patterns in their phenotypic response across populations or demes. In this study, we investigate a threatened population of fall chinook salmon (*Oncorhynchus tshawytscha*) in the Snake River of Idaho, in which a significant fraction of the juvenile population have been shown to exhibit a yearling out-migration strategy which had not previously been thought to exist. It has been suggested that dam-related environmental changes may have altered the selective pressures experienced by out-migrating fall chinook, driving evolution of a later and more selectively advantageous migration strategy. Using isotopic analysis of otoliths from returning adult spawners, we reconstructed the locations of individual fish at three major

juvenile life stages to determine if the representation of the yearling life history was geographically structured within the population. We reconstructed juvenile locations for natal, rearing and overwintering life stages in each of the major spawning areas in the basin. Our results indicate that the yearling life-history strategy is predominantly represented within one of the main spawning regions, the Clearwater River, rather than being distributed throughout the basin. Previous studies have shown the Clearwater River to have cooler temperatures, later hatch dates, and later outmigration of juveniles, indicating a link between environment and expression of the yearling life history. Our data suggest that this new yearling life history may be disproportionately represented in returning adult spawners, indicating selection for this life history within the population.

**Keywords** Phenotypic plasticity · Local adaptation · Chinook salmon · Juvenile migration · Otolith microchemistry

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## Introduction

Human disturbances to ecosystems have created challenges to populations worldwide (Foley et al. 2005; Vitousek et al. 1997). Populations can show resilience to disturbances by responding phenotypically in ways that increase their fitness under current conditions (Ghalambor et al. 2007; Gotthard and Nylin 1995; Hendry et al. 2008; Waples et al. 2008). Numerous examples exist of populations that have demonstrated changes in life-history traits in response to major anthropogenic disturbances such as climate change (Crispo et al. 2010; Parmesan 2006). In many cases, these examples of population response can serve as unplanned experiments to potentially provide insights into patterns of

population fitness under dynamic environmental conditions. For example, Smith (2008) showed evidence of phenotypic change and heritable selection between African birds inhabiting anthropogenically altered and unaltered forest.

When a population is subjected to multiple disturbances throughout its life cycle, relating a particular phenotypic response to a particular disturbance is difficult. For example, complex interactions have been shown on the effect of environmental and behavioral reactions in the life-history trajectories of damselflies and frogs (Altwegg 2002; Johansson et al. 2001). Further, in species with complex life histories, such as migratory species, an observed life-history trait may be the result of trade-offs expressed across several life stages (Crozier et al. 2008; Taborsky 2006) and even across generations (Giménez and Torres 2004). Illustrating this complexity, De Block and Stoks (2005) found that food availability and hatch date in damselflies created expected growth tradeoffs in the juvenile stages, but unexpected sex-linked survival differences in the adult stage. One approach to examining population responses to disturbance in species with complex life histories is to study species that exhibit spatial patterns in their phenotypic response across populations or demes (Decker et al. 2003; Marcel et al. 2003). By relating this differential response to the variable conditions experienced across the landscape, we can begin to understand the driving forces behind the population change. We conducted this type of analysis on the life-history variability of Snake River fall chinook salmon (*Oncorhynchus tshawytscha*), which are listed as threatened under the US Endangered Species Act.

Pacific salmon (*Oncorhynchus* spp.) have been subjected to a litany of disturbances across multiple life stages, including impacts from hatcheries, harvest, and habitat destruction (Ruckelshaus et al. 2002). In the Columbia River basin in the northwestern United States, the development of hydroelectric dams has greatly altered ecosystems by blocking spawning habitat, inflicting direct mortality during migration, creating favorable conditions for predators, decreasing water velocity, and changing thermal regimes (Waples et al. 2009). Snake River fall chinook salmon, have been particularly impacted, with impassable dams blocking the vast majority of their historical spawning area (Williams et al. 2008). Current spawning occurs in areas with conditions substantially different from their historic spawning sites (Waples et al. 1991). In addition, juveniles must pass up to eight hydroelectric dams that prolong downstream migration and may influence survival patterns (Connor et al. 2003a; Keefer et al. 2004; Raymond 1979).

It appears that these pronounced disturbances have elicited an adaptive response in Snake River fall chinook. The vast majority of these fish historically expressed an outmigration strategy in which juveniles migrate as

subyearlings within a few months of hatching (Groot and Margolis 1991). Connor et al. (2005) recently demonstrated that a significant fraction of the population now exhibit a yearling out-migration strategy. The temperature, hydrology, and effects of hydropower vary between spawning streams indicating that, for the fall chinook population, the selective advantage of this novel migration strategy may vary geographically, and could be linked to cooler temperatures in the Clearwater River (Connor et al. 2002). This offers an opportunity to understand the geographic distribution of life-history strategies, the environmental conditions that favor them, and the fitness advantages they confer. Although the recent appearance of the yearling out-migration strategy is well documented, the geographic details of yearling migration timing are not well understood due to seasonal loss of ability to detect PIT tags during winter and very early spring (Connor et al. 2005), and the relatively coarse spatial resolution of tagging data in general.

Advances in linking the life-cycle stages of migratory organisms using chemical and isotopic tracers has greatly improved our understanding of the relationships between source habitats, population regulation and life-history strategies (Hamann and Kennedy 2012; Marra et al. 1998; Wassenaar and Hobson 1998, 2000). We used strontium (Sr) isotopes in the otoliths of returning fish to reconstruct a detailed record of their juvenile migration. Otoliths are unique in their ability provide a detailed temporal and spatial record of changes in water chemistry and growth through daily deposition of growth rings throughout the life of the fish (Campana 2005). This makes otoliths useful for investigating the geographic diversity of life history of Snake River fall chinook salmon with resolution that has not been previously available. Specifically, chemical and isotopic patterns stored in otoliths provide a record of fish movement with enough resolution to uncover the geographic representation of juvenile out-migration strategies in unmarked and untagged natural origin fish (Bacon et al. 2004; Campana and Thorrold 2001; Kennedy et al. 2000, 2002). Understanding these strategies and their geographic representation is a prerequisite to unraveling the selective pressures acting on life history in Snake River fall chinook salmon.

