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Publication Date

2023

Peer reviewed|Thesis/dissertation

Build it and they will come: Evidence of a natal-origin Chinook salmon population
reestablishing following stream restoration

By

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THESIS

Submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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2023

Abstract

California's Chinook salmon populations (*Oncorhynchus tshawytscha*) are undergoing severe and widespread population declines and extirpations, and examples of recovered or restored wild runs of salmon in California are rare. Most salmon returning to California streams are of hatchery origin and have largely replaced salmon of natural origin. I provide a case history for the dynamics of a Chinook salmon population currently recovering in a dam-controlled stream. Following implementation of a functional flow regime and other restoration actions, spawning Chinook salmon returned to Lower Putah Creek, a tributary of the Sacramento River, for the first time since the waterway was dammed in 1958. The return of Chinook salmon to Putah Creek following restoration efforts presents a novel opportunity to understand how salmon may become established in freshwater systems in response to direct restoration actions that enhance habitat suitability, providing insight on population dynamics and recolonization processes in systems of restoration and conservation concern. It remains uncertain whether spawning salmon in Putah Creek produce progeny that return to Putah Creek to spawn in subsequent years, and to what degree the yearly spawning cohort is inflated by straying hatchery-origin fish. In this thesis, I used otolith microchemistry and microstructure methods to evaluate natal origin and population age structure across five spawning cohorts of adult Chinook salmon recovered at Putah Creek from 2016 through 2021. Demonstrating the presence of natal-origin fish in Putah Creek spawning cohorts is the first step in the potential development of a self-sustaining and locally-adapted Chinook salmon run in Putah Creek. I found evidence of successful salmon reproduction in Putah Creek and of the presence of natal individuals in spawning cohorts, although hatchery-origin fish were the most abundant origin class in every cohort studied. The proportion of wild-origin and Putah Creek-origin fish increased with

successive cohorts, and the population structure of the spawning population varied among study years.

1. Introduction

Understanding how fish populations respond to manifold anthropogenic and climatic changes is of increasing interest in conservation ecology, especially for threatened species of fishes (Lynch et al. 2016; Bardot et al. 2019; Till et al. 2019). The impacts of dams and similarly disruptive water management practices are of critical importance due to their profound impacts on native fishes and freshwater ecosystems (Bain et al. 1988; Pringle et al. 2000; Carlisle et al. 2019). California's inland waterways demonstrate this research need: rapid human population growth and agricultural development has generated extreme demand for freshwater, resulting in extensive ecological modifications. For example, damming and alterations to California's freshwater ecosystems have resulted in the imperilment of 83% of California native fishes (Moyle et al. 2011). Chinook salmon (*Oncorhynchus tshawytscha*) are emblematic of these trends: dams and water management practices have wrought severe population declines and extirpations on their populations (Yoshiyama et al. 1998; Katz et al. 2013). At present, two of the four genetically distinct Chinook salmon runs found in the Central Valley are listed for protection under the US Endangered Species Act

As trends in water and flow management in the American West shift away from traditional strategies, restoring waterway connectivity and promoting resilience of freshwater fishes has been strongly emphasized (Quinones et al. 2015; Bellmore et al. 2016; Foley et al. 2017). There is growing interest in evaluating how species of conservation interest, such as Chinook salmon, may become reestablished in systems which were previously unavailable because of barriers to anadromous fish passage (Anderson et al. 2014; Brewitt 2016; Brady Allen et al. 2016). Yet there is considerable debate in scientific, academic, and management communities regarding whether restored waterways should be stocked with hatchery-origin fish

or allowed to reestablish naturally as a result of natural straying behavior of spawning salmon over time (Brenkman et al. 2019; Neutzel et al. 2023). Straying salmon that colonize newly available waterways likely possess some degree of local adaptation to their natal system. For example, the presence of founder individuals from many sources may confer adaptive traits that are effective in the reestablishment process. Yet there are concerns regarding the use of hatchery-origin stocks as source populations for Chinook salmon recolonization events, including that hatchery fish may lack the genotypic and phenotypic diversity necessary for adaptation to the new habitat (Evans et al. 2019). Domestication effects from hatchery rearing could reduce the fitness of Chinook salmon founding a novel wild population (Blouin et al. 2021; Neutzel et al. 2023). Either of these two mechanisms could slow or jeopardize a founding population's ability to become established. However, introducing or supplementing hatchery-reared Chinook salmon has been proposed to promote reestablishment (Deredec and Courchamp 2007), especially in cases when wild-source populations are not located nearby (Anderson et al. 2014a) or would colonize on undesirably slow timelines (Anderson et al. 2014b).

California's Central Valley, including the Sacramento and San Joaquin river systems and their tributaries, historically supported an abundant Chinook salmon fishery and four genetically distinct runs (Yoshiyama et al. 1998; Yoshiyama et al. 2001). However, habitat loss due to damming and impoundments resulted in the loss of 70% of Chinook spawning habitat by the start of the 21st century (Yoshiyama et al. 2001). Following substantial habitat alterations, hatchery rearing programs were quickly developed in large Central Valley rivers in order to ensure that sufficient stocks of Chinook salmon were available to support commercial and recreational fishing (Sturrock et al. 2019). Yet this change ultimately resulted in hatchery salmon accounting for up to 90% of the Chinook salmon stock in California's Central Valley (Barnett-

Johnson et al. 2007). Climate change and drought have reduced survival probabilities of outmigrating Central Valley juvenile Chinook salmon (Huber and Carlson 2015). In response, many hatcheries have adopted methods to assist migration within the last two decades, such as trucking and estuarine net pen releases to ensure high juvenile survival at ocean entry (Sturrock et al. 2019). Although this management method ensures a higher proportion of hatchery-origin juvenile salmon enter the ocean to support fishery production, trucked hatchery-origin juveniles are unable to imprint on their migration pathways (Dedrick and Baskett 2018). Consequently, hatchery-origin Chinook salmon exhibit high rates of straying into non-natal waterways on their return migrations as spawners (Bond et al. 2016; Sturrock et al. 2019). This management action results in hatchery-origin spawning salmon migrating to facilities other than their hatchery of origin or migrating to hatchery-free rivers where they spawn alongside wild-origin Chinook salmon. Further, hatchery-origin spawning salmon may also pursue inappropriate cues and become trapped in water diversions, at which point they are salvaged and returned to viable migration channels or transported to hatcheries. Thus, while hatchery trucking and release of juvenile Chinook has been adopted to promote the survival of Central Valley salmon in high numbers (Huber and Carlson 2015), widespread straying of hatchery-origin salmon has had a number of major impacts. Trucking has led to genetic homogenization of hatchery- and wild-origin populations (Williamson and May 2004), reduced temporal variability of run timings which weaken the portfolio effect (Satterthwaite and Carlson 2015), masked declines in wild-origin fish (Johnson et al. 2012), and introduced less fit genotypes into wild populations via hatchery-origin fish (Ford 2002; Araki et al. 2007; Neutzel et al. 2023).

Naturally occurring stable isotopes of strontium (Sr) vary in their presence and abundance due to differences in underlying geology, which results in variations in Sr isotope

ratios among local watersheds (Chesson et al. 2012). Matching Sr isotope ratios observed in organisms with those mapped from water and soil samples can establish habitat use and migration of mobile animals (Hobson et al. 2009). Sr isoscapes for California's Central Valley, which were developed by mapping Sr isotope ratios of water samples from major tributaries and hatcheries, have been used to identify the natal origins of Chinook salmon by measuring Sr isotope ratios measured in the core region of adult salmon otoliths (Barnett-Johnson et al. 2008). Otoliths, or earstones, are calcareous structures which begin to develop during a salmon's freshwater natal residence, accreting daily and annual growth rings that reflect local water chemistry and can identify the natal river and hatchery- or wild- origin of a given fish.

Lower Putah Creek (California, USA), a small tributary of the Sacramento River, is an ideal study system in which to deploy geochemical tools for the improved understanding of salmon recolonization. Historical reports (Shapovalov 1940, Shapovalov 1947) document that Chinook salmon and steelhead trout accessed Putah Creek during wet years when there was enough flow to attract migrating fishes. In 1957, two dams were built that fragmented the stream ecosystem (Fig. 1). One large dam (Monticello Dam) forms Berryessa Reservoir, an 8100 ha impoundment used for both recreation and water storage. A smaller dam was constructed downstream (Putah Diversion Dam), which forms Lake Solano and diverts the majority of the water for agricultural and urban usage. Both impoundments blocked anadromous fish access to upper Putah Creek, and dam management practices provided permanent flows to only a short segment of the creek immediately downstream of the dams (Kiernan et al. 2012). Further, in the decades following impoundment, the stream ecosystem had insufficient flows to support most native fishes (Jacinto et al. 2023).

Legal action in the 1990s required increased flows in Lower Putah Creek, which comprises the segments of the waterway downstream of Putah Diversion Dam and the recipient of the remaining water that is not diverted into the Putah South Canal. A new flow regime was implemented in 2000 with the intent of restoring biologically relevant flows to Lower Putah Creek (Kiernan et al. 2012). The new ‘natural’ flow regime (e.g., Poff et al. 1997) included flows to promote attraction of anadromous fishes in the fall (attraction ‘pulse’ flows), rearing of juvenile fishes in the spring, and permanent flows for the length of the creek downstream of the Putah Diversion Dam (approximately 42 river kilometers). Subsequent monitoring studies found that native fishes displaced non-native fishes in many segments of Putah Creek following the implementation of the flow regime (Kiernan et al. 2012; Jacinto et al. 2023), and adult Chinook salmon began to appear in Putah Creek more consistently and with greater frequency from 2014 onward (Willmes et al. 2021; Jacinto et al. 2023).

While the return of Chinook salmon to Putah Creek has been hailed as a local conservation and restoration success story, many questions remain regarding the life histories of Chinook salmon. Namely, it remains unknown whether the adult salmon observed spawning in Putah Creek each year are of natal origin (i.e., hatched in Putah Creek, migrated out to sea, then successfully navigated a return migration to return and spawn in Putah Creek). Alternatively, the population may be comprised exclusively of straying hatchery-origin fish. If the population contains natal-origin fish, it may be possible that the Putah Creek population will develop into an established, wild-origin salmon population, which would have conservation and management consequences. Reestablishing another locally-adapted, self-sustaining wild salmon population in California’s Central Valley would generate additional diversity among natal salmon populations,

and promote population resiliency and conservation overall (Sullaway et al. 2021; Price et al. 2021; Stier et al. 2020).

In this thesis, I examine whether there is evidence of Putah Creek-origin fish returning to spawn in Putah Creek following restoration and management efforts. I assess (1) whether the presence and prevalence of natal Putah Creek salmon in the spawning population changes over successive years; (2) whether spawning Chinook salmon in Putah Creek are predominantly of natal or hatchery origin; (3) and whether the demographics of the spawning salmon population change over time.

I hypothesized (1) that spawning Chinook salmon population will exhibit evidence of natal origins of some Putah Creek fish in the first seven years of Chinook salmon spawning in Putah Creek. Since Chinook salmon generation times are between 2-4 years in the Central Valley (Waples 1990), it is possible that the seven-year period this study will be able to capture between two to three full generations since colonization.

