










Integrating otolith and genetic tools to reveal intraspecific biodiversity in a highly impacted salmon population

Malte Willmes^{1,2}  | Anna M. Sturrock^{3,4}  | Flora Cordoleani^{2,5}  |
 Sara Hugentobler⁶  | Mariah H. Meek^{6,7}  | George Whitman³  |
 Kimberly Evans³ | Eric P. Palkovacs²  | Natalie J. Stauffer-Olsen⁸  |
 Rachel C. Johnson^{3,5} 

¹Norwegian Institute for Nature Research, Trondheim, Norway

²Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, California, USA

³Center for Watershed Sciences, University of California Davis, Davis, California, USA

⁴School of Life Sciences, University of Essex, Colchester, UK

⁵National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, California, USA

⁶Department of Integrative Biology, Michigan State University, East Lansing, Michigan, USA

⁷The Wilderness Society, Bozeman, Montana, USA

⁸Trout Unlimited, Emeryville, California, USA

Correspondence

Malte Willmes, Norwegian Institute for Nature Research, Høgskoleringen 9, 7034 Trondheim, Norway.

Email: malte.willmes@nina.no

Anna M. Sturrock, School of Life Sciences, University of Essex, Wivenhoe Park, Colchester, UK.

Email: anna.sturrock@essex.ac.uk

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Abstract

Intraspecific biodiversity is vital for species persistence in an increasingly volatile world. By embracing methods that integrate information at different spatiotemporal scales, we can directly monitor and reconstruct changes in intraspecific biodiversity. Here we combined genetics and otolith biochronologies to describe the genotypic and phenotypic diversity of Chinook salmon (*Oncorhynchus tshawytscha*) in the Yuba River, California, comparing cohorts that experienced a range of hydroclimatic conditions. Yuba River salmon have been heavily impacted by habitat loss and degradation, and large influxes of unmarked hatchery fish each year have led to concern about introgression and uncertainty around the viability of its wild populations, particularly the rarer spring-run salmon. Otolith strontium isotopes showed that Yuba River origin fish represented, on average, 42% (range 7%–73%) of spawners across six return years (2009–2011, 2018–2020), with large interannual variability. The remainder of adult Chinook salmon in the river were primarily strays from the nearby Feather River hatchery, and since 2018 from the Mokelumne River hatchery. Among the Yuba-origin spawners, on average, 30% (range 14%–50%) exhibited the spring-run genotype. The Yuba-origin fish also displayed a variety of outmigration phenotypes that differed in the timing and size at which they left the Yuba river. Early-migrating fry dominated the returns (mean 59%, range 33%–89%), and their contribution rates

Anna Sturrock should be considered joint first author.

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were negatively correlated with freshwater flows. It is unlikely that fry survival rates are elevated during droughts, suggesting that this trend reflects disproportionately low survival of larger later migrating parr, smolts, and yearlings along the migratory corridor in drier years. Otolith daily increments indicated generally faster growth rates in non-natal habitats, emphasizing the importance of continuing upstream restoration efforts to improve in-river growing conditions. Together, these findings show that, despite a long history of habitat degradation and hatchery introgression, the Yuba River maintains intraspecific biodiversity that should be taken into account in future management, restoration, and reintroduction plans. The finding that genotypic spring-run are reproducing, surviving, and returning to the Yuba River every year suggests that re-establishment of an independent population is possible, although hatchery-wild interactions would need to be carefully considered. Integrating methods is critical to monitor changes in key genetic, physiological, and behavioral traits to assess population viability and resilience.