The overall objective of this paper is to determine the geographic representation of the yearling out-migration strategy within the naturally spawned populations of Snake River fall chinook salmon. We examined spatial differences in yearling representation in light of geographically distinct temperature and hydrologic differences between spawning and rearing streams in the basin. We characterized the geochemical variability (temporally and spatially) of all spawning and rearing habitats for the Snake River fall chinook population. Using Sr isotope chemistry within otoliths of individual fish, we determined natal, rearing,

and overwintering location and the timing of juvenile entry into the ocean. We then determined the geographic representation of yearling fish within each major spawning area of the population. Subsequently, we reconstructed rearing location of all fish, and overwintering location of all yearling fish. These life stages are then examined for differences in juvenile fall chinook salmon out-migration strategy across distinct spawning populations and between yearling and sub-yearling life histories. We hypothesize that the proportion of yearling fish is higher, and out-migration timing is later, in tributaries known to have lower temperatures and later emergence timing.

## Materials and methods

### Study site

The Snake River, the largest tributary to the Columbia River on the west coast of North America, drains an area of 280,000 km<sup>2</sup> over six states. The river originates in Wyoming and flows 1,670 km to its confluence with the Columbia River in western Washington State with the majority of the basin located in the state of Idaho (Fig. 1). Because the Snake River flows through diverse geology, whereby each of its major tributaries flows through watersheds exhibiting large variations in mafic and felsic geology (Fig. 1), it is likely that differences exist in geochemical signatures among major watersheds in the basin. Geologic age also affects <sup>87</sup>Sr/<sup>86</sup>Sr signatures. Within the spawning area of Snake River fall chinook salmon, geologic age largely covaries with Mafic and Felsic rock type, with the oldest rocks being associated with the large felsic batholith of central Idaho (Foster and Fanning 1997) and large areas of young mafic rock within the Columbia River flood basalts (Hooper et al. 2007).

Fall chinook salmon runs, which once numbered as many as 500,000 returning adults per year, have been affected by the placement of dams within the Snake River basin. Upstream access to 80 % of their historic spawning grounds was blocked by the construction of the Hells Canyon Dam complex in the middle Snake River in 1959 (Waples et al. 1991) (Fig. 1). Four downstream dams on the Snake have impounded the river from Ice Harbor Dam near the confluence with the Columbia to the port of Lewiston, Idaho. Dworshak Dam, an impassable dam on the North Fork of the Clearwater River, blocks salmon migration and supplies cold, hypolimnetic water that cools the lower portion of the Clearwater River during hatching and rearing seasons. Outflows from Dworshak Reservoir are managed during late summer to aid juvenile fall chinook out-migration by creating cool refugia in otherwise warm downstream reservoirs as a part of the Columbia and

Snake River salmon management plan (Connor et al. 2003a). The Salmon River, flowing through the largely pristine Frank Church River of No Return Wilderness, remains the only tributary of the Snake River unaffected by hydropower. Based upon aerial redd surveys, it is estimated that the majority of current fall chinook salmon spawning occurs in two locations, the Hells Canyon reach of the Snake River (usually divided into two reaches, above and below the confluence with the Salmon River) and the Clearwater River. Less significant spawning occurs in the Lower Snake, Salmon, Grande Ronde, Tucannon and Imnaha Rivers (Garcia et al. 2008).

