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Article

Juvenile life history, migration, and habitat use of natural-versus hatchery-origin Chinook Salmon

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ABSTRACT

Objectives: Our overall objective was to directly compare the early life history and migration patterns of hatchery- and natural-origin fish and determine when hatchery fish provide good surrogates for natural-origin winter-run Chinook Salmon *Oncorhynchus tshawytscha* in the Sacramento River system. Specifically, our objectives were to compare the juvenile freshwater habitat use, residence time in freshwater habitats, and size at age and relative growth of juveniles.

Methods: Using otoliths that were collected from adult carcasses, we reconstructed the freshwater life history of hatchery- and natural-origin fish through microstructural and chemical analyses. We analyzed the otolith strontium isotope chemistry and daily increment widths to characterize habitat use, migration timing, and growth.

Results: Following their hatchery-rearing period, hatchery fish had much shorter residence times (11 d, SD = 16 d) in the river than natural-origin fish (129 d, SD = 37 d). Beyond the reduced duration of river residence, hatchery fish occupied fewer areas of the watershed during ocean out-migration. Despite these differences in out-migration behaviors, adults from both groups reached saltwater during their downstream out-migration at similar sizes (natural-origin fish: 633 µm, SD = 68 µm; hatchery-origin fish: 625 µm, SD = 63 µm) and ages (natural-origin fish: 161 d old, SD = 20 d; hatchery-origin fish: 165 d old, SD = 22 d) as juvenile smolts.

Conclusions: Considering the differences in habitat use and timing between hatchery- and natural-origin fish is critical to avoiding bias when applying data that are collected from hatchery fish to manage and conserve natural populations. Explicitly considering the presence of winter-run Chinook Salmon in habitats beyond the migratory corridor during habitat management is needed to promote and enable the contribution of multiple life histories for productivity, resilience, and ultimately recovery.

KEYWORDS: nonnatal rearing, otoliths, out-migration, Sacramento River, winter-run Chinook Salmon

LAY SUMMARY

Chinook Salmon that are released from hatcheries use freshwater habitats less extensively and for shorter durations than their natural counterparts do, which can result in underestimating the importance of these habitats to natural populations when directly applying data that are collected from hatchery fish for managing natural populations.

INTRODUCTION

Wild Pacific salmon and trout (*Oncorhynchus* spp.) can exhibit complex variation in their life history expression, such as the phenology of their migration and maturation. Within a single population, juveniles may migrate soon after emergence or rear in their natal habitats for months and years before beginning downstream migration. Nonnatal habitats such as off-channel areas, tributaries, floodplains, and estuaries can augment growth and/or survival by reducing density and density-dependent effects (Ebersole et al., 2006; Jeffres et al., 2020; Rossi et al., 2024; Schroeder et al., 2016). Variation diversifies the number of strategies in a population and increases the population's resilience against catastrophic environmental events. This life history diversity spreads risk across the landscape and

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can increase overall population productivity (Greene et al., 2010). Environmental conditions in the wild that shape the life history of fish can be dramatically altered in a hatchery, potentially altering postrelease life history expression and the degree of trait variability in hatchery fish (Berejikian et al., 2001; Shearer et al., 2006; Yamamoto & Reinhardt, 2003).

Chinook Salmon *Oncorhynchus tshawytscha* in hatcheries are limited to the rearing conditions of the hatchery prior to their release. Hatchery fish may be released at sizes and times that deviate from those of their natural life histories to increase survivorship and minimize interactions with natural populations (del Real et al., 2012; Huber & Carlson, 2015; Huber et al., 2024). A handful of studies have explored how migratory tactics and habitat use differ between hatchery and wild fish, typically reporting that hatchery fish migrate more quickly and use a subset of the available habitats that wild fish use (del Real et al., 2012; Levings et al., 1986). Differences in behavior, life history, and survival between hatchery- and natural-origin fish have the potential to lead to disruptions to population dynamics that reduce the long-term ecological resilience of the species (Naish et al., 2007; Sturrock et al., 2019).

Due to their abundance and accessibility, hatchery salmon are often used as surrogates of wild fish to infer the conditions experienced by their wild counterparts. Prior to release, large numbers of hatchery fish can be implanted with tags to estimate reach-specific and lifetime survival rates and provide insights into the river and ocean conditions that wild fish may be experiencing. Indeed, tagged hatchery fish often serve as proxies for wild fish in management and research (Fujiwara et al., 2011; Michel et al., 2021; O'Farrell et al., 2012; Weitkamp, 2010). However, the influence of the hatchery environment and release methods on the behavior and life history of hatchery fish raises questions about whether they are reliable surrogates for natural-origin fish in evaluating their behavior (Yamamoto & Reinhardt, 2003), migration (del Real et al., 2012), and age at maturity (Chen et al., 2023). Understanding the potential biases when using hatchery fish as a proxy is critical to accurately interpreting management models and making informed decisions for the natural population.

The California Central Valley, which includes the Sacramento River and San Joaquin River drainages, comprises a large fraction of the state and has been highly altered by human activities (Yoshiyama et al., 1998). The watershed hosts four distinct runs of Chinook Salmon, historically supporting high total abundances through diverse life histories. Today, most major rivers in the system are blocked by large impassable dams that block access to the majority of suitable spawning and rearing habitat (Lindley et al., 2006) or alter downstream flow regimes (Brown & Bauer, 2010), resulting in the loss and reduction of many salmonid populations. Out-migrating juvenile salmon experience elevated mortality in the heavily altered Sacramento–San Joaquin Delta due to habitat degradation, major water diversion projects (e.g., Kimmerer, 2008), and the introduction of nonnative predators (Michel et al., 2020). In recent years, biotelemetry studies on hatchery fish that were implanted with acoustic tags have allowed for a more detailed understanding of migration survival and movement. However, most of these studies have focused on larger, smolt-size hatchery fish of at least 80 mm because they are large enough to be implanted with a tag without a tag burden that affects their health or behavior (Buchanan et al., 2018; Hassrick et al., 2022; Perry et al., 2010).

Otolith chemistry represents another approach for evaluating fish movement, using natural tags from the ambient water to provide insight into the early life stages of fish that are too small to physically tag. Otoliths are internal calcified structures that are frequently used to understand the age and life history of fish because they typically grow isometrically to body length and growth rings are deposited both daily (Neilsen & Geen, 1982) and annually (Campana & Thorrold, 2001). As they grow, otoliths incorporate ions from the surrounding environment, making it possible to determine the habitat that was used by an individual during a specific period of life (Campana & Thorrold, 2001; Claiborne & Campbell, 2016). Recovering and analyzing otoliths from the carcasses of returning spawners is a noninvasive method for studying the movement and growth of successful individuals. Within the Sacramento River basin, some tributaries have unique geologic composition and strontium isotope ratios ($^{87}Sr/^{86}Sr$), resulting in an $^{87}Sr/^{86}Sr$ "isoscape" that makes it possible to assess natal origin and movement between regions of the watershed (Barnett-Johnson et al., 2008; Phillis et al., 2018). The strontium concentration and isotope ratio also differ between marine and freshwater, making it possible to identify when the fish had entered the ocean (Miller et al., 2010).

Winter-run Chinook Salmon in the Sacramento River are currently listed as endangered under the federal and California Endangered Species Acts (Good et al., 2005). Their designated critical habitat includes the Sacramento main stem, the westward margin of the Sacramento–San Joaquin Delta, and the northern half of the San Francisco Bay (U.S. Office of the Federal Register, 1993). Conserving the population requires relying on information on their habitat use needs and how aspects of the riverscape influence their growth and survival and, ultimately, their reproductive success (Johnson et al., 2017). Previous work using otolith isotope chemistry revealed that natural-origin winter-run Chinook Salmon are the most nomadic of all Central Valley salmon runs, making extensive use of the watershed and often rearing in habitats outside of the designated critical habitat (Morais et al., 2025; Phillis et al., 2018). Another recent study using acoustic-tagged hatchery fish evaluated how the residence time of winter-run hatchery fish varies with spring flows in the upper Sacramento River (Hassrick et al., 2022), but it is unclear whether these residence times and flow sensitivities also apply to natural-origin fish that initiate downstream migration months earlier than hatchery fish. Using data that were collected from hatchery fish for managing the natural-origin population could potentially bias assessments and lead to less effective actions if managers do not account for differences.

