

RESEARCH

Variation in Juvenile Salmon Growth Opportunities Across a Shifting Habitat Mosaic

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ABSTRACT

Historically, Chinook Salmon in the California Central Valley reared in the vast wetlands of the Sacramento–San Joaquin Delta. However, more than 95% of floodplain, riparian, and wetland habitats in the Delta have become degraded because of anthropogenic factors such as pollution, introduced species, water diversions, and levees. Despite pronounced habitat loss, previous work using otolith reconstructions has

revealed that some juvenile salmon continue to successfully rear for extended periods in the Delta. However, the extent to which the Delta functions to promote salmon growth relative to other habitats remains unknown. In this study, we integrated otolith microstructure (daily increment count and width) and strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) records to fill this critical knowledge gap by comparing the growth of natural-origin fall-run Chinook Salmon from the American River that reared in the Delta with those that remained in their natal stream. Using generalized additive models, we compared daily otolith growth rates among rearing habitats (Delta vs. American River) and years (2014 to 2018), encompassing a range of hydrologic conditions. We found that juvenile Chinook Salmon grew faster in the Delta in some years (2016), but slower in the Delta during drought conditions (2014 to 2015). The habitat that featured faster growth rates varied within and among years, suggesting the importance of maintaining a habitat mosaic for juvenile salmonids, particularly in a dynamic environment such as the California Central Valley. Linking otolith chemistry with daily growth increments provides a valuable approach to explore the mechanisms governing interannual variability in growth across habitat types, and a useful tool to quantify the effects of large-scale restoration efforts on native fishes.

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KEY WORDS

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INTRODUCTION

The stability and resiliency of salmon populations depends partially on a juvenile salmon's ability to access and utilize suitable freshwater rearing habitats during emigration to the ocean. Juvenile salmon often utilize a diverse mosaic of habitat types off the main migratory corridor—such as shallow-water wetlands, tidal marshes, and floodplains—which can provide increased feeding opportunities (Sommer et al. 2001; Williams 2006; Jeffres et al. 2008; Limm and Marchetti 2009). This habitat diversity increases growth opportunities for juvenile salmon in freshwater habitats (Brennan et al. 2019), which is critical for age class success because early growth during freshwater residence can significantly affect marine survival (Woodson et al. 2013). However, the spatial distribution of habitat patches shifts in response to abiotic factors at different scales, but may be particularly pronounced interannually as a result of large-scale climactic forcing, such as those observed during flooding and drought. The concept of the “Shifting Habitat Mosaic” (Stanford et al. 2005) is that habitat conditions are variable in space and time, and therefore one location may produce optimal growth in one season or year, and an alternate habitat may be more favorable in another. In California, juvenile salmon face additional challenges in accessing rearing habitats because anthropogenic factors—such as urban development, water diversions, and agriculture—have led to extensive freshwater habitat loss, which has simplified and homogenized the landscape (Moyle et al. 2017). The loss of habitat diversity in river systems has also led to reductions in phenotypic and genetic variation, which may negatively affect the ability of salmon populations to respond to environmental changes (McClure et al. 2008). To maintain diverse habitats and enhance salmon populations, it is critical to understand

the temporal and spatial variation in habitat availability and use by juvenile salmon, and how these modified freshwater habitats function to promote salmon growth.

The Sacramento–San Joaquin River system in the California Central Valley supports four runs of Chinook salmon. They are listed under the Endangered Species Act (ESA) as either endangered (winter run), threatened (spring run), or a species of concern (fall run and late-fall run) (Williams 2006). Fall-run Chinook Salmon (hereafter, “fall run”) are the most abundant run in the California Central Valley, and support large recreational and commercial fisheries in California and Oregon (Williams 2006). Adult fall run migrate upstream from June through December, and spawn from late September through December (Williams 2012). In the winter and early spring, fry emerge from the gravel and rear in freshwater for weeks to several months before emigrating to the ocean (Williams 2012). Juvenile fall run exhibit several migratory behaviors, with some emigrating from their natal river soon after emergence as fry, then rearing downstream in the Sacramento–San Joaquin Delta (hereafter, “the Delta”), while others remain in their natal river over a longer duration of time to rear until they emigrate as parr or smolts (Williams 2012; Sturrock et al. 2020).

Regardless of their migratory behavior, all naturally produced juvenile California Central Valley fall run use the Delta as a migration corridor. While juvenile fall run experience increased growth in shallow-water wetlands and floodplains in the Delta (Sommer et al. 2001), access to these habitats is limited because urban development, levee construction, and increased agricultural activities have replaced more than 95% of the historical Delta rearing habitat (Williams 2006; Robinson et al. 2014). Alongside the extensive habitat loss and associated reduction in local food production, juvenile fall run can experience high mortality in the Delta as a result of the combined effect of high temperatures, contaminant loads, and increased predation (Kjelson et al. 1982; Marine and Cech 2004; Grossman 2016; Michel et al. 2020).

Yet, otolith chemistry reconstructions of adult Chinook Salmon indicate that fry emigrants can successfully rear in the Delta (Miller et al. 2010; Sturrock et al. 2015; Phillis et al. 2018; Sturrock et al. 2020). However, the growth rates of these individuals relative to their upstream rearing counterparts remain unknown.

Otolith chemistry is widely used to track the individual movements and habitat use of anadromous fishes (Campana and Thorrold 2001; Brennan et al. 2015). In the California Central Valley, otolith strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) can be used to track the origin and migration histories of Chinook Salmon (Sturrock et al. 2015; Phillis et al. 2018; Sturrock et al. 2020) because many of the tributaries exhibit statistically different $^{87}\text{Sr}/^{86}\text{Sr}$ signatures with minor overlap (Ingram and Weber 1999; Barnett-Johnson et al. 2008; Phillis et al. 2018). Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ is a particularly powerful geographic marker because the water $^{87}\text{Sr}/^{86}\text{Sr}$ signature remains stable across years as the isotope ratios vary, based on the age and bedrock composition of the freshwater environments (Kennedy et al. 2000). The formation of daily otolith increments also provides a record of the temporal changes in $^{87}\text{Sr}/^{86}\text{Sr}$ (Campana 1999), and the otolith increment widths provide a chronological estimate of the fish's daily growth rate, given that the otolith grows proportionally to fish size (Chittaro et al. 2015). In the present study, we combined otolith chemistry ($^{87}\text{Sr}/^{86}\text{Sr}$) and microstructure (daily increment count and width) to reconstruct early freshwater habitat use and evaluate the habitat-specific growth rates of juvenile fall run from the American River that reared non-natally in the Delta, versus their counterparts that reared natively. Here, natal American River habitat is defined as the habitat on the mainstem American River downstream of Nimbus Dam to the confluence with the mainstem Sacramento River. Non-natal Delta habitat is defined as the freshwater habitat in the legal Delta between Discovery Park and Chippis Island. We focused on juvenile fall run originating from the American River because the $^{87}\text{Sr}/^{86}\text{Sr}$ signature of the American River is easily distinguishable from the other tributaries in the

California Central Valley, mainstem Sacramento River, and the Delta (Ingram and Weber 1999; Barnett-Johnson et al. 2008; Phillis et al. 2018).