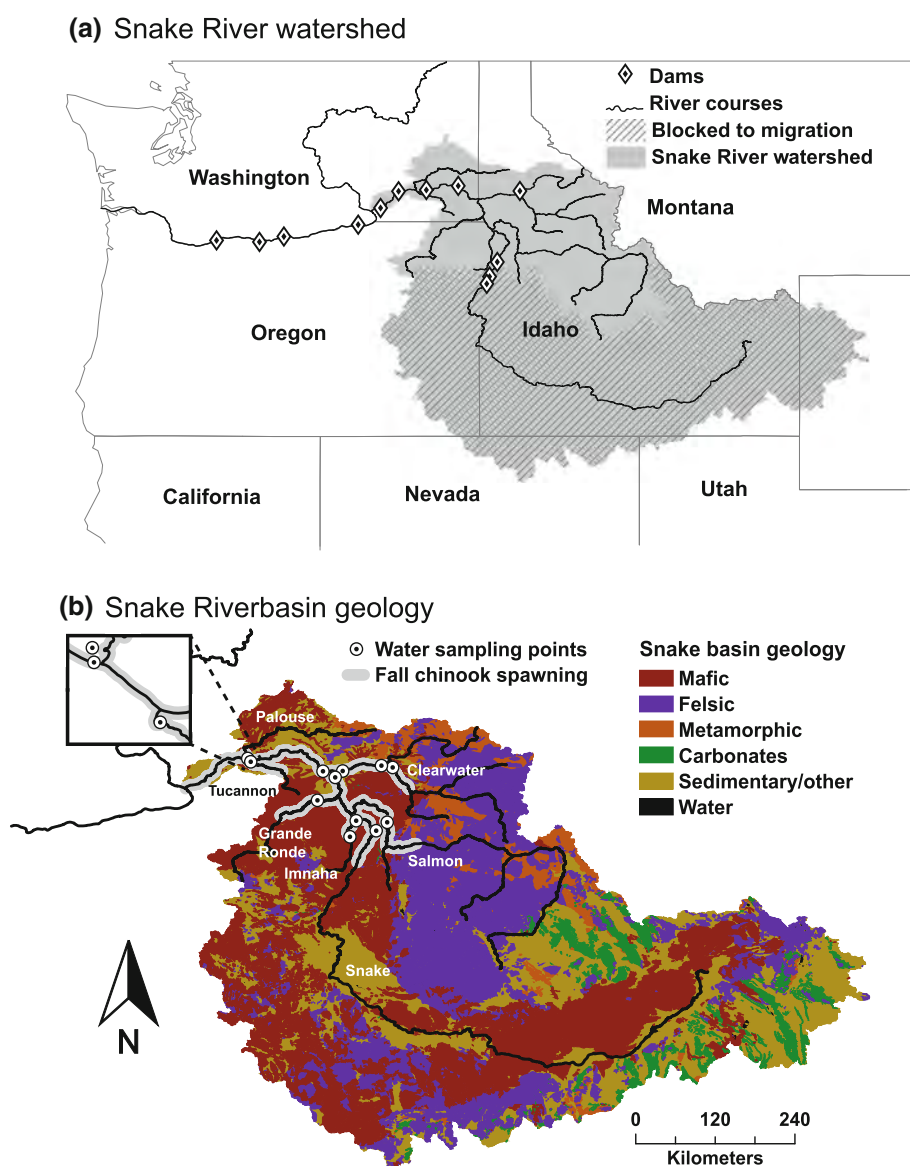
### Water chemistry

To quantify the spatial variation of <sup>87</sup>Sr/<sup>86</sup>Sr ratios within the Snake River basin, water samples were taken from the major spawning tributaries and at sites along the main stem of the Snake River (Fig. 1). Sampling points were determined based on the locations of significant fall chinook spawning activity with some additional sampling to capture hypothesized geochemical changes, such as the impounded section of the Lower Snake River. The Upper Snake River was defined as the free flowing river from the confluence with Salmon River upstream to Hells Canyon Dam. The Lower Snake River was defined as the free flowing section downstream of the Salmon River confluence downstream to the impounded section, located near confluence of the Clearwater River, created by the lower Snake River dams. The reservoirs were considered as a separate river section. Though no spawning occurs in this reach it is considered to be an important rearing area (Connor et al. 2002).

Samples were collected using established methods (Kennedy et al. 2000) from each site during spring, summer and fall seasons of 2008, with replicate fall samples collected in 2009 (Table 1). All samples were analyzed for <sup>87</sup>Sr/<sup>86</sup>Sr ratios using a Finnigan MAT 262 Multi-Collector thermal ionization mass spectrometer (TIMS). Throughout the research period, replicate analysis of the National Institute of Standards and Technology standard reference material (SRM-987) yielded mean <sup>87</sup>Sr/<sup>86</sup>Sr = 0.710231 (SD = 1.6 × 10<sup>-5</sup>, n = 16).

Water sampling points were grouped statistically based on similarity in <sup>87</sup>Sr/<sup>86</sup>Sr ratios. Grouping was determined using the non-parametric Kruskal–Wallis rank sum test (Hollander and Wolfe 1973) with post hoc non-parametric multiple comparisons tests ( $\alpha = 0.05$ ). Non-parametric tests were used due to the differences in variance between river groups, which violate the assumptions of ANOVA. Multiple comparisons were completed using results of Behrens–Fisher multiple comparisons tests (Munzel and Hothorn 2001) using the npmc package for R (<http://cran.r-project.org/>). Successive Kruskal–Wallis tests

**Fig. 1** The geology and extent of the Snake River basin, Idaho, USA is shown with **a** the extent of the Snake River watershed, the area blocked to fall chinook salmon (*Oncorhynchus tshawytscha*) spawning, and the location of hydroelectric dams indicated. No fish passage facilities exist at Hells Canyon dam on the Snake River, blocking upstream migration. **b** Snake River watershed geology showing rock types with strong impacts on  $^{87}\text{Sr}/^{86}\text{Sr}$ . Rock types are categorized by mantle origin (*Mafic*) or crustal origin (*Felsic*). *Metamorphic* rocks were grouped by protolith where known, or classified as metamorphic where protolith was unknown. *Carbonates* were classified separately due to their potential to affect  $^{87}\text{Sr}/^{86}\text{Sr}$  due to weathering effects or high  $^{87}\text{Sr}/^{86}\text{Sr}$  values. If no protolith could be determined rocks were classified as *Sedimentary/Other*. The location of water samples and the extent of documented fall chinook spawning are indicated. Geologic data from Preliminary Integrated Geologic Maps of the Western and Central States (Ludington et al. 2005; Stoesser et al. 2006)



were performed, with water sample data aggregated into river groups until multiple comparisons showed all groups to be significantly different ( $\alpha = 0.05$ ).

#### Otolith collection

Left sagittal otoliths from returning adult fall chinook salmon of presumed wild (natural origin), based upon a lack of marks or tags, were collected over 3 years (2006–2008) during spawning operations at Lyons Ferry Fish Hatchery (Lyons Ferry, WA). In each year, a fraction of the wild population (<10 %) is randomly selected for inclusion in hatchery operations to maintain genetic diversity. These fish are randomly sampled at Lower Granite Dam for hatchery broodstock and to estimate the

run size and are considered to be the most representative sample of the run available for the basin (Milks et al. 2009). We randomly selected otoliths from within this wild subsample to include in our analysis to ensure that our analysis reflects the proportions of yearling and subyearling fish migrating during a given year.

Otoliths were prepared for growth and microchemical analysis using established methods (Secor et al. 1991). Otoliths were ground using alumina slurry on a lapping wheel. Analyses were performed on the dorsal side of the otoliths in the region perpendicular to the sulcus (Fig. 2) as this area contained the most repeatable and clear growth rings. Scale samples were taken for all fish at the time of otolith removal and analyzed by Washington State Department of Fish and Wildlife to estimate hatchery or

**Table 1** Water sample  $^{87}\text{Sr}/^{86}\text{Sr}$  data for the Snake River basin 2008–2009 shows spatial variation among river groups (i.e., tributaries and major reaches) but not among sites within a river group

