FEATURE

Researcher Eric Chapman holding a Chinook Salmon carcass collected from Putah Creek, Yolo County, California. Photo credit: Ken Davis, Aquatic Biologist, Wildlife Photojournalist.

# Geochemical Tools Identify the Origins of Chinook Salmon Returning to a Restored Creek


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Populations of Chinook Salmon *Oncorhynchus tshawytscha* in California are in decline due to the combined effects of habitat degradation, water diversions, and climate change. Reduced life history diversity within these populations inhibits their ability to respond to these stressors. Putah Creek, a small creek in California's Central Valley that once supported Chinook Salmon, is undergoing restoration to provide spawning habitats for this imperiled species. Beginning in 2014, increasing numbers of Chinook Salmon spawned throughout the creek, and emigrating juveniles were observed in the following months. Here we used otolith annual growth bands and microchemistry to investigate the age structure and natal origins of the adult spawners. Most individuals were 2 or 3 years old, and they originated from at least seven different natal sources, overwhelmingly from Central Valley hatcheries (~88%). These findings highlight that straying fall-run Central Valley Chinook Salmon can rapidly utilize restored habitats, potentially establishing new populations. However, to facilitate local adaptations, straying rates and gene flow will have to be managed over time. Reconnecting migratory pathways and restoring many small and diverse streams, like Putah Creek, provides an opportunity to increase life history diversity, strengthening the recovery and resilience of Chinook Salmon.

## INTRODUCTION

The need for enhanced connectivity and other strategies to promote population resiliency is evident for most salmonid runs (Bourret et al. 2016), but especially for those in the Central Valley of California. California holds the southernmost spawning streams for Chinook Salmon *Oncorhynchus tshawytscha*, with four evolutionarily distinct run types (spring, fall, late-fall, winter). Each run is named after the season when the adults return to fresh water to spawn, and each has distinctive genetic and life history traits (Moyle 2002; Williams 2006). This diversity among runs, as well as the diversity within runs across rivers, has allowed Chinook Salmon to persist within California's highly variable climate by providing population-level resilience to environmental variability, both in freshwater and marine habitats (Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015; Herbold et al. 2018; Sturrock et al. 2019a). However, riverine habitat loss and degradation, water diversions, fish harvest, and the construction of dams have led to drastic population declines (Yoshiyama et al. 1998), jeopardizing their long-term sustainability (Moyle et al. 2017; Herbold et al. 2018). As a result, spring- and winter-run Chinook Salmon of California's Central Valley are listed as threatened and endangered, respectively, under the Federal Endangered Species Act, while fall- and late-fall-run are considered species of concern (NMFS 1999, 2005).

The Chinook Salmon fishery in California is largely supported by hatchery production of fall-run juveniles (HSRG 2012). The transfer of fish among hatcheries and high straying rates of returning adults has led to their genetic homogenization (Williamson and May 2005). This valleywide homogenization combined with processes of genetic introgression from hatchery-origin fish into wild populations is likely reducing the local adaptation of wild populations and exacerbating their decline (Katz et al. 2012; Quiñones et al. 2014; Franks and Lackey 2015; Willmes et al. 2018a). California Chinook Salmon recently experienced high straying rates of hatchery adults, partially resulting from the trucking of hatchery-produced juveniles downstream to the estuary. Trucking efforts were accelerated during an extended drought (2012–2015) to improve outmigration survival to the ocean (Moyle et al. 2017; Sturrock et al. 2019b). These practices also disrupt the juveniles' olfactory map of the emigration corridor and thus result in higher straying rates of returning adults into nonnatal streams (Huber and Carlson 2015).

Given the negative impacts of this loss in genetic and life history diversity, one potential avenue for future management lies in the restoration of degraded habitats and the establishment of new populations in many smaller creeks within the Central Valley. In principle, each of these populations may develop local adaptations, driven by the selective forces unique to each watershed, and thereby increase the overall life history diversity of Central Valley Chinook Salmon. The observed high straying rates may facilitate the rapid use of reconnected, rehabilitated, or restored habitats. However, while these straying fish may provide the basis for establishing new populations and beginning the long-term process of building new diversity, continued high straying rates may also hamper the resurgence of genetic diversity in the future. Therefore, active management of straying adults may be required to leverage this natural process for the benefit of the species.

Putah Creek, a small stream in California's Central Valley, provides an opportunity to evaluate the straying of Chinook Salmon as a mechanism for population recovery. Putah Creek originates in the Vaca Mountains of the Coast Range of California and flows east into the Central Valley through Yolo and Solano counties and into the Yolo Bypass, from which it drains through the Cache–Lindsey slough complex and then into the lower Sacramento River (Figure 1A). Historically, the stream was intermittent in summer, with winter and spring floods creating large wetlands and multiple meandering channels in its lower reaches that supported a diverse flora and fauna, including many native fishes (Shapovalov 1947). Conversion of the floodplain to farmland, groundwater pumping, gravel mining, realignment, and diking forced the lower creek into a single, deeply incised channel with intermittent deep, wide pools. Then, construction of Monticello Dam in 1957 created Berryessa Reservoir, which drowned the principal salmonid spawning area in Putah Creek. The Putah Creek Diversion Dam, 13 km below Monticello Dam, diverted most of the water released from the reservoir for agricultural and urban use, causing the creek to cease flowing below the diversion dam in summer months. Putah Creek supported a diverse group of native fishes, including a small population of fall-run Chinook Salmon that spawned where the reservoir is today and a winter-run steelhead *Oncorhynchus mykiss*, which reproduced and reared in the permanent cold water of upstream tributaries (Shapovalov 1947); however, both runs disappeared with the construction of the dams. An agreement in 2000 (Putah Creek Accord) between the Solano County Water Agency, which is responsible for the oversight and management of dam and reservoir operations, and various stakeholders resulted in a flow regime designed to provide perennial flows for native fishes between the Putah Creek Diversion Dam and the Yolo Bypass (Figure 1; Kiernan et al. 2012). Additionally, fall flow pulses were designed to attract upstream migrating adult Chinook Salmon, even though initially there were few adults observed