Given the well-documented transformation of wetland habitats in the Delta (Robinson et al. 2014), we hypothesized that juvenile fall run rearing natively in the American River would have higher growth rates than those rearing non-natally in the Delta. While other studies have used otolith microstructure to quantify the growth of salmon rearing in the California Central Valley (Titus et al. 2004; Limm and Marchetti 2009), this is the first study to combine otolith microstructure and otolith chemistry to reveal habitat-specific growth rates of naturally produced California Central Valley fall run. During the study period, the state of California experienced variable hydrologic conditions, including extreme drought in 2014 and 2015, and flood conditions in 2017 (Figure 1). Since habitat patch availability and suitability is likely influenced by both hydrology and temperature, evaluating the habitat-specific growth rates of juvenile fall run in the California Central Valley within and among years will provide empirical evidence for the importance of different habitats under variable conditions, as described in the shifting habitat mosaic concept. Quantifying habitat-specific growth rates among years will provide insights into the mechanisms that govern growth variability. Furthermore, because there is a pressing need to improve habitat quality in the Delta, tracking and evaluating habitat-specific growth will provide a useful metric to understand the influence of regional restoration efforts.

MATERIALS AND METHODS

Fish and Otolith Sampling

For the present study, unmarked juvenile fall run were collected by the Delta Juvenile Fish Monitoring Program (DJFMP) using a 15-m beach seine, Kodiak trawl, and midwater trawl at 15 different sites in the Delta from January to June during 2014 to 2018 (Figure 2). Fish were kept on ice then in the freezer until analysis. The right and left sagittal otoliths were dissected from thawed fish, rinsed with deionized water, then

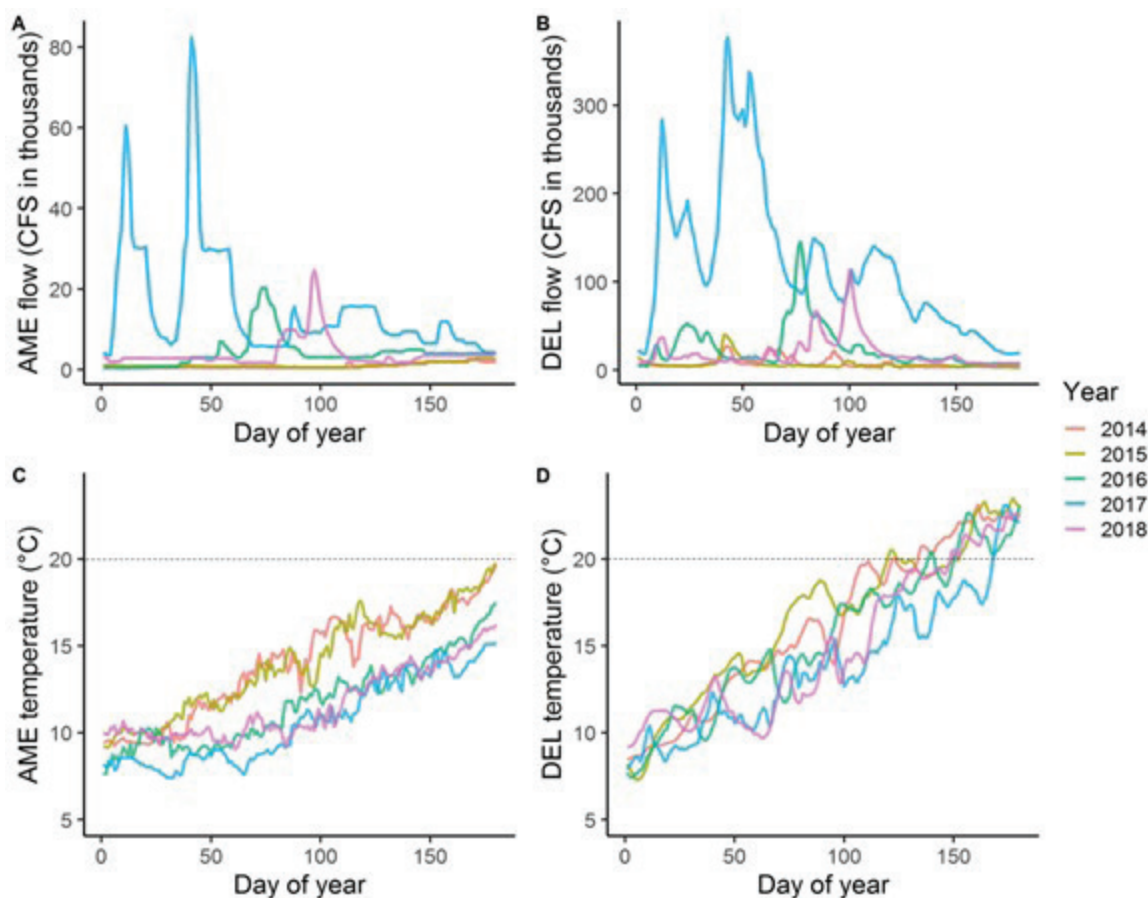


Figure 1 Mean daily flow (in thousand cubic feet per second (CFS; **A** & **B**) and mean daily temperature (°C; **C** & **D**) in the lower American River (*left column*) and Sacramento–San Joaquin Delta (*right column*) in 2014–2018. American River flow was measured at Fair Oaks (FAO; USGS gauge no. 11446500), and because of the large tidal influence in the Delta, the Department of Water Resources-calculated 'Delta Outflow' metric was used for Delta flow values. Temperature was measured in the American River at William B. Pond Park (CDEC station 'AWP'), and in the Delta in the lower Sacramento River at Rio Vista (CDEC station 'RIV'). The *horizontal dashed line* represents the temperature threshold at which growth and physiological performance can become impaired for salmon. *Source:* Marine and Cech (2004).

dried in open 1.5-ml polypropylene vials. Once the otoliths were dry, either the right or left otolith from each fish was ground and polished with sandpaper and diamond lapping film until the primordia and daily increments were exposed in the sagittal plane, according to established techniques (Barnett-Johnson et al. 2007). The second otolith was only used if the first otolith was missing, broken, or vateritic (i.e., pertaining to the calcium carbonate formation that prohibits examination of otolith microstructure).

Otolith Strontium Isotope and Increment Analyses

For each otolith, daily growth increments were measured and counted along a standardized

90-degree transect (Barnett-Johnson et al. 2007) using a Leica DM1000 microscope and Image Pro Plus software. Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ were measured from the core to the edge of each otolith along the same standardized 90-degree transect at the UCD Interdisciplinary Center for Plasma Mass Spectrometry by multiple-collection, laser-ablation, inductively-coupled, plasma mass spectrometry (MC-LA-ICPMS; Nu plasma HR interfaced with a New Wave Research Nd:YAG 213-nm laser) following methods presented in Sturrock et al. (2015).