In this study, we provide a much-needed comparison of the out-migration behaviors of hatchery- and natural-origin winter-run Chinook Salmon. We did this by reconstructing the freshwater life history of hatchery- and natural-origin fish through microstructural and chemical analyses of otoliths that were collected from returning adults. Specifically, we compared (1) juvenile freshwater habitat use, (2) residence time in the system, and (3) size at age and relative growth of juveniles. Our approach allowed us to directly compare the early life history and migration patterns of hatchery- and natural-origin fish

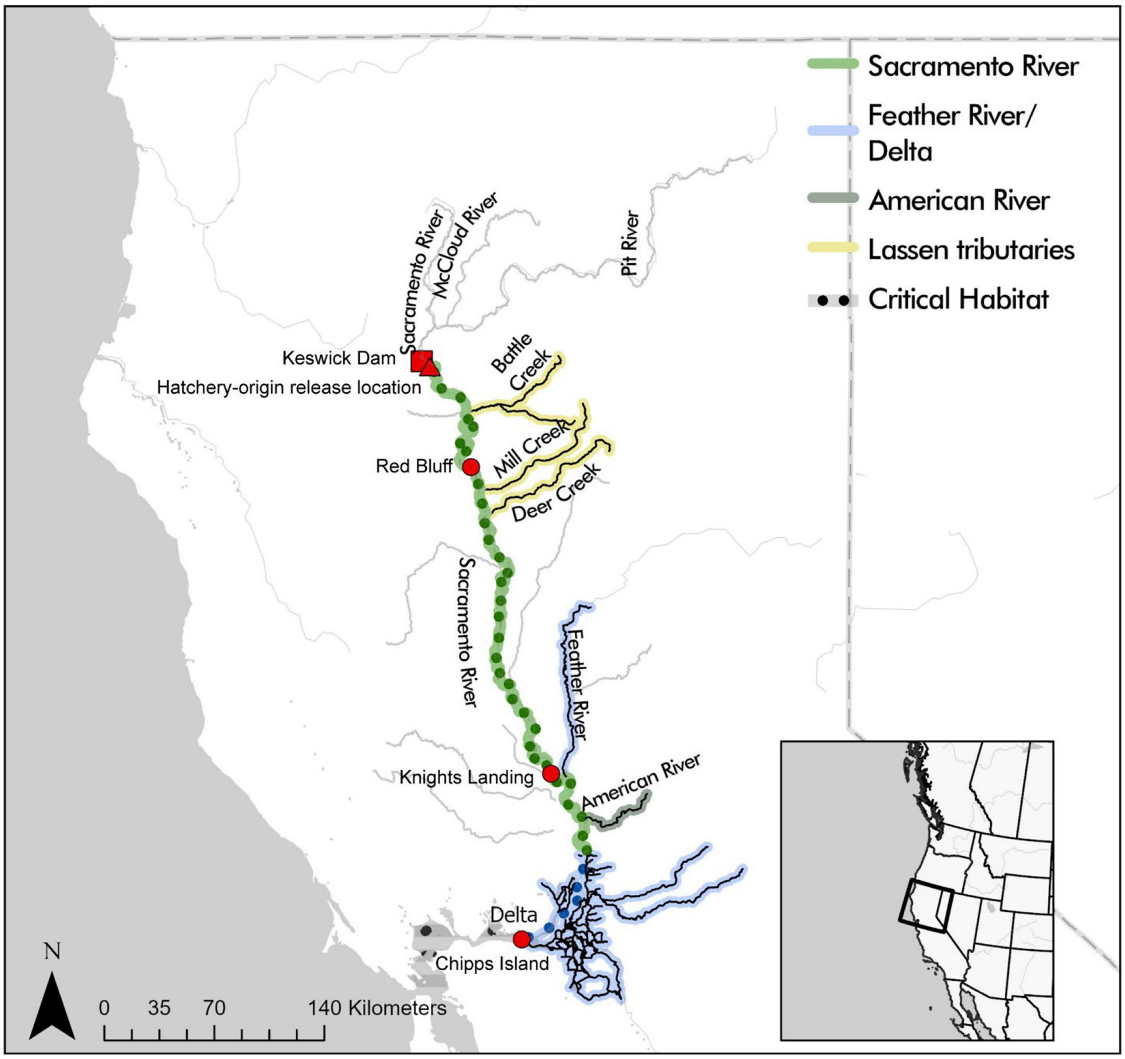

Figure 1. Map of the main-stem Sacramento River, major tributaries, and Sacramento–San Joaquin Delta (Delta). Shades indicate groupings of areas with similar $^{87}Sr/^{86}Sr$ ranges. Dotted regions indicate critical habitat areas of Sacramento River winter-run Chinook Salmon designated in the Endangered Species Act.

and determine when hatchery fish provide good surrogates for natural-origin winter-run Chinook Salmon.

METHODS

Study site and population

Winter-run Chinook Salmon in the Sacramento River are their own evolutionary significant unit and have a unique life history that is not found elsewhere in the native range of Chinook Salmon. Their evolutionary life history has been shaped by their ancestral waters, which are characterized by cold reliable springs in high-elevation habitats, allowing their eggs to thrive during the hottest times of the year. Unlike other runs of Chinook Salmon, which typically spawn in the fall and winter, winter-run Chinook Salmon spawn from May to July, and fry typically emerge in August and September (Jennings & Hendrix, 2020). In most years, the majority of juveniles migrate past Red Bluff in the upper Sacramento River in October and peak migration occurs through the lower Sacramento River past Knights Landing between November and March, depending on the timing of high-flow events during the wet season (Figure 1; Bellido-Leiva et al., 2021; del Rosario et al., 2013). Based on trawl surveys, smolts typically exit the Sacramento–San Joaquin Delta near Chipps Island in March and April (del Rosario et al., 2013). In the ocean, winter-run Chinook Salmon tend to remain off the California coast and are primarily encountered by recreational and commercial fisheries in the Monterey and San Francisco areas south of Point Arena (Satterthwaite et al., 2015). Winter-run Chinook Salmon rear for 1 to 3 years at sea, and adults reenter the watershed from November onward to spawn as 2-, 3-, and 4-year-olds (Chen et al., 2023; Killam, 2021). Winter-run Chinook Salmon have a more homogenous age structure than other runs of Chinook Salmon, with most of both natural- and hatchery-origin spawners returning at age 3 (Chen et al., 2023).

Winter-run Chinook Salmon historically comprised multiple populations that spawned in the upper Sacramento River and its tributaries, where they were stewarded since time immemorial by the Wintu, Yana, Achomawi, and Atsugewi peoples (Good et al., 2005; University of California Berkeley, 1995;

Table 1. Summary of hydrology and sample sizes in years included in the analysis. Otolith chemistry informed habitat use at size, and the addition of a daily increment analysis on a subset of samples informed residence times and relative growth rates.

Escape year	Brood year[a]	Migrant year[a]	Start flow[b]	Peak flow[c]	Mean flow[d]	Year type[e]	Otolith chemistry—natural	Otolith chemistry—hatchery	With increment analysis—natural	With increment analysis—hatchery	Previously reported in
2007	2004	2005	Dec 8	40645	8263	AN	29	0	0	0	Phillis et al., 2018
2008	2005	2006	Dec 2	88950	20929	W	86	0	0	0	Phillis et al., 2018
2009	2006	2007	Dec 13	28946	7970	D	67	5	0	0	Phillis et al., 2018
2015	2012	2013	Nov 30	37441	7957	D	298	58	0	0	Morais et al., 2025
2016	2013	2014	Mar 4	19604	5804	C	183	2	0	0	Morais et al., 2025
2017	2014	2015	Dec 4	63646	7020	C	27	3	0	0	Morais et al., 2025
2018	2015	2016	Dec 21	44458	9518	BN	126	106	80	39	This manuscript
2019	2016	2017	Nov 20	93096	23784	W	130	84	71	37	This manuscript

[a]The brood year and out-migration year assume all individuals returned at age 3 (Chen et al., 2023).
[b]Start flow is the first date starting September 1 of the brood year when daily mean flow exceeds 15,000 ft^3/s (424.7527 m^3/s) at Bend Bridge gauge station (California Department of Water Resources, 2023).
[c]Peak flow is the highest recorded mean daily flow (in ft^3/s) at Bend Bridge gauge station from September 1 of the brood year to March 31 of the migrant year.
[d]Mean flow is the mean daily flow at Bend Bridge gauge station from September 1 of the brood year to March 31 of the migrant year each year.
[e]Sacramento Valley water year classification according to the California Department of Water Resources for October 1 of brood year to October 1 of migrant year (W = wet; AN = above normal; BN: below normal; D = dry; C = critical) (California Department of Water Resources, 2023).

Yoshiyama et al., 1998). Establishment of major water and flood control projects, including reservoirs, diversions, and levees, has dramatically disrupted the habitat conditions for Sacramento River winter-run Chinook Salmon (Yoshiyama et al., 1998). Construction of the Shasta and Keswick dams flooded tribal villages and extirpated salmon from their ancestral spawning and rearing habitats. Currently, the vast majority of natural-origin winter-run Chinook Salmon spawn as a single population below Keswick Dam (Figure 1). River escapement of winter-run Chinook Salmon has averaged 4,188 spawners (SD = 2,891 spawners) during the past decade (2014–2023), considerably fewer than was observed for fall-run Chinook Salmon escapement in the upper main stem of the Sacramento River (14,114 spawners, SD = 11,005 spawners) during the same period (Pacific Fishery Management Council, 2025). Efforts are underway to reintroduce winter-run Chinook Salmon to their historic habitats, such as Battle Creek and the McCloud River, to expand and diversify the evolutionary significant unit and restore winter-run Chinook Salmon in their historical range (ICF International, 2016; National Marine Fisheries Service [NMFS], 2016; U.S. Office of the Federal Register, 2023).