River Group	Site Name And Map Number	Sample Size	Site Average	River Group Average
USK	1. U. Snake (Pittsburg Landing)	4	0.708685±97	0.708685±97
CWS	2. Salmon River	5	0.713318±555	0.713308±832
	3. L. Clearwater (Below North Fork)	2	0.713809±668	
	4. L. Clearwater (Lapwai Creek)	4	0.713586±840	
	5. U. Clearwater (Orofino)	3	0.712292±25	
LSK	6. L. Snake (Lewiston)	2	0.709677±37	0.709699±124
	7. L. Snake (Chief Timothy)	4	0.709781±101	
	8. Lyons Ferry Hatchery	1	0.709659	
	9. L. Snake (Lyons Ferry)	2	0.709576±177	
TGI	11. Grand Ronde	3	0.706488±163	0.70681±320
	12. Imnaha (Cow Creek)	1	0.707204	
	13. Imnaha (Imnaha, OR)	1	0.707340	
	14. Tucannon	4	0.706756±130	

Sample points maintained temporal stability across seasons with of the Salmon and Lower Clearwater Rivers. Variation is expressed as 1 standard deviation in the last decimal place (i.e.  $\pm 97$  equals  $\pm 9.7 \times 10^{-5}$ ). The average within-sample standard error was  $\pm 1.3 \times 10^{-5}$  for all samples

Bold lines enclose samples which were not significantly different (Kruskal–Wallis, post-hoc Behrens–Fisher  $\alpha = 0.05$ )

wild origin, age, and yearling or sub-yearling migration strategy. The results of scale and otolith determination of migration strategy were compared (Table 2).

The otoliths from seven juvenile fish PIT tagged at known locations throughout the basin (Clearwater,  $n = 1$ ; Lower Snake,  $n = 3$ ; Upper Snake,  $n = 3$ ), were collected at Lower Granite Dam and used as validation samples for fish classification (Table 2). Their capture location at Lower Granite Dam also provided a known signature at the time of rearing/outmigration. In addition, otoliths from nine yearling juveniles from the 2008 brood year at Lyons Ferry Hatchery were analyzed for natal origin and included in the validation sample for natal location classification.

#### Otolith microchemistry

Otoliths were analyzed for  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio at each life history time point (i.e. emergence, rearing and outmigration). Sr isotopic ratios were analyzed at the GeoAnalytical Laboratory at Washington State University 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-ICPMS).

A marine shell standard, which was assumed to be in equilibrium with the global marine value of  $^{87}\text{Sr}/^{86}\text{Sr}$  (0.70918), was used to evaluate measurement error. The shell standard was analyzed periodically throughout a day

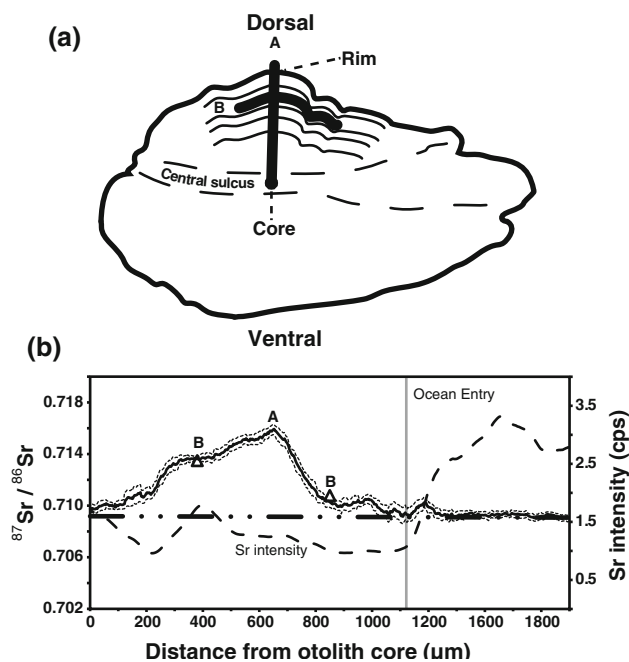
of analysis with no more than 15 samples run between standard runs. The mean marine shell value over the length of the study was 0.709214 (SD = 0.00013,  $n = 166$ ). A daily correction factor was calculated for each analysis day based upon the average deviation of the shell standard from the marine value and otolith  $^{87}\text{Sr}/^{86}\text{Sr}$  values were adjusted accordingly.

Two laser ablation approaches were combined to measure the otolith Sr isotope ratios (Fig. 2). First, a transect was analyzed from the otolith edge to its core at  $90^\circ$  from the sulcus on the dorsal side. If clear rings were not present in that region, the analysis was shifted to the nearest location with more distinct rings. The laser was set to ablate the sample at a constant speed (30  $\mu\text{m}/\text{s}$ , 40  $\mu\text{m}$  laser spot size, 0.262 s integration time). This scan recorded changes in  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio across the otoliths with excellent temporal resolution but lower precision ( $\pm 0.00028$ , 2 SE). To capture a more precise  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio for each life stage, transect ablations were followed by analyses which ablated a curved path along individual rings of the otolith (subsequently referred to as ring analyses) at points of stable signature within the natal, rearing and overwintering sections of the otolith (10  $\mu\text{m}/\text{s}$ , 30  $\mu\text{m}$  laser spot size, 0.262 integration time, 100 integrations). This method can provide very precise measures of isotopic chemistry ( $\pm 0.00012$ , 2 SE) within specific timepoints of the otolith. In cases where a more precise scan was not completed, signatures were determined using the appropriate section of

a transect scan. This was done by calculating the mean of the corrected  $^{87}\text{Sr}/^{86}\text{Sr}$  integration points within a region of stable  $^{87}\text{Sr}/^{86}\text{Sr}$  corresponding to the life stage being analyzed.