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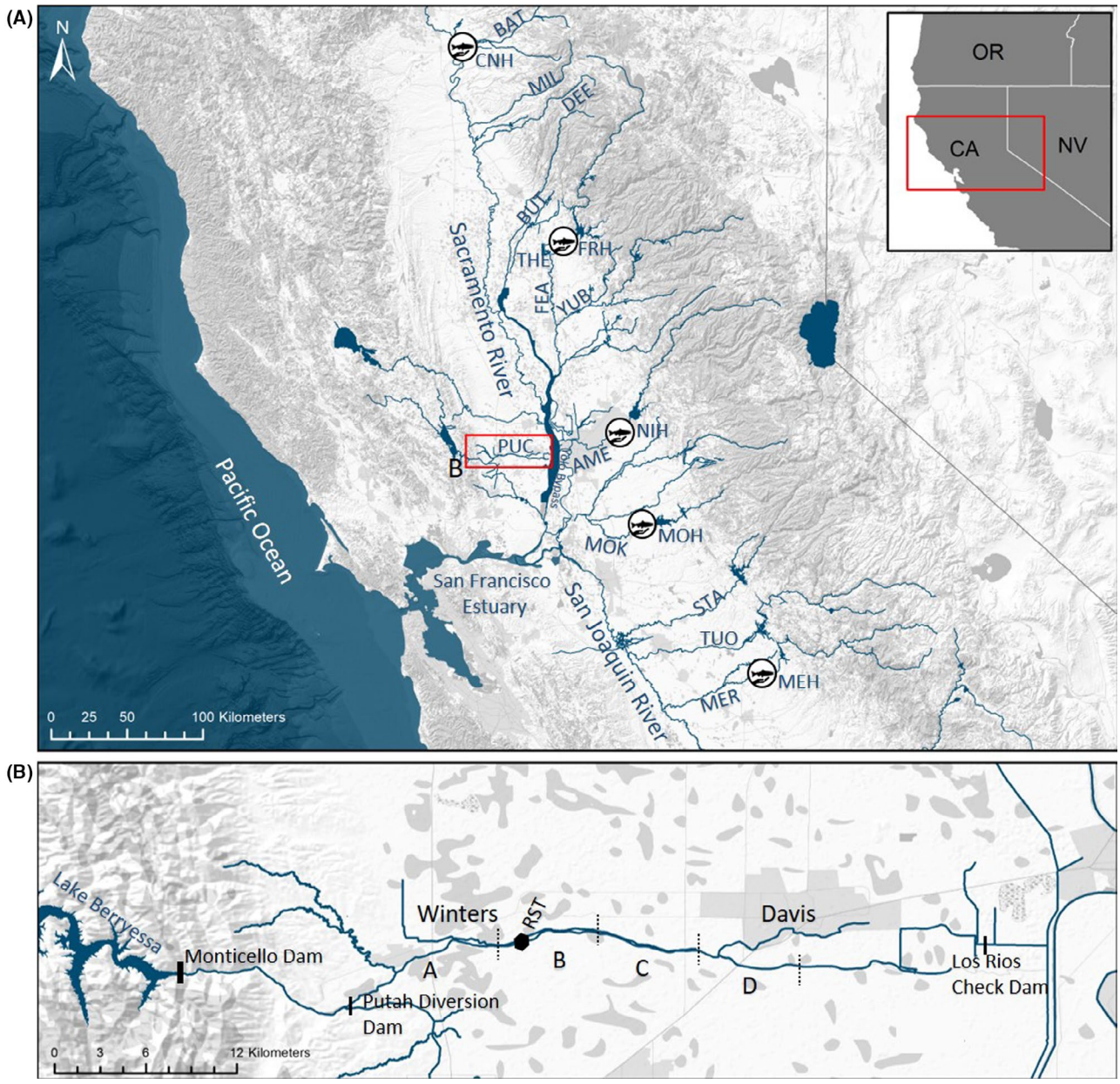


Figure 1. Panel **(A)** shows an overview map of the major Central Valley Chinook Salmon rivers and hatcheries. The abbreviations are as follows: BAT = Battle Creek, MIL = Mill Creek, DEE = Deer Creek, BUT = Butte Creek, SAC = upper Sacramento River, CNH = Coleman National Fish Hatchery, THE = Thermalito Annex, FEA = Feather River, PUC = Putah Creek, STA = Stanislaus River, MOK = Mokelumne River, FRH = Feather River Hatchery, MOH = Mokelumne River Hatchery, TUO = Tuolumne River, YUB = Yuba River, MER = Merced River, MEH = Merced River Hatchery, NIH = American River Nimbus Fish Hatchery, and AME = American River. Panel **(B)** is a map of Putah Creek showing the four sections surveyed for adult salmonid carcasses (labeled A–D) and the location of the rotary screw trap (RST) used to sample emigrating juveniles. The Putah Diversion Dam is the upper limit for the stream reach accessible to Chinook Salmon. Data for the base layers comes from the National Hydrography and Watershed boundary Dataset, U.S. Geological Survey, and the California Fish and Wildlife Service.

spawning there. Spring pulse flows were also designed to facilitate survival of emigrating juveniles and other native fishes through the upper reaches of the creek. These flows were not designed to be as large as historical flows but were intended to mimic the historical patterns with the idea to partially restore historical processes (Beechie et al. 2010). Putah Creek is currently also undergoing other active restoration initiatives, including rechanneling at various points, uncovering of previously silted spawning gravels, addition of new gravel habitats, and improvements within the surrounding riparian landscape.

Following the Putah Creek Accord, the initiation of regulated flows, and the seasonal opening of a barrier in Lower Putah Creek (Los Rios Check Dam), adult fall-run Chinook Salmon began appearing in the creek. Surveys conducted on behalf of Solano County Water Agency and by researchers from the University of California Davis showed adult numbers increased from < 10 per year prior to 2014 to over 500 in each of the following 3 years (~200 to 500 in 2014, ~500 to 700 in 2015, ~1,500 to 1,700 in 2016, and ~600 to 700 in 2017; estimates made by Peter Moyle, Ken Davis, and Eric Chapman).