Each fish was classified to a river or hatchery of origin using a random forest classification model

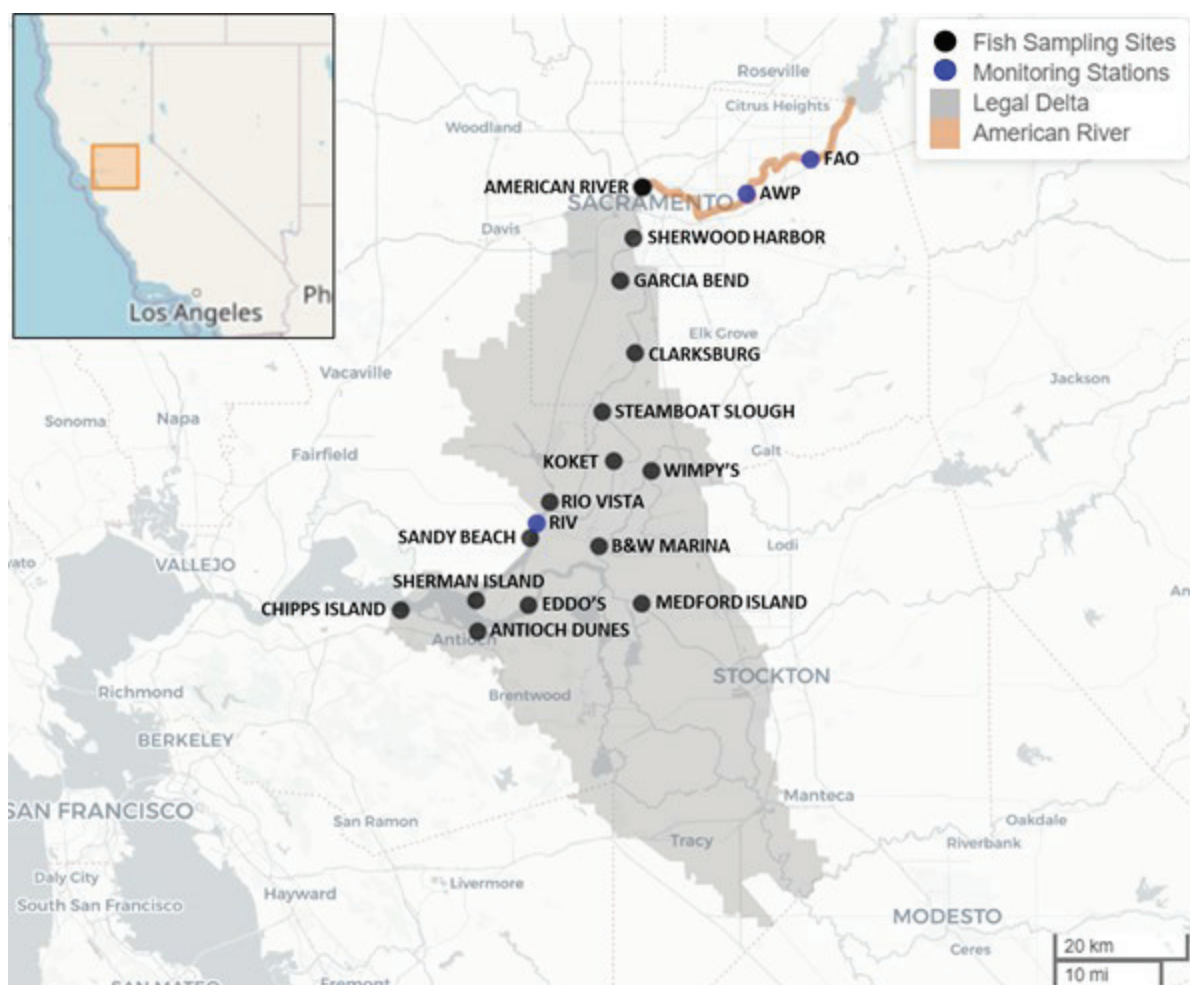


Figure 2 Map of the 15 sampling sites (black circles) in the Sacramento–San Joaquin Delta where juvenile fall-run Chinook Salmon were captured between 2014 and 2018 by the DJFMP. Sherwood Harbor and Chipps Island are sampled by trawl, the rest by beach seine. Temperature and flow monitoring stations (CDEC stations ‘AWP’ and ‘RIV’ and USGS gauge ‘FAO’), depicted by blue circles.

(‘randomForest’ package; Liaw and Wiener 2020), similar to Willmes et al. 2021. The model included three predictors: otolith $^{87}\text{Sr}/^{86}\text{Sr}$ values at distances of 160 μm and 170 μm from the core, and a visual score of the prominence of the exogenous feeding check averaged over multiple readers per otolith, to improve discrimination of hatchery vs. natural-origin fish (Barnett-Johnson et al. 2007; Sturrock et al. 2020). Note that the exogenous feeding check (assumed to coincide with depletion of the yolk sac and emergence of the salmon fry from the gravel) typically occurs around 220 μm from the core. Most classification models in the literature intending to characterize the $^{87}\text{Sr}/^{86}\text{Sr}$ in the natal habitat avoid using $^{87}\text{Sr}/^{86}\text{Sr}$ values

before this point (i.e., within the core), because it typically reduces classification power because of the integration of isotopically different material from the maternal yolk. However, the American River has a unique $^{87}\text{Sr}/^{86}\text{Sr}$ signature within the Central Valley region (Barnett-Johnson et al. 2008) that is discernible even with this “physiological noise.” A key advantage of utilizing core material in the current study is that it provided a powerful approach to identify American River-origin fish that left the natal stream immediately after emergence and reared in the Delta. All freshwater habitats downstream of the American River have significantly lower $^{87}\text{Sr}/^{86}\text{Sr}$ values (Phillis et al. 2018), and thus early migrants would likely be

misclassified if the model were trained using only otolith material deposited after exogenous feeding. To extract $^{87}\text{Sr}/^{86}\text{Sr}$ values at consistent distances across each otolith, we fitted a spline to serial $^{87}\text{Sr}/^{86}\text{Sr}$ measurements, varying the degrees of freedom per otolith to maximize the fit (n observations - 1), then predicted $^{87}\text{Sr}/^{86}\text{Sr}$ values at 160 μm and 170 μm from the core.