The winter-run Chinook Salmon hatchery program at Livingston Stone National Fish Hatchery was established in 1997 and has the overarching purpose to sustain and recover the population (Good et al., 2005). A primary objective of this conservation hatchery is to maintain stock integrity and minimize harmful genetic and ecological interactions with natural-origin fish (U.S. Fish and Wildlife Service, 2016). To do this, the hatchery program uses natural-origin fish as broodstock whenever possible and selects individuals for inclusion in the broodstock with traits (e.g., run timing and size) that are representative of the entire run. Juvenile fish are released in the upper Sacramento River during high-flow events in February after most natural-origin fish have initiated their downstream migration (Figure 1). Hatchery winter-run fish that are implanted with acoustic tags spend about 30 d rearing and migrating in the main stem of the Sacramento River, although this can vary among individuals and across years (Hassrick et al., 2022). When adults return to spawn, the proportion of hatchery- to natural-origin fish on the spawning grounds has usually been less than 30%, but the proportion was over 80% in 2017 and 2018 due to large hatchery cohorts in 2014 and 2015 during a multiyear drought when survival of natural-origin fish was exceptionally low (Meyers, 2021). The production of hatchery fish has increased over time, including a 50% increase in 2022 in response to low recent escapement and concerns about the poor productivity of natural-origin fish (NMFS, 2023).

Sample collection and analysis

We analyzed sagittal otoliths that were collected from adult carcasses during spawning ground surveys on the Sacramento River by the U.S. Fish and Wildlife Service and California Department of Fish and Wildlife and from the Livingston Stone National Fish Hatchery (Table 1). Winter-run Chinook Salmon spawn from May to July when no other runs are spawning, eliminating the possibility of other runs in our samples. In the brood years that are included in our study (Table 1), nearly all (99.3%) winter-run hatchery Chinook Salmon had their adipose fin clipped prior to release. A sample was considered natural origin if the adipose fin was present, although misclips and adipose fin regeneration can occur (Kinziger et al., 2022). Intact adipose samples were later evaluated and reclassified as hatchery fish if their strontium isotope profiles had higher isotope ratios than the values of the Sacramento River main stem for the initial months after exogenous feeding because of the marine-derived diet in the hatchery. Ultimately, 20 intact adipose samples (2% of intact adipose samples) were reclassified as hatchery fish. For this analysis, otoliths from natural-origin fish that returned to spawn during 2007–2009 and 2015–2019 ($n = 946$) were compared with hatchery-origin otoliths from 2009 and 2015–2019 ($n = 258$), primarily from 2015, 2018, and 2019 due to the larger sample sizes that were available in

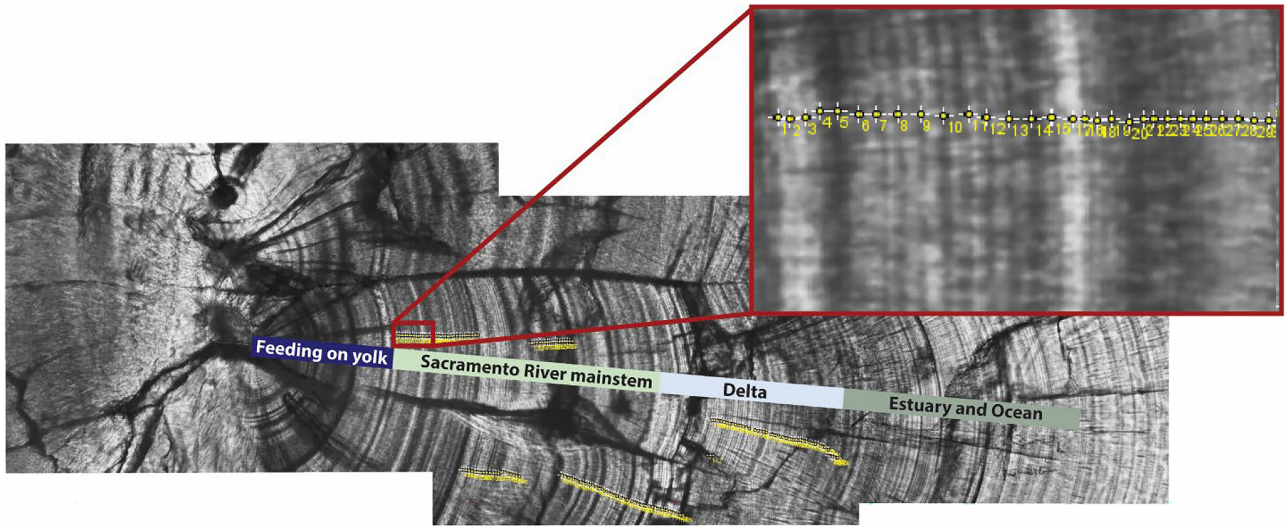

Figure 2. Dorsal side of an otolith sample with annotations. The transect that is shown is labeled according to the habitat assigned based on the measured $^{87}Sr/^{86}Sr$ values. Yellow points in the figure and inset indicate individual increments.

those years (Table 1). Most of the otolith samples were aragonite (versus vaterite), and only aragonite otoliths were prepared and analyzed. The otoliths were thin-sectioned in the sagittal plane by rough-polishing both sides until the core and early increments were exposed using 600 and 1,500 grit wet/dry sandpaper. A final smooth polish was achieved using 3- and 1-μm Al_2O_3 lapping films (Barnett-Johnson et al., 2007).

Otolith $^{87}Sr/^{86}Sr$ and total strontium voltage were measured using multiple collection laser ablation inductively coupled mass spectrometry (MC-LA-ICPMS) at the UC Davis Interdisciplinary Center for Plasma Mass Spectrometry following established protocols (Barnett-Johnson et al., 2007; Sturrock et al., 2015). The strontium measurements were sampled with a spot transect, starting from the core and extending 800 μm toward the dorsal edge, far enough to include the entire natal portion of the otolith and past the transition into ocean residence (Figure 2). Each spot was 40 μm in diameter, encompassing approximately 10–20 daily increments, depending on increment width, and pulsed at 10 Hz for 20 s, with a fluence of ~4–6 J/cm^2. Each measurement reflected the average $^{87}Sr/^{86}Sr$ across the 40-μm diameter. Instrument bias and drift were monitored by periodically measuring the ocean residence portion within the sampled otoliths, which have a known $^{87}Sr/^{86}Sr$ global marine value of 0.70918. The analyzed otoliths were later imaged in 100× magnification with a Q-Imaging digital camera (MicroPublisher 6 CCD), and the distance of each spot (i.e., otolith radius) was measured from the most dorsal-posterior primordia along a standardized transect in Image-Pro Premier. We interpolated the changes in isotope ratio from spot to spot by assuming a linear relationship between the centers of each spot.

Reconstructions of habitat use

We characterized the habitat use of individual fish by assigning sections of the otolith transect to parts of the watershed or the ocean based on the measured $^{87}Sr/^{86}Sr$ values and the logical progression of downstream migration (Figure 3). Individuals were characterized into a juvenile freshwater life history based on their habitat use (e.g., main stem only, partial nonnatal tributary residence, extended delta rearing). For the isoscape, we used the $^{87}Sr/^{86}Sr$ ranges that were established in Phillis et al. (2018), which were based on a series of water and juvenile otolith sample collections, to assign a habitat to every section of the otolith (Table 2). We assumed that all natural-origin fish were born in the Sacramento River, even though early $^{87}Sr/^{86}Sr$ values were sometimes higher because the fish were still receiving nutrients from the maternally derived yolk sac, which has marine-derived nutrients and thus an elevated isotopic ratio.

Sections of the otolith transect with $^{87}Sr/^{86}Sr$ values below the range of those for the Sacramento River main stem were considered to indicate periods of nonnatal rearing in tributaries in the Lassen volcanic region including Mill, Deer, Battle, Mud, Dye, Toomes, and Antelope creeks (Morais et al., 2025). These creeks have overlapping $^{87}Sr/^{86}Sr$ values that are all below the $^{87}Sr/^{86}Sr$ range for the Sacramento River main stem, and the measurements in this range were collectively grouped as the "Lassen tributaries." The Feather River and Sacramento–San Joaquin Delta have similar $^{87}Sr/^{86}Sr$ values and were not distinguished separately, although fish that rear in the Feather River may sometimes show a subsequent decrease in $^{87}Sr/^{86}Sr$ as they reenter the Sacramento River. The Sacramento–San Joaquin Delta is on the migration route to the ocean and most fish show periods of being in the delta. Fish can stop and reside in the delta, and we considered a span of measurements greater than 120 μm (approximately 40 d) in this range to be an indicator of residing in the Sacramento–San Joaquin Delta or Feather River. Fish with sections spanning less than 120 μm in this range were considered to have only used the Sacramento–San Joaquin Delta as a migratory corridor.