#### Life stage determination

We examined three distinct life cycle stages within the juvenile section of each adult otolith in the study: natal, rearing, and overwintering. The first stable signature



**Fig. 2** Otolith analysis was performed on **a** the dorsal section such that laser ablation transects (A) were at  $90^\circ$  to the sulcus and moved from the otolith core to rim. Ablation paths along rings (B, triangles in **b**) were used to determine more precise estimates of time-specific signatures. **b** Changes in  $^{87}\text{Sr}/^{86}\text{Sr}$  (solid line) and Sr intensity (dashed line) are shown across the otolith transect. Error for A (fine dotted lines) and B (triangles) is expressed as  $\pm 2$  times standard error (error bars for B are smaller than the marker). A characteristic increase in strontium intensity followed by convergence to the global marine signature (dot-dashed line) indicates ocean entry. The inflection point of strontium intensity was used as the point of ocean entry (vertical line)

beyond  $110\ \mu\text{m}$  and within  $250\ \mu\text{m}$  from the otolith core on the dorsal side was considered to be the natal signature. If no stable signature was detected, the first peak or valley in  $^{87}\text{Sr}/^{86}\text{Sr}$  was used as the natal signature. This range (i.e.,  $110\text{--}250\ \mu\text{m}$ ) was used in order to most closely approximate the natal location, while ensuring that a portion of the otolith was selected that was outside the area of maternal influence in the microchemical signature, yet before migration to downstream rearing habitat. These distances corresponded to hatching checks and downstream migration initiation in previous studies of fall chinook (Barnett-Johnson et al. 2005; Zabel and Chittaro, unpublished data).

Rearing signature was considered to be the first stable, freshwater signature between  $250$  and  $800\ \mu\text{m}$ . An overwintering signature was considered to be the first stable signature or peak beyond  $800\ \mu\text{m}$  from the otolith core. This distance was based on calculations of otolith size at length for fall chinook juveniles (Zabel et al. 2010), which indicated that  $800\ \mu\text{m}$  exceeded the expected size for a fish outmigrating past Lower Granite Dam in October, when bypass captures for the year and sub-yearling fall chinook outmigration have ended. These results were checked against scale analysis to confirm similarity in determination of yearling life history (78 % similarity; see Table 2). Scale analysis to determine yearling life history was compared with otolith results as a way to crosscheck scale analysis results however; validation of this scale method was incomplete at the time of this study. The similarity of results between the two methods indicates some degree of confidence in the results; however, otolith data was used to determine yearling or sub-yearling status of all fish. Any fish exhibiting a freshwater signature beyond  $800\ \mu\text{m}$  from the otoliths core was considered a yearling fish for subsequent analysis.

#### Discriminant function classification

Adult fish were classified to their natal, rearing and overwintering location using linear discriminant function analysis (LDFA) with equal prior probability and leave-one-out cross validation.  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures for all water sampling points within the basin were pooled, based on the

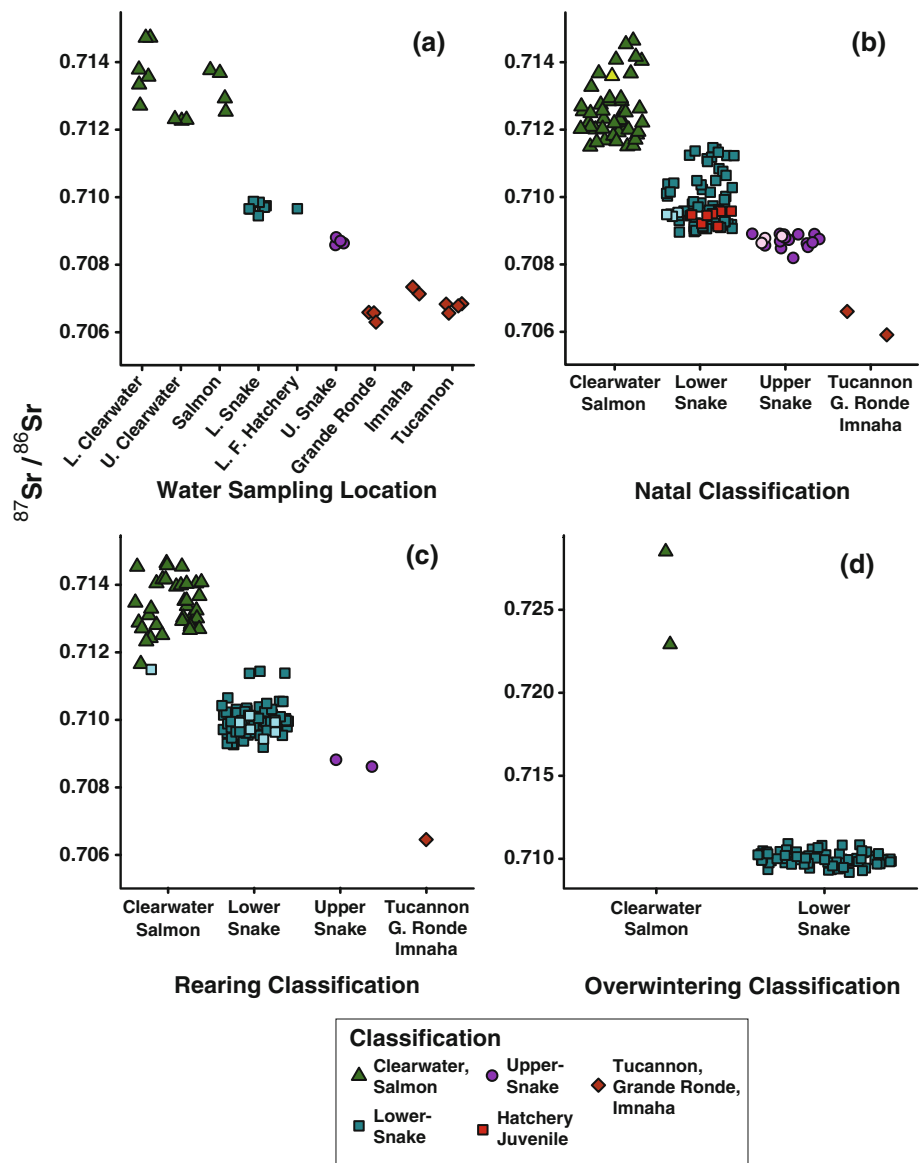
**Table 2** Summary statistics of adult fall chinook (*Oncorhynchus tshawytscha*) captured between 2006 and 2008 at Lower Granite Dam and sampled as a part of hatchery spawning operations at Lyons Ferry Hatchery