Some fish were known to be of hatchery origin based on their lack of an adipose fin, which is clipped from 25% of fall-run hatchery salmonids produced in the Central Valley (Bergman et al. 2012; Kormos et al. 2012).

Here we analyzed annual growth bands and microchemistry in otoliths ("ear stones") to reconstruct age structure and natal origins of spawning adult Chinook Salmon in Putah Creek. Our main questions were as follows: (1) What are the origins of Chinook Salmon spawning in Putah Creek? (2) Is there evidence that juvenile Chinook Salmon produced in Putah Creek are returning as adults to spawn? (3) Is the age structure of adult Chinook Salmon spawning in Putah Creek similar to that of fall-run Chinook Salmon throughout the Central Valley? Enhanced understanding of the origins of adult fish that strayed into this restored habitat will highlight conditions that foster the establishment of new populations and ultimately may provide a blueprint for how small stream restorations can contribute to the long-term conservation of Chinook Salmon in California.

## METHODS

### *Otolith Analyses*

Otoliths are paired calcium carbonate structures located in the inner ear of most teleost fishes used for balance and hearing. They are metabolically inert and accrete continuously, forming incremental growth layers. Consequently, they can preserve a record of age, growth, and environmental conditions throughout the life of a fish (Campana 1999). Strontium (Sr) substitutes for calcium in the mineral lattice of otoliths, resulting in element concentrations and isotope ratios ($^{87}Sr/^{86}Sr$) that reflect environmental sources (Kennedy et al. 1997; Hobbs et al. 2005). In turn, $^{87}Sr/^{86}Sr$ in the environment varies predictably between different geologic provinces, based on their age and geochemical composition (Capo et al. 1998), due to the radioactive $\beta^-$ decay of $^{87}Rb$ (Rubidium) to $^{87}Sr$. Through weathering, Sr is transferred into the hydrosphere and ecosphere and subsequently integrated into biological tissues. This allows us to use $^{87}Sr/^{86}Sr$ as a tracer to reconstruct individual fish movements across different rivers and within estuaries. For Chinook Salmon in the Central Valley, $^{87}Sr/^{86}Sr$ has been successfully used to identify life history diversity, natal origins, and nonnatal rearing habitats and to distinguish hatchery and wild origins (Ingram and Weber 1999; Barnett-Johnson et al. 2008; Sturrock et al. 2015, 2019a; Phillis et al. 2018; Willmes et al. 2018a).

### *Field Survey and Sample Collection*

For the 2016 field survey (November 2016 to January 2017), Putah Creek was divided into four sections (A–D) stretching from below the Putah Diversion Dam to Old Davis Road in Davis, California (Figure 1B), encompassing the majority of suitable habitat available to spawning Chinook Salmon. Samples were collected by canoe from all carcasses encountered throughout the creek by this stratified sampling approach on a weekly basis, and GPS location, date, sex, and fork lengths were recorded. For several fish, it was not possible to determine fork length due to the state of the carcass. Fish were dissected on site and otoliths were removed, air dried, and stored in plastic vials. Heads were collected and frozen from fish carcasses missing an adipose fin, an indication of a fish released by the Constant Fractional Marking Program and containing a coded wire tag. Heads were then transferred to the California Department of Fish and Wildlife Coded Wire Tag Laboratory in Sacramento, California, where the coded wire tags were extracted and the individual fish were linked to a hatchery, release year, and release location. We used these known fish origins and ages for validation of otolith age and natal origin. In total, 126 carcasses were collected; however, 22 otoliths were damaged during dissection or sample preparation, resulting in 104 otoliths (18 paired with coded wire tags) being analyzed (Table 1). These 104 fish represent ~ 6% of the total estimated number of ~ 1,500 to 1,700 adult Chinook Salmon returning to Putah Creek that year. In addition, juveniles were collected by beach seine in 2016 ($n$ = 6) and from incidental mortalities in a rotary screw trap (river section B, Figure 1B) in spring of 2017 ($n$ = 13; Table 1), and their otolith microchemistry was used as a baseline for the $^{87}Sr/^{86}Sr$ variability in Putah Creek.

Table 1. Number of Chinook Salmon otoliths analyzed by recovery location (see Figure 1B) in the Putah Creek, California.

| Sample type and total | Recovery location | Number of fish analyzed |
|---|---|---|
| Juvenile Chinook Salmon | Beach seine (2016) | 6 |
| | Rotary screw trap (2017) | 13 |
| Total juvenile | | 19 |
| Adult Chinook Salmon | River section A | 64 |
| | River section B | 32 |
| | River section C | 7 |
| | River section D | 1 |
| Total adult | | 104 |

### *Otolith Preparation*

Adult Chinook Salmon sagittal otoliths were mounted in Epoxicure (Buehler Scientific) epoxy resin and transversely sectioned with an Isomet diamond cutting saw to remove the rostral and postrostral ends. Thin sections were adhered to glass microscope slides with Crystal Bond thermoplastic resin (Crystalbond 509; Ted Pella, Redding, California), sanded to the core on both sides with 800–1,200 grit wet/dry sandpaper, and polished with 0.3-µm MicroPolish II Alumina (Buehler Scientific) on a polishing cloth, following established methods (Wells et al. 2003). We used the transverse section instead of the sagittal preparation, which is typically used for juvenile habitat use and growth reconstructions (Woodson et al. 2013; Sturrock et al. 2015, 2019a), to preserve the outer rings in the convex adult otoliths. Whole juvenile otoliths were mounted in the sagittal plane, then sanded and polished using the same procedure as the adult otoliths. Digital images of otoliths were taken on a CH30 Olympus compound microscope using transmitted light at 40× and 200× magnification and a 12-megapixel digital camera, using AM Scope (MU1000).