One challenge to using $^{87}Sr/^{86}Sr$ to infer habitat use in the Sacramento River basin is that the lower end of the American River $^{87}Sr/^{86}Sr$ range overlaps with the $^{87}Sr/^{86}Sr$ range of the San Francisco Estuary and ocean. To distinguish whether $^{87}Sr/^{86}Sr > 0.7082$ reflects the American River or the estuary and ocean, we inferred the otolith strontium concentration from strontium voltage. Concentrations of strontium in freshwaters of the Sacramento basin, including the American River,

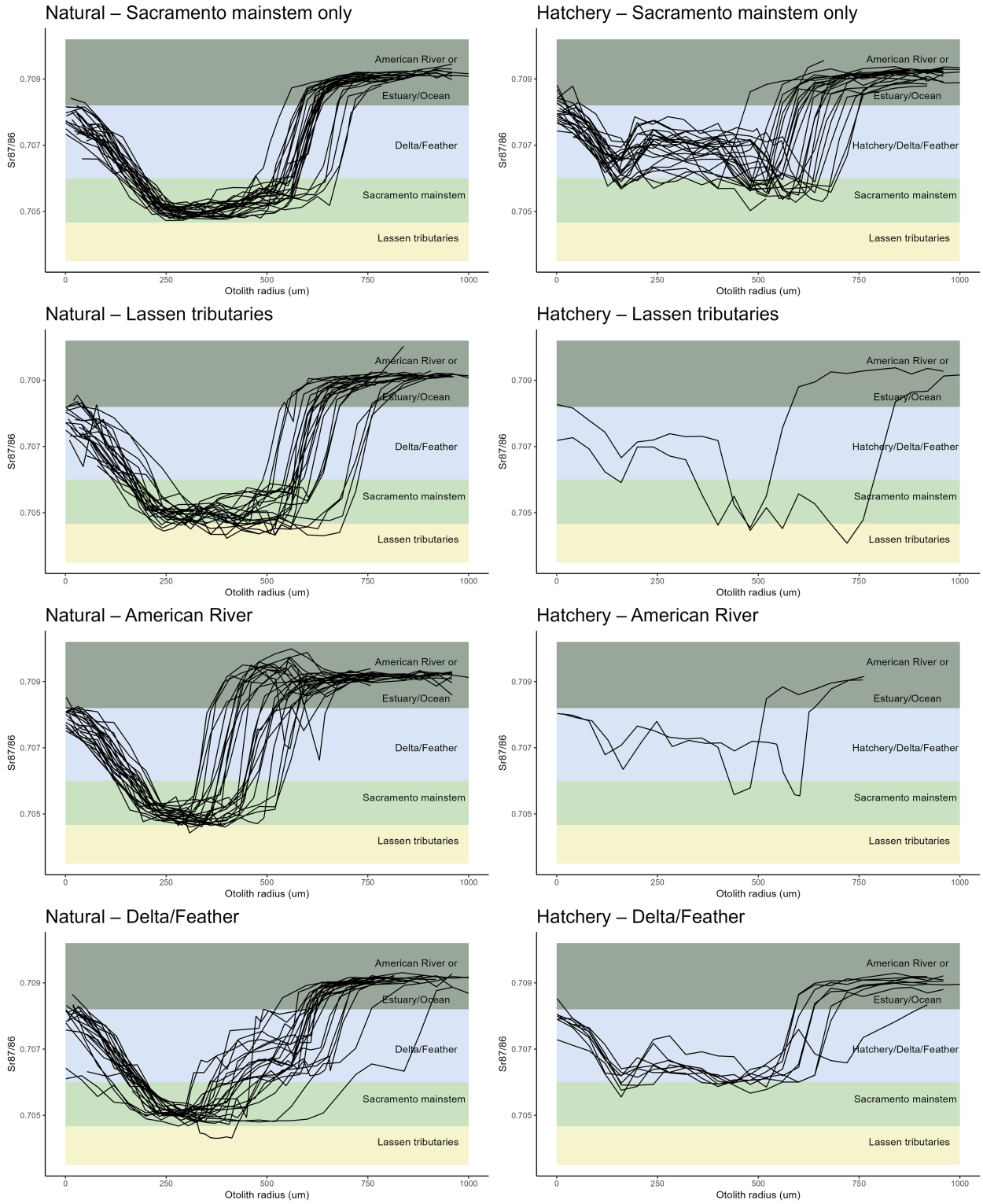

Figure 3. Strontium isotopic ratio profiles of natural-origin life histories (left) and hatchery-origin life histories (right) during their freshwater-rearing and ocean-entry phases. Otolith radii were measured starting from the most dorsal-posterior primordia (near the center of the otolith). The average exogenous feeding check occurred at 190 μm (SD = 20 μm), and strontium isotope values prior to exogenous feeding reflect nutrients from a maternally derived yolk sac. A maximum of 25 samples were randomly selected among analyzed the samples for each rearing strategy and origin for this figure. All samples are presented in Supplementary Materials.

are multiple orders of magnitude lower than they are in marine waters (Phillis et al., 2011; Weber, 2002). Therefore, $^{87}Sr/^{86}Sr$ values that exceed 0.7082 but do not have a corresponding increase in strontium voltage were assumed to be from the American River (Phillis et al., 2018). We identified the transition point to brackish water in the strontium voltage profile,

Table 2. Obtained $^{87}Sr/^{86}Sr$ values for the ocean and regions of the Sacramento River watershed, sorted based on $^{87}Sr/^{86}Sr$ range. The Feather River and Sacramento–San Joaquin Delta (Delta) have similar $^{87}Sr/^{86}Sr$ and were not distinguished separately. The American River and San Francisco Estuary (Estuary)/Ocean) were further distinguished using strontium voltage, a proxy for strontium concentration (see below and supplemental material for Phillis et al., 2018).

Region	$^{87}Sr/^{86}Sr$ range
Lassen tributaries	<0.70467
Sacramento River	0.70467–0.70600
Delta or Feather River	0.70600–0.7082
American River	>0.7082
Estuary/Ocean	>0.7082

identifying a single transition point through breakpoint analysis. A breakpoint analysis for each sample is robust to the variation of strontium voltage values that is observed across samples. A breakpoint was identified that divides the strontium voltage profile into two lines of different slopes while minimizing the residuals (Zeileis et al., 2022). Sections of the otolith transect with $^{87}Sr/^{86}Sr > 0.7082$ were considered periods of rearing in the American River if they occurred prior to the breakpoint in the strontium voltage profile.

Although winter-run Chinook Salmon were rearing in the hatchery, $^{87}Sr/^{86}Sr$ was generally higher than the $^{87}Sr/^{86}Sr$ of the Sacramento River main stem where the hatchery is located because of their marine-derived diet, often overlapping with the $^{87}Sr/^{86}Sr$ range of the Sacramento–San Joaquin Delta (Barnett-Johnson et al., 2008; Weber, 2002). We identified when a hatchery fish was released into the upper Sacramento River when $^{87}Sr/^{86}Sr$ was first within the range of the $^{87}Sr/^{86}Sr$ values for the Sacramento main stem. In many instances, hatchery fish migrated downstream quickly and no rearing in the main stem was detected, making it difficult to distinguish delta rearing from hatchery rearing without main-stem $^{87}Sr/^{86}Sr$ values separating the two stages. Consequently, we excluded these samples ($n = 39$) when estimating residence time and growth in the hatchery and delta for hatchery-origin fish. Finally, the $^{87}Sr/^{86}Sr$ value of water within the delta does not exceed 0.7082, so measurements greater than 0.7082 that were not categorized as the American River were considered to reflect rearing in the estuary and ocean. We refer to this as "ocean entry," although this may include rearing in the San Francisco Estuary.

Residence time

Residence time in each habitat was estimated for a subset of otoliths from 2018 and 2019 that were imaged and had their microstructure analyzed (Figure 2). The specific samples analyzed and included in the residence time analyses were chosen based on the visibility of daily increments. Next, we viewed the otoliths at 200× magnification using a Canon Rebel XS camera and program EOS Utility 2 (Version 2.14) and marked and measured them using ImageJ (Version 1.53). Following the same transect as $^{87}Sr/^{86}Sr$ measurements, we measured the widths of increments from the dorsal-posterior primordia toward the dorsal side of the otolith (Figure 2). We measured at least the first 200 increments, starting from the exogenous feeding check to evaluate the age and size of fish within the individual's first 200 d from exogenous feeding (Barnett-Johnson et al., 2007). To evaluate the residence time in each habitat, we counted the increments that were present within each section of the otolith that was assigned to a particular habitat (Neilsen & Geen, 1982). We summarized the residence time in each habitat for natural- and hatchery-origin fish and conducted Mann–Whitney *U* tests for habitats in which there were sufficient sample sizes to compare natural- and hatchery-origin residence time (i.e., the Sacramento main stem and Sacramento–San Joaquin Delta).

Size, age, and relative growth

The size and age at which the fish transitioned to a new habitat was estimated by measuring the otolith radius and counting the increments that were present between the exogenous feeding check and the first increment within the new habitat's $^{87}Sr/^{86}Sr$ range (Claiborne & Campbell, 2016). To test whether the size and age at ocean entry differed between origin types and among years, we compared the otolith radius and age at ocean entry in hatchery- and natural-origin fish across years using two-way analyses of variance (ANOVAs) after evaluating the data for normality and homoscedasticity. Because of limited hatchery-origin microstructure samples prior to 2018, we only compared samples from 2018 and 2019 when there were sufficient and comparable sample sizes in the two-way ANOVA for ocean entry age.

We used daily increment widths during their first 200 d to assess whether habitat, life history type, origin, and/or escapement year affected juvenile salmon growth. Habitat was a time-varying covariate, whereas life history type, origin, and escapement year were individual-level covariates. Growth may vary by life history (i.e., faster or slower growing individuals may be more or less likely to use nonnatal habitats). Juvenile salmon growth rates vary ontogenetically (Coleman et al., 2022), and the samples in this study exhibited a nonlinear relationship between increment width and age. We fit a generalized additive mixed-effects model using a smoothing function for distance from center using the R package *mgcv* (Wood, 2023). Because increment measurements within each sample are not independent, we included a random intercept effect for each sample and specified an autocorrelation structure of order 1 (Coleman et al., 2022). Habitat, life history, origin, and escapement year were included as covariates in the full model, and nested versions of the full model were compared using Akaike information criterion scores (Burnham & Anderson, 2002). We checked the models for lack of residual autocorrelation and checked the residuals for normality and homoscedasticity.