Further, I predict (2) that hatchery-origin fish will predominate in spawning cohorts found in Putah Creek during early cohort years, because³ hatchery strays likely form the majority of the individuals available to form a founder population. I also predict the proportion of natal-origin fish will increase, but slowly, primarily due to low outmigration survival rates of juvenile Chinook in the Central Valley (Michel et al. 2015) but the proportion of fish of Putah Creek natal origin will increase as they successfully reproduce.

Lastly, I predict (3) that if natal-origin fish become more prevalent over time, demographics of the spawning cohort will shift towards higher proportions of older age-class fish since hatchery-origin fish tend to reproduce at younger ages.

2. Methods

2.1. Study Area

The 42 rkm of Putah Crrek downstream of Putah Diversion Dam comprise the reaches of the waterway that are accessible to anadromous fishes ('Lower Putah Creek'). The water present in this section of the creek is that not diverted into Putah South Canal at Putah Diversion Dam.

Lower Putah Creek flows past the cities of Winters, CA and Davis, CA. Flows into Lower Putah Creek are released from the second dam as stipulated by the Putah Creek Accord ('The Accord'). The Accord resulted from a lawsuit settled in 2000 requiring a natural flow regime (Yarnell et al. 2020), including minimum flows to benefit Chinook salmon and other native fish species.

Outmigrating juvenile Chinook salmon transit through the most downstream reach of Lower Putah Creek located in the Yolo Bypass floodplain area, a managed floodplain of the Sacramento River, and then join the Sacramento River complex via the Toe Drain.

2.2. Field Methods

Since 2016, the adult Chinook salmon population of Lower Putah Creek was monitored using weekly canoe-based carcass surveys. Surveys were conducted in an upstream to downstream direction and live salmon were counted. Carcasses were detected from visual observation and the location of each carcass was recorded using a handheld GPS. A uniquely numbered metal or plastic tag was zip-tied to the mandible of each carcass for individual identification and carcass resighting.

2.2.1. Carcass Sampling

When the condition of deteriorating carcasses allowed, fork length of the carcass was measured (mm) and the presence or absence of an adipose fin was documented. Hatcheries operating in the California Central Valley participate in a marking program in which a constant fraction of released juvenile fish are injected with a microscopic coded wire tag (CWT) in their nasal cavity coded with hatchery and release information; these fish also have their adipose fin removed to indicate the potential presence of a CWT (Nandor et al. 2010). In the event that a carcass was too deteriorated to evaluate adipose fin presence, it was assumed that the adipose fin was missing. For carcasses missing (or presumed missing) an adipose fin, the snout of the carcass was removed and frozen for Coded Wire Tag (CWT) recovery at the California Department of Fish and Game Coded Wire Tag Laboratory in Sacramento, CA (Nandor et al. 2010). CWTs extracted from carcasses were thus linked to a hatchery and year and location of release. For each carcass in suitable condition, a fin clip was removed with scissors, placed in Whatman filter paper, folded and air dried in labeled coin envelopes for genetic analysis. Similarly, sagittal otoliths were removed on site and air dried in Falcon tubes and eye lenses were removed on site, placed in film canisters, and frozen for stable isotope analysis. All sampling and collections were conducted in accordance with California Department of Fish & Wildlife scientific collecting permit S-183530003-18360-003.

2.2.2. Juvenile Sampling

Downstream migrant trapping was conducted in each spring following spawning adult carcass surveys to evaluate juvenile production (UC Davis IACUC Protocol #22677). A rotary screw trap (RST) was operated during every study year except 2020, during which a fyke net was operated instead to allow for social distancing of field staff during the Covid-19 pandemic.

The use of a fyke also removed need for accessing private properties during pandemic precautions. Juvenile mortalities in traps were collected in 2017, 2018, and 2021 and frozen. Juvenile mortalities were later sampled for otoliths, eye lenses, and fin tissue.

2.3.1. Adult Otolith Preparation

After air drying, sagittal otoliths collected from 2017 through 2021 were photographed whole at a magnification of 0.5x and weighed. The length (distance from the midpoint of the rostrum, through the primordium, to posterior edge) and width of each otolith to the nearest 0.001mm was measured from photographs using ImagePro Plus software. Otoliths were snapped posterior to the core region mounted sulcal side up on round glass slides in Crystal Bond thermoplastic resin in the sagittal plane, as preparations in this method both expose the core and preserve annual growth rings with high fidelity. Mounted otoliths were ground until the core region was exposed using an AccuStop specimen holder on 800 – 1200 grit wet/dry sandpaper and polished. The sanded side was adhered to a small glass slide using superglue, then the otolith was flipped and sanded using the same methods until the core region was exposed and polished. Otoliths collected in 2016 incorporated into this dataset from a previous study in this system (Willmes et al. 2021) were prepared identically to otoliths from 2017 – 2021 with the exception that 2016 otoliths were prepared using a transverse section.

2.3.2 Otolith Age Estimations

Adult Chinook salmon otoliths accrete material constantly throughout the life of the fish, and annual periods of growth are visible as an alternating series of opaque and translucent bands (Welch et al. 1993; Willmes et al. 2021). Annuli are represented by one translucent zone

followed by one opaque zone. Two readers independently counted annual growth rings for each otolith to estimate the annual age of each fish (Barnett-Johnson et al. 2007). When the age estimates generated by the two readers were in disagreement, concert reads were used (both readers assessed the otolith together). If the two readers could not reach a consensus or the bands were too obscure to read, the otolith was excluded from the final age dataset.

2.3.3. Otolith Strontium Isotope Analysis & Natal Origin Classification

Otoliths were mounted onto petrographic glass slides (six otoliths per slide) using double-sided tape. $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios for each otolith were analyzed at the University of California, Davis Interdisciplinary Center for Plasma Mass Spectrometry using established techniques (Barnett-Johnson et al. 2008). A Nd:YAG 213nm laser (New Wave Research UP213) coupled to a New Plasma HR multi-collector inductively-coupled plasma mass spectrometer (MC-ICP-MS) (Nu032) was used for Sr isotope analyses. A 40 μm laser beam transect was pulsed along the otolith from the dorsal edge, through the core, to the ventral edge at a speed of 10 $\mu\text{m}/\text{s}$. Isotope data were reduced using IsoFishR (Willmes et al. 2018) to yield Sr isotope ratio profiles along the transect line of the otolith. Laser run times were converted to transect lengths (in μm) using known laser run speed of 10 $\mu\text{m}/\text{s}$. Natal regions of Sr profiles were identified by eye and subsampled for incorporation into natal origin classification modeling.

Following laser ablation, each otolith was photographed at 10x magnification using Image-Pro Plus software and utilizing the 'live tiling' function. Laser transect orientations were reconciled with otolith axes using the Line function in Image-Pro Plus to trace laser transect lines and otolith axis lines, and marking lengths (in μm) to known landmarks (e.g., laser start, otolith start, ventral lobe bands, core, dorsal lobe bands, otolith end, laser end) between the two lines. A

classification and regression trees (CART) model was used to make the highest probability prediction for each fish's natal origin by matching the isotope signals of the natal region for each otolith's Sr profile with known $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios for different California rivers and fish hatcheries (Barnett-Johnson et al. 2008; Sturrock et al. 2019). The $^{87}\text{Sr}/^{86}\text{Sr}$ signal for the wild Feather River population is known to fully overlap with the wild Putah Creek $^{87}\text{Sr}/^{86}\text{Sr}$ signal (Fig. 2).

2.3.4. *Otolith Trace Element Analysis*

For all individuals classified by the CART model as Putah Creek-origin or of uncertain classification between Putah Creek origin and wild Feather River origin, otoliths were analyzed for variation in trace elements to inform natal origin classifications with greater certainty. Juvenile Chinook salmon otoliths recovered from incidental mortalities in rotary screw traps were used to assess known trace element concentrations for wild-caught Feather River (2022: n=10; 2019: n=5; 2015: n=5) and wild Putah Creek (2022: n=3; 2018: n=2) classifications. Juvenile and adult otoliths were analyzed for element concentrations using a 193nm laser coupled to an Agilent 7700x Quadrupole Inductively Coupled Plasma Mass Spectrometer at the Stable Isotope Laboratory, University of California, Davis. The laser was set with a repetition rate of 10 Hz and fluence of 1.44 J/cm^3 , each sample was preablated at a slit size of $100 \mu\text{m}$ and a run speed of $100 \mu\text{m/s}$, and ablation transect lines were set with a slit length of $40 \mu\text{m}$ and a run speed of $10 \mu\text{m/s}$. For juvenile otoliths, transect lines were drawn on the ventral lobe before the core to the dorsal edge and bent to intersect the core. For adult otoliths, transect lines $1000 \mu\text{m}$ long were drawn from the core through the dorsal lobe to capture the natal, freshwater residence region of the otolith. Element species measured were ^{24}Mg , ^{43}Ca , ^{44}Ca , ^{55}Mn , ^{66}Zn , ^{88}Sr , and

^{137}Ba . Analysis cycle time was approximately 1.0s, allowing each element to be sampled for every second, with varying dwell times depending upon element abundance (see Table 1). Before and after each set of samples was ablated, three sets of four reference materials were ablated along 300 μm transects in the following order: NIST 610, NIST 612, SrNano, Macs3. Laser run times were converted to transect lengths (in μm) using known laser run speed of 10 $\mu\text{m/s}$.

Data were reduced using Iolite v4 software (Paton et al. 2011). Elements were then expressed as ratios against ^{43}Ca and grouped according to their origin (e.g., Putah Creek juvenile; Feather River juvenile; unknown adult; Fig. 3). Ratios of Ba/Ca and Sr/Ca were most distinct between known Feather River and known Putah Creek juvenile samples and were utilized as tracers for subsequent natal origin classification analysis. Adult otoliths were classified as either Putah Creek or Feather River origin using a linear discriminant analysis, with elemental concentrations of Ba/Ca and Sr/Ca from juvenile otoliths of known natal origin used as the training dataset.

All analyses were conducted in R Studio version 4.2.0 (R Core Development Team 2022).