### *Otolith Ages and Microstructure*

Chinook Salmon otoliths contain a time series of translucent and opaque bands that are deposited on a daily and seasonal basis in response to photoperiod, temperature, diet, and endogenous rhythms (Neilson and Geen 1982; Campana and Neilson 1985). In adult otoliths, a translucent zone followed by

an opaque zone signifies 1 year of otolith growth, representing winter and summer seasons, respectively (Welch et al. 1993). Annual ages were estimated from digital images along the transverse plane of the ventral lobe, counting each sequence of winter (translucent) and summer bands (opaque). Bands were counted after identifying checks produced at hatching (hatch check), those produced by the onset of exogenous feeding (exogenous feed check), and those from ocean entry (ocean entry check; Figure 2). These are distinct bands that are often produced during periods of stress and environmental change (Campana and Neilson 1985; Woodson et al. 2013). Ages were validated by comparing age counts to known-age hatchery fish with physical tag information ($n$ = 18) between five age readers following the methods proposed by Campana (2001) and using the FSA package (Ogle et al. 2020) in R (R Core Team 2019).

### *Otolith Microchemical Analysis*

Otoliths were mounted on petrographic glass slides, with 12 individual otoliths per slide. The $^{87}Sr/^{86}Sr$ isotope ratios were measured at the University of California–Davis Interdisciplinary Center for Plasma Mass Spectrometry. For the Sr isotope analyses a Nd:YAG 213-nm laser (New Wave Research UP213) was coupled to a Nu Plasma HR multi-collector inductively-coupled plasma mass spectrometer (MC-ICP-MS) (Nu032). A laser beam 40 µm in diameter was traversed across the otolith from the core to the ventral edge at 5 µm/s, with the laser pulsing at a 10-Hz frequency and 5–15 J/cm$^2$ photon output. For all juvenile Chinook Salmon, and a subset of the adults, full profiles were also obtained from the dorsal edge to the core to the ventral edge (Figure 2). The $^{87}Sr/^{86}Sr$ isotope ratio was normalized for instrumental mass discrimination by monitoring the $^{86}Sr/^{88}Sr$ isotope ratio ($^{86}Sr/^{88}Sr$ = 0.1194), and $^{87}Rb$ was corrected by monitoring the $^{85}Rb$ signal and normalized by the same mass bias coefficient as Sr. Krypton interference ($^{86}Kr$) originating from the argon supply was corrected using on-peak subtraction before each analysis. Accuracy and reproducibility of the LA-MC-ICP-MS were evaluated using in-house reference materials consisting of a modern marine coral from the South China Sea and a modern marine otolith from a White Seabass *Atractoscion nobilis* collected offshore of Baja California. Replicate analyses yielded a $^{87}Sr/^{86}Sr$ value for the coral of 0.70921 ± 0.00006 (mean ± 2 SDs; $n$ = 32) and for the otolith of 0.70919 ± 0.00005 ($n$ = 53). These values are in good agreement with the global average $^{87}Sr/^{86}Sr$ value of modern seawater of 0.70918 (McArthur et al. 2001; Mokadem et al. 2015).

Processing of otolith microchemistry data was performed using the IsoFishR application (Willmes et al. 2018b). A five-point average was applied to the raw data collected by the mass spectrometer, with an integration time of 0.2 s resulting in one data point per second. Then a 20-point moving average was applied to the raw data and outliers were removed based on 2 SD outlier criterion using a 40-point moving average window. For each otolith, the core was visually identified from the growth structure in the otolith image and the spike in $^{88}Sr$ V. Following the core, the freshwater and ocean habitats were assigned based on the observed $^{87}Sr/^{86}Sr$ pattern as distinct

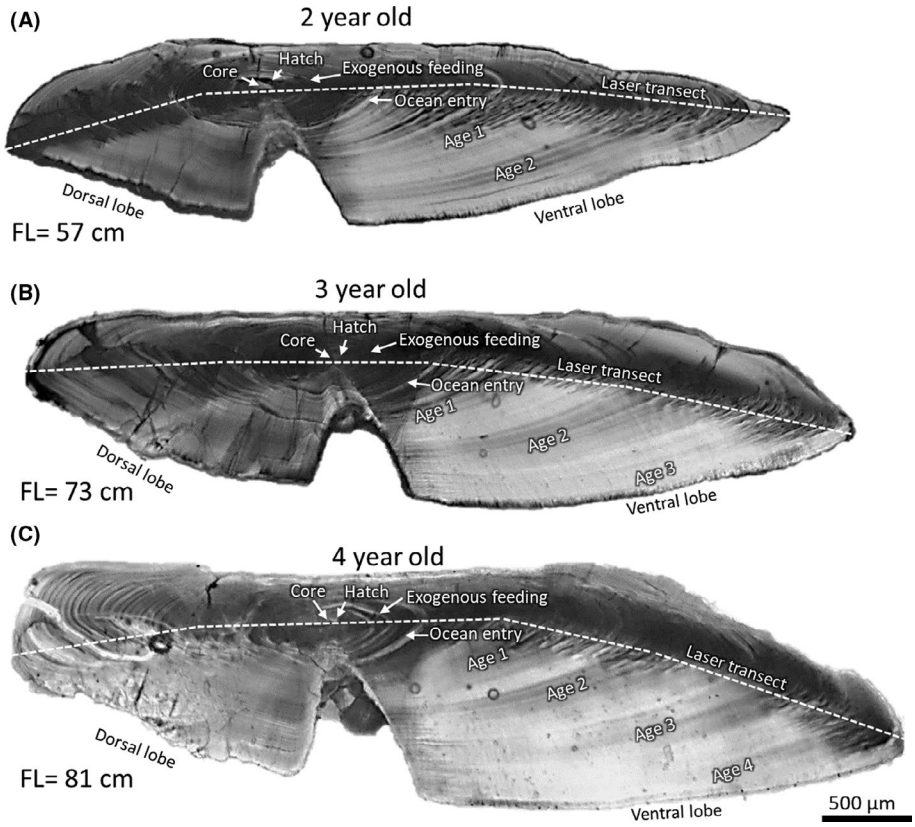


Figure 2. Three examples of Chinook Salmon otoliths showing the position of checkmarks produced at hatching (hatch check), those produced by the onset of exogenous feeding (exogenous feed check), and those produced by ocean entry (ocean entry check). Annual ages were estimated based on the sequence of winter (translucent) and summer bands (opaque). The dotted white line shows the laser ablation transect.