RESULTS

Habitat use

Examining the otolith $^{87}Sr/^{86}Sr$ patterns across sources revealed that natural-origin fish used the basin much more extensively than hatchery fish did following release (Figure 3). Importantly, a mean of 48.4% of returning natural-origin fish across years used nonnatal tributaries as juveniles. In particular, 19.4% (SD = 6.9%) reared in tributaries within the Lassen volcanic region (e.g., Battle Creek, Deer Creek, Mill Creek) and 13.4% (SD = 8.2%) showed evidence of rearing in the

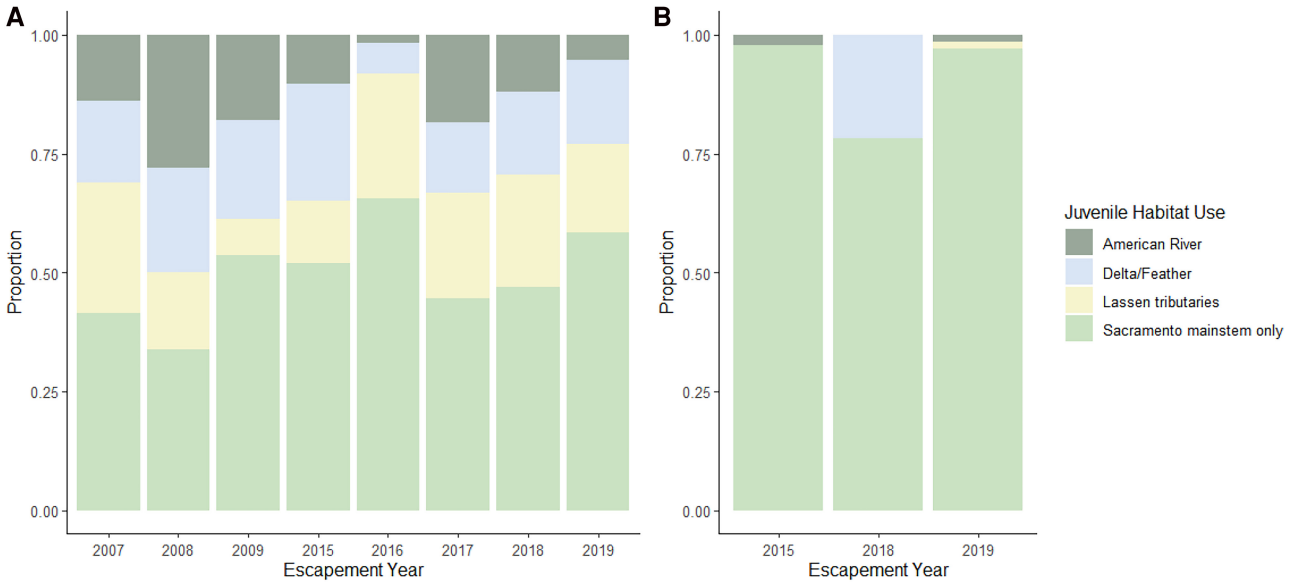

Figure 4. Juvenile freshwater habitat use of returning (A) natural-origin and (B) hatchery-origin winter-run Chinook Salmon by escapement year. The years 2008, 2009, and 2016 were excluded from the figure for hatchery samples because of limited sample sizes ($n = 3$, 2, and 2, respectively). Abbreviation is as follows: Delta = Sacramento–San Joaquin Delta.

American River (Figure 4) across 2007–2009 and 2015–2019. Another 17.7% (SD = 5.5%) of the natural-origin fish reared in the Feather River or Sacramento–San Joaquin Delta for an extended period (at least ~40 d) in those years. Overall, large proportions of natural-origin winter-run fish reared in nonnatal habitats every year (Figure 4), including years with different hydrologies (summarized in Table 1).

In contrast, of the 258 hatchery-origin otoliths that we analyzed, only 11 samples (~4%) showed evidence of nonnatal rearing (Figure 3). Because of the resolution of the strontium isotope transect measurements, we may not detect the Sacramento River main-stem signature if the fish were only in the main stem for a short period prior to ocean entry. This occurred in approximately 30% of the hatchery fish samples and was highly variable across years (range: 0–70%; see online Supplementary Material).

Residence time, size, age and relative growth

Hatchery fish spent a mean of 118 d (SD = 31 d) after emergence rearing in the hatchery and had a mean otolith radius of 489 µm (SE = 6 µm; SD = 71 µm) when we first detected the main stem's $^{87}Sr/^{86}Sr$ range for fish in which we were able to detect the transition from the hatchery to the Sacramento River main stem. At the same age (118 d), natural-origin fish had a mean otolith radius of 512 µm (SE = 4 µm; SD = 43 d), suggesting that these natural-origin fish grew more quickly than those from the hatcheries. Hatchery fish reared for a much shorter time in the Sacramento main stem once they were released than natural-origin fish did (Mann–Whitney $U = 11{,}432$, $P = 2.20 \times 10^{-16}$). The mean duration of hatchery fish being detected in the Sacramento River main stem, including samples with no main-stem rearing detected, was 11 d (SD = 16 d) across samples, but natural-origin fish were detected in the main stem for an average of 129 d (SD = 37 d) from exogenous feeding (Figure 5). Natural-origin fish had shorter residence times in the Sacramento–San Joaquin Delta (mean = 21 d, SE = 2 d, SD = 20 d) than hatchery-origin fish (mean = 24 d, SE = 2 d, SD = 15 d; Mann–Whitney $U = 2{,}031$, $P = 0.010$). Faster-migrating hatchery fish without any measurements within the main-stem $^{87}Sr/^{86}Sr$ range were excluded from our estimates of residence time in the hatchery and the Sacramento–San Joaquin Delta because we were unable to distinguish hatchery from delta rearing, which may bias the mean residence times if these individuals reared in the hatchery or delta for longer or shorter periods.

The fish that reared in nonnatal tributaries that are located higher in the watershed and closer to the spawning grounds (i.e., the Lassen tributaries) were smaller (mean otolith radius for natural-origin fish = 371 µm, SE = 6 µm) and younger (mean = 70 d, SE = 5 d) when they entered these habitats than were fish that reared in the American River farther downstream (mean otolith radius for natural-origin fish = 405 µm, SE = 7 µm; mean age = 82 d, SE = 13 d). The hatchery individual that was considered to have reared in one of the tributaries in the Lassen region was first detected in this isotopic range at 473 µm, whereas the two hatchery individuals that were considered to have reared in the American River were first detected at 484 µm and 608 µm—sizes that are larger than when natural-origin fish first used these tributaries. These fish were also older than the average age at which natural-origin fish first used the tributaries. For natural-origin fish that we categorized as having reared in Lassen tributaries, we estimated that they reared in these tributaries for an average of 43 d (SD = 38 d) across individuals based on the number of daily increments within the appropriate strontium isotopic range. For natural-origin fish that we detected having reared in the American River, we estimated mean rearing time to be 79 d (SD = 28 d), although this may be biased high because the $^{87}Sr/^{86}Sr$ range of the American River is considerably higher and fish that are in the American River for short periods may have an intermediate

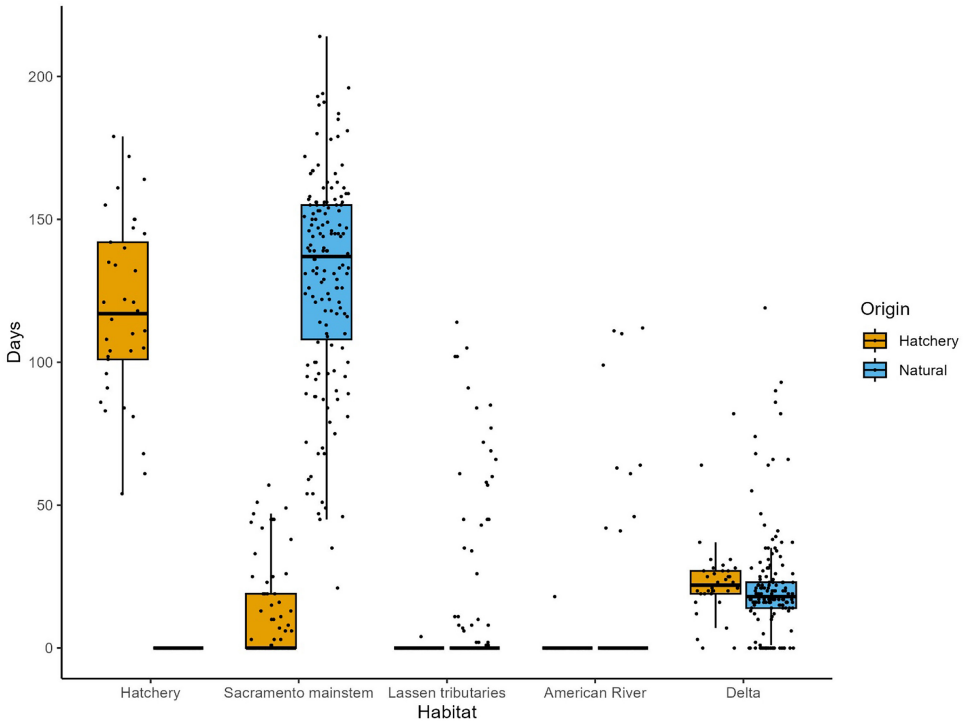

Figure 5. Number of daily increments counted in hatchery- versus natural-origin winter-run Chinook Salmon otoliths in each habitat. Bold lines indicate the median, boxes indicate the interquartile range, and whiskers are 1.5 times interquartile range. Hatchery samples in which there were no Sacramento main-stem $^{87}Sr/^{86}Sr$ values detected were excluded from estimating residence time in the hatchery and Sacramento–San Joaquin Delta (Delta).

