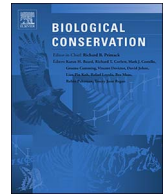




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Short communication

Endangered winter-run Chinook salmon rely on diverse rearing habitats in a highly altered landscape

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ABSTRACT

Protecting habitats for imperiled species is central to conservation efforts. However, for migratory species, identifying juvenile habitats that confer success requires tracking individuals to reproduction. Here, we used otolith strontium isotope ratios (⁸⁷Sr/⁸⁶Sr) to reconstruct juvenile habitat use by endangered Sacramento River winter-run Chinook salmon that survived to adulthood. The isotope data revealed that 44–65% of surviving adults reared in non-natal habitats, most of which is not designated as critical habitat under the Endangered Species Act. Juveniles entered these non-natal habitats at small sizes, yet left freshwater at a similar size to those that reared in the mainstem Sacramento River, suggesting these alternate rearing habitats provide suitable growth conditions. These findings indicate Sacramento River winter-run Chinook salmon rely on rearing habitats across a broader geographic region than previously known, potentially opening up greater restoration and conservation opportunities for species recovery.

1. Introduction

Identifying essential habitat is central to the conservation of endangered species. This can be particularly challenging for migratory species given their broad geographic range and the need to understand how the use of habitat through time affects survivorship (Runge et al., 2014). The issue of tracking is further complicated for salmon that distribute risk by sharing waterways with multiple populations (Schindler et al., 2015). Advancements in isotopic analyses show promise for reconstructing habitat linkages across life stages in a diversity of migratory taxa including bats, birds, fish, invertebrates and whales (Rubenstein and Hobson, 2004). Here, we demonstrate the use of natural isotopic variations to identify previously unknown rearing habitats that contribute to the long-term survival of endangered Sacramento winter-run Chinook salmon (hereafter, ‘winter run’).

Four runs of Chinook salmon (*Oncorhynchus tshawytscha*) with unique life histories spawn in the California Central Valley (CCV) basin (Fisher, 1994) named after the seasons adults return to spawn, including the endangered winter run. Sacramento River winter-run Chinook salmon are genetically distinct and exhibit rare life history behaviors across their life cycle. Juveniles rear in freshwater for 5–10 months before migrating to the ocean and show a more southerly

ocean distribution than other Chinook salmon. Adults typically mature after two years at sea before returning in the winter prior to spawning in the summer (Fisher, 1994; Satterthwaite et al., 2015, 2017). As a distinct Evolutionary Significant Unit (ESU; Waples, 1991) they are managed as a “species” under the Endangered Species Act (ESA). Historically, winter run spawned in the headwaters of the Sacramento River and its tributaries, such as the McCloud and Pit Rivers, but Shasta and Keswick Dams have prevented access to these upstream reaches since the early 1940s (Fig. 1). The ESU is vulnerable to extinction primarily because it is restricted to a single spawning population below Keswick Dam reliant on cold water releases that are insufficient to mitigate temperature dependent mortality during droughts, and projected to become increasingly scarce with climate change (Johnson and Lindley, 2016; Martin et al., 2017). The population declined dramatically in the 1970s to fewer than 200 spawners in the early 1990s, and was the first Pacific salmon to be state and federally listed as endangered in 1989 and 1994, respectively (California Code of Regulations, 1989, Federal Register, 1994). The freshwater habitat designated under the ESA as critically important for the long-term persistence of winter run is the mainstem Sacramento River downstream of Keswick Dam to the Golden Gate Bridge (~485 km), but excludes tributaries to the Sacramento River, much of the freshwater