3. Results

A total of 326 adult fish from five spawning cohorts of Chinook salmon were analyzed for natal origins using otolith $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios (2016: n=104; 2017: n=49; 2018: n=47; 2020: n=51; 2021: n=75; Table 2). Otoliths sampled from five spawning cohorts of Chinook salmon recovered in Putah Creek were identified to have natal origins from sixteen sources in California's Central Valley, including eleven rivers and five hatcheries (Fig. 4). The CART

model confidently assigned a total of eight Chinook salmon otoliths as potential Putah Creek- or Feather River wild-origin fish (2016: n=1; 2017: n=1; 2020: n=1; 2021: n=10) and one fish between Putah Creek- and Stanislaus River wild-origin (2021: n=1). These 14 fish were subsequently analyzed for trace elements along with 25 juvenile fish of known Feather River or Putah Creek origin. The aim of this analysis was that the unknown fish may be assigned more confidently as either Feather River- or Putah Creek-origin if the signatures of their elemental tracers more closely reflected those of known juveniles originating from either system. Linear discriminant analysis of Ba/Ca and Sr/Ca ratios assigned 13 of the 14 unknown fish as Putah Creek origin (Fig. 5), with these fish clustering closely with known-Putah Creek origin juvenile fish, and one fish was grouped in uncertain classification as a result of low confidence in assignment. Hatchery-origin fish were the most abundant group in every spawning cohort studied, though the proportion of wild-origin fish was greater in the four later cohorts (2016=0.028; 2021=0.217 ; Fig. 4). A Pearson's chi-squared test indicated there were large differences in number of hatchery-origin, wild-origin, and Putah Creek-origin fish among study years ($\chi^2 = 49.234$, $df = 12$, $p < 0.0001$); however, the conclusions are tentative because of the high frequency of zero-values for the number of Putah Creek-origin fish, which violates assumptions of the chi-squared test. Similarly, the low number of wild-origin fish in certain cohorts also resulted in low expected ($n < 5$) observations, which is also a violation of the chi-squared test (Table 3). Pairwise post-hoc comparison tests found large differences in the frequency of different natal classifications between 2016 and 2017 ($p=0.045$), 2016 and 2020 ($p=0.016$), and 2016 and 2021 ($p=0.00086$), although violations of the chi-squared test as noted above resulted in two post-hoc comparisons presenting null values: 2016 and 2018, and 2018 and

2020, owing to zero-values for observed Putah Creek-origin fish in 2016 and 2018, and of unknown fish for 2018 and 2020.

Of the 326 otoliths with age estimations, readers were able to form a consensus on 317 otoliths (97%), with the remaining otoliths excluded from age structure analyses. Demographics of the spawning population varied in the five cohorts studied. Age-two and age-three fish were present in near-equal proportions in the first cohort (Fig. 6). In every subsequent cohort, age-three fish predominated and proportions of age-two and age-four fish varied among cohorts. A Pearson's chi-squared test supported the observed differences in the frequency of age classes between study years ($\chi^2 = 37.58$, $df = 8$, $p < 0.0001$). However, the conclusions drawn by this test are limited as the low number of age-four fish observed resulted in expected frequencies of age-four fish of $n < 5$ for three of the five study years, which is a violation of the assumptions of the chi-squared test (Table 3). Post-hoc pairwise comparisons found that there were significant differences in the observed frequencies of the age classes between 2016 and 2018 ($p=0.010$), 2016 and 2020 ($p=0.00033$), 2016 and 2021 ($p=0.042$), 2017 and 2020 ($p=0.042$), and 2020 and 2021 ($p=0.0048$). Most hatchery spawner populations are comprised of primarily two-year-old fish, which have poorer reproductive success than older age-class fish (Shedd et al. 2022). Fork lengths (in mm) were larger for fish of older age classes (Fig. 7), though size discrimination was weak between the older age classes (age 3 and age 4 fish). Fork lengths of age-two fish were skewed slightly positive, while fork lengths of age-three and age-four fish were not skewed (Table 4). Fork lengths had a leptokurtic distribution for age-two fish, mesokurtic for age-three fish, and platykurtic for age-four fish (Table 4).

4. Discussion

We studied the origins and population structure of a recolonizing Chinook salmon population in a restored stream in California's Central Valley. Our results show that while hatchery-origin fish are the most abundant natal group across five spawning cohorts, there is strong empirical evidence of successful salmon reproduction and full life cycle completion in Putah Creek. Adult Putah Creek-origin salmon appear in later spawning cohorts, with the proportion of Putah Creek-origin and wild-origin fish increasing in the four later spawning cohorts. Age- and size-classes of the spawning Chinook salmon population at Putah Creek varied substantially among years.

4.1. Natal origins of Putah Creek spawning Chinook salmon cohorts

The CART model used in this study (which assigned natal origin classifications to spawning adult Chinook salmon using natal region $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios) identified several Putah Creek-origin fish in later spawning cohorts. Previously uncertain natal classifications resulting from overlap in strontium isotope signals were resolved using trace elements analyses of Ba/Ca and Sr/Ca, resulting in greater confidence in natal origin classifications for spawning Chinook salmon of putative Putah Creek origin. This finding represents the first documentation of Putah Creek-spawned Chinook salmon surviving and successfully returning to Putah Creek to spawn using two strong and separate lines of evidence. Most of the fish assigned as Putah Creek-origin were observed in spawning cohorts from later study years, and this delayed observation of Putah Creek-origin fish is consistent with expectations for increasing numbers of natal spawners over time. Chinook salmon have only consistently been observed in Putah Creek since 2014; this study examines cohorts of spawning salmon present between two and seven years following the first substantial observations of Chinook salmon in Putah Creek. Since salmon in the Central

Valley are between 2-4 years of age at spawning, this study only captures up to three generations of salmon spawning in Putah Creek and likely represents early stages of the salmon recolonization process (Pess et al. 2011; Brady Allen et al. 2016; Liermann et al. 2017). Consequently, this study's finding of natal-origin salmon in spawning cohorts within the first ten years of recolonization is a promising sign that Lower Putah Creek may be viable Chinook salmon natal habitat overall and may suggest the potential for Putah Creek to develop a locally-adapted, self-sustaining Chinook salmon run. However, this potential assumes that the system continues to be managed for suitable flows and migration access and timing.

In all but one survey year, three-year old fish were the most abundant age class observed in Putah Creek Chinook spawning cohorts, and older fish were generally of larger size than younger fish (Fig. 7). The earliest cohort had near-equal numbers of age-two and age-three fish. Older, larger salmon may have greater fitness and reproductive success than younger, smaller individuals (Berejikian et al. 2010; Williamson et al. 2010; Anderson et al. 2012; Christie et al. 2014), and hatchery-origin individuals tend to spawn at younger ages (Hankin et al. 2009; Macaulay et al. 2023). The higher proportion of older spawning individuals in the Putah Creek salmon population could promote higher rates of reproductive success compared to other Central Valley salmon populations, aiding juvenile production and Chinook salmon population establishment in Putah Creek.

4.2. Potential for an established natal Chinook salmon population at Putah Creek

In each spawning cohort, hatchery-origin Chinook salmon were most abundant, and wild and hatchery sources contributed variably to several years of Putah Creek spawning cohorts. Multiple source populations may result in a higher degree of genetic variation present in the

Putah Creek founding population. Such genetic diversity could in turn provide more genes and traits upon which selection may act to determine which source populations will be most successful in contributing to the Chinook salmon recolonization process at Putah Creek (Neutzel et al. 2023).

One mechanism influencing the high number of hatchery-origin Chinook salmon observed spawning in Putah Creek is the management of juvenile Chinook salmon during drought years in California. During droughts, hatchery-origin juveniles are trucked or barged to estuaries and released rather than released directly at the hatchery (Sturrock et al. 2019). This management method, while effective at producing higher outmigration survival during droughts, results in hatchery-origin Chinook salmon lacking natal imprinting, and consequently straying at high rates during their spawning migrations (Bond et al. 2016; Dederick and Baskett 2018; Sturrock et al. 2019). Since the trucking of juvenile hatchery-origin Chinook is still widely practiced in the Central Valley, despite concern about the effectiveness of this strategy (California Hatchery Scientific Review Group 2012), it is highly likely that hatchery-origin fish will continue to present in high numbers in future spawning cohorts at Putah Creek. Further, hatchery inputs are not shown to result in poorer reproductive success after the first generation (Neutzel et al. 2023). However, high inputs of hatchery-origin fish in later recolonization stages may slow the development of a natal Putah Creek Chinook salmon population or homogenize the emerging Putah Creek population with other Central Valley populations.

Without pressure from straying hatchery fish, natal salmon could become better adapted to conditions and migratory timings of Putah Creek and could have greater spawning success than hatchery-origin fish (Ford 2002; Araki et al. 2007; Anderson et al. 2012). Similar phenomena have been observed in other salmonid populations (McClure et al. 2008; Berntson et

al. 2011; Nuetzel et al. 2023), in which natal individuals typically exhibit greater reproductive success than straying hatchery individuals. Natal Chinook salmon at Putah Creek may be especially likely to develop a degree of local adaptation as a result of selective pressures from local dam operations. For example, the privately operated agricultural impoundment dam (Los Rios Check Dam) located near the terminus of Putah Creek in the Yolo Bypass (Fig. 1) is currently operated such that Putah Creek is inaccessible to spawning Chinook salmon until late October or early November each year, late in the run timing window for fall-run Chinook. Salmon are often present at the dam as early as September, but without passage, many ultimately migrate farther up the Yolo Bypass to the Wallace Weir. Ultimately, current management of the dam selects for a reduced number of Putah Creek spawners that have a delayed run timing. The dam's flashboards are also reinstalled every spring when need arises for agricultural water pumping, usually in May. Reinstallation of the dam then restricts the outmigration timing and success of juvenile salmon produced in Putah Creek (Miner 2022). As a result, the spring reinstallation timing of the dam may select for juveniles that develop and outmigrate earlier, as later-arriving juveniles become trapped behind the dam and are unable to continue their migrations towards the estuary (Miner 2022). Together, the dam's selections for late-migrating adults and early-migrating juveniles put high selective pressure on both juvenile and adult life stages of Chinook salmon utilizing Putah Creek. If natal-origin salmon are able to leverage the dam's selective pressures towards specific migration timing traits, they could develop a fitness advantage over straying fish. Such differential reproductive success could help promote the faster emergence of a Putah Creek natal population despite high annual inputs of hatchery-origin strays. Further, if management recommendations to reduce or eliminate the trucking of hatchery-origin juveniles are implemented (California Hatchery Scientific Review Group 2012), straying

hatchery-origin spawners may begin to decline in abundance in Putah Creek and other Central Valley systems.

While the presence of several Putah Creek natal-origin Chinook salmon documented in the 2021 spawning cohort of this study was promising, these individuals were ultimately unable to spawn. All salmon from the 2021 spawning cohort documented in this study died near the junction of Lower Putah Creek and the Sacramento Toe Drain, many kilometers downstream of the nearest viable spawning habitat on Putah Creek. An atmospheric river event coincided with the timing of fall attraction flows on Lower Putah Creek, and high inputs of debris, organic matter, and ammonia-saturated tailwaters during a storm runoff. Warmer than average waters and rapid decomposition of organic matter ultimately resulted in a prolonged hypoxic event. The event affected the most downstream reach of Putah Creek as well as several kilometers of downstream aquatic habitats in the Yolo Bypass and Toe Drain. It is a significant, but not insurmountable, setback that the spawning cohort with the greatest proportion of Putah Creek-origin fish was unable to contribute to the next generation of Putah Creek juvenile production. It is likely that future spawning cohorts that consist of offspring produced during this season will have lower numbers of Putah Creek-origin fish, since the poor juvenile production on Putah Creek during this season fundamentally restricts the number of Putah Creek origin fish available to join future spawning cohorts. However, variability in ages at spawning for Central Valley Chinook salmon (Table 4; Fig. 7) demonstrate a mechanism of resilience. Age diversity within the run could help distribute the impact of this poor production year and stabilize the population during its emerging years.