$^{87}Sr/^{86}Sr$ value that is below the range for the American River $^{87}Sr/^{86}Sr$ due to signal averaging.

Based on their otolith radius, hatchery fish had size distributions that were similar to those of natural-origin fish at ocean entry (Figure 6). The otolith radius of natural-origin fish upon ocean entry was 633 µm (SE 2 µm; SD = 68 µm), and the mean otolith radius for hatchery fish was 625 µm (SE 4 µm; SD = 63 µm; ANOVA: $F = 1.78$, df = 1201, $P = 0.18$). Ocean entry size differed across years (ANOVA: $F = 2.52$, df = 1201, $P = 0.014$), but the difference in mean radius between the years with the largest (652 µm in 2007) and smallest (612 µm in 2009) otolith radius was 40 µm, less than the overall standard deviation of ocean entry size across all samples (67 µm).

The age of ocean entry differed between sources and across years (ANOVA: *origin*—$F = 4.64$, df = 207, $P = 0.033$; *year*—$F = 14.5$, df = 207, $P = 0.00019$), but the difference in mean age between hatchery- and natural-origin fish was only 4 d. Hatchery fish were on average 165 d old (SE = 3 d; SD = 22 d) since exogenous feeding when they entered the ocean, and natural-origin fish were on average 161 d old (SE = 2 d; SD = 20 d; Figure 6). Adults returning in 2019 reared in the basin for around 2 weeks longer as juveniles than adults returning in 2018 (natural: 160 d in 2018 versus 174 d in 2019; hatchery: 168 d in 2018 versus 181 d in 2019). Most of the adults in 2019 likely migrated downstream in 2017, a wet water year, whereas most of the adults in 2018 likely migrated downstream in 2016, a below-normal water year.

The generalized additive mixed-effects model with the optimal fit that was selected to model juvenile salmon growth included habitat, origin, and escapement year as covariates but not life history type (Table A1). Based on the daily increment widths, hatchery fish had lower growth rates than natural-origin fish at all life stages regardless of habitat (Figure 7; Figure 8). Rearing in the Lassen tributaries was associated with significantly lower relative growth ($P = 0.036$) than rearing in the main-stem Sacramento River, and rearing in the Sacramento–San Joaquin Delta/Feather River and in the estuary/ocean were associated with higher daily growth rates (Sacramento–San Joaquin Delta/Feather River $P = 0.037$; estuary/ocean $P = 3.3 \times 10^{-5}$; Table A2). Higher growth was also observed in 2019 adults than in 2018 adults ($P = 3.8 \times 10^{-7}$; Figure 7; Table A2).

DISCUSSION

We found large spatial variation in the freshwater rearing patterns of returning winter-run Chinook Salmon in the Sacramento River system, including considerable evidence of natural-origin fish moving into and rearing in nonnatal tributaries and the Sacramento–San Joaquin Delta, similar to Phillis et al. (2018) and Morais et al. (2025). Among natural-origin fish, nearly half of adults returning to spawn showed evidence of having reared for an appreciable length of time in a nonnatal habitat during their out-migration. Rearing in nonnatal habitats reduces the population's density in a single habitat and dampens the effect of environmental perturbations in individual habitats (Cordoleani et al., 2022). Many of the nonnatal habitats that were used by winter-run Chinook Salmon are outside of the Endangered Species Act's critical habitat designation (U.S. Office of the Federal Register, 1993). In contrast, fish that were

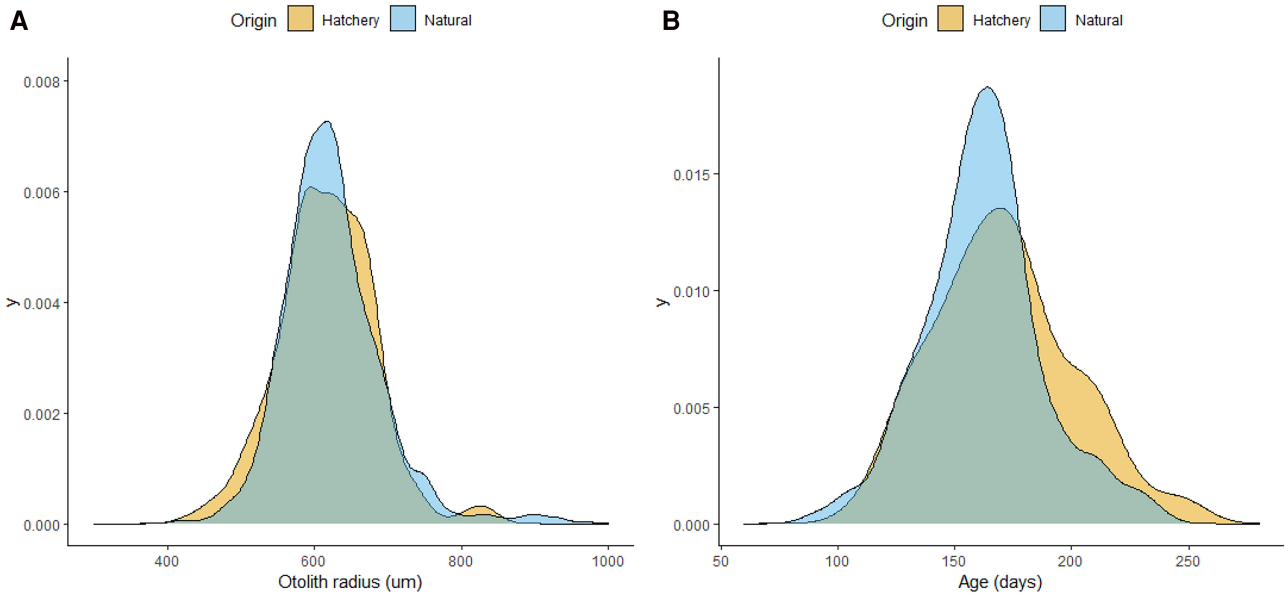

Figure 6. (A) Otolith radius (a proxy for fish size) and (B) age at ocean entry for hatchery and natural-origin winter-run Chinook Salmon.

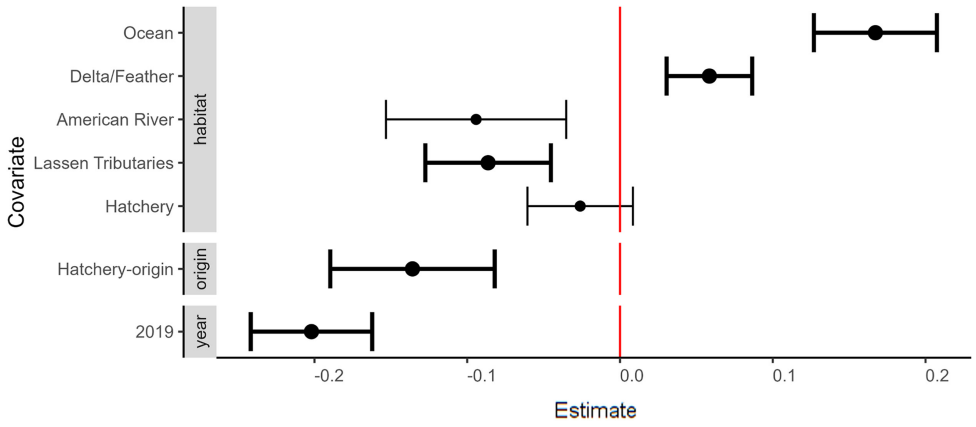

Figure 7. Coefficient estimates for the optimal generalized additive mixed-effects model predicting otolith daily increment widths (μm; a proxy for fish growth rate; error bars indicate standard error). The estimates reflect differences from baseline—habitat: Sacramento River, origin: natural, and year: 2018. For instance, the positive coefficient for the ocean indicates higher growth rate relative to the baseline habitat, the Sacramento River. Coefficient estimates with $P < 0.05$ are bolded. Abbreviation is as follows: Delta = Sacramento–San Joaquin Delta.

limited to rearing in the hatchery for the first part of their life moved quickly through the system to the ocean after release, using the system primarily as a migratory corridor.