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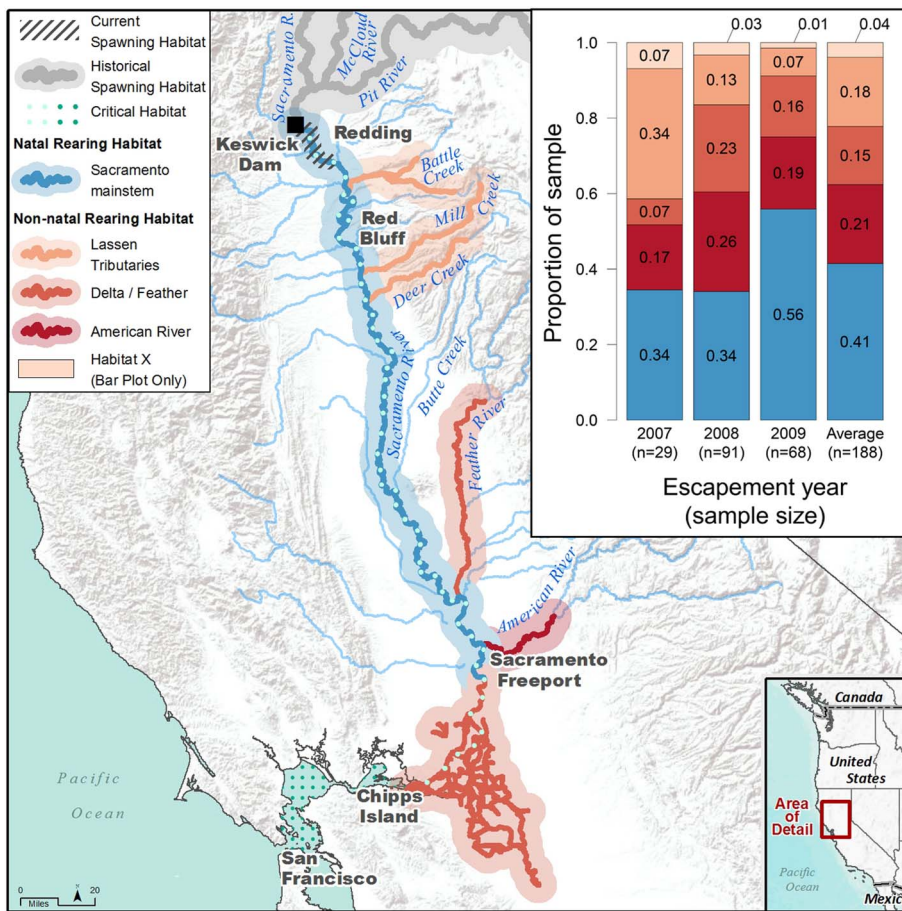


Fig. 1. Map of the California Central Valley winter run spawning grounds and migratory corridor, from Keswick Dam on the Sacramento River to Chipps Island, where they exit the freshwater Delta. Red shaded areas identify the regions identified isotopically as potential non-natal rearing habitats. Inset barplot shows the proportion of winter run in different “rearing groups” by escapement year, and averaged across years.

Delta, and South San Francisco Bay (Federal Register, 1993; Fig. 1). To date our understanding of winter run habitat use in the CCV is limited to older juveniles large enough for acoustic tags (> 80 mm); however, monitoring data suggest the majority of individuals disperse from the spawning reach as much smaller fry (< 46 mm, Fig. S1; del Rosario et al., 2013, Poytress et al., 2014). Anecdotal evidence suggests that the early-dispersing fry may use non-natal habitats (Maslin et al., 1996; Silva and Bouton, 2015), as has been found in other systems (Murray and Rosenau, 1989; Bradford et al., 2001), but it remains unclear whether this strategy contributes meaningfully to the adult population.

Here we use strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) in otoliths (calcium carbonate ‘ear stones’) to reconstruct the juvenile freshwater migration of winter run. $^{87}\text{Sr}/^{86}\text{Sr}$ varies among many of the rivers in the CCV, producing distinct and reproducible geographic markers across the landscape that are recorded in the otolith (Ingram and Weber, 1999; Barnett-Johnson et al., 2008). We determine the relative contribution of different juvenile rearing habitats to spawning winter run that returned in 2007–2009 based on the frequency of use, as recorded in adult winter-run otoliths. Our primary objectives were to determine (1) which juvenile rearing habitats contributed to the spawning population, (2) whether there was evidence for among-year variation in habitat use, and (3) whether size at freshwater exit differed among rearing groups.