4.3 Management recommendations for Chinook salmon in Putah Creek

Evidence for successful production of natal Chinook salmon at Putah Creek has important management implications. Putah Creek is a viable Chinook salmon spawning stream accessible from the Yolo Bypass and the sole accessible tributary on the west side of the Sacramento River. Therefore, Putah Creek may be an important alternate spawning stream for both natal and straying spawning salmon that migrate into these waterways. Prior to evidence of a Putah Creek Chinook salmon population, all salmon migrating through the Yolo Bypass Wildlife Area and the Toe Drain were considered hatchery-origin strays. Indeed, salmon that migrate past Putah Creek in the Yolo Bypass either spawn (likely unsuccessfully) and die in the Yolo Bypass or are rescued by CDFW biologists at the Wallace Weir and released into the Sacramento River. The most recent severe drought year resulted in an extensive loss of connectivity between the Toe Drain and the Wallace Weir during fall-run Chinook salmon migration periods, making Putah Creek the sole available stream for spawning Chinook salmon migrating through the Toe Drain. Current policy considers all Chinook salmon that migrate into the Toe Drain as destined for the Wallace Weir. Incorporating Putah Creek into Chinook salmon management plans for the Toe Drain and Yolo Bypass will provide an alternative route for Chinook salmon using these waterways, perhaps especially when the Wallace Weir site is hydrologically disconnected during drought years.

To prevent fish kills like the one experienced in 2021, it will be essential to monitor and adaptively manage passage for adult salmon entering into Putah Creek. The Los Rios Check Dam, which blocks passage at times, is operated for both agriculture (primarily rice farming) and to maintain water levels in the Yolo Basin Wildlife Area for waterfowl habitat in the fall. When the dam is closed, adult salmon congregate below the dam, waiting for passage, making them vulnerable to poor water quality conditions. Dynamic, integrative, and potentially real-time

management of pulse flows timing, passage barriers, and stakeholder engagement and activation would be helpful in streamlining communications, aligning management priorities, and initiating timely actions during future periods of poor water conditions. Ultimately, these actions will promote greater resilience in the Chinook salmon population at Putah Creek, which is becoming an explicit management aim for California's Central Valley Chinook salmon populations overall (Herbold et al. 2018).

4.4 Future Directions

Future studies in this system should consider the population genetics of both adult and juvenile life stages of Chinook salmon present in Putah Creek to evaluate measures of genetic diversity in the hatchery- versus wild-origin members of Putah Creek spawning cohorts using measures of heterozygosity, genes under selection, and other population genetics approaches. These studies would assess the diversity of hatchery-origin, wild-origin, and Putah Creek-origin founders and if there are signatures of selection present in the nascent Putah Creek population. Population genetic approaches may also be used to evaluate whether natal Putah Creek Chinook salmon become locally-adapted, with consequences for fitness overall (McClure et al. 2008; Neutzel et al. 2023).

Utilizing genetics would allow parentage-based tagging (PBT; Steele et al. 2019; Beacham et al. 2021). Kinship analyses may help identify lineages of Putah Creek natal-origin fish and confirm natal assignments generated by otolith microchemistry. Using PBT to link spawners and juvenile recruits could be used to generate assessments of reproductive success for hatchery-origin, wild-origin, and Putah Creek-origin fish. These data could also be used to understand which adults are contributing disproportionately to juvenile production, and the

extent to which the timing of spawning is linked to successful recruitment. If a Putah Creek natal Chinook salmon run begins to emerge over time.

Additional questions in the Putah Creek system that may be evaluated using otoliths, such as evaluating daily growth rates for juvenile Chinook salmon produced in Putah Creek to compare with other salmon populations in the Central Valley (Sommer et al. 2001; Jeffres et al. 2008). Diet and food web studies of juvenile Chinook salmon rearing in Putah Creek would provide insight regarding the availability of forage and prey items for juvenile Chinook salmon and identify any habitat-related shifts in diet during development and outmigration (Bell-Tilcock et al. 2021).

4.5 Conclusions

We provide evidence of successful natal production of Chinook salmon at Putah Creek by recent spawning cohorts following community-led restoration initiatives and changes in streamflow management. Individuals of Central Valley hatchery origin remain the most abundant in each studied spawning cohort, though the proportion of wild-origin and Putah Creek-origin spawners is increasing through subsequent cohorts. The dynamic, collaborative management of the Putah Creek system in the future will play an important role in determining the fate and resilience of the Chinook salmon population at Putah Creek.

Ensuring earlier migratory access to Putah Creek, providing alternate migration pathways into Putah Creek, and developing a real-time response system for future emergency situations will likely determine the timeline for observing increased establishment of the Putah Creek natal Chinook salmon population. The role of hatchery straying in recolonizing and interbreeding with wild salmon populations will continue to be a controversial topic in the fisheries community as

climate change, dam removal initiatives, and habitat restoration projects continue to operate and evolve. Preliminary evidence from this study suggests that it is possible to have a variety of source populations colonizing restored habitats and resulting in the initial establishment of recovered natal populations.

Data from the reestablishment of Chinook salmon at Putah Creek provide context for other Pacific salmon runs, many of which are in decline or already extirpated (Nehlsen et al. 1991; Irvine and Fukuwaka 2011). While many sweeping and expensive management actions that have been taken in recent decades to abate or slow declines in salmon populations, most have been unsuccessful (Knudsen and McDonald 2020). As other river systems with Pacific salmonid populations consider restoration and dam management or removal efforts, Lower Putah Creek provides a case study for what other systems may expect as they anticipate their own reintroductions and reestablishments. It is also important to recognize that salmon recovery began to occur only following the restoration of a natural flow regime. Thus, habitat restoration represents a major key to fisheries recovery (Geist and Hawkins 2016; Marttila et al. 2019). This study also highlights that the recolonization process is likely slow, and prone to possible setbacks. Rehabilitation efforts appear to result in viable habitat that may provide new resilience for Pacific salmonid populations against a changing climate.

5. Acknowledgements

Firstly, I would like to extend my deep thanks to Solano County Water Agency, especially the current and former Putah Creek Streamkeepers, Dr. Max Stevenson and Rich Marovich, as well as Duc Jones, Alex Rabidoux, Roland Sanford, and the rest of the staff at

SCWA for their support of this project and of salmon research on Putah Creek. I also thank local stakeholders and landowners who permitted access to their properties for this research, especially J. Pickerell, D. Kilkenny, and J. & E. Hasbrook, as well as the many community members and university affiliates who care so deeply about the Putah Creek ecosystem. I would also like to thank E.D. Chapman, G. Singer, E.E. Jacinto, M.C. Miner, J. Colby, A. Boyd, S.G. Gonzales, and the many undergraduate and graduate student volunteers and junior specialists who helped conduct field surveys and operate the rotary screw trap to obtain the samples used in this study.

I thank R. Johnson, G. Whitman, and CDFW staff for access to juvenile Chinook salmon otoliths collected from RSTs they operate on the Feather River, and for allowing inclusion of these otoliths in this study for establishing baselines in the trace element work. I thank Lea Koerber and the staff of the CDFW CWT laboratory for their assistance in recovering CWTs and hatchery origin data for fish included in this study. This research was also supported by grants received from the Erica Kelly Memorial Award, the UC Davis Jastro-Shields Fund, and Yolo Basin Foundation, and I thank each of them for their financial support of this work. I extend my gratitude to M. Willmes, G. Whitman, K.R. Evans, F. Torres, M. Emard, F. Cordoleani, C.A. Jeffres, and R. Johnson for so readily sharing their knowledge of otoliths and salmon with me, and for providing valuable expertise in the technical methods and resources required to carry out this study's microchemistry and microstructure work. I thank J.J.G. Glessner, L. Lewis, M. Willmes, G. Whitman, K.R. Evans, S. Araya, and R. Johnson for technical support in operating the mass spectrometers and analyzing spectrometer data. My deepest thanks to M. Willmes, G. Whitman, C.A. Jeffres, R. Johnson, P.B. Moyle, and J.R. Durand for thoughtful discussions and feedback on this work.

6. Works Cited

- Anderson, J.H., P.L. Faulds, W.I. Atlas, and T.P. Quinn. 2012. Reproductive success of a captive bred and naturally spawned Chinook salmon colonizing newly accessible habitat. *Evolutionary Applications* 6(2): 165-179. <https://doi.org/10.1111/j.1752-4571.2012.00271.x>
- Anderson, J.H., P.L. Faulds, K.D. Burton, M.E. Koelher, W.I. Atlas, and T.P. Quinn. 2014a. Dispersal and productivity of Chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon colonizing newly available habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 72(3). <https://doi.org/10.1139/cjfas-2014-0180>
- Anderson, J.H., G.R. Pess, R.W. Carmichael, M.J. Ford, T.D. Cooney, C.M. Baldwin, and M.M. McClure. 2014b. Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management* 34(1): 72-93. <https://doi.org/10.1080/02755947.2013.847875>
- Araki, H., B. Cooper, and M.S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318(5847): 100-103. <https://doi.org/10.1126/science.1145621>
- Bain, M.B., J.T. Finn, and H.E. Booke. 1988. Streamflow regulation and fish community structure. *Ecology* 69(2): 382-392. <https://doi.org/10.2307/1940436>
- Bardot, S., L. Avvadie, A. Auclerc, C. Barthelemy, E. Berille, P. Billet, P. Clergeau, J.N. Consales, M. Deschamp-Cottin, A. Davis, C. Devigne, V. Dham, Y. Dusza, A. Gaillard, E. Gonzalez, M. Hedont, D. Labarraque, A.M. Le Bastard, J.L. Morel, Y. Petit-Berghem, E. Remy, E. Rochelle-Newall, and M. Veyrieres. 2019. Urban ecology, stakeholders and the future of ecology. *Science of the Total Environment* 667: 475-484. <https://doi.org/10.1016/j.scitotenv.2019.02.410>
- Barnett-Johnson, R., C.B. Grimes, C.F. Royer, and C.J. Donohoe. 2007. Identifying the contribution of wild and hatchery Chinook salmon (*Oncorhynchus tshawytscha*) to the ocean fishery using otolith microstructure as natural tags. *Canadian Journal of Fisheries and Aquatic Sciences* 64(12). <https://doi.org/10.1139/f07-129>
- Barnett-Johnson, R., T.E. Pearson, F.C. Ramos, C.B. Grimes, and R.B. MacFarlane. 2008. Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. *Limnology and Oceanography* 53(4): 1633-1642. <https://doi.org/10.4319/lo.2008.53.4.1633>
- Beacham, T.D., C.G. Wallace, K. Jonsen, B. McIntosh, J.R. Candy, K. Horst, C. Lynch, D. Willis, W. Luedke, L. Kearey, and E.B. Rondeau. *Evolutionary Applications* 14(5): 1365-1389. <https://doi.org/10.1111/eva.13203>