Relative to natural-origin fish, we found simple migratory behavior among hatchery releases. Hatchery-produced winter-run Chinook Salmon juveniles were at liberty in the river for much shorter periods (mean = 11 d) prior to entering the ocean than were their natural-origin counterparts (mean = 129 d). Releasing all individuals within a short span of time condenses migration timing and aggregates downstream movement, potentially resulting in a more homogenous response of the hatchery fish to the environment and reduced stability in downstream survival across years (Sturrock et al., 2019). However, releasing fish over a narrow range of dates may also be beneficial in terms of predator swamping. In general, hatchery fish are released at a size and stage that is more ready for ocean rearing; thus, it is not too surprising that they migrate downstream faster than natural-origin fish do. Because of their shorter residence in freshwater, winter-run hatchery fish likely do not pose a major competition risk to natural-origin fish during freshwater rearing. Many hatchery fish (~30%) migrated downstream so quickly (within ~2 weeks) that we did not detect a main-stem isotopic signature in the otolith (i.e., the residence time was too short to result in a $^{87}Sr/^{86}Sr$ measurement reflecting the Sacramento River in the 40-μm windows that we measured). Unlike natural-origin fish, hatchery fish generally stay within and are protected by the critical habitat designation (U.S. Office of the Federal Register, 1993). Hatchery fish are larger upon release than natural-origin fish are when they go into nonnatal tributaries, suggesting they may not require extended rearing in the basin, which might explain why nonnatal rearing was not frequently observed in hatchery fish. Although a majority of returning hatchery fish only reared in the river for a short period, there was a large range of migration

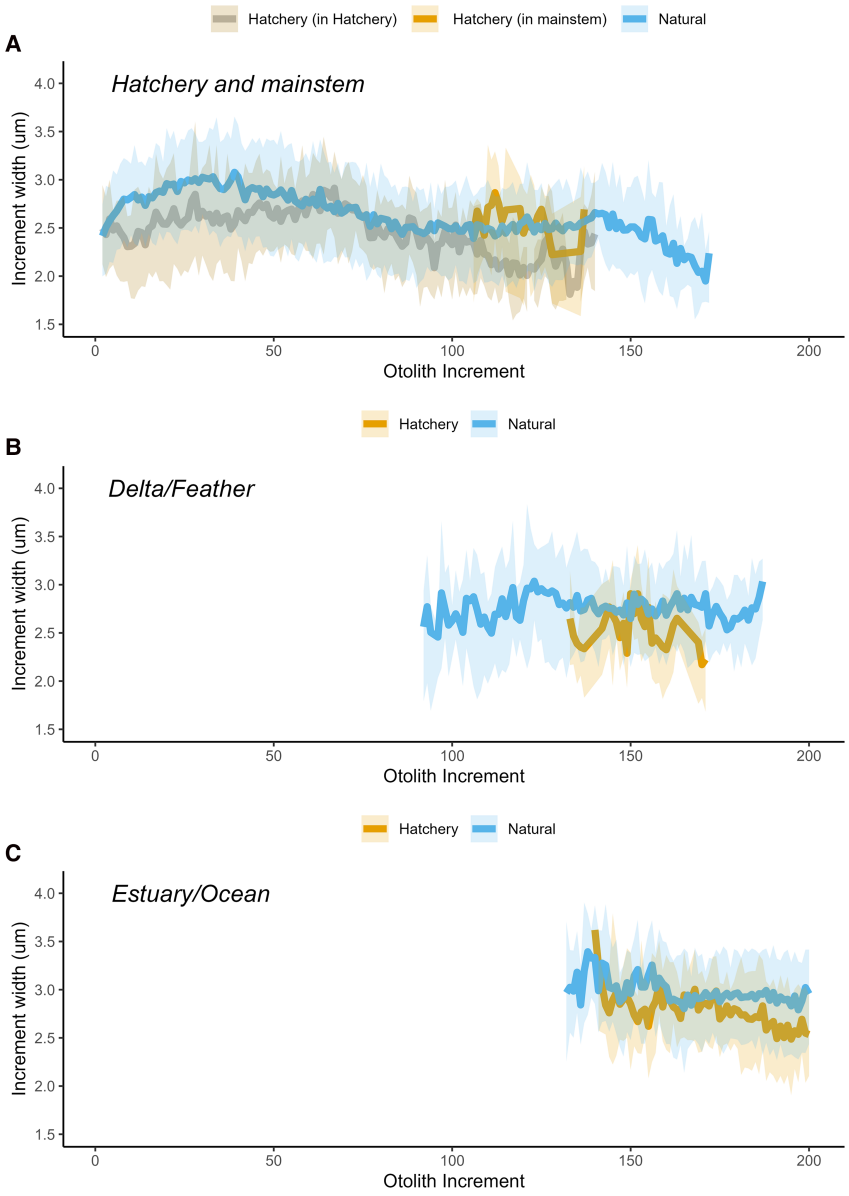

Figure 8. Otolith daily increment widths (a proxy for fish growth rate) for natural-origin (blue) and hatchery-origin (brown) individuals while in the (A) hatchery and Sacramento River main stem, (B) Sacramento–San Joaquin Delta (Delta)/Feather River, and (C) San Francisco Estuary (Estuary) or ocean. The lines indicate the mean increment widths and are plotted when there were at least 10 individuals per habitat at the increment, and shading indicates the interquartile range.

rates and some fish were observed rearing in the basin for extensive periods, including some tributary rearing. Hatchery fish had slower growth across habitats than natural-origin fish, potentially because of reduced natural fitness and foraging ability. These results are among surviving individuals and indicate that hatchery fish have slow growth postrelease, which can lead to lower survival (Brown & Laland, 2005; Ersbak & Haase, 1983). In the years of our study that overlap with Hassrick et al. (2022), there were similar year-to-year patterns in migration rate in the studies (i.e., hatchery fish had a lower migration speed during the wet year of 2017 versus the below-normal year of 2016). The hatchery residence times that we measured in the main stem using otoliths (averaging 6 d in migrant year 2016 and 16 d in migrant year 2017) were shorter than the residence times that were estimated through acoustic tags in Hassrick et al. (2022), averaging 13 d in 2016 and 48 d in 2017. This is likely because hatchery fish were not categorized as being in the Sacramento River until their otolith chemistry had entered the $^{87}Sr/^{86}Sr$ range of the Sacramento main stem. Given that the measurements typically integrate around 2 weeks, regions of the otolith when the fish were transitioning from the hatchery to the main-stem isotopic range were classified as hatchery residence, so the estimates of main-stem rearing in hatchery-origin fish may be underestimated by up to 2 weeks. However, the residence time difference between acoustic-tagged fish and otolith reconstructions from returning fish in 2017 was greater than 2 weeks, suggesting higher overall survival among the fish that moved out of the system faster.

Although hatchery fish reared in the river for much shorter periods and exhibited lower diversity in habitat use, returning

hatchery-origin fish entered the ocean at a size and age similar to those of returning natural-origin fish. Natural- and hatchery-origin migrants were typically 4–6 months postexogenous feeding when they exited the Sacramento–San Joaquin Delta and entered the estuary, which corresponds to approximately January–March if the fish emerge in mid-September (Jennings & Hendrix, 2020; Torres et al., 2023). These date estimates are close to when natural- and hatchery-origin winter-run fish are captured by trawl sampling in the estuary at Chipps Island. Fish that are the size of natural-origin winter-run Chinook Salmon are captured from December to April, peaking in March (del Rosario et al., 2013), whereas hatchery fish are captured soon after their release in February to April (Pacific States Marine Fisheries Commission, 2020). Overall, this suggests that hatchery practices have not greatly altered the size or timing at ocean arrival, but the paths that the fish take to arrive at those sizes and timings differ greatly.

Survival during the first year in the ocean is one of the periods of lowest survival for Chinook Salmon and is determined by marine environmental conditions, such as food availability and temperature, and individual attributes, such as a fish's ocean size and arrival timing (Beamish & Mahnken, 2001; Satterthwaite et al., 2014; Woodson et al., 2013). Similar ocean entry timing and size among hatchery- and natural-origin fish suggest that they may have more similar early ocean survival rates than expected. Although there are estimates for winter-run Chinook Salmon survival from downstream migration to the start of age 2 (Winship et al., 2014), there are no estimates of ocean survival alone (excluding downstream migration) for winter-run Chinook Salmon. Winship et al. (2014) estimated hatchery-origin fish to have much higher survival rates from release to age 2 than their wild counterparts from downriver migration to age 2, but it is unknown whether this is because they experience greater survival or because they are released later. Returning hatchery fish had standard deviations in their ocean entry age and size that were similar to those of natural-origin fish, which was surprising given that hatchery fish all rear under the same conditions and are all released within the span of a few weeks. It is also important to note that our results only reflect surviving fish, so the actual variation in ocean entry may differ between hatchery- and natural-origin fish. The similarity in size and timing at ocean entry observed here could also partly reflect strong selection during early ocean residence (Satterthwaite et al., 2014; Woodson et al., 2013).