Strontium Isotope Natal Assignment Model and Validation

Our reference samples for the natal assignment model comprised otoliths from known-origin hatchery fish, natural-origin juveniles caught in rotary screw traps before they had left their natal stream, and a selection of spring- and winter-run adults to characterize the upper Sacramento River and Lassen tributaries where we had limited known-origin juvenile samples (see Appendix A, Table A1). Fourteen potential salmon sources (strata or classes) were included: American River (AME), Nimbus Hatchery (NIH), Lassen tributaries (LAS, combining Mill, Deer, and Battle Creeks because of isotopic overlap), Coleman National Hatchery (CNH), Upper Sacramento River (SAC_B, combining Sacramento River mainstem and Butte Creek because of isotopic overlap), Yuba River (YUB), Feather River (FEA), Feather River Hatchery (FEH), Mokelumne River (MOK), Mokelumne River Hatchery (MOH), Stanislaus River (STA), Tuolumne River (TUO), Merced River (MER), and Merced River Hatchery (MEH) (see Appendix A, Figure A1). Before fitting the model, we split the reference samples into training (80%) and test (20%) data, sub-sampling randomly within strata. We fit the model using training samples ($n=500$ trees), and estimated assignment accuracy using test samples (i.e., out-of-sample predictions). To balance class sizes when generating each tree, training data were sub-sampled without replacement from each of the 14 strata ($n=10$ observations per class, defined by the class with the lowest sample size, which here was LAS).

We used the final model to predict the natal origin of all fish in our test data set ($n=96$ of which five were AME-origin). Key to this study was having the ability to accurately track a single

population (AME) from fish caught at multiple locations and times. Even though we did not sub-sample the test data to balance samples sizes within each stratum, after aggregating predictions into AME vs. non-AME sources, 99% of fish were correctly classified. While some caution should be applied, given the low sample size in our reference set ($n=5$), 100% of the known-origin AME fish were correctly classified (Table A2 in Appendix A). However, 20% (1 of 6) known-origin Nimbus Hatchery fish (NIH, located on the American River) were incorrectly classified as AME origin, resulting in an overall accuracy rate for AME (“positive predicted value”) of 83%, with all misclassifications occurring between NIH and AME.

Importantly, most of our study samples were caught in the Delta before hatcheries had started releasing any unmarked juveniles. Thus, to increase assignment accuracy, after running the model, we forced the assignment probability for a fish to be from a hatchery to zero if their capture date preceded the first unmarked release from said hatchery that year; we then re-assigned that individual to the source that exhibited the next-highest assignment probability. Among the random subset of AME-assigned fish that were used for growth analyses ($n=118$), 79% were caught before Nimbus Hatchery had started releasing any juveniles that year, and we are thus highly confident of their assignment. Of the remaining 21%, if we assumed a 17% “false positive rate” (see above), it would mean 3% of our final data set were misclassified NIH fish. However, it was likely our error rate was even lower than that, because within this 21%, some individuals were caught many miles upstream of the NIH release site (e.g., Clarksburg vs. San Pablo Bay) and/or had left the American River as a fry-sized fish (NIH have not released fry-sized fish for many years; Huber and Carlson 2015).

Habitat Reconstructions in American River-Origin Juveniles

We measured $^{87}\text{Sr}/^{86}\text{Sr}$ across the otoliths of unmarked fish caught in the Delta, then used the assignment model outlined above to identify their natal origin. We selected individuals classified

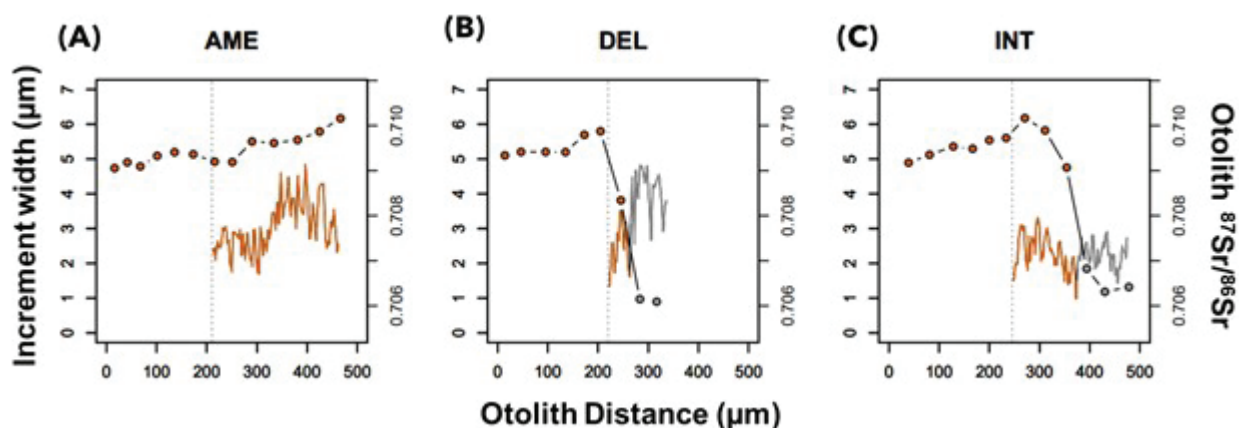


Figure 3 Illustration of how we coupled the otolith strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) measurements and daily growth increment widths for juvenile fall-run Chinook Salmon that reared in (A) the American River, (B) the Delta, and (C) both habitats (“intermediate” fish, which was only observed once in this data set). Plots show otolith $^{87}\text{Sr}/^{86}\text{Sr}$ measurements from the core to edge, and daily growth increment widths starting from the exogenous feeding check (black dashed vertical line). The $^{87}\text{Sr}/^{86}\text{Sr}$ measurements were assigned with the following colors: AME = American River in orange and DEL = the Delta in gray. Increments deposited in the transition between rearing habitats were excluded from our analysis.

as AME-origin for growth rate analysis. To determine rearing habitat-specific (i.e., Delta v. American River) growth rates, we combined isotopic and microstructural analyses by measuring their distance from the otolith core along the same dorsal axis, then we used each $^{87}\text{Sr}/^{86}\text{Sr}$ measurement (typically 40 μm diameter integrating approximately 10 days of growth) to assign a rearing habitat to each of the growth increments that overlapped with it (Figure 3). We assigned each increment a rearing habitat based on the $^{87}\text{Sr}/^{86}\text{Sr}$ value it intersected, based on a well-established baseline of water and otolith $^{87}\text{Sr}/^{86}\text{Sr}$ signatures (Barnett-Johnson et al. 2008; Phillis et al. 2018; Sturrock et al. 2020). Specifically, an increment was assigned to “American River” if $^{87}\text{Sr}/^{86}\text{Sr} > 0.70814$ and “Delta” if $^{87}\text{Sr}/^{86}\text{Sr} < 0.70785$. We converted the otolith radius measured at each daily growth increment into a fish fork length following methods presented in Sturrock et al. 2020, then used to estimate somatic growth rates by year and habitat to facilitate comparisons to other growth studies in the California Central Valley. Since salmon emigrate from the American River directly into the Sacramento River at the northern edge of the Delta (Figure 2) and each laser spot typically encompasses about 10 days of growth (Figure 3), we excluded $^{87}\text{Sr}/^{86}\text{Sr}$ values between 0.70785 and

0.70814 as “transitional,” given that we could not confidently assign those increments to one habitat or the other. Given the challenges associated with reliably measuring $^{87}\text{Sr}/^{86}\text{Sr}$ values at the otolith edge, we excluded fry migrants caught < 10 days post-emergence, where the outermost increments could not be reliably linked to a rearing habitat ($n=11$). In total, we performed growth and habitat reconstructions for 118 AME-assigned juveniles (Table 1), equating to 4,674 daily otolith increments.