- Bell-Tilcock, M., C.A. Jeffres, A.L. Rypel, M. Willmes, R.A. Armstrong, P. Holden, P.B. Moyle, N.A. Fangue, J.V.E. Katz, T.R. Sommer, J.L. Conrad, and R.C. Johnson. *PLOS ONE* **16**(10): e0257444. <https://doi.org/10.1371/journal.pone.0257444>
- Bellmore, J.R., J.D. Duda, L.S. Craig, S.L. Greene, C.E. Torgersen, M.J. Collins, and K. Vittum. 2016. Status and trends of dam removal research in the United States. *WIREs Water* **4**(2): e1164. <https://doi.org/10.1002/wat2.1164>
- Berejikian, B.A., D.M. Van Doornik, R.C. Endicott, T.L. Hoffnagle, E.P. Tezak, M.E. Moore, and J. Atkins. 2010. Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Fisheries and Aquatic Sciences* **67**(12). <https://doi.org/10.1139/F10-112>
- Berntson, E.A., R.W. Carmichael, M.W. Flesher, E.J. Ward, and P. Moran. 2011. Diminished reproductive success of steelhead from a hatchery supplementation program (Little Sheep Creek, Imnaha Basin, Oregon). *Transactions of the American Fisheries Society* **140**(3): 685-698. <https://doi.org/10.1080/00028487.2011.584489>
- Blouin, M.S., M.C. Wrey, S.R. Bollman, J.C. Skaar, R.G. Twibell, and C. Fuentes. 2021. Offspring of first-generation hatchery steelhead trout (*Oncorhynchus mykiss*) grow faster in the hatchery than offspring of wild fish, but survive worse in the wild: Possible mechanisms for inadvertent domestication and fitness in hatchery salmon. *PLOS ONE* **16**(12): e0257407. <https://doi.org/10.1371/journal.pone.0257407>
- Bond, M.H., P.A.H. Westley, A.H. Dittman, D. Holecek, T. Marsh, and T.P. Quinn. 2016. Combined effects of barge transportation, river environment, and rearing location on straying and migration of adult Snake River fall-run Chinook salmon. *Transactions of the American Fisheries Society* **146**(1): 60-73. <https://doi.org/10.1080/00028487.2016.1235614>
- Brady Allen, M., R.O. Engle, J.S. Zendt, F.C. Schrier, J.T. Wilson, and P.J. Connolly. 2016. Salmon and steelhead in the White Salmon River after the removal of Condit Dam – Planning efforts and recolonization results. *Fisheries* **41**(4): 190-203. <https://doi.org/10.1080/03632415.2016.1150839>
- Brenkman, S.J., R.J. Peters, R.A. Tabor, J.J. Geffre, K.T. Sutton. 2019. Rapid recolonization and life history responses of bull trout following dam removal on Washington's Elwha River. *North American Journal of Fisheries Management* **39**(3): 560-573. <https://doi.org/10.1002/nafm.10291>
- Brewitt, P.K. 2016. Do the fish return? A qualitative assessment of anadromous Pacific salmonids' upstream movement after dam removal. *Northwest Science* **90**(4): 433-449. <https://doi.org/10.3955/046.090.0405>

- California Hatchery Scientific Review Group (California HSRG). 2012. *California Hatchery Review Report*. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries Commission: June 2012. 100 pgs. <https://swfsc-publications.fisheries.noaa.gov/publications/CR/2012/2012California.pdf>
- Carlisle, D.M., D.M. Wolock, and M.R. Meador. 2010. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment*. **9**(5): 264-270. <https://doi.org/10.1890/100053>
- Chesson, L.A., B.J. Tipple, G.N. Mackey, S.A. Hynek, D.P. Fernandez, and J.R. Ehleringer. 2012. Strontium isotopes in tap water from the coterminous USA. *Ecosphere* **3**(7): 1-17. <https://doi.org/10.1890/ES12-00122.1>
- Christie, M.R., M.J. Ford, and M.S. Blouin. 2014. On the reproductive success of early-generation hatchery fish in the wild. *Evolutionary Applications* **7**(8): 883-896. <https://doi.org/10.1111/eva.12183>
- Dedrick, A.G., and M.L. Baskett. 2018. Integrating genetic and demographic effects of connectivity on population stability: The case of hatchery trucking in salmon. *The American Naturalist* **192**(2). <https://doi.org/10.1086/697581>
- Deredec, A., and F. Courchamp. 2007. Importance of the Allee effect for reintroductions. *Ecoscience* **14**(4): 440-451. [https://doi.org/10.2980/1195-6860\(2007\)14\[440:IOTAEF\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2007)14[440:IOTAEF]2.0.CO;2)
- Evans, M.L., M.A. Johnson, D. Jacobson, J. Wang, M. Hogansen, and K.G. O'Malley. 2019. Evaluating a multi-generational reintroduction program for threatened salmon using genetic parentage analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **73**(5): 844-852. <https://doi.org/10.1139/cjfas-2015-0317>
- Foley, M.M., J.R. Bellmore, J.E. O'Connor, J.J. Duda, A.E. East, G.E. Grant, C.W. Anderson, J.A. Bountry, M.J. Collins, P.J. Connolly, L.S. Craig, J.E. Evans, S.L. Greene, F.J. Magilligan, C.S. Magirl, J.J. Major, G.R. Pess, T.J. Randle, P.B. Shafroth, C.E. Torgersen, D. Tullos, and A.C. Wilcox. 2017. Dam removal: Listening in. *Water Resources Research* **53**(7): 5229-5246. <https://doi.org/10.1002/2017WR020457>
- Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* **16**(3): 815-825. <https://doi.org/10.1046/j.1523-1739.2002.00257.x>
- Geist, J., and S.J. Hawkins. 2016. Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. *Aquatic Conservation* **26**(5): 942-962. <https://doi.org/10.1002/aqc.2702>

- Hankin, D.G., J. Fitzgibbons, and Y. Chen. 2009. Unnatural random mating policies select for younger age at maturity in hatchery Chinook salmon (*Oncorhynchus tshawytscha*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **66**(9). <https://doi.org/10.1139/F09-085>
- Herbold, B., S.M. Carlson, R. Henery, R.C. Johnson, N. Mantua, M.M. McClure, P.B. Moyle, and T. Sommer. 2018. Managing for salmon resilience in California's variable and changing climate. *San Francisco Estuary and Watershed Science* **16**(2). <https://doi.org/10.15447/sfews.2018v16iss2art3>
- Hobson, K.A., R. Barnett-Johnson, and T. Cerling. 2009. Using isoscapes to track animal migration. In: West, J., G. Bowen, T. Dawson, and K. Tu, (eds) *Isoscapes* pp.273-298. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-3354-3_13
- Huber, E.R., and S.M. Carlson. 2015. Temporal trends in hatchery releases of fall-run Chinook salmon in California's Central Valley. *San Francisco Estuary and Watershed Science* **13**(2). <https://doi.org/10.15447/sfews.2015v13iss2art3>
- Irvine, J.R., and M. Fukuwaka. 2011. Pacific salmon abundance trends and climate change. *ICES Journal of Marine Science* **68**(6): 1122-1130. <https://doi.org/10.1093/icesjms/fsq199>
- Jacinto, E., N.A. Fangué, D.E. Cocherell, J.D. Kiernan, P.B. Moyle, and A.L. Rypel. 2023. Increasing stability of a native freshwater fish assemblage following flow rehabilitation. *Ecological Applications* e2868. <https://doi.org/10.1002/eap.2868>
- Jeffres, C.A., J.J. Opperman, and P.B. Moyle. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes* **83**: 449-458. <https://doi.org/10.1007/s10641-008-9367-1>
- Johnson, R.C., P.K. Weber, J.D. Wikert, M.L. Workman, R.B. MacFarlane, M.J. Grove, and A.K. Schmitt. 2012. Managed metapopulations: Do salmon hatchery 'sources' lead to in-river 'sinks' in conservation? *PLOS ONE* **7**(2):e28880 <https://doi.org/10.1371/journal.pone.0028880>
- Katz, J., P.B. Moyle, R.M. Quinoñes, J. Israel, and S. Purdy. 2013. Impending extinction of salmon, steelhead, and trout (*Salmonidae*) in California. *Environmental Biology of Fishes* **96**: 1169-1186. <https://doi.org/10.1007/s10641-012-9974-8>
- Kiernan, J.D., P.B. Moyle, and P.K. Crain. 2012. Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications* **22**(5): 1472-1482. <https://www.jstor.org/stable/41722867>
- Knudsen, E.E., and D. McDonald (Eds). 2020. *Sustainable fisheries management: Pacific salmon*. CRC Press.

- Liermann, M., G. Pess, M. McHenry, J. McMillan, M. Elofson, T. Bennett, and R. Moses. 2017. Relocation and recolonization of Coho salmon in two tributaries to the Elwha River: Implications for management and monitoring. *Transactions of the American Fisheries Society* **146**(5): 955-966. <https://doi.org/10.1080/00028487.2017.1317664>
- Lynch, A.J., B.J.E. Myers, C. Chu, L.A. Eby, J.A. Falke, R.P. Kovach, T.J. Krabbenhoft, T.J. Kwak, J. Lyons, C.P. Paukert, and J.E. Whitney. 2016. Climate change effects on North American inland fish populations and assemblages. *Fisheries* **41**(7): 346-361. <https://doi.org/10.1080/03632415.2016.1186016>
- Macaulay, R., E. Barrett, G. Penunuri, and E.E. Goldwyn. 2023. A statistical analysis of the change in age distribution of spawning hatchery salmon. *Spora* **9**: 12-19. <https://doi.org/10.30707/SPORA9.1.1675492827.538909>
- Marttila, M., P. Louhi, A. Huusko, T. Vehanen, A. Maki-Petays, J. Erkinaro, J.T. Syrjanen, and T. Muotka. *Reviews in Fish Biology and Fisheries* **29**: 513-527. <https://doi.org/10.1007/s11160-019-09557-z>
- McClure, M.M., F.M. Utter, C. Baldwin, R.W. Carmichael, P.F. Hassemer, P.J. Howell, P. Spruell, T.D. Cooney, H.A. Schaller, and C.E. Petrosky. 2008. Evolutionary effects of alternative artificial propagation programs: implications for viability of endangered anadromous salmonids. *Evolutionary Applications* **1**(2): 356-375. <https://doi.org/10.1111/j.1752-4571.2008.00034.x>
- Michel, C.J., et al. 2015. Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. *Canadian Journal of Fisheries and Aquatic Sciences* **72**(11). <https://doi.org/10.1139/cjfas-2014-0528>
- Miner, M.C. 2022. *Migratory phenology and spatial distributions of a recovering Chinook salmon run in a flow regulated creek, considerations for management* [unpublished master's thesis]. University of California, Davis. <https://escholarship.org/uc/item/93z321vk#main>
- Moyle, P.B., J.V.E. Katz, and R.M. Quinones. 2011. Rapid decline of California's native inland fishes: A status assessment. *Biological Conservation* **144**(10): 2414-2423. <https://doi.org/10.1016/j.biocon.2011.06.002>
- Nandor, G.F., J.R. Longwill, and D.L. Webb. 2010. Overview of the coded wire tag program in the greater Pacific region of North America. *PNAMP Special Publication: Tagging, Telemetry, and Marking Measures for Fish Populations – A compendium of new and recent science for use in informing technique and decision modalities*: 5-16.
- Nehlsen, W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* **16**(2): 4-21. [https://doi.org/10.1577/1548-8446\(1991\)016%3C0004:PSATCS%3E2.0.CO;2](https://doi.org/10.1577/1548-8446(1991)016%3C0004:PSATCS%3E2.0.CO;2)