Years	Sample size	Mean age	% Female	% Yearling female	% Yearling	% Otolith/scale agree
2006	15	4.3	100	67	67	87
2007	38	3.7	42	63	66	80
2008	67	4.0	72	60	57	75
Overall	120	4.0	66	62	62	78

All fish were first determined to be yearling or sub-yearling based on scale analysis



**Fig. 3** Plots of  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio from **a** water samples and the classification of adult and juvenile chinook salmon otoliths to their **b** natal, **c** rearing, and **d** overwintering locations in the Snake River. Points are coded by *color and shape* according to statistical classification to river groups. Misclassified fish appear as a different color or shape from the classification column. *Lighter colored points* indicate juvenile fish of known origin. Wide variation (a) in the Clearwater—Salmon group is driven largely by seasonal variation in  $^{87}\text{Sr}/^{86}\text{Sr}$  signature. Results of (a) natal location LDFA classification of 120 adults and 14 known-origin juveniles. Results of (b) rearing location LDFA classification of 120 wild adults and 7 known-origin juveniles show distinct grouping between source river groups (six of seven known origin samples were correctly classified). Results of (d) overwintering location LDFA classification of 74 wild adults show the majority of overwintering juveniles residing in the Lower Snake River reservoirs. Note the change in scale in (d) of the y-axis and two points with much higher signatures that likely overwintered in the Columbia River system, outside our study area



non-parametric multiple comparisons (see “Water chemistry” above), into distinguishable groups. These groups were used as the training set to develop the LDFA. Overwintering was determined using otolith ocean entry signature ( $>800 \mu\text{m}$  = yearling). Known origin juvenile otoliths were included in the classification to provide validation of our ability to correctly classify fish.

We tested the hypothesis that expression of the yearling juvenile life history is non-randomly distributed within the basin using a two-tailed Fisher’s exact test of proportions (Routledge 2005). We compared the proportion of yearling fish originating from each of the classification groups to the pooled proportion of yearlings for the other river groups within the basin, to determine if statistically significant differences in yearling proportion exist between spawning areas.

**Results**

Water chemistry

Water  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures vary substantially in the major reaches of the Snake River basin (Table 1; Fig. 3) with significant differences between reaches (Kruskal–Wallis,  $\chi^2 = 104.6, P < 0.001$ ). Pairwise comparison tests indicated four major groups of distinguishable spawning site signatures in the basin. These groups were combined into a reduced model for the purpose of fish classification. The Tucannon, Grande Ronde, and Imnaha Rivers (TGI) were grouped based upon similar isotopic signatures. The Clearwater and Salmon Rivers (CWS) were grouped into a second group. Lyons Ferry Hatchery, the impounded section of the Lower Snake River, and the free-flowing Lower

Snake River below the Salmon River confluence made up a third group (LSK). The Upper Snake River (USK) made up a fourth group. All comparisons were significant in this reduced model (Behrens–Fisher,  $P < 0.001$ ). (Table 1)

The  $^{87}\text{Sr}/^{86}\text{Sr}$  values of water samples from the TGI, CWS, LSK and USK groups were used as a training set to create a linear discriminant function for subsequent fish classification. Cross-validation was used to estimate the true classification error rate and prior probability of group membership was assumed to be equal. The cross validation error rate for this model was 0 %. This linear discriminant function was subsequently used to classify fish to location at discrete juvenile life history stages.

We expected  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures to remain relatively temporally stable as reported in past studies of otolith microchemistry (Bain and Bacon 1994; Kennedy et al. 2000). The Clearwater and Salmon Rivers, however, showed high seasonal variation, resulting in high variation in their average signatures (Table 1). Both rivers generally decreased in  $^{87}\text{Sr}/^{86}\text{Sr}$  values during the spring and increased during the summer and fall, with the exception of the Lower Clearwater, which had an unexpectedly high summer signature. The relatively high signature for the Lower Clearwater during summer is likely due to large releases of water from Dworshak Dam on the North Fork Clearwater (Connor et al. 2003a). The Upper Clearwater River section, however, sampled 4 miles upstream of the North Fork confluence, and above possible dam effects, maintains a steady signature throughout the seasons with very little variation (Table 1). While Dworshak Dam likely affects the Sr chemistry of the Lower Clearwater River during summer, other seasonal variation in both the Clearwater River and the Salmon River (which is undammed) may be due to spatial variation in snowmelt patterns, the effect of seasonal saturation of soils with different weathering rates or isotopic signatures, or the effect of snow trapped windblown dust (Clow et al. 1997).

#### Life stage determination

#### Natal location classification

We classified all adult otoliths ( $n = 120$ ), as well as known origin juveniles ( $n = 14$ ), to their natal location based on the  $^{87}\text{Sr}/^{86}\text{Sr}$  signature recovered from the natal section of their otoliths (100–250  $\mu\text{m}$ ) using the previously developed LDFA model (Table 3). The LSK claimed the largest share of natal fish (58 fish, 48 %), followed by CWS (44 fish, 37 %), USK (16 fish, 13 %), and lastly, TGI (2 fish, 2 %). Classification was successful for 100 % of the known origin juveniles (Fig. 3).

To compare the occurrence of the yearling life history between natal locations, the percentage of yearling fish

(ocean entry  $>800 \mu\text{m}$  from otoliths core) was calculated for each group from the LDFA (Table 3). The CWS group contained the largest percentage of yearling fish (77, 74 % female), while the LSK and USK groups consisted of 62 and 13 % yearling fish (55 and 37 % female), respectively. Lastly, the TGI group was made up of 50 % yearling fish (100 % female); however, the sample size was small (2 fish). Based on these proportions of yearling fish, we found the CWS group to be significantly higher than the pooled proportion in the rest of the basin (Fisher's exact test,  $P = 0.01$ ). In contrast, the USK group contained a significantly lower proportion of yearling fish than the rest of the basin using the same test ( $P < 0.001$ ). The LSK and TGI groups did not show significant differences. The latter, however, had a small sample size and thus statistical power was insufficient to draw a conclusion.