Table 1 Summary of the total number of juvenile fall-run Chinook Salmon per year (2014 to 2018) per rearing habitat (AME = American River, DEL = Delta) whose daily otolith growth was examined in the present study. In some cases, a single fish may have deposited increments in both rearing habitats; thus, data presented here is the number of fish per year per dominant habitat, which is determined by the rearing habitat in which a fish deposited the majority (> 50 %) of its increments.

| Year | n AME | n DEL |
|------|------------|------------|
| 2014 | 7 | 7 |
| 2015 | 15 | 2 |
| 2016 | 27 | 22 |
| 2017 | 7 | 14 |
| 2018 | 4 | 13 |

Table 2 Summary of reported average growth rates (mm d^{-1}) and standard deviations (SD) or standard errors (SE) of California Central Valley Chinook Salmon in the Delta, Yolo Bypass, Sacramento River, and American River

| Reference | Region | Method | Year | Growth rate (mm d^{-1}) | SD | SE |
|---------------------|--------------------------------------|--|------|------------------------------------|------|------|
| This study | American River | Back-calculated FL from otolith increment widths | 2014 | 0.63 | 0.08 | |
| This study | American River | " " | 2015 | 0.6 | 0.06 | |
| This study | American River | " " | 2016 | 0.54 | 0.13 | |
| This study | American River | " " | 2017 | 0.55 | 0.12 | |
| This study | American River | " " | 2018 | 0.47 | 0.08 | |
| This study | Delta | " " | 2014 | 0.52 | 0.09 | |
| This study | Delta | " " | 2015 | 0.53 | 0.16 | |
| This study | Delta | " " | 2016 | 0.57 | 0.19 | |
| This study | Delta | " " | 2017 | 0.55 | 0.15 | |
| This study | Delta | " " | 2018 | 0.49 | 0.09 | |
| Kjelson et al. 1982 | Upper Sacramento River | Mark & Recapture/Seine & Trawl | 1981 | 0.33 | | |
| Kjelson et al. 1982 | Delta | " " | 1981 | 0.53 | | |
| Kjelson et al. 1982 | Delta | " " | 1980 | 0.86 | | |
| Sommer et al. 2001 | Lower Sacramento River | Mark & Recapture/Trawl | 1998 | 0.52 | | 0.18 |
| Sommer et al. 2001 | Yolo Bypass, Delta | " " | 1998 | 0.8 | | 0.06 |
| Sommer et al. 2001 | Lower Sacramento River | " " | 1999 | 0.43 | | 0.03 |
| Sommer et al. 2001 | Yolo Bypass, Delta | " " | 1999 | 0.55 | | 0.06 |
| Titus et al. 2004 | American River (hatchery population) | Back-calculated FL from otolith size | 1998 | 0.43 | 0.12 | |
| Titus et al. 2004 | American River | " " | 1998 | 0.5 | 0.19 | |
| Katz et al. 2017 | Yolo Bypass, Delta | PIT tagged – free swimming | 2012 | 0.7 | 0.09 | |
| Katz et al. 2017 | Yolo Bypass, Delta | PIT tagged – enclosure | 2012 | 0.68 | 0.08 | |
| Katz et al. 2017 | Yolo Bypass, Delta | Free Swimming | 2012 | 0.76 | 0.11 | |
| Holmes et al. 2021 | Yolo Bypass, Delta | Enclosure | 2013 | 0.96 | | |
| Holmes et al. 2021 | Yolo Bypass, Delta | Enclosure | 2014 | 0.99 | | |
| Holmes et al. 2021 | Yolo Bypass, Delta | Enclosure | 2015 | 0.81 | | |
| Holmes et al. 2021 | Yolo Bypass, Delta | Enclosure | 2016 | 1.28 | | |
| Jeffres et al. 2020 | Yolo Bypass, Delta | Enclosure | 2016 | 0.93 | 0.15 | |
| Jeffres et al. 2020 | Yolo Bypass, Delta | Enclosure | 2016 | 0.31 | 0.10 | |
| Jeffres et al. 2020 | Yolo Bypass, Delta | Enclosure | 2016 | 0.18 | 0.09 | |

Table 3 Candidate GAMs with AR 1 correction for temporal auto-correlation used to explain variation in otolith daily increment width of juvenile fall-run Chinook Salmon, ranked by AICc value. Fish age was consistently included as a smooth term (s), with the more complex models (1 to 5) creating a separate smooth for each rearing habitat * year combination. Note whenever there is an interaction term, the individual terms are also included. Sample ID was included as a random effect in all models, allowing the y intercept to vary by individual fish.

| Model number | Predictors | AICc | Δ AICc |
|--------------|---|--------|---------------|
| 1 | s(age by rearing habitat * year) + rearing habitat * year | 9650.9 | 0 |
| 2 | s(age by rearing habitat * year) + rearing habitat + year | 9653.2 | 2.3 |
| 3 | s(age by rearing habitat * year) + rearing habitat | 9653.2 | 2.3 |
| 4 | s(age by rearing habitat * year) | 9661.7 | 10.8 |
| 5 | s(age by rearing habitat * year) + year | 9665.1 | 14.2 |
| 6 | s(age) + rearing habitat + year + rearing habitat | 9700.0 | 49.1 |
| 7 | s(age) + rearing habitat + rearing habitat | 9700.8 | 49.9 |
| 8 | s(age) + year * rearing habitat | 9704.5 | 53.6 |

Growth Models

We used mixed effects generalized additive models (GAM) ('mgcv' package; Wood 2017) to investigate drivers of fish growth, including Sample ID as a random effect to account for repeated observations within individual fish. Specifically, we performed a series of increasingly complex GAMs to explore how otolith daily increment widths were influenced by year, rearing habitat, and age (otolith increment number), as well as their interactions (Table 3). We included only the first 60 days past emergence of growth for all fish, given limited numbers ($n < 2$) of individuals within each habitat-year combination older than this (Appendix A, Figure A2). We added a penalty term in the smoothness selection procedure (Marra and Wood 2011) to effectively exclude unimportant predictors from the fit and incorporated an AR 1 correction to account for temporal auto-correlation ('itsadug' package; van Rij et al. 2017). GAMs were fitted using maximum likelihood (ML) and ranked using the Akaike's information criterion corrected for small sample sizes (AICc; Table 3). The model with the lowest AICc was selected as the final model (Zurr et al. 2009). To statistically compare growth rates among each habitat-year combination, we used Tukey's pairwise comparisons ('emmeans' package;

Lenth 2021). Note that to use Turkey's pairwise comparisons, we used a simplified model to fit a global smooth to fish age (Model 8, Table 3). All analyses were completed in R v3.6.1 (R Core Team 2020).