regions (minimum >50 µm, often >100s of µm, if no change in $^{87}Sr/^{86}Sr$ isotope values). The natal period was defined as part of the freshwater region immediately following the exogenous feeding check, outside of the influence of maternally derived Sr (Bacon et al. 2004; Barnett-Johnson et al. 2007; Miller and Kent 2009). For each region mean values and standard deviations were calculated.

### *Natal Habitat Assignment*

A random forest model was used to classify the natal origins to their respective river source as determined by the strontium isoscape of the Central Valley. The $^{87}Sr/^{86}Sr$ baseline for Central Valley rivers and Chinook Salmon hatcheries was compiled from published water and juvenile otolith data (Ingram and Weber 1999; Barnett-Johnson et al. 2008; Sturrock et al. 2015, 2019a; Phillis et al. 2018; Willmes et al. 2018a) and augmented with new data based on juvenile Chinook Salmon in Putah Creek. Random forest is a supervised ensemble machine learning method. It is generally used for data with many variables, but also proved to be more stable for single variate data than alternative classification techniques, such as classification and regression trees or discriminant function analyses. To create the forest, the strontium isoscape data was split 50%, bootstrapped with replacement and a sample size of 100 stratified by source, and 500 trees were generated. The mean $^{87}Sr/^{86}Sr$ value of the natal region from the otoliths was used to predict natal origin of each fish, choosing the highest probability (≥80%) as the likely natal origin. Assignment was carried out independently on two levels, first on aggregated hatchery and wild origins and second for individual river and hatchery strata. When a fish could not be assigned to a single natal source with high classification confidence, then we combined the best matches until they reached ≥80% classification confidence to create a combined natal origin. For example, if a fish was assigned to the Feather River Hatchery (44%) and Mokelumne River Hatchery (46%), it was assigned to a combined group of Feather River Hatchery–Mokelumne River Hatchery fish. While this approach does not yield a natal origin on the level of distinct river or hatchery, it still allows broader-scale classification.

## RESULTS

### Age and Length

Annuli counts from otoliths provided reliable estimations of fish age, with age estimates of known-age fish (determined from coded wire tags), spanning 2-, 3-, and 4-year-old fish, exhibiting 100% accuracy ($n$ = 18). Age estimations between the five age readers across all otoliths reached an initial agreement of 82% ($n$ = 104, average coefficient of variation = 4.5, average percent error = 3.2). For fish with age disagreements, ages were assigned based on majority vote if at least three readers were in agreement. Age estimates for most Chinook Salmon were 2 years (44%) or 3 years old (42%; Figure 3A), while 4-year-old fish were in the minority (13.5%). All fish showed an ocean entry check before the year-1 annuli, indicating that they all emigrated from the freshwater system of the Central Valley to the Pacific Ocean as subyearlings, which is typical for this region and run type (Woodson et al. 2013). Average adult fork length was determined for 64 fish and increased with age from 61.0 cm at age 2 to 88.9 cm at age 4, but there was considerable overlap among the age-classes (Figure 3B; Table 2).

### Strontium Isoscape

Generally, $^{87}Sr/^{86}Sr$ signatures differed among the rivers and hatcheries of the Central Valley (Figure 4), largely following expected patterns based on the age and composition of the watershed geology. In some cases, however, considerable overlap exists between sources, which can complicate natal assignment to the river and hatchery level. The $^{87}Sr/^{86}Sr$ value of Putah Creek is based on natal values of juvenile otoliths from 2016 ($n$ = 6) and 2017 ($n$ = 13) and was on average 0.70630 ± 0.00016 (mean ± 2 SDs; $n$ = 19). Unfortunately, this $^{87}Sr/^{86}Sr$ value overlaps considerably with the isotopic signature of the spawning reaches of the Feather River and Stanislaus River (but not the Feather River Hatchery). However, Putah Creek is isotopically different from other major salmonid producing rivers and hatcheries in the Central Valley (Figure 4). The main stem of the San Joaquin River is not included in the $^{87}Sr/^{86}Sr$ isoscape because it does not currently represent an important natal habitat for fall-run Chinook Salmon (Buchanan et al. 2018).

Random forest models achieved an accuracy of 91% (CI = 87–94%; kappa = 0.80) for classifying baseline samples of known origin as either hatchery or wild (Supplement Table S1). For models classifying fish to their individual river or hatchery origin, accuracy decreased to 74% (CI = 68–79%; kappa = 0.72) as a result of overlap between some of the rivers and hatcheries in the Central Valley (Supplement Table S2).

### Life History and Natal Origins

For each fish, the adult and natal regions of the otolith $^{87}Sr/^{86}Sr$ profiles (Figure 5A) were assessed. Adult $^{87}Sr/^{86}Sr$ values were on average 0.70919 ± 0.0002 (mean ± 2 SDs; $n$ = 104), overlapping with the modern ocean average of 0.70918 (McArthur et al. 2001; Mokadem et al. 2015), reflecting the expected pattern of prolonged foraging in the ocean (typically 1.5–3.5 years). We also observed a change in the $^{87}Sr/^{86}Sr$ values at the very edge of the otoliths, reflecting the last weeks or months of each fish's life, when they returned to freshwater habitats to spawn.