Data that are collected continuously across years are invaluable to understanding how populations respond to variation in annual conditions. For Chinook Salmon in the Central Valley, egg-to-fry and downstream survival rates vary across years and are positively related to flow and its related parameters (Hassrick et al., 2022; Henderson et al., 2018). We expected hydrological conditions to shift the habitat mosaic in the basin across time, changing the productivity and importance of habitats in years with different rainfall patterns (Coleman et al., 2022; Cordoleani et al., 2022). For example, drier conditions are expected to reduce habitat availability and quality and potentially disconnect small tributaries and off-channel habitats (Bellido-Leiva et al., 2021; Moidu et al., 2023). Although greater flows in the main stem tend to result in a higher occurrence of nonnatal rearing (Morais et al., 2025), we still found evidence of considerable nonnatal rearing in all years. Surprisingly, we found that growth rates in nonnatal tributaries tended to be lower than in the main stem despite evidence of potential growth benefits in other studies (Maslin et al., 1996) and growth benefits being a primary hypothesis for why salmon use these habitats (Morais et al., 2025; Phillis et al., 2018). Although, on average, tributary rearers were overall slower growing than main-stem rearers, the effect of life history type was not significant. The high contribution rates of tributary rearing life histories to the spawning population suggest that there are other advantages to rearing in these tributaries. Our results reflect successful individuals that have survived through all life stages only. Considerable spatial diversity in freshwater rearing and the contribution of nonnatal-rearing life histories to the returning population warrant closer investigation into how nonnatal habitat use differs across years with different escapement sizes and hydrologies. With environmental conditions expected to become more variable and extreme with climate change, understanding how a population's use of the habitat mosaic contributes to a diverse portfolio of life histories is critical to supporting their habitat needs.

Currently much of the habitat supporting the spatial diversity of winter-run Chinook Salmon is outside of the critical habitat that was designated in 1993 under the Endangered Species Act. Otolith chemistry studies (i.e., Morais et al., 2025; Phillis et al., 2018; and here) and field sampling (i.e., Maslin et al., 1996) documenting habitat use throughout the basin since then suggest the need for an updated designation to better support the diversity of migratory strategies within natural-origin winter-run Chinook Salmon. Although there is overlap between the habitat use of winter-run Chinook Salmon and the critical habitat that is designated for other listed species (e.g., spring-run Chinook Salmon, steelhead *Oncorhynchus mykiss*, Delta Smelt *Hypomesus transpacificus*), protections and flow releases that are intended for these species may not be as effective or match temporally with the habitat needs of winter-run Chinook Salmon. Explicitly considering the presence of winter-run Chinook Salmon in habitats beyond the migratory corridor during habitat management (e.g., restoration and flow management) is needed to promote and enable the contribution of multiple life histories for productivity, resilience, and ultimately recovery.

Information from hatchery-origin fish is often used for managing natural-origin populations because data from natural-origin fish can be difficult to attain, particularly for endangered species such as Sacramento River winter-run Chinook Salmon. However, hatchery-origin fish may not be representative of natural-origin fish because of differences in life history due to the hatchery selection, rearing, and release processes (Chen et al., 2023; del Real et al., 2012; Vainikka et al., 2010; Yamamoto & Reinhardt, 2003). This bias should be considered and quantified whenever possible. In management and conservation models for Sacramento River winter-run Chinook Salmon—for example, the juvenile production estimate that was described in O'Farrell et al. (2018) and the life cycle model that was described in Hendrix et al. (2017)—smolt survival rates from acoustically tagged hatchery fish are used to calculate smolt abundance of natural-origin fish that reach the lower river. Because hatchery fish generally spend much shorter durations in the river, we expect their downstream survival rate to be considerably higher than

that for natural-origin fish and therefore to potentially overestimate natural-origin survival during downstream migration and number of smolts reaching the Sacramento–San Joaquin Delta and entering the ocean. Hatchery-origin fish were estimated to have much higher survival in the first year of life, which includes in-river rearing, than their wild counterparts in Winship et al. (2014), and this can be partly attributed to different in-river durations. One practical solution is to normalize survival rates to a rate per day as a lower end estimate of survival; however, this still does not account for other potential influences on survival, such as size and time of year. Hatchery fish migrate downstream in the spring, whereas natural-origin fish generally migrate through the same reaches the previous fall and winter, which can have very different flow conditions that affect turbidity (and therefore visibility to predators), flow velocity, and predator abundance and lead to further differences in downstream survival of hatchery- versus natural-origin fish (Henderson et al., 2018; Matern et al., 2002). When possible, hatchery fish with life histories that are the most similar to those of natural-origin fish—for example, in size and migration time—should be used to estimate natural-origin parameters of interest.

Our study compared the juvenile freshwater life history patterns of hatchery- and natural-origin fish with the goal of evaluating the suitability of applying measurements and results that are obtained from one group to the other. Studying otoliths that are taken from carcasses does not involve handling or sacrificing fish and provides the ability to identify rearing patterns throughout an individual's lifetime. However, there are aspects of otolith analysis that make their estimates not directly comparable to those from other methods. Otoliths are collected only from adults that have survived to spawn and therefore reflect the life history and habitat use of successful individuals, which may differ from sampling the early life stages of that same cohort in situ. Sampling for juvenile life history while fish are juveniles would likely reveal a far broader spectrum of life histories and habitat use patterns (Sturrock et al., 2020).

Although otoliths are useful for measuring residence history throughout an individual's lifetime, short residency periods and residency in some habitats may not always be detected. Measurements of otolith chemistry in this study were generally performed at 40-µm resolution, encompassing approximately 10–20 daily increments depending on increment width. Each $^{87}Sr/^{86}Sr$ measurement reflects the average $^{87}Sr/^{86}Sr$ across the measurement period. This resolution would likely mean that excursions that occurred for only short, subweekly periods would be undetected, depending on when rearing occurred relative to where point isotopic measurements were taken and the resulting average value. Furthermore, the upper and lower Sacramento River have similar strontium isotope chemistry, so it is not possible to distinguish upper river rearing from lower river rearing to understand the distribution of winter-run Chinook Salmon within the main stem of the Sacramento River. Some tributaries and intermittent streams have isotopic signatures that are in the same range as those in the main-stem Sacramento River (e.g., Lower Butte, Red Bank, and Dibble Creek; Morais et al., 2025). Consequently, any nonnatal rearing in these tributaries would not be detected with this method, even though winter-run-sized fish have been found in these tributaries (Maslin et al., 1996). These limitations generally result in underestimating the true variation in freshwater rearing patterns in winter-run Chinook Salmon. Other forms of monitoring and sampling, such juvenile trapping, tagging, and environmental DNA sampling, could further inform juvenile habitat use and nonnatal rearing in aspects that currently are not possible using otoliths.

In response to the increasing frequency of drought conditions in California and the possibility of high in-river egg mortality, hatchery production and densities have increased threefold within Livingston Stone since 2014, including a 50% increase in production in 2022 from 2021 (Johnson et al., 2023; NMFS, 2023). Increasing densities can slow physiological development (Schreck et al., 1985) and alter behavior (Cogliati et al., 2023) in juvenile Chinook Salmon but do not definitively lead to differences in postrelease survival (Banks & LaMotte, 2002; Brockmark et al., 2007; Olson & Paiya, 2013). When the mechanisms for shaping behavior and life history are not well understood, mimicking natural conditions to the greatest extent possible lowers negative hatchery effects. Studying whether increased densities affect juvenile in-hatchery, out-migration, and postrelease survival will be necessary to achieve production levels of winter-run Chinook Salmon that meet conservations goals (U.S. Fish and Wildlife Service, 2016). Identifying sources of divergence between hatchery and naturally produced fish and developing practices to avoid artificial selection is critical to the long-term benefits to the populations that conservation programs support.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Transactions of the American Fisheries Society* online.

DATA AVAILABILITY

Data and code that support the findings of this study are available on GitHub: https://rb.gy/6ltwu5, and Dryad: https://doi.org/10.5061/dryad.47d7wm3rp.

ETHICS STATEMENT

There were no ethical guidelines applicable to this study.

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CONFLICTS OF INTEREST

None declared.

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APPENDIX: Juvenile salmon growth model selection and coefficients of selected model

Appendix Table 1. Generalized additive mixed-effects model candidate models for increment widths and their Akaike information criterion (AIC) scores and difference (ΔAIC) from the optimal model. All models include a random intercept effect grouped by individual samples and an autocorrelation structure of order 1.

Model	AIC	ΔAIC
~ s(Otolith Radius) + Origin + Habitat + Escapement Year	62,401.05	0
~ s(Otolith Radius) + Origin + Life History + Habitat + Escapement Year	62,404.87	4
~ s(Otolith Radius) + Origin + Escapement Year	62,417.60	17
~ s(Otolith Radius) + Origin	62,440.19	39
~ s(Otolith Radius)	62,448.67	48

Appendix Table 2. Coefficient estimates for the optimal generalized additive mixed-effects model modeling increment widths. Estimates reflect difference from baseline habitat: Sacramento River, origin: natural, and year: 2018. Abbreviations are as follows: Delta = Sacramento–San Joaquin Delta.

Covariate	Coefficient (SE)	*p*
Intercept	2.92 (0.0304)	2.2×10^{-16}
Habitat (Hatchery)	−0.0261 (0.0345)	0.45
Habitat (Lassen tributaries)	−0.0863 (0.0410)	0.036
Habitat (American River)	−0.0941 (0.0590)	0.11
Habitat (Delta/Feather)	0.0585 (0.0280)	0.037
Habitat (Ocean)	0.167 (0.0403)	3.3×10^{-5}
Origin (Hatchery)	−0.135 (0.0538)	0.012
Escapement (2019)	−0.202 (0.0398)	3.8×10^{-7}