- Neutzel, H.M., P.F. Galbreath, B.A. Staton, C.A. Crump, L.M. Naylor, and G.E. Shippentower. 2023. Improved productivity of naturalized spring Chinook salmon following reintroduction from a hatchery stock in Lookingglass Creek, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* **80**: 375-392. <https://doi.org/10.1139/cjfas-2022-0114>
- Paton, C., Hellstrom, J., Paul, B., Woodhead, J., Hergt, J., 2011. Iolite: Freeware for the visualisation and processing of mass spectrometric data. *Journal of Analytical Atomic Spectrometry*. **26**: 2508. <https://doi.org/10.1039/C1JA10172B>
- Pess, G.R., P.M. Kiffney, M.C. Liermann, T.R. Bennett, J.H. Anderson, and T.P. Quinn. 2011. The influences of body size, habitat quality, and competition on the movement and survival of juvenile Coho salmon during the early stages of stream recolonization. *Transactions of the American Fisheries Society* **140**(4): 883-897. <https://doi.org/10.1080/00028487.2011.587752>
- Poff, N.L. J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow regime. *BioScience* **47**(11): 769-784. <https://doi.org/10.2307/1313099>
- Price, M.H.H., J.W. Moore, B.M. Connors, K.L. Wilson, and J.D. Reynolds. 2021. Portfolio simplification arising from a century of change in salmon population diversity and artificial production. *Journal of Applied Ecology* **58**(7): 1477-1486. <https://doi.org/10.1111/1365-2664.13835>
- Pringle, C.M., M.C. Freeman, and B.J. Freeman. 2000. Regional Effects of Hydrologic Alterations on Riverine Macrobiota in the New World: Tropical-Temperate Comparisons: The massive scope of large dams and other hydrologic modifications in the temperate New World has resulted in distinct regional trends of biotic impoverishment. While neotropical rivers have fewer dams and limited data upon which to make regional generalizations, they are ecologically vulnerable to increasing hydropower development and biotic patterns are emerging. *BioScience* **50**(9): 807-823. [https://doi.org/10.1641/0006-3568\(2000\)050\[0807:REOHAO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0807:REOHAO]2.0.CO;2)
- Quiñones, R.M., Grantham, T.E., Harvey, B.N. et al. 2015. Dam removal and anadromous salmonid (*Oncorhynchus* spp.) conservation in California. *Reviews in Fish Biology and Fisheries* **25**: 195–215. <https://doi.org/10.1007/s11160-014-9359-5>
- Satterthwaite, W.H., and S.M. Carlson. 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences* **72**(12). <https://doi.org/10.1139/cjfas-2015-0169>
- Shapovalov, L. 1940. Report on the possibilities of establishment and maintenance of salmon and steelhead runs in Cache and Putah Creeks. *California Fish and Game* BR40-16.

- Shapovalov, L. 1947. Report on fisheries resources in connection with the proposed Yolo-Solano Development of the United States Bureau of Reclamation. *California Fish and Game* **33**:61-88.
- Sommer, T.R., M.L. Nobriga, W.C. Harrell, W. Batham, and W.J. Kimmerer. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **58**(2). <https://doi.org/10.1139/f00-245>
- Steele, C.A., M. Hess, S. Narum, and M. Campbell. 2019. Parentage-based tagging: Reviewing the implementation of a new tool for an old problem. *Fisheries* **44**(9): 412-422. <https://doi.org/10.1002/fsh.10260>
- Stier, A.C., A.O. Shelton, J.F. Samjhour, B.E. Feist, and P.S. Levin. 2020. Fishing, environment, and the erosion of a population portfolio. *Ecosphere* **11**(11): e03283. <https://doi.org/10.1002/ecs2.3283>
- Sturrock, A.M., W.H. Satterthwaite, K.M. Cervantes-Yoshida, E.R. Huber, H.J.W. Sturrock, S. Nussle, and S.M. Carlson. 2019. Eight decades of hatchery salmon releases in the California Central Valley: Factors influencing straying and resilience. *Fisheries* **44**(9): 433-444. <https://doi.org/10.1002/fsh.10267>
- Sullaway, G.H., A.O. Shelton, and J.F. Samjhour. 2021. Synchrony erodes spatial portfolios of an anadromous fish and alters availability for resource users. *Journal of Animal Ecology* **90**(11): 2692-2703. <https://doi.org/10.1111/1365-2656.13575>
- Till, A., A.L. Rypel, A. Bray, and S.B. Fey. 2019. Fish die-offs are concurrent with thermal extremes in north temperate lakes. *Nature Climate Change* **9**: 637-641. <https://doi.org/10.1038/s41558-019-0520-y>
- Waples, R.S. 1990. Conservation genetics of Pacific salmon II. Effective population size and the rate of loss of genetic variability. *Journal of Heredity* **81**(4): 267-276. <https://doi.org/10.1093/oxfordjournals.jhered.a110989>
- Welch, T.J. et al. 1993. Precision and relative accuracy of striped bass age estimates from otoliths, scales, and anal fin rays and spines. *North American Journal of Fisheries Management* **13**: 616-620. [https://doi.org/10.1577/1548-8675\(1993\)013%3C0616:PARAOS%3E2.3.CO;2](https://doi.org/10.1577/1548-8675(1993)013%3C0616:PARAOS%3E2.3.CO;2)
- Williamson, K.S., and B. May. 2004. Homogenization of fall-run Chinook salmon gene pools in the Central Valley of California, USA. *North American Journal of Fisheries Management* **25**(3): 993-1009. <https://doi.org/10.1577/M04-136.1>
- Williamson, K.S., A.R. Murdoch, T.N. Pearsons, E.J. Ward, and M.J. Ford. 2010. Factors influencing the relative fitness of hatchery and wild spring Chinook salmon

- (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 67(11). <https://doi.org/10.1139/F10-099>
- Willmes, M. et al. 2018. IsoFishR: An application for reproducible data reduction and analysis of strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) obtained via laser-ablation MC-ICP-MS. *PLoS One*: <https://doi.org/10.1371/journal.pone.0204519>
- Willmes, M. et al. 2021. Geochemical tools identify the origins of Chinook salmon returning to a restored creek. *Fisheries* 46(1). <https://doi.org/10.1002/fsh.10516>
- Yarnell, S.M., E.D. Stein, J.A. Webb, T. Grantham, R.A. Lusardi, J. Zimmerman, R.A. Peek, B.A. Lane, J. Howard, and S. Sandoval-Solis. 2020. A functional flows approach to selecting ecologically relevant flow metrics for environmental flow applications. *River Research and Applications* 36(2): 318-324. <https://doi.org/10.1002/rra.3575>
- Yoshiyama, R.M. et al. 1998. Historical abundance and decline of Chinook salmon in the Central Valley region of California. *North American Journal of Fisheries Management* 18: 487-521. [http://doi.wiley.com/10.1577/1548-8675\(1998\)018<0487:HAADOC>2.0.CO;2](http://doi.wiley.com/10.1577/1548-8675(1998)018<0487:HAADOC>2.0.CO;2)
- Yoshiyama, R.M., E.R. Gerstung, F.W. Fisher, and P.B. Moyle. 2001. Historical and present distribution of Chinook salmon in the Central Valley drainage of California. *California Department of Fish and Game Fish Bulletin* 179(1): 71-176.

Table 1. Trace elements laser dwell times.

Element	Dwell time (s)
²⁴ Mg	0.1
⁴³ Ca	0.03
⁴⁴ Ca	0.03
⁵⁵ Mn	0.3
⁶⁶ Zn	0.3
⁸⁸ Sr	0.1
¹³⁷ Ba	0.1

Table 2. Number of Chinook salmon carcasses recovered in Lower Putah Creek by study year and the number of carcasses from which salmon otolith microchemistry was analyzed.

Year	Total carcasses recovered	Total otoliths analyzed
2016	126	104
2017	208	49
2018	211	47
2020	70	51
2021	81	75

Table 3. Observed and expected counts of different natal origin assignments by study year (top) and different age classes by study year (bottom). Values in bold indicate values violating assumptions of the chi-squared test.

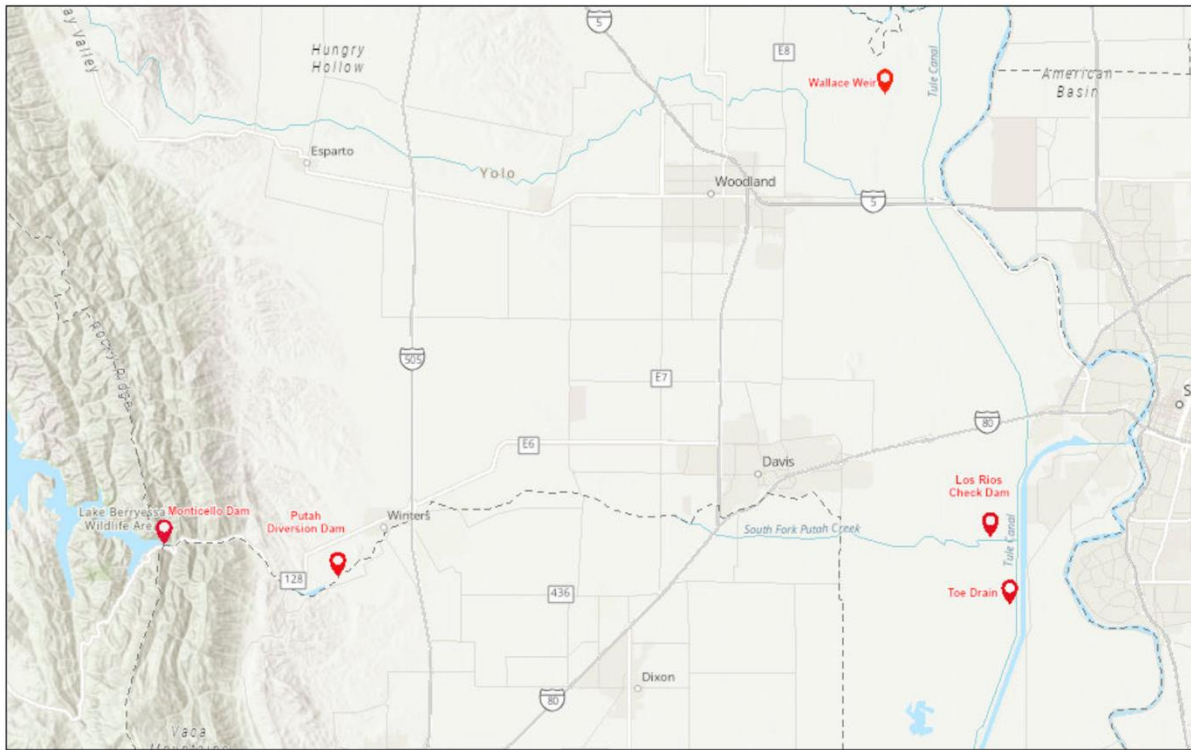
Natal Origin Observed					
	2016	2017	2018	2020	2021
Hatchery-stray	92	38	39	42	58
Wild-stray	3	8	8	8	6
Unknown	9	2	0	0	1
Putah Creek	0	1	0	1	10

Natal Origin Expected					
	2016	2017	2018	2020	2021
Hatchery-stray	86	40	38	42	61
Wild-stray	11	5	4.8	5	7
Unknown	4	2	2	2	2
Putah Creek	4	2	2	2	2
Age Class Observed					
	2016	2017	2018	2020	2021
Age 2	46	13	9	3	21
Age 3	44	32	33	33	46
Age 4	14	3	2	10	3
Age Class Expected					
	2016	2017	2018	2020	2021
Age 2	31	14	13	14	21
Age 3	63	29	27	28	42
Age 4	11	4.9	4.5	4.7	7

Table 4. Age-fork length summary statistics.