KEYWORDS

GREB1L, hidden biodiversity crisis, intraspecific biodiversity, phenotypic plasticity, strontium isotopes

1 | INTRODUCTION

Intraspecific biodiversity increases species and ecosystem resilience and stabilizes ecosystem services (Bolnick et al., 2011; Luck et al., 2003; Nicastro et al., 2020; Roches et al., 2017). Genetic and phenotypic variations within and among populations of the same species create diverse life histories that can buffer populations in dynamic systems by way of the portfolio effect (Figge, 2004). The loss of this intraspecific diversity often goes unnoticed despite progressing at an alarming rate, and has thus been termed the “hidden biodiversity crisis” (Hughes et al., 1997; Luck et al., 2003; Roches et al., 2021). Furthermore, this silent loss is considered a precursor to species extinction. Thus, identifying and monitoring changes in intraspecific biodiversity through time is crucial for the conservation and management of species and ecosystems.

Pacific salmonids demonstrate a high level of intraspecific diversity that helps stabilize populations in the face of a changing climate (Greene et al., 2010; Moore et al., 2014; Schindler et al., 2010). They have highly adaptable life histories underpinned by genetic and phenotypic diversity that results in populations that are adapted to local climatic and hydrological conditions (Quinn, 2018). Consequently, effective salmon conservation and management relies on understanding their genotypic and phenotypic diversity, including behavior, physiology, and life-history traits. A diverse salmon population complex of Chinook salmon (*Oncorhynchus tshawytscha*) can be found in California's Central Valley (CCV), at the southern end of the native species range (Moyle, 2002). Chinook salmon in the CCV co-occur as three evolutionarily significant units (ESUs) that differ in many key life-history traits, including adult and juvenile migration timing (Moyle, 2002; Moyle et al., 2017; Williams, 2006). CCV Chinook

salmon are in decline as a result of anthropogenic pressures such as habitat loss, overfishing, and water diversions (Crozier et al., 2019; Herbold et al., 2018; Moyle et al., 2017). The remaining populations are constrained to less than 30% of their historical habitat (Yoshiyama et al., 2001), exposed to low streamflows and increasingly extreme droughts (Herbold et al., 2018), and are also impacted by hatchery fish across all life stages (Cline et al., 2019; Huber & Carlson, 2015; Sturrock et al., 2019). The high numbers of hatchery strays and their introgression with wild populations has led to genetic and demographic homogenization (Katz et al., 2012; Quiñones et al., 2014; Williamson & May, 2005), with increased synchrony and instability in population abundances in recent decades signaling erosion of portfolio effects (Carlson & Satterthwaite, 2011; Carvalho et al., 2023). Despite all these stressors and homogenizing forces, intraspecific diversity in CCV Chinook salmon still exists and warrants monitoring and protection to increase resiliency to future environmental change (Meek et al., 2020).

The three CCV Chinook salmon ESUs are primarily defined by run timing. The fall- and late-fall-run ESU that spawns primarily on the valley floor now dominates the stock complex and ocean fishery. Yet fall-run are still classified as a “species of concern” and are heavily supported by five production hatcheries (HSRG, 2012; Myers, 1998). The winter-run ESU has exhibited large declines (Yoshiyama et al., 1998) and is listed as endangered under the Endangered Species Act. Winter-run historically spawned in the tributaries of the upper Sacramento River watershed but are now largely constrained to a short stretch of the mainstem Sacramento River just below the impassable Keswick dam (Lindley et al., 2004). Finally, the spring-run ESU was once highly abundant before the construction of large, impassable dams through the 1900s, but is now listed as

“threatened”, and numbers of spawners in some rivers are often only in the hundreds (Lindley et al., 2004; Yoshiyama et al., 1998). Historically, spring-run used the higher spring flows created by snowmelt to gain access to high-elevation cold-water pools that allowed them to avoid the high summer and early-fall temperatures on the valley floor (Cordoleani et al., 2021). Today, natural origin spring-run populations not actively supplemented by hatchery production remain only in Mill, Deer, Butte, and Battle Creeks, out of 19 historic independent populations (Figure 1, Yoshiyama et al., 2001). Questions remain around their persistence in tributaries assumed to be dominated by fall-run salmon that receive high influxes of hatchery fish, such as the Yuba River (Lindley et al., 2004, 2007; NMFS, 2014). For tributaries supporting multiple runs, understanding how hatchery and streamflow management can help to maintain the genetic integrity of each

population and run can only be fully achieved if the presence and frequencies of fall- and spring-run phenotypes are monitored. Importantly, recent advances in genomics have made it possible to identify the run type of CCV Chinook salmon, using the region of the genome linked with early (winter- and spring-run) and late (fall- and late-fall) adult migration timing (GREB1L) (Kelson et al., 2019, 2020; Meek et al., 2020; Narum et al., 2018; Prince et al., 2017; Thompson et al., 2019).