#### Rearing location classification

All adult otoliths ( $n = 120$ ), as well as juveniles of known rearing location ( $n = 7$ ), were classified to rearing location based on the  $^{87}\text{Sr}/^{86}\text{Sr}$  rearing signature from their otoliths (250–800  $\mu\text{m}$ ) using the LDFA model (Table 3). The LSK group contained 78 fish (66 %), the CWS group contained 37 fish (31 %), the USK group contained 2 fish (2 %), and the TGI group contained only 1 fish (1 %).

To compare the occurrence of the yearling life history between rearing locations, the percentage of yearling fish (ocean entry  $>800 \mu\text{m}$  from otoliths core) was calculated for each group from the LDFA (Table 3). Yearling representation varied between rearing locations such that the LSK and CWS groups contained 58 and 76 % yearling fish (71 and 61 % female), respectively, while both the TGI and USK groups did not contain yearling fish.

Classification of juveniles of known rearing location was successful for six of the seven samples (Fig. 3); one fish was misclassified to the CWS group, possibly as a result of use of using the CWS as rearing habitat either before tagging or between recapture events.

#### Overwintering location

All adult yearlings ( $n = 74$ ) were classified to overwintering location (Fig. 3) based upon the  $^{87}\text{Sr}/^{86}\text{Sr}$  signature in the overwintering portion of their otoliths ( $>800 \mu\text{m}$ ) (Table 3). Specifically, 72 fish (97 %) were classified to the LSK group, while 2 fish (3 %) were classified to the CWS group (these groups consisted of 68 and 50 % female fish, respectively). The signatures of the CWS group fish were far higher than any measured within our study reach, and are more similar to the Columbia River (Barnett-Johnson et al. 2010; Miller et al. 2011). The TGI and USK groups did not contain any fish.

**Table 3** Results of the LDFA used to classify adult fish to their natal, rearing, and overwintering river group based upon <sup>87/86</sup>Sr ratio

River groupings (codes)	Natal location (%)	Sub-yearling	Yearling (%)	Juvenile validation samples	% Female	% Yearling female
Grande Ronde, Innaha, Tucannon (TGI)	2 (2)	1	1 (50)	0	100	100
Clearwater, Salmon (CWS)	44 (37)	10	34 (77) <sup>c</sup>	1 <sup>a</sup>	71	74
Lower Snake (LSK)	58 (48)	22	36 (62)	10 <sup>a</sup>	55	58
Upper Snake (USK)	16 (13)	12	2 (13) <sup>bc</sup>	3 <sup>a</sup>	37	100
Total sample size	120	45	73 (62)	14		
River groupings (codes)	Rearing location (%)	Sub-yearling	Yearling (%)	Juvenile validation samples	% Female	% Yearling female
Grande Ronde, Innaha, Tucannon	1 (1)	1	0	0	0	0
Clearwater, Salmon	37 (31)	9	28 (76)	1	61	61
Lower Snake	78 (66)	33	45 (58) <sup>b</sup>	6 <sup>a</sup>	65	71
Upper Snake	2 (2)	2	0	0	–	–
Total sample size	120	45	73 (62)	7		
River groupings (codes)	Overwintering location (%)	Sub-yearling	Yearling (%)	Juvenile validation samples	% Female	% Yearling female
Grande Ronde, Innaha, Tucannon	0	–	–	–	–	–
Clearwater, Salmon	2 (3)	–	–	–	50	–
Lower Snake	72 (97)	–	–	–	68	–
Upper Snake	0	–	–	–	–	–
Total sample size	74					

River groupings were determined from water chemistry (see Table 1). Juvenile validation samples consisted of juvenile fish of known origin (Wild = 7, Hatchery = 9) and were used to test the classification. River grouping is given in first column with remaining columns reporting the number of fish at each life stage. Percentage of fish classified to each life stage is given in parentheses

<sup>a</sup> Indicates successful classification to known source river group

<sup>b</sup> Yearling signatures for two fish were unrecoverable and were excluded from yearling analysis

<sup>c</sup> Indicates yearling proportion is significantly different from the rest of the basin (Fisher's Exact Test)

## Discussion

As environments undergo rapid change, adaptive changes in life history strategies may provide population resilience in the face of habitat changes and decoupling of ecological systems (Grottoli et al. 2006; Hughes et al. 2003; Jiguet et al. 2007; Reed et al. 2011). The extent to which adaptive shifts are the result of phenotypic plasticity or evolution is an important ecological question which may determine the ability of species to persist when the frequency or scope of the environmental pressures change (Chevin et al. 2010). Salmon, in particular, have exhibited a long history of resilience and adaptation in a changing environment (Montgomery 2000; Waples et al. 2008). Their ability to adapt and survive in the face of recent anthropogenic changes, however, has been questioned (Waples et al. 2009). Given the spatial variation of anthropogenic environmental changes, and the recent changes in life history expression, Snake River fall chinook salmon offer a compelling case study for understanding adaptation to recent anthropogenic change.

Our data support the hypothesis that novel life history strategies are spatially structured within the study population. Specifically, the yearling life history is expressed primarily in fish originating in the Clearwater River spawning area. Our data confirm prior studies (Connor et al. 2002, 2005) showing that the current population is made up of both yearling and sub-yearling juvenile migrants. We also provide evidence that the majority of yearling fish overwinter in the Snake River reservoirs, with a small fraction potentially moving downstream to the Columbia River. The majority of this new diversity in migration strategy is concentrated in only one spawning area, the Clearwater River.

The aggregation of watersheds into river groups with similar  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures had the potential to introduce ambiguity into the interpretation of our results, particularly comparison of the CWS and USK, the two largest spawning areas. Combining the Salmon River with the Clearwater River to form the CWS group does not significantly effect our interpretation of data. The CWS group is expected to be made up of less than 1 % fish from the Salmon River based on redd count data (Garcia et al. 2008), indicating that the vast majority of fish in this group are of Clearwater Origin. The free-flowing Snake River below the Salmon River confluence is grouped together with the Lower Snake River reservoirs within the LSK group, potentially obscuring the downstream movements of fish hatching below the Salmon River. Our results, however, correspond well to beach seine data showing fish throughout the basin moving into Lower Granite reservoir during the rearing phase (Connor et al. 2003b). Thus, during the natal stage, fish in the LSK group must be considered to have hatched in the free flowing section

below the Salmon River confluence. During rearing and overwintering stages, the LSK group can be considered to be residing in the downstream reservoirs, as beach seine data shows that fish do not remain in the free-flowing reach during these phases. The significantly smaller contribution of the Tucannon, Grande Ronde and Imnaha Rivers as source populations resulted in these sites being underrepresented in our sampled population, making their aggregation less problematic.