Age Class	n	Minimum FL (mm)	Maximum FL (mm)	Mean FL (mm)	Standard Deviation (mm)	Skewness	Kurtosis
2	190	452	860	634	76	0.7	3.7
3	97	563	1030	770	88	-0.1	2.9
4	30	725	1030	877	76	0.2	2.2

Putah Creek, CA, USA



5/4/2023

1:314,475
0 2 4 8 mi
0 3.25 6.5 13 km
Esri, NASA, NGA, USGS, County of Sacramento, Yolo County, California State Parks, Esri, HERE, Garmin, SafeGraph, FAO, METINASA, USGS

Fig. 1. Map of Putah Creek, CA, USA and surrounding area. Putah Creek flows from west to east and is constrained by three dams. From most upstream to most downstream, Monticello Dam is the largest and forms Berryessa Reservoir; Putah Diversion Dam forms Lake Solano and diverts water into Putah South Canal or into Lower Putah Creek. The reaches of Lower Putah Creek downstream of Putah Diversion Dam until its confluence with the Sacramento Toe Drain are accessible to anadromous fishes. One rkm upstream of the Toe Drain confluence is the smallest dam, Los Rios Check Dam (LRCD), an agricultural water diversion that is seasonally installed and removed.

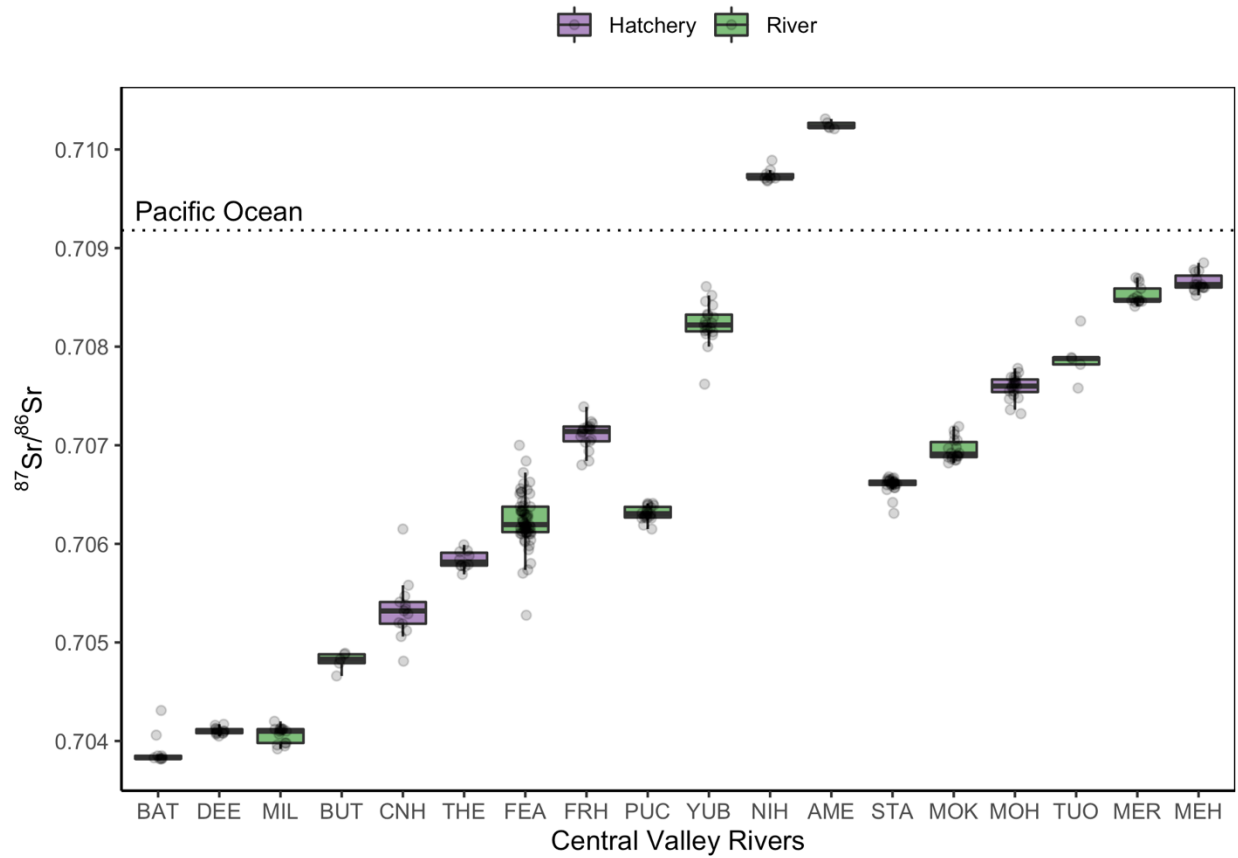


Fig. 2. $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios for Central Valley wild river populations (blue) and hatchery populations (orange) derived from Barnett-Johnson et al. (2008) and Willmes et al. (2021). Note that the signal for the Feather River wild population (FEA) completely overlaps the Putah Creek wild (PUC) signal.

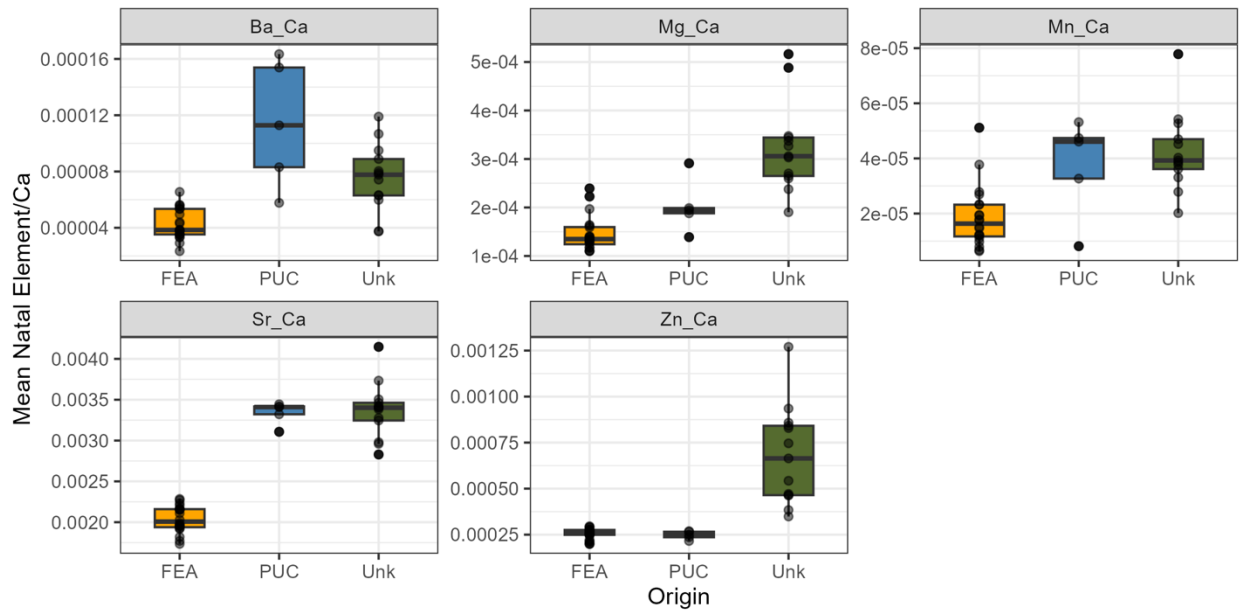


Fig. 3. Trace elements concentrations expressed as ratios of element X /⁴³Ca for known Feather River wild juveniles, known Putah Creek wild juveniles, and unknown adults of uncertain natal classification. Ba/Ca and Sr/Ca were utilized in linear discriminant analysis for classifications of unknown fish.

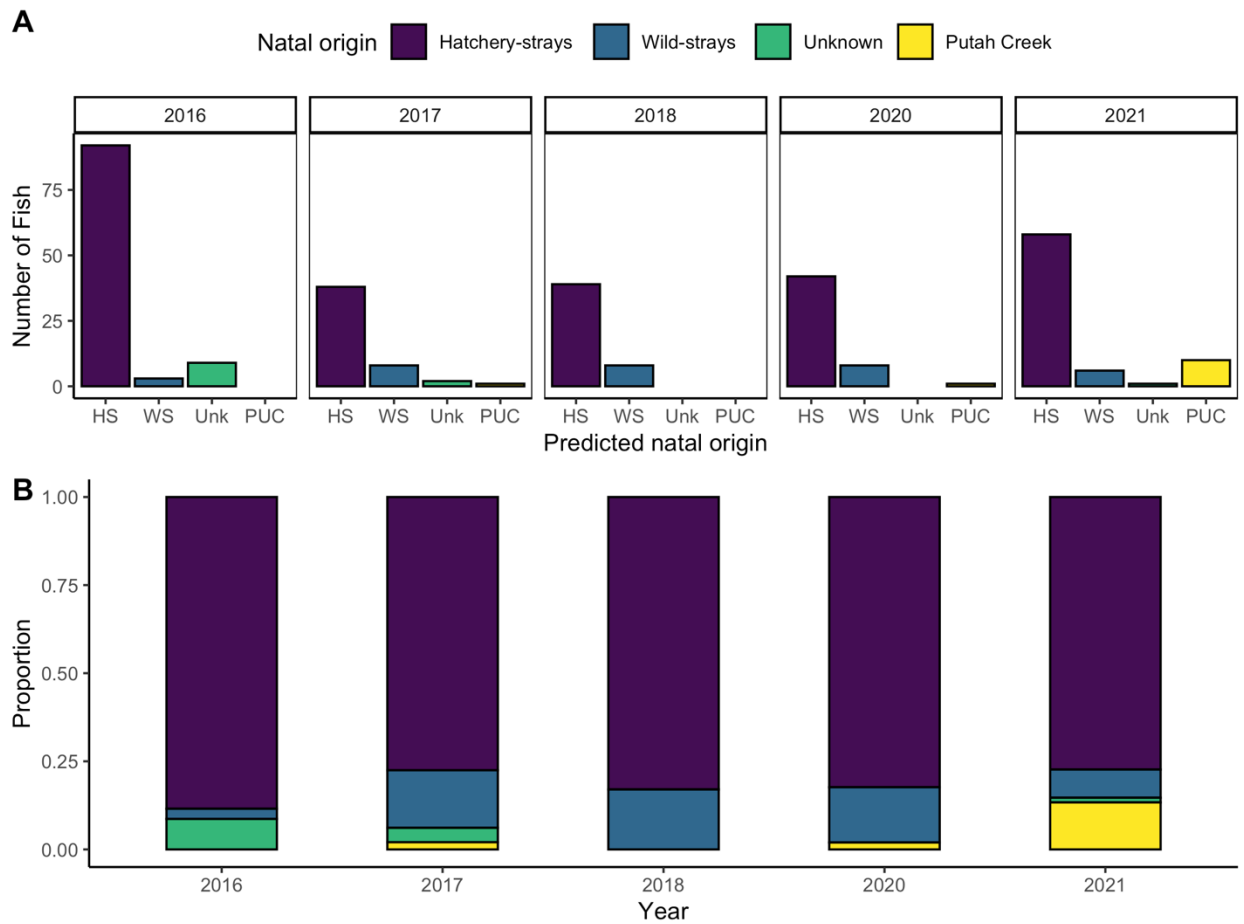


Fig. 4. Natal origin classifications by category (hatchery-origin, wild-origin, unknown-origin, or Putah Creek-origin) by study year. 2016 cohort data first published in Willmes et al. (2021). Wild fish were observed in the lowest frequency in the 2016 spawning cohort.