Increment Analysis Quality Control

Among-reader precision and accuracy were estimated by performing multiple increment reads on a sample of otoliths ($n=34$), including 16 reference otoliths of known age from CNH (age range = 21 to 84 days). Among-reader precision—calculated as the average coefficient of variation for multiple reads of the same otolith by 2 to 4 independent readers—was 6.2%, which is well within optimal reproducibility for age and growth laboratories (Campana and Thorrold 2001). The mean difference between estimated vs. known age of hatchery-origin juveniles was 0.2 ± 3.3 days (mean absolute difference of 2.4 ± 2.2 days), based on reads performed by 2 to 4 independent readers, which suggests high reproducibility.

RESULTS

Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ profiles of the 118 American River-origin juveniles revealed largely binary rearing strategies: (1) juveniles that left the American River as fry soon after emergence

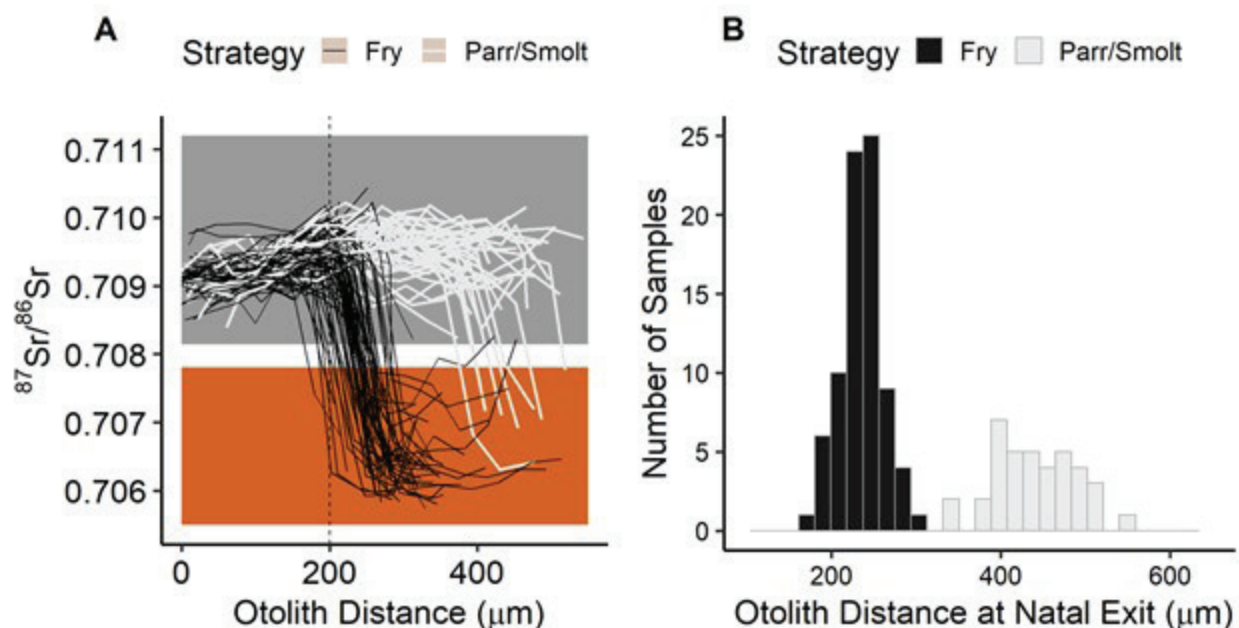


Figure 4 (A) Otolith strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) profiles of juvenile American River-origin fall-run Chinook Salmon included in this study, with the isotopic thresholds used to assign daily growth increments to a rearing habitat indicated by varying colors: American River (orange), Transition (white) and the Delta (gray). The typical distance of the exogenous feeding check is indicated by a vertical dashed line. (B) The size distribution of the two rearing strategies (black = fry; gray = parr/smolt), separated by an otolith distance of about 320 μm , which is roughly equivalent to a fork length of 45 mm.

and reared in the Delta ($n=64$), and (2) juveniles that reared in the natal stream and emigrated later as parr ($n=56$) or smolts ($n=8$) (Figure 4A). As indicated by Figure 4B, there was a natural size break point at an otolith distance of approximately 320 μm , roughly equivalent to a fork length of 45 mm, based on the otolith size-fish size relationship used in Sturrock et al. (2020). As such, we used this break point to delineate individuals as fry (<45 mm) or parr/smolt (>45 mm) emigrants, despite it being smaller than the 5 mm fry-parr size cut off used in Sturrock et al. (2015, 2020). The average daily growth (mm d^{-1}) between 2014 and 2018 varied between 0.47 ± 0.08 to 0.63 ± 0.08 mm in the American River, and 0.49 ± 0.09 to 0.57 ± 0.19 mm in the Delta, which is consistent with other growth studies conducted in the California Central Valley (Table 2).

The final GAM (Model 1, Table 3) explained about half of the variation in otolith daily increment widths (deviance explained, akin to a pseudo r^2 value = 0.49; Table 4). Overall, there was no consistent difference in growth rate between fish

that reared natively in the American River (parr/smolt emigrants) and those that reared non-natively in the Delta (fry emigrants). However, predicted otolith widths suggest that growth rates were typically higher in the Delta than in the American River in 2016 and vice versa in 2014, 2015, and 2017, particularly later in the season as the fish grew older (Figure 5). Pairwise comparisons support the trends shown in Figure 5, suggesting that different rearing habitats provide variable growth opportunities among years (Figure 6). Fish that emigrated to and reared in the Delta in 2016 and 2018 grew faster than those that stayed in the American River (Figure 6). Conversely, the fish that showed the highest average growth rate across all year-habitat combinations were juveniles that reared in the American River (and survived until capture) in drought year 2015 (Figure 6). The only within-year difference in growth (averaged across the entire season) was in 2016, when fish that reared in the Delta grew significantly faster than their counterparts that reared in the American River. However, significant smooth terms in the GAM

Table 4 Model coefficients \pm standard error (SE) from the most parsimonious GAM (Model 1, Table 3) explaining variation in daily growth rate (otolith increment width) for American River-origin juvenile fall-run Chinook Salmon that reared natally in the American River vs. non-natally in the Delta (DEL) in 2014 to 2018

| | Estimate (\pm S.E) | t-value | p-value |
|-----------------------------|-----------------------|---------|---------|
| Intercept | 2.97 (0.192) | 15.51 | < 0.001 |
| Rearing habitat (DEL) | -0.166 (0.217) | -0.76 | 0.445 |
| 2015 | 0.356 (0.243) | 1.47 | 0.143 |
| 2016 | -0.243 (0.218) | -1.12 | 0.264 |
| 2017 | 0.041 (0.251) | 0.17 | 0.869 |
| 2018 | -0.661 (0.273) | -2.42 | 0.016 |
| Rearing habitat (DEL): 2015 | 0.052 (0.320) | 0.16 | 0.872 |
| Rearing habitat (DEL): 2016 | 0.550 (0.242) | 2.27 | 0.023 |
| Rearing habitat (DEL): 2017 | 0.085 (0.263) | 0.32 | 0.747 |
| Rearing habitat (DEL): 2018 | 0.688 (0.274) | 2.51 | 0.012 |