2. Materials and methods

Adult winter-run otoliths were collected from the Livingston Stone National Fish Hatchery (LSNFH) throughout the May–July spawning season in 2007 ($n = 29$), 2008 (91), and 2009 (68). The adults sampled represent $\sim 1\%$ of the total population (2541–4537) and $\sim 50\text{--}85\%$ of the winter run spawned at the hatchery (Table A1). Winter run mature

predominately at age 3 ($> 90\%$; Fisher, 1994, Satterthwaite et al., 2017) so we assume the samples are representative of the 2004, 2005, and 2006 brood years. All adults sampled had adipose fins and therefore were assumed to be of natural origin because LSNFH removes the adipose fin of 100% of their hatchery juveniles prior to release. Otoliths were prepared using the methods described in (Barnett-Johnson et al., 2005). Strontium isotope ratios and the intensity of the Sr ion beam (Sr V, used as a proxy for Sr concentration) were measured by multiple collection laser ablation inductively coupled plasma mass spectrometry at the UC Davis Interdisciplinary Center for Plasma Mass Spectrometry (details provided in the Supplementary Material).

To reconstruct the habitat-use of juvenile winter run, habitat classification rules were developed using a baseline of $^{87}\text{Sr}/^{86}\text{Sr}$ signatures for salmon habitats in the Sacramento Basin and freshwater Delta (Weber, 2002; Barnett-Johnson et al., 2008; Sturrock et al., 2015), updated to ensure extensive spatial and temporal coverage (Table A2, Supplementary Material). We identified four isotopically unique “rearing groups”: (1) fish that reared only in the Sacramento River mainstem, and fish that also spent at least 3 weeks in (2) Mount Lassen Tributaries (e.g. Mill, Deer and Battle Creeks), (3) the Feather River or Delta, and (4) the American River (Figs. 1, 2). An additional group (“Habitat X”) was included containing individuals that exhibited clear non-natal rearing patterns in the otolith transect, but uncertainty in the geographic location(s). Of these rearing groups, only the Sacramento River mainstem and westward margin of the Delta are designated critical habitat for winter run (Fig. 1). We used changes in $^{87}\text{Sr}/^{86}\text{Sr}$ values along the otolith transect to identify two key habitat shifts to reconstruct the size at which individuals exited (1) the “natal” habitat (defined here as the mainstem Sacramento River from Keswick Dam to Freeport; Fig. 1), and (2) freshwater (Chipps Island, river kilometer 73). Because Chinook salmon otoliths grow proportionally with body length