Mean natal $^{87}Sr/^{86}Sr$ values were variable, ranging from 0.7053 to 0.7100, indicating that these adult spawners originated from a variety of different rivers and hatcheries (Figure 5B). Random forest accuracy varied by river and hatchery, with some sources showing poor discrimination, such as the Feather River Hatchery and the Mokelumne River Hatchery (Supplement Table S2). Using coded-wire-tagged fish with known hatchery origin ($n$ = 18), we tested the accuracy of the random forest model and found that all were correctly classified as hatchery fish. However, some of the known origin Mokelumne River Hatchery fish were classified to the combined Feather River Hatchery–Mokelumne River Hatchery strata with poor differentiation between these two sources.

Based on the random forest model, we estimated that fish from at least seven sources contributed to the Putah Creek Chinook Salmon population in 2016 (Table 3). Posterior probabilities for assigning fish to individual sources were generally high ($n$ = 64; ≥80%), and fish with lower posterior probabilities ($n$ = 40) were assigned to grouped sources due to lower confidence in the unique origins (Supplement Figure S1). Nearly all fish contributing to the current Putah Creek Chinook Salmon run were of hatchery origin ($n$ = 92; ~88%), mostly from the Mokelumne River Hatchery ($n$ = 27) and the Feather River Fish Hatchery ($n$ = 24) or from the combined Mokelumne

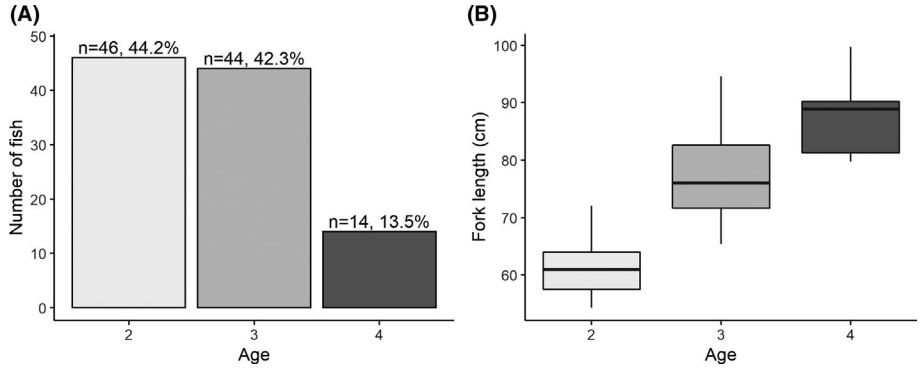


Figure 3. **(A)** Age distribution and **(B)** fork length by age for the adult Putah Creek Chinook Salmon. For the box and whisker plot (panel B) the bottom of the box corresponds to the 1st quantile (Q1), the horizontal line to the 2nd quantile (Q2=median), and the top the 3rd quantile (Q3). The inter quantile range (IQR) is calculated as Q3-Q1, and the whiskers are defined as Q1- 1.5*IQR for the lower whisker and Q3+1.5*IQR for the upper whisker.

River Hatchery–Feather River Fish Hatchery group ($n$ = 30), with smaller contributions from the American River Nimbus Fish Hatchery ($n$ = 8), Coleman National Fish Hatchery ($n$ = 2), and the Merced River Fish Hatchery ($n$ = 1).

Wild-origin fish were classified to the Mokelumne River ($n$ = 2) or to the Feather River–Putah Creek group ($n$ = 1). In total, wild fish contributed only ~ 3% to the fish found in Putah Creek. Finally, nine fish could not be classified as either hatchery or wild origin belonging to the combined groups of Feather River Fish Hatchery–Mokelumne River ($n$ = 6), Merced River Fish Hatchery–Merced River ($n$ = 2), and Mokelumne River Hatchery–Tuolumne River ($n$ = 1). Given the prevalence of hatchery fish in the system it is likely that these fish were also of hatchery origin, but this could not be confirmed using otolith strontium isotope ratios.

## DISCUSSION

Chinook Salmon have adapted to thrive in dynamic marine and riverine environments, including the Central Valley of California. Anthropogenic changes in the last ~ 150 years have drastically modified the landscape, and these changes exert a driving force on regional Chinook Salmon populations. This has been exacerbated by management practices that encourage homogenization and loss of life history diversity, thus reducing resiliency to new or ongoing threats (Yoshiyama et al. 1998; Satterthwaite et al. 2015; Herbold et al. 2018; Sturrock et al. 2019a). Here we described the return of Chinook Salmon to a previously highly degraded stream, following habitat restoration efforts and the introduction of a managed flow regime aimed at promoting habitat suitability for salmonids. Using otolith microstructure and microchemistry, we found that individuals were almost uniformly 2 to 3 years old and originated from at least seven different natal sources within the Sacramento and San Joaquin watersheds, overwhelmingly from hatcheries. Because not all fish returning to Putah Creek could be sampled, it is possible that low numbers of salmonids from other rivers also contributed to the composition of the run but were not observed.

Hatchery-origin fall-run Chinook Salmon vastly outnumber naturally produced Chinook Salmon in California's Central Valley and are known to exhibit higher straying rates, which is related to hatchery management practices such as trucking and the release of fish directly into the San Francisco Estuary (Huber and Carlson 2015; Lasko et al. 2015; Dedrick and Baskett 2018; Sturrock et al. 2019b). The trucking of hatchery fish likely greatly increased straying rates into Putah Creek because adults in 2016 emigrated as smolts in 2012–2014 during the drought of 2012–2016. During these years, high mortality was expected along the natural migratory corridor, thus Central Valley fall-run hatcheries trucked most or all of their production directly to the San Francisco Estuary and Delta (Sturrock et al. 2019b). Coded wire tag recoveries from adult carcasses in Putah Creek revealed that all of the marked fish in Putah Creek were trucked and released in locations far downstream from their source hatchery.