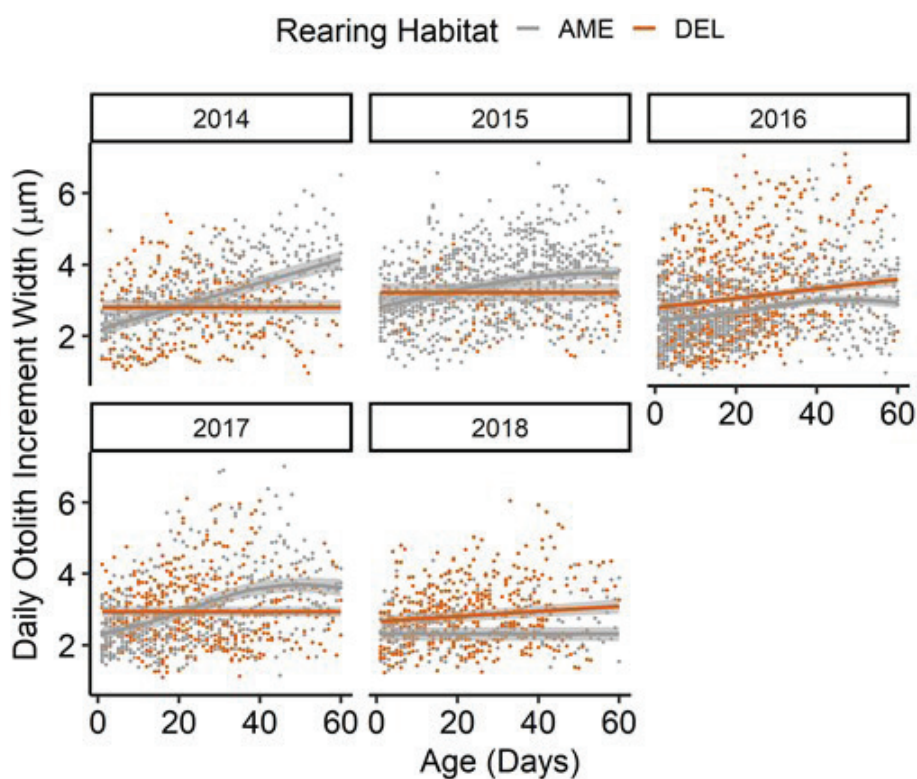


Figure 5 Growth rates of juvenile American River-origin fall-run Chinook Salmon inferred by daily otolith increment widths. Circles indicate measured increment widths for the first 60 days of life for each fish per year, and their assigned rearing habitat (AME = American River in orange, DEL = the Delta in gray). Smooths represent the predicted otolith increment widths (\pm SE) for each year-rearing habitat combination using the most parsimonious GAM (Table 3, Model 1).

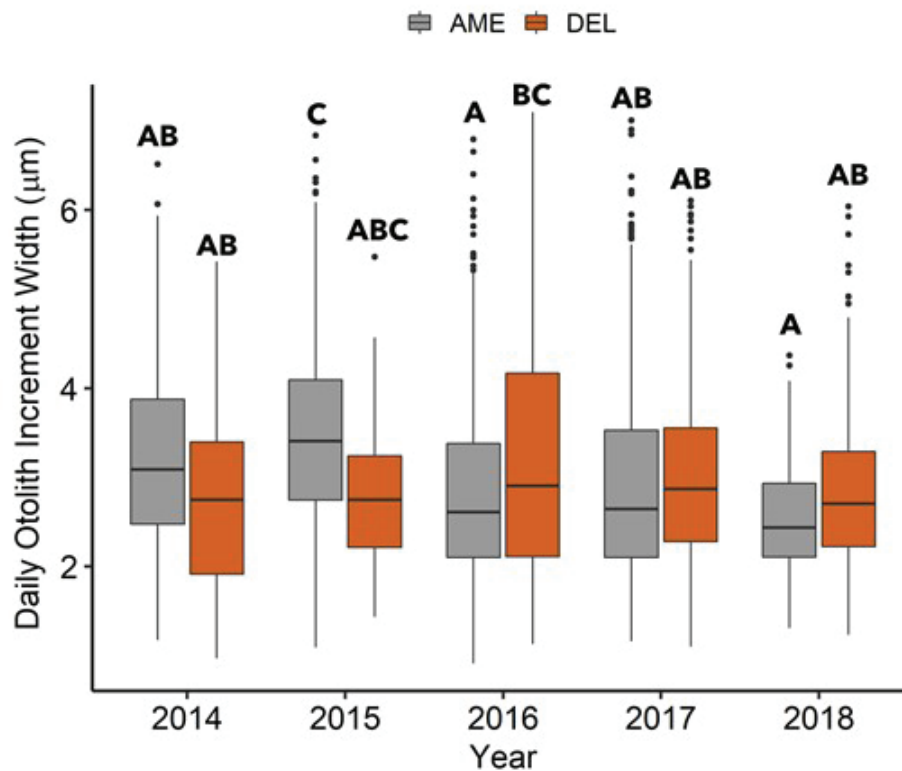


Figure 6 Boxplot illustrating growth rates of juvenile American River-origin fall-run Chinook Salmon inferred by otolith daily increment widths, based on the first 60 days of life for each fish per year, and rearing habitat (AME = American River in orange, DEL = Delta in gray). Boxes that do not share the same letter are significantly different (Tukey's test, $p < 0.05$). Horizontal bars in each box represent the median.

model (Figure 5) suggest further within-habitat and within-year growth variation in the American River in all years except 2018, and in the Delta in 2016 and 2018.

DISCUSSION

One of the greatest unknowns for salmon in the California Central Valley is the extent to which the contemporary Delta still can provide adequate non-natal rearing habitat for juvenile salmon. Here, we used innovative techniques to identify the natal origin, habitat use, and habitat-specific growth rates of emigrating fall run to compare the early growth of fish that reared in their natal river with the growth of fish that emigrated early and reared non-natally downstream. Results indicated that the rearing habitat that promoted the highest early growth in juvenile fall-run salmon varied within and among years. Specifically, juvenile fall-run salmon exhibited

faster growth in the Delta in some years (2016), but the American River provided greater growth opportunities during drought conditions (2015 in particular). These results suggest that while there has been extensive loss and degradation of juvenile salmon rearing habitat in the Delta (Williams 2006; Robinson et al. 2014), under certain conditions, it still provides habitat features that support faster juvenile growth than one of the main salmon-producing rivers. Furthermore, variation in juvenile salmon growth between and within the two rearing habitats across years provides evidence for the shifting habitat mosaic concept because the rearing habitat that provides increased growth opportunities changes through time and space.