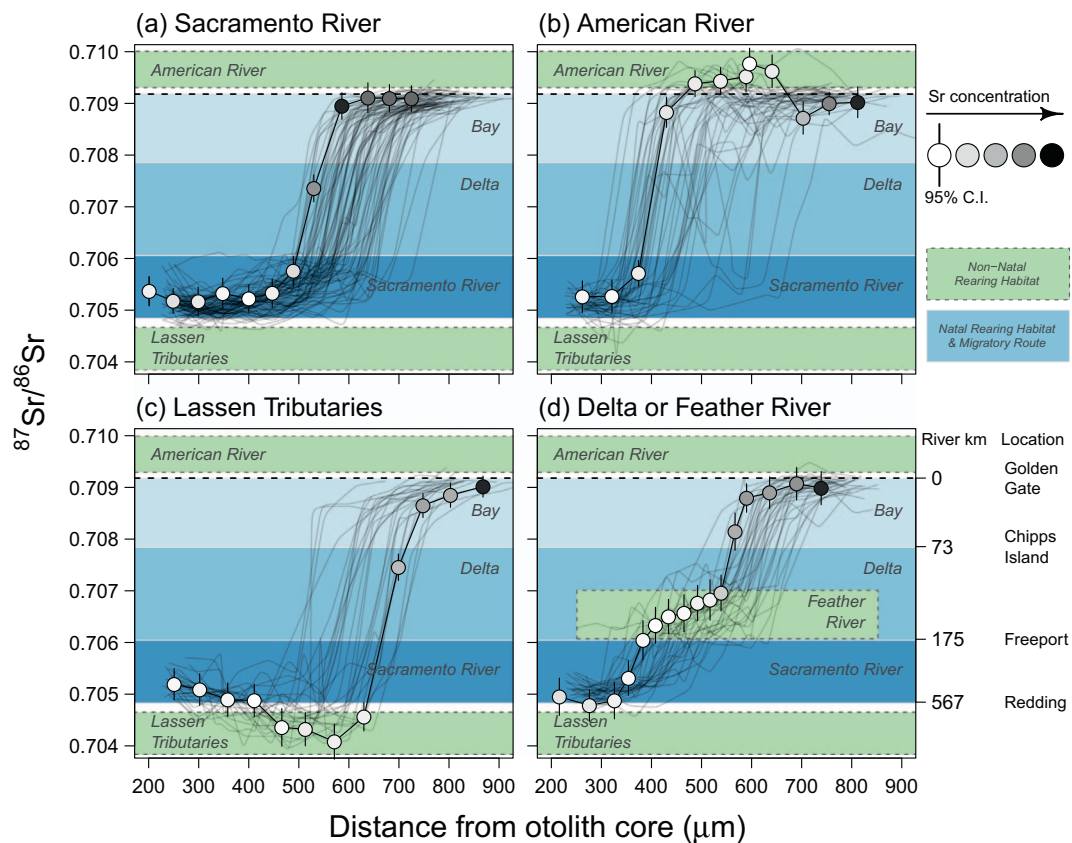


Fig. 2. Individual otolith $^{87}\text{Sr}/^{86}\text{Sr}$ profiles by rearing group (thin lines). In each group a representative example has been highlighted (circles with 95% confidence intervals showing measurement error), and shaded by relative strontium concentration as inferred using Sr V.

during juvenile freshwater residence (Miller et al., 2010; Sturrock et al., 2015), otolith radius was used as a proxy for juvenile fish size (see Supplementary Material for further details).

We fit linear models to test for differences in size at natal and freshwater exit associated with rearing group and escapement year. As fish in Habitat X could have resided in multiple non-natal habitats, these individuals were included in the latter but not the former. We reduced individual rearing group (4 or 5 levels) to natal or non-natal rearing (2 levels) following model selection with AIC corrected for small sample sizes. Analyses were performed in R 3.3.1 (R Core Team, 2016).

3. Results

The otolith isotope data reveal 44–65% of returning winter-run adults reared as juveniles in non-natal habitats (Fig. 1). Of these, the American River (17–26%), Lassen tributaries (7–34%), Feather River and most of the Delta (7–23%) are not designated as critical habitat for endangered winter run (Fig. 1). This diversity in rearing behavior was consistent among years, although escapement year 2009 (brood year 2006) contained a higher proportion of adults that had reared solely in the Sacramento River (56%). Of the individuals assigned to the ‘Delta or Feather River’ rearing group, the majority (> 86%, 2007 = 2 of 2, 2008 = 18 of 21, 2009 = 10 of 11) exhibited increasing $^{87}\text{Sr}/^{86}\text{Sr}$ values over time followed by ocean entry, suggesting Delta (rather than Feather River) rearing (see Supplementary Material). Five individuals reared in multiple non-natal habitats, exhibiting $^{87}\text{Sr}/^{86}\text{Sr}$ values consistent with rearing in Lassen tributaries followed by the American River or Delta, and were categorized according to the habitat they spent the greatest duration of time.

Fish that reared in non-natal habitats left the Sacramento River at significantly smaller sizes than fish that remained in the Sacramento

mainstem until ocean migration, but size did not vary with escapement year (Fig. 3a; Table A3). The average otolith radius of fish that had reared non-natally was 151 μm smaller (127–175 μm , 95% confidence interval) at natal exit than those that had reared solely in the Sacramento mainstem. While there is currently no winter-run-specific otolith-fish size calibration model available necessary for producing accurate size reconstructions (Zabel et al., 2010), a fall-run specific model (Sturrock et al., 2015) suggests a 26 mm difference in mean fork length at natal exit between natal and non-natally rearing fish (Fig. 3a). Yet, all fish exited freshwater at comparable sizes (Fig. 3b), with an average of 230 μm otolith growth (roughly equivalent to 39 mm fork length) occurring between natal and freshwater exit in fish that used non-natal habitats. Size at freshwater exit was relatively constrained (95% CI: 516–754 μm ; 75–116 mm fork length equivalent), but on average, individuals from escapement year 2009 were marginally, but significantly smaller when they left freshwater than those that returned in 2007–08 (Fig. 3c; Table A3).