Straying is a key characteristic of salmonid life history strategies, contributing to their long-term persistence and genetic variability. However, in hatchery-dominated systems, excessive straying rates are considered detrimental to wild, locally adapted populations because it can lead to maladaptive gene flow and genetic and demographic homogenization. This weakens the portfolio effect, resulting in reduced resilience of the population to environmental change (Quinn 1997; Schindler et al. 2010; Brenner et al. 2012; Keefer and Caudill 2014; Brennan et al. 2019). Here, increased straying rates are arguably beneficial for Putah Creek by providing a mechanism for Chinook Salmon from diverse geographic origins to utilize

Table 2. Summary of ages and associated fork lengths for the collected samples of Chinook Salmon. For several fish, it was not possible to determine fork length due to the state of the carcass.

| Age | | | | Fork length (cm) | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Total age | Freshwater annuli | Saltwater annuli | *N* | Minimum | Quantile 1 | Median | Quantile 1 | Maximum | *N* |
| 2 | 0 | 2 | 46 | 54.3 | 57.5 | 61.0 | 64.0 | 72.0 | 31 |
| 3 | 0 | 3 | 44 | 65.4 | 71.7 | 76.0 | 82.6 | 94.6 | 24 |
| 4 | 0 | 4 | 14 | 79.7 | 81.3 | 88.9 | 90.2 | 99.7 | 9 |

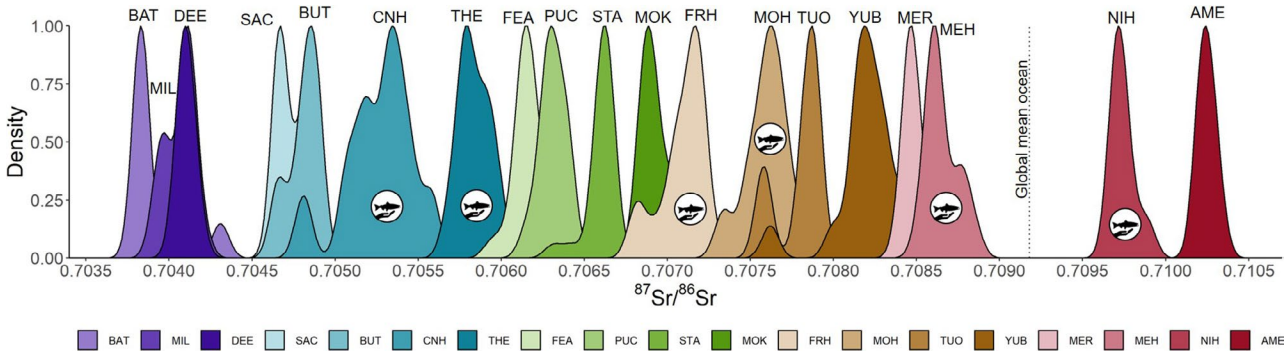


Figure 4. Kernel density plot showing the $^{87}Sr/^{86}Sr$ (Strontium) ranges of the major rivers in the Central Valley, with the white circle symbols indicating hatcheries. River and hatchery abbreviations are defined in Figure 1. The dashed line indicates the mean global ocean $^{87}Sr/^{86}Sr$ value. Data are compiled from published water and juvenile otolith data (*n* = 266) (Ingram and Weber 1999; Barnett-Johnson et al. 2008; Sturrock et al. 2015, 2019a; Phillis et al. 2018; Willmes et al. 2018a).