In addition to genetic run diversity, CCV salmon also exhibit considerable diversity in the size, timing, and age at which they outmigrate from their natal stream and into the ocean (Cordoleani et al., 2021; Moyle et al., 2017; Munsch et al., 2020; Sturrock et al., 2020). This has allowed these populations to buffer the large interannual variations in coastal upwelling patterns characteristic of

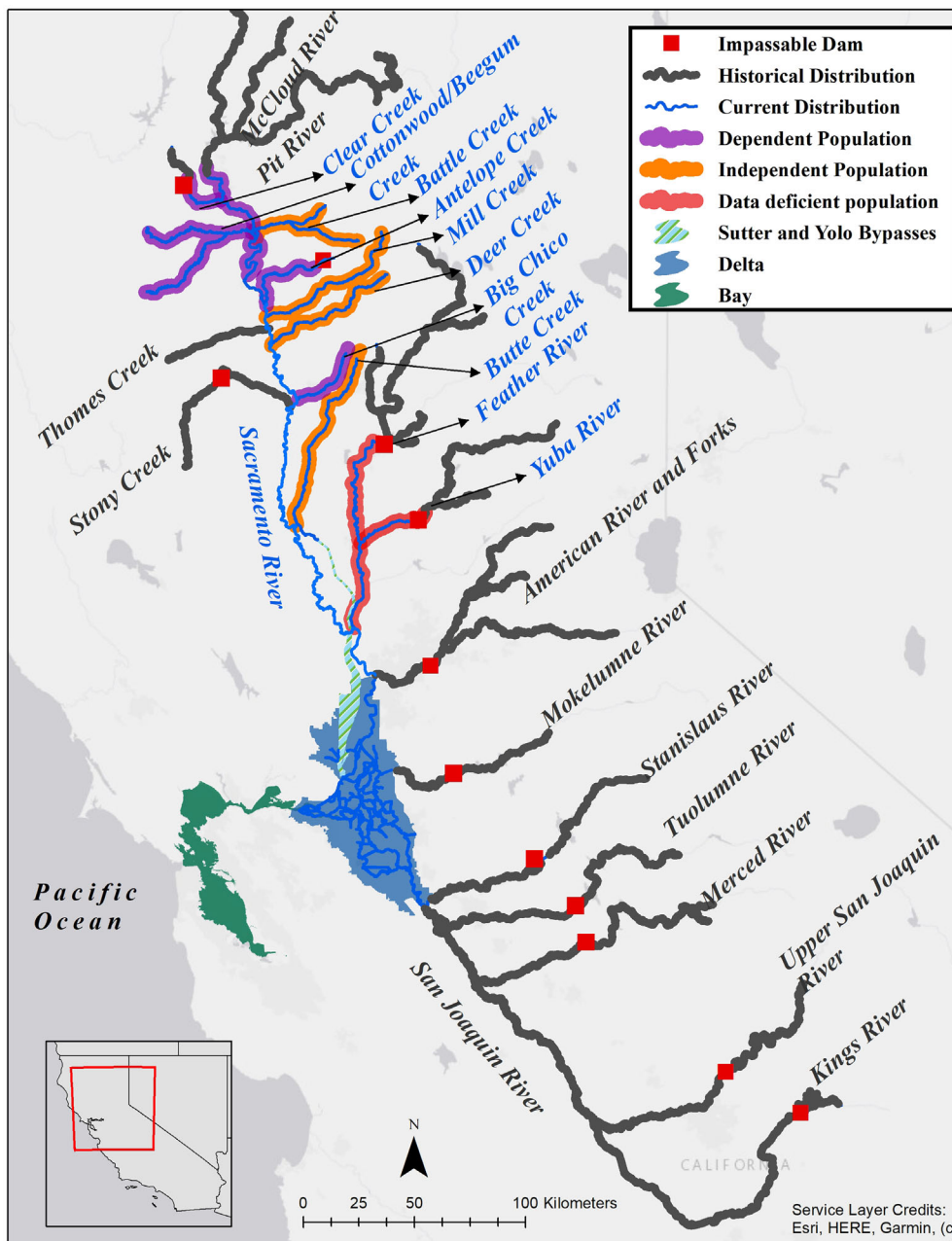


FIGURE 1 Historic and current distribution of spring-run Chinook populations. Independent populations correspond to populations that were historically not significantly altered by exchanges of individuals with other populations, while dependent populations likely would have not persisted without immigration from other streams (Lindley et al., 2004, 2007; NMFS, 2014).

the region that affect the timing, location, and abundance of prey species that are key to salmon survival (Spence & Hall, 2010). In particular, juvenile spring-run (and occasionally fall-run) sometimes over-summer in their natal stream, outmigrating as much larger yearlings in the fall, experiencing vastly different riverine, Delta, and ocean conditions to their subyearling counterparts (Cordoleani et al., 2021). In this region, where water scarcity and high spring and summer temperatures play a disproportionate role in setting cohort strength (Michel, 2019; Sturrock et al., 2015, 2020), this phenotypic diversity is thought to contribute significantly to population persistence by spreading risk in space and time (Cordoleani et al., 2021; Spence & Hall, 2010; Sturrock et al., 2020).

Monitoring migration timing and pathways is typically achieved through tagging studies, but these can be biased towards larger life stages. Otolith (“ear stone”) chemical analysis can provide an alternative approach. Otoliths are formed of daily concentric layers of CaCO_3 and protein, with the older layers occupying the central core region and younger layers sequentially formed on top. This process continues throughout the lifetime of the fish while simultaneously incorporating ambient water