4. Discussion

A successful migratory life history relies on an organism's ability to access suitable habitats during all phases of their life cycle (Runge et al., 2014). Here, we reveal that endangered winter run are relying on habitats outside of the critical habitat designated for preservation of the Sacramento River winter-run Chinook salmon ESU. On average, only 41% of juveniles reared in the mainstem Sacramento River for the duration of their juvenile life stage. Rather, the majority of winter run spent at least 3 weeks rearing in non-natal habitat, of which only the westward margin of the Delta is designated as critical habitat for winter run (Federal Register, 1993). In the CCV the majority of rivers are regulated and managed for multiple uses (Grantham and Viers, 2014); and all of the waterways involved in this study contain water

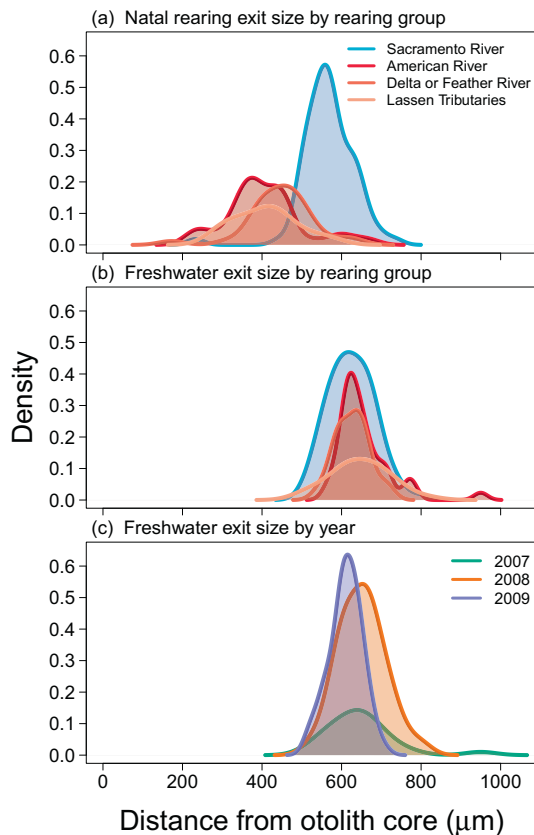


Fig. 3. Otolith distance (proxy for fish size) at (a) “natal” and (b–c) freshwater exit comparing rearing groups (a–b) and among escapement years (c). Data are presented as computed kernel density estimates weighted by the samples sizes of the rearing groups (a–b) or escapement years (c).

diversions. Therefore, identifying and maintaining suitable conditions in these waterways and other potential winter-run habitats may be paramount to the species' conservation.

Chinook salmon across their species range are recognized for their heritable diversity in life histories within populations and across ESUs that make them adapted to diverse environmental conditions. Non-natal rearing by juveniles has been observed in Chinook salmon in other parts of their range (Murray and Rosenau, 1989; Scrivener et al., 1994; Bradford et al., 2001; Brennan et al., 2015; Bourret et al., 2016), and it may be especially common in systems where conditions in the natal habitat or migratory corridor become adverse. For example, Bradford et al. (2001) found that a small, groundwater-fed tributary provided an important temperature refuge for overwintering juveniles in the Yukon River. In the Fraser River, juveniles move from the margins of the mainstem river into non-natal tributaries, likely to escape high flows and sediment concentrations associated with the spring freshet (Scrivener et al., 1994). Recent tagging and otolith studies have indicated that small fry that disperse downstream to rear are a viable migratory behavior commonly represented in the adult population (Shrimpton et al., 2014; Sturrock et al., 2015), and may experience higher smolt-to-adult survival than fry that rear in their natal reach (Copeland et al., 2014). However, identifying the non-natal habitats most commonly used by these successful individuals, and thus the specific habitats that may warrant conservation attention, remains elusive.