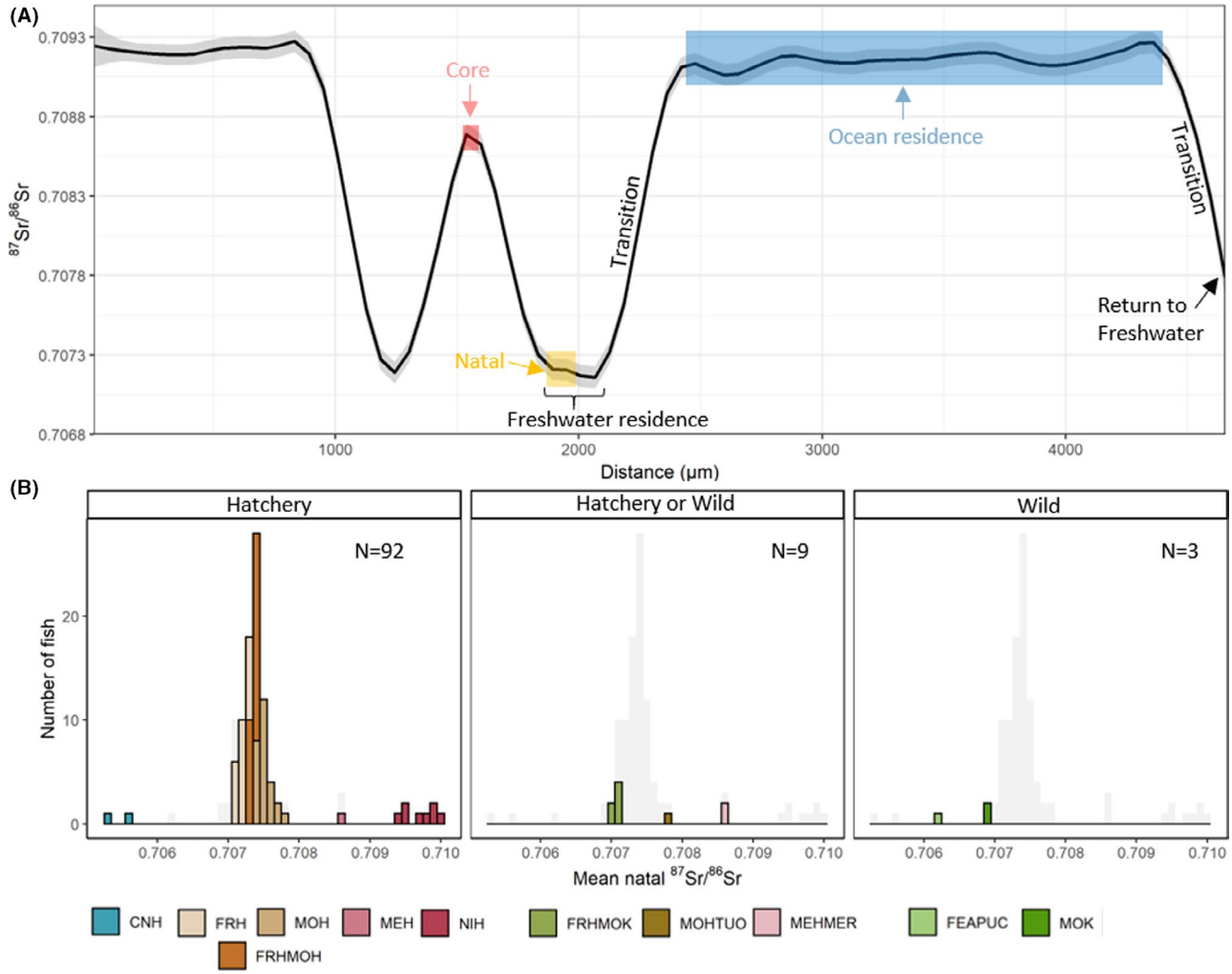


Figure 5. **(A)** Example $^{87}Sr/^{86}Sr$ (Strontium) profile of a Chinook Salmon otolith, with the freshwater and ocean residence areas marked, and **(B)** predicted natal origins for 104 Chinook Salmon collected from Putah Creek. Several different distinct natal origins were classified and grouped as either hatchery, hatchery or wild, and wild origin. Light gray shading shows the entire distribution. Abbreviations are defined in Figure 1.

this newly restored habitat. This may prove beneficial because life history traits are affected by habitat conditions experienced by juvenile stages (Roddam and Ward 2017) and local adaptations can evolve, even within populations that show high levels of gene flow (Meek et al. 2019). Therefore, restoring a natural, locally adapted run in Putah Creek could benefit from the high straying rates, at least initially. Over time, mechanisms to capture, identify, and remove straying fish (e.g., a

Table 3. Natal origins of 104 Chinook Salmon analyzed in this study. The acronyms are NIH (American River Nimbus Fish Hatchery), MEH (Merced River Hatchery), MOH (Mokelumne River Hatchery), FRH (Feather River Hatchery), CNH (Coleman National Fish Hatchery), MOK (Mokelumne River), MER (Merced River), TUO (Tuolumne River), FEA (Feather River), PUC (Putah Creek).

| Natal origin | Group | *n* | Total per group |
|---|---|---|---|
| NIH | Hatchery | 8 | |
| MEH | Hatchery | 1 | |
| MOH | Hatchery | 27 | |
| FRH | Hatchery | 24 | |
| FRHMOH | Hatchery | 30 | |
| CNH | Hatchery | 2 | 92 |
| FRHMOK | Hatchery or Wild | 6 | |
| MEHMER | Hatchery or Wild | 2 | |
| MOHTUO | Hatchery or Wild | 1 | 9 |
| MOK | Wild | 2 | |
| FEAPUC | Wild | 1 | 3 |

weir and natural or physical tags) will likely be important for reducing gene flow and promoting local adaptation.

The observed age distribution of Chinook Salmon in Putah Creek was shifted toward younger fish compared to age distributions of natural spawning grounds in other Central Valley tributaries, such as those from the Feather River (Grover and Kormos 2008; Mesick et al. 2009; Willmes et al. 2018a), where 3 and 4-year old fish typically dominate the spawning population. Size is positively correlated with fecundity in Chinook Salmon (Healey and Heard 1984). In Putah Creek, a younger age distribution and hatchery-dominated spawning population may exhibit lower fitness than other spawning runs in the system (Williamson et al. 2010). However, the high abundance of emigrating juveniles (~33,000) in 2018 and their mean Fulton's condition factor of 1.04 (Miner et al. 2019) suggests that Putah Creek provided suitable spawning and rearing habitat for these fish.

Currently, little is known about juvenile survival during emigration from Putah Creek and how straying behaviors and accompanying gene flow may impede the ability of Putah Creek spawners to establish a self-sustaining Putah Creek population. The finding of one fish of potential Putah Creek–Feather River origin (3 years old) highlights the need for continued monitoring during coming years; this fish emigrated during 2014 when only ~10 adults were observed in Putah Creek. Specifically, monitoring of phenotypic and genetic diversity of the returning adults and estimating their spawning success by quantifying the number, condition, and size of juvenile emigrants per spawner are essential to assess the effects of restoration and flow management efforts. The application of parentage-based analyses and additional otolith tracers ($\delta^{18}O$, $\delta^{34}S$, Sr, Ba, Li) that distinguish Putah Creek from other salmonid streams in the Central Valley, especially from the Feather River, will be crucial to confirming the establishment of a self-sustaining Putah Creek Chinook Salmon run.

Salmonids have evolved resilient and plastic life histories and retain the ability to utilize new habitats as they arise. However, in human-dominated environments, it can often be a long process to move from degraded to rehabilitated ecosystems. Through leveraging and restoring many small, spatially distinct systems, like Putah Creek, and restoring ecological processes that generate biological complexity, we may be able to develop a diverse network of populations that experience a range of habitat and environmental conditions and thus differ in susceptibility to natural and anthropogenic risks (Beechie et al. 2010). Under this framework, the benefits of creating a new habitat that can support even small numbers of spawners are greater than those resulting from increased capacity for spawners in an existing system. Coordination across basins and watersheds will be required to create a diverse portfolio of life histories and runs that can be resilient in the face of climate change and other threats (Schindler et al. 2010; Brennan et al. 2019). This research shows that restoring natural processes and habitats to small systems like Putah Creek may be enough to attract straying spawners, the first and critical step for the establishment of a new population. Reconnecting migratory pathways and restoring many diverse rearing and spawning habitats is essential to increase and support life history diversity for Chinook Salmon in California (Herbold et al. 2018; Sturrock et al. 2019a), which in turn can lead to more stable and predictable salmonid stocks (Hilborn et al. 2003; Schindler et al. 2010; Brennan et al. 2019).

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Figure S1
Table S1–S2
Table S3 AFS

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