Interestingly, the most parsimonious model included an interaction between fish age (equivalent to time in days), rearing habitat, and year, suggesting that while there may be an

ontogenetic trend in growth across all individuals, daily otolith growth rates were plastic and likely influenced by dynamic spatio-temporal variation in environmental conditions (Figure 1) as well as by demographic (e.g., density dependence) factors (Marine and Cech 2004; Connor et al. 2013; Lusardi et al. 2020). It is important to note that a limitation of this study is that we could only differentiate between relatively large geographic regions using otolith strontium isotope ratios, and within each rearing habitat (i.e., the American River and the Delta) there could be numerous microhabitats that change spatially and temporally. In particular, the “habitat” defined here isotopically as “the Delta” comprises fast-flowing, leveed channels (Robinson et al. 2014) as well as productive patches of relict, restored and managed wetland and floodplain habitats, such as Liberty Island, Yolo Bypass, Sherman Island, and Browns Island. Furthermore, during wet years like 2017, the lower American River inundates Discovery Park (Cannon and Kennedy 2006) creating a large, ephemeral floodplain within the natal stream that likely would have supported increased food production and growth (Sommer et al. 2001).

Daily otolith growth varied considerably in individual juvenile fall run examined in this study (Figure 5), suggesting the importance of multiple interconnected abiotic and biotic factors. Although identifying the specific mechanisms that promote juvenile salmon otolith growth in the Delta vs. the American River is beyond the scope of this study, variation in water flow and temperature (Figure 1) were likely the primary abiotic factors that generated differences in growth opportunities in each habitat within and among years. During the drought years 2014 and 2015, juveniles encountered extremely low flows and high temperatures in both rearing habitats (Figure 1). Water temperatures were particularly high in the Delta later in the season (Figure 1). This likely led to decreased daily otolith growth in the Delta (0.52 mm d^{-1} in 2014, and 0.53 mm d^{-1} in 2015; Table 2; Figure 5) because juvenile salmon growth and physiological performance typically becomes impaired at temperatures above 20°C (Marine and Cech 2004; Lehman et al.

2017). However, mean daily otolith growth was higher for Delta rearers during high (0.55 mm d^{-1} in 2017; Table 2) and “normal” flow conditions (0.57 mm d^{-1} in 2016; Table 2). These results agree with a mark-and-recapture study from Kjelson et al. (1982) that found the somatic growth of hatchery-produced fall-run fry released during a wet year in the northern Delta was higher (0.53 mm d^{-1} ; Table 2) than their counterparts released in the upper Sacramento River (0.33 mm d^{-1} ; Table 2). This is to be expected, because during wet conditions, juvenile salmon have increased access to productive floodplains and shallow-water habitats (Kjelson et al. 1982), and fish that rear in these shallow-water habitats grow more quickly than those in the mainstem river as a result of increased food availability and warmer temperatures (Sommer et al. 2001; Jeffres et al. 2008; Limm and Marchetti 2009).

Temperature and water flow also affect biotic factors such as food availability and density-dependent competition, which in turn, also affect juvenile salmon growth. During low flow periods, food availability decreases, and, when combined with high temperatures, can create stressful and fatal conditions for juvenile salmon (Lusardi et al. 2020). Because of the high temperatures observed in the Delta during the drought, we were surprised that our data did not show more pronounced within-year differences in growth in 2014 and 2015 between the American River and the Delta. This suggests that while juvenile salmon encountered low flows and high temperatures in the Delta and experienced reduced growth, some individuals were likely able to exploit food-rich habitats to offset the effects of prolonged exposure to high temperatures (Lusardi et al. 2020). Another hypothesis to explain the limited within-year variation between the Delta and American River during the drought is that there was increased density-dependent competition in the American River as a result of decreased access to shallow-water habitats that are inundated at higher flows. It is possible that increased competition in the American River “forced” smaller and weaker individuals to emigrate early from the American River, resulting in the perceived reduction in

growth observed in the Delta (Connor et al. 2013). Similarly, growth differences among years and habitats could have been dampened by variation in the strength of growth-selective mortality, with the individuals that survived to be sampled during the drought representing the strongest and fastest-growing individuals within the population, while individuals sampled in cooler wetter years represented a broader cross-section of the life history portfolio. Furthermore, this study did not address the extent to which individuals rearing in the warmer Delta had lower survival from increased predation (Michel et al. 2020).

Our results show that juvenile fall run exhibited two distinct rearing strategies, resulting in different temporal and spatial patterns of habitat use and growth, which is consistent with previous observations of juvenile fall run from the American River (Kjelson et al. 1982; Williams 2001). This variation in migratory timing allowed juveniles to find suitable rearing conditions across the array of habitats between the American River and the Delta, and to take advantage of the dynamic “foodscapes” produced through space and time. The observed differences in growth within and among habitats and years show how habitat quality, along the migratory pathway, shifts dynamically in response to various abiotic and biotic processes, consistent with the shifting habitat mosaic concept (Stanford et al. 2005; Brennan et al. 2019). Our results suggest that age class survival may also vary between rearing strategies, given the dynamic nature of habitat quality. There is strong evidence that fish which grow faster and larger upon ocean entry are more likely to survive their first year in the ocean (Beamish and Mahnken 2001). While our otolith reconstructions showed reduced growth in Delta-rearing fish under extreme drought conditions, the Delta typically provided comparable and sometimes superior growth opportunities for juvenile fall run in this study. This is evident in the “intermediate” strontium isotope profile and daily otolith increment widths presented in [Figure 3C](#). This particular fish was the only one in our study that spent an extended period of time rearing in both habitats, and when it moved from the American River to the Delta, we did not observe a dramatic decrease in daily otolith

growth ([Figure 3C](#)). This supports our conclusion that while much of the Delta is severely degraded, some areas can still provide adequate rearing habitat for juvenile Chinook Salmon. It is also important to note that the growth rates estimated in this study were consistently lower than for fish reared on floodplain habitats (e.g., Sommer et al. 2001; Jeffres et al. 2008; Katz et al. 2017) and also in a study conducted in the Delta almost 40 years ago (Kjelson et al. 1982) ([Table 2](#)), underscoring the importance of continued habitat restoration across the full migratory corridor.

CONCLUSION

Our results provide empirical evidence to support the concept of the shifting habitat mosaic, adding to the consensus that maintaining habitat heterogeneity is critical to enhance the resilience and productivity of salmon populations (Brennan et al. 2019). Management actions aiming to improve salmon resilience and growth should consider the importance of maintaining and restoring a diversity of rearing habitats along the full migratory corridor of fall run. Measuring growth of salmon across multiple habitats and through time (both within and among years) using otolith reconstructions provides key data to model habitat performance across different hydroclimatic conditions. It also provides baseline data to compare demographic patterns in salmon growth before and after large-scale habitat restoration efforts, or after flow actions aimed to benefit salmon and other native fishes. While it is impossible to return the Delta to its former state, it is possible to increase habitat quality and diversity by increasing the amount of tidal and sub-tidal habitats and by altering flow regimes (Moyle et al. 2010). Future work in this system should examine the role of different micro-habitats and their distribution and organization across the migratory corridor in promoting salmon growth and climate resilience.

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