In the CCV, opportunistic and often anecdotal observations support the presence of winter run in non-natal habitats. Juvenile Chinook salmon of winter-run size have been observed in tributaries of Mount Lassen (Mill, Deer, and Antelope Creeks; Matthew Johnson personal communication) and coded-wire tagged hatchery winter run have been

recovered in a number of nearby intermittent streams (Maslin et al., 1996, 1998). Recently, genetic analyses have confirmed presence of winter run in the American River (Silva and Bouton, 2015). While these observations have been documented in occasional reports, the frequency of their occurrence in non-natal habitats was thought to be minimal and rare. Presently, no explicit monitoring occurs for winter run in these habitats (Johnson et al., 2017). Presence of winter run in non-natal habitats alone does not necessarily signify their value to the species. However, coupled with our isotope analyses from otoliths of returning adults, these habitats are revealed to contribute meaningfully to the population, warranting consideration for inclusion as critical habitat.

Early dispersing winter run appear to exit their natal Sacramento River at small sizes to rear for an extended duration in non-natal habitats and/or further downstream in the Delta prior to entering the ocean (Fig. 3a). However, at freshwater exit, all winter-run juveniles, regardless of rearing habitat, were comparable in size (mean otolith radius = 635 μm , SD = 61 μm ; mean fork length equivalent = 96 mm, SD = 10 mm; Fig. 3b). The constrained size at which juvenile winter run exit freshwater is likely due to physiological limitations associated with smoltification and/or size selective mortality in the marine environment (Woodson et al., 2013). Thus, non-natal habitats are providing both suitable growth opportunities for juveniles as well as contributing to the adult population in demographically relevant numbers.

The role of non-natal habitats appears important in all years, yet access to these habitats and the quality of the habitat likely varies as a function of hydrology. For example, non-natal rearing in the Lassen tributaries show the greatest variability in among-year contribution to the adult population (Fig. 1). These watersheds usually have adequate flows during winter; however, during drought conditions in January 2014, juvenile salmon mortalities were observed when Mill Creek was dewatered near the confluence with the Sacramento River (Matt Johnson personal communication). Further, several intermittent streams draining the Mount Lassen region are not wetted during the winter run rearing period in every year. Conversely, large storm events can back the Sacramento River water up into the American River by at least 13 km (Silva and Bouton, 2015). Juvenile winter run that establish territories in the American River after Sacramento River waters recede would likely benefit from being larger and thus more likely to out-compete the local fall-run population that typically emerges around December.

In addition to increasing the total area of potential juvenile rearing habitat, non-natal habitats may provide improved growth and survival conditions relative to the mainstem Sacramento River. In a survey of Chinook rearing habitats, Limm and Marchetti (2009) observed faster juvenile growth rates, greater prey density, and warmer water temperatures in non-natal tributaries compared to the mainstem Sacramento River. Similarly, Maslin et al. (1998) report faster growth rates in intermittent streams. The authors argue that because the intermittent streams go dry for months at a time, populations of piscivorous fish are not established. In the absence of predators, energy that would be expended on predator avoidance is directed towards growth. Future efforts would benefit from understanding the extent to which juveniles rearing in these alternative habitats are experiencing growth benefits relative to mainstem Sacramento rearing habitats. Additionally, by establishing a monitoring program that could estimate the proportion of winter-run juveniles rearing in these locations and the duration of time spent in each habitat, a quantitative estimate of their relative importance to the population can be estimated using otolith reconstructions (Walsworth et al., 2015; Brennan et al., 2015).

5. Conclusions

Access to diverse juvenile rearing habitats for winter run promotes phenotypic diversity which is likely to be important in dynamic environments, such as the CCV (Schindler et al., 2015). While our data

suggests these non-natal rearing habitats are consistently used, their relative importance to the population may fluctuate with California's hydrologic extremes. Annually collecting and analyzing adult otoliths ensures changes in habitat use and life history diversity can be monitored through time (Johnson et al., 2017). Maintaining and protecting a diversity of habitat options can buffer against extinction risk and needs to be incorporated into the winter run conservation strategy. Failure to protect these key habitats limits recovery opportunities and may increase the extinction risk of Sacramento winter-run Chinook salmon that currently rely on non-natal habitats.

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Appendix A. Supplementary data

Method details, including decision rules used to categorize adult Sacramento River winter run Chinook salmon into rearing groups. Supplementary data associated with this article can be found in the online version, at <https://doi.org/10.1016/j.biocon.2017.10.023>.

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