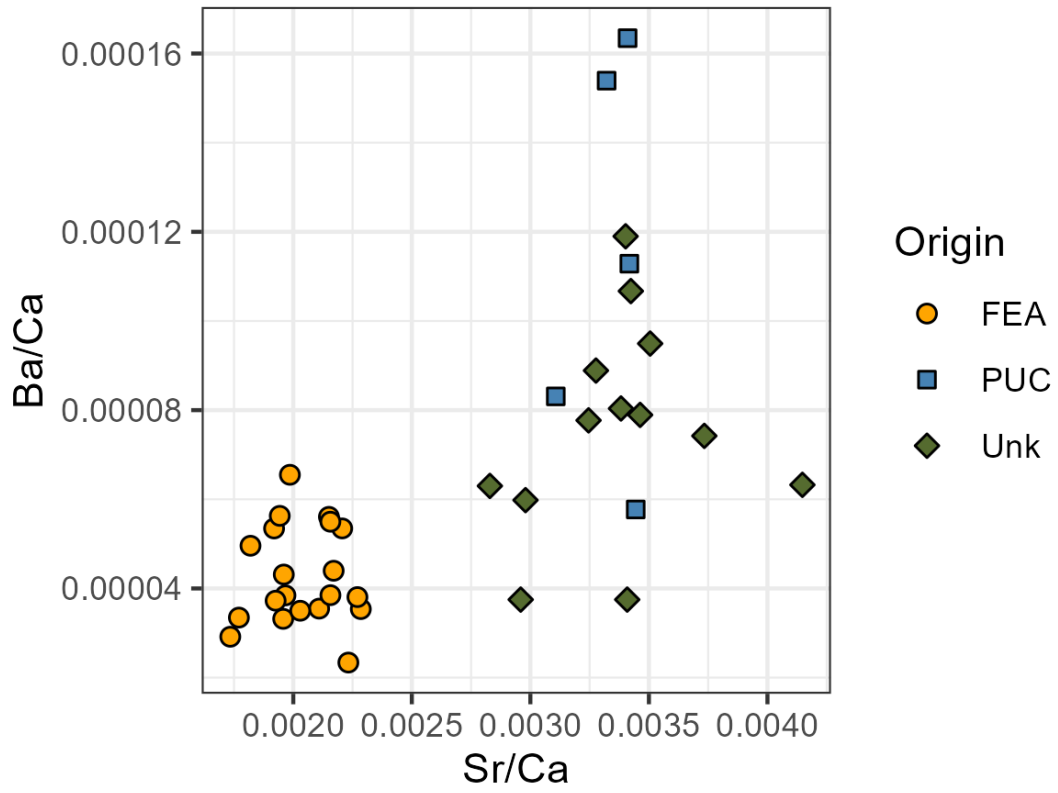


Fig. 5. Trace Sr/Ca and Ba/Ca ratios for each otolith grouped by natal origin classification.

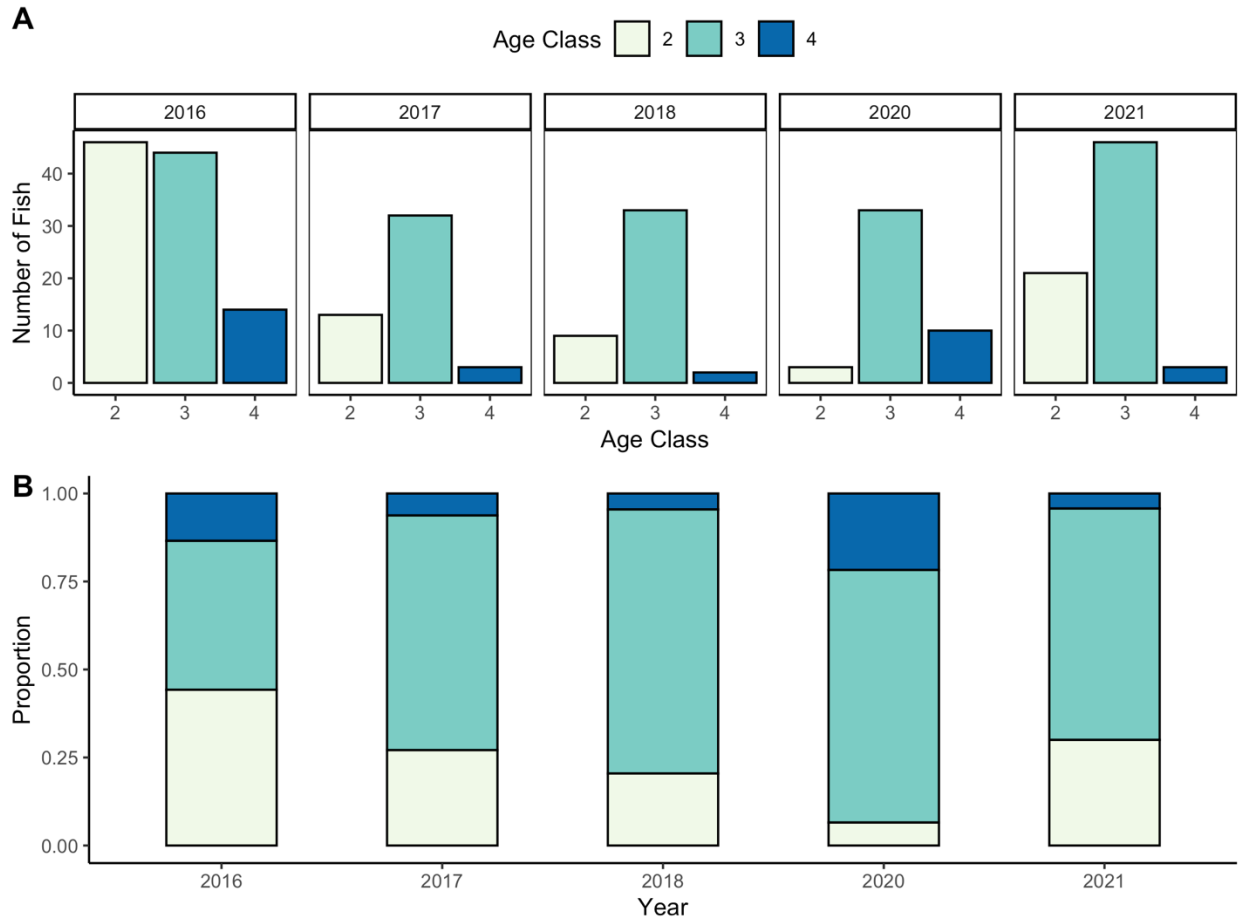


Fig. 6. Number of fish per age class by survey year. 2016 cohort data first published in Willmes et al. (2021). Age 2 and age 3 fish were observed in similar proportions in 2016, but for all other survey years age 3 fish were the most abundant age classification.

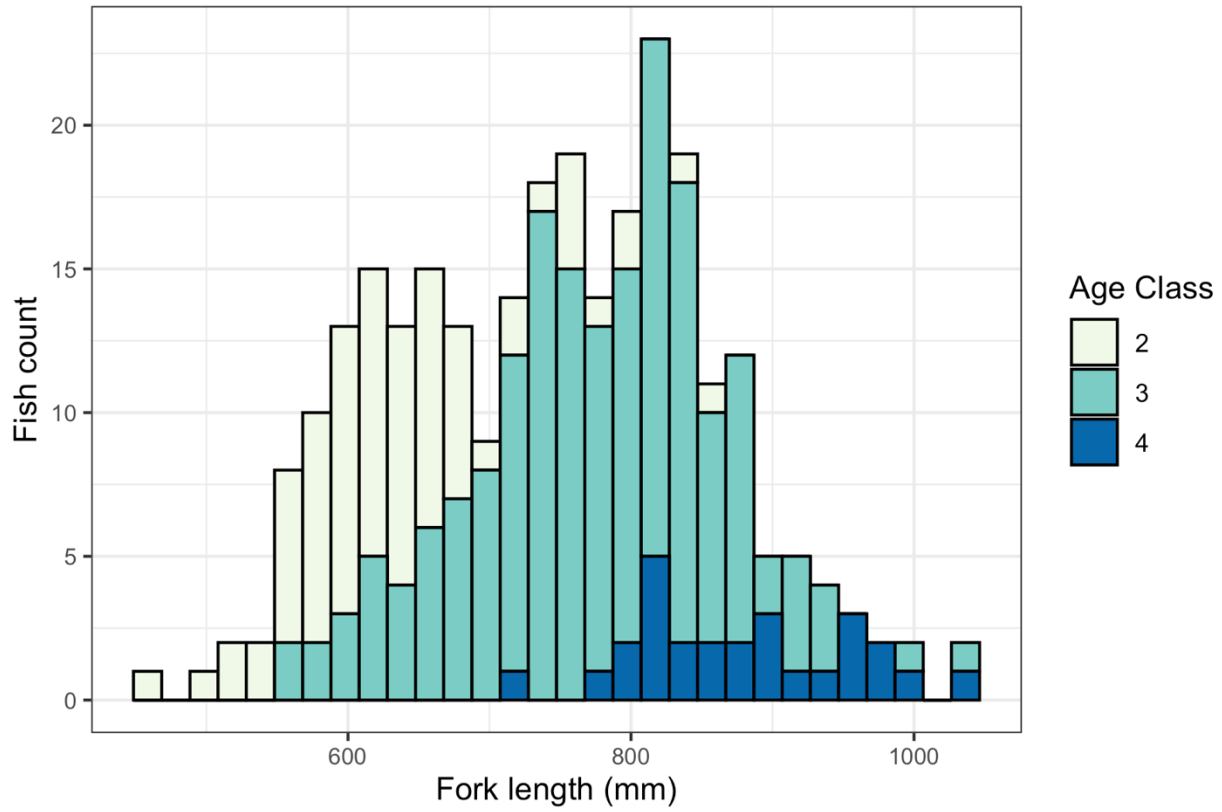


Fig. 7. Distribution of fish fork lengths (in mm) for each age class of Putah Creek adult Chinook salmon, all years combined.