Our results strengthen the case for a link between natal stream temperatures and expression of the yearling salmon outmigration strategy. As their range has decreased, the importance of relatively cooler spawning habitat in the Clearwater River has increased (Waples et al. 1991). Outflows from Dworshak Reservoir further cool the lower reach of the Clearwater River and are managed during key summer migration periods to provide temperature refugia in the downstream reservoirs and increase smolt survival (Connor et al. 2003a). The Clearwater River averages 9 °C, a significantly lower temperature than the Snake River (Connor et al. 2002). Previous studies have linked the cooler temperatures and later hatch dates in the Clearwater to a shift toward later juvenile migration and increased abundance of yearling fish (Connor et al. 2002). Given that temperature can be a significant determinant of juvenile growth and survival in salmon (Connor et al. 2003a; McCullough 1999), these anthropogenic effects have the potential to create selective pressures toward changes in juvenile migration timing.

We found 13 % of fish originating from the USK, which averages 11.8 °C in spring (Connor et al. 2002), followed a yearling life history. In comparison, 77 % of CWS juveniles followed a yearling life-history strategy (Table 3). This confirms previous studies that indicated large numbers of yearlings originating in the Clearwater River (Connor et al. 2005). Further, our data show that fish from the Clearwater remain in the Clearwater until later in the year and move to rearing areas in the Lower Snake River later than other spawning groups (Fig. 3). Whether this is a result of later emergence, slower growth, or differences in life history expression is unknown, but supports the observations of Connor et al. (2002) that early emergence, temperature, or growth opportunity seem to play a part in determining yearling behavior.

While sample sizes were not large, the percentage of yearling fish from the CWS and USK was significantly higher than the pooled percentage of the remaining basin. The representative sampling of fish at Lower Granite dam indicates that even with relatively small sample sizes the proportions should be robust. Further, our results seem to fit well with previous studies which show the Clearwater River likely contain the largest number of yearling juveniles. Still, exact proportions of yearling fish from each

spawning area, or for a given hatch year, will require larger sample sizes. It is important to also note that our data come from adult fish which survived to return. Therefore, the proportions we calculated integrate both the actual percentage of fish following a given strategy as juveniles as well as any differential survival between these strategies throughout their lives.

Demonstrating whether this apparent increase in juvenile life-history diversity is an example of individual plasticity or adaptive evolution would depend upon genotypic differences among juvenile strategies and whether natural selection is changing genotypes in the population. Selection for a yearling life-history strategy requires differential survival between the two life-history strategies. Because our study was limited to otoliths from returning adult fish, direct estimation of differential survival cannot be calculated. Still, we would expect the representation of yearlings returning to spawn would be greater if a higher probability of survival exists for this population. We found that 62 % of returning fish had followed a yearling juvenile life history (Table 3), a high percentage considering the Clearwater River provides only 36 % of the total juvenile production for the Snake River basin (Garcia et al. 2008). Connor et al. (2005) also noted that a large percentage of returning adults (41 %) had followed a yearling life history. While this does not establish increased survival among yearling fish it provides evidence of possible selection for the yearling life history.

Williams et al. (2008) argue that these differences in representation may be evidence of selection for the yearling migration strategy. If this is the case, it would indicate a wider ability to adapt to the environmental changes of hydropower than has been observed previously in Pacific Salmon populations (Waples et al. 2009). Evidence exists for rapid evolution of salmon populations in response to changing environments, both in the recent and distant past (Quinn et al. 2000; Waples et al. 2004). Still, life-history changes, even if they are evolutionarily advantageous, do not provide evidence of a solution to population declines within the Snake River population or among other Pacific Salmonids. Rather, it is an interesting counterpoint to the conclusions of Waples et al. (2009), who argue that restoration efforts must attempt, as much as possible, to mimic natural disturbance regimes because salmon may not have the ability to adapt to the high frequency of anthropogenic disturbances across the landscape. Our data provide additional indication that, at least in the case of Snake River fall chinook salmon, Pacific salmon may have more adaptive plasticity than previously thought and that this plasticity may result in divergent migratory behaviors at the meta-population scale.

This study shows that otolith microchemistry and watershed scale  $^{87}\text{Sr}/^{86}\text{Sr}$  variation can provide important

tools to examine life-history expression at the level of the individual. Further, the temporal and spatial precision of otolith studies may be improved by combining  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios with other elemental signatures within the otolith (Thorrold et al. 2001; Walther et al. 2011). By combining individual migration data from otoliths with growth and survival estimates, we can begin to make specific predictions regarding the fitness advantages of observed migration strategies. Comparing the success of migration strategies under spatially heterogeneous environmental regimes may also inform our understanding of the relative contribution of evolution and phenotypic plasticity within Snake River fall chinook salmon.

The results of this study have important implications for understanding the population-level responses to changing environmental regimes and anthropogenic impacts that may not be evenly distributed across their range. Detailed study of alternate life histories creates opportunities to improve management at important life-history stages. For example, our results indicate that the majority of fall chinook juveniles in the Snake River overwinter in the reservoirs of the lower Snake River with a minority of fish potentially overwintered in the Columbia based upon their  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures. Understanding the location and timing of overwintering and early spring outmigration of this population group may allow managers the opportunity to target management actions toward individual life histories within the population. Further study of the environmental factors acting on expression of multiple life histories may allow managers to predict and mitigate the survival and fitness consequences of climate change or other anthropogenic disturbances.

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