chemistry, resulting in a daily chemical record of the fish's local environment. When geochemistry data are linked to daily and annual otolith growth bands, detailed information about the timing of movements among habitats and the growth rates within different habitats can be reconstructed (Campana, 1999). Strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) in otoliths are powerful geochemical tracers for retrospective geolocation of Chinook salmon in the CCV (Barnett-Johnson et al., 2008; Johnson et al., 2016; Phillis et al., 2018; Sturrock et al., 2015; Willmes, Hobbs, et al., 2018). The underlying principle is that water $^{87}\text{Sr}/^{86}\text{Sr}$ varies predictably between rivers, based on differences in the local geology, and these differences are recorded in the otolith as it grows (Barnett-Johnson et al., 2008; Brennan et al., 2016; Capo et al., 1998). Furthermore, otolith size varies predictably with fish size (Campana, 1990; Campana & Thorrold, 2001), allowing us to reconstruct the size at which individual Chinook salmon moved among rivers and into the sea during their early life (Coleman et al., 2022; Cordoleani et al., 2022; Sturrock et al., 2015, 2020). Faster growth during early life stages is often assumed to correlate with higher survival (Sogard, 1997), but the strength of selection can vary considerably among years (Woodson et al., 2013), likely due to variations in food availability and timing (e.g., match-mismatch theory; Cushing, 1990). Exploring variations in juvenile migration behavior and growth among genotypic run types provides a rare opportunity to understand the interplay between genotype, phenotype, and environmental conditions in an increasingly unpredictable climate.

Both spring-run and fall-run Chinook salmon populations can be found in the Yuba River, and although its spring-run population was historically independent (i.e., unique genetically and isolated geographically, with limited hatchery influence; Lindley et al., 2004), its current status is uncertain (Lindley et al., 2007; NMFS, 2014). The Yuba River is located in close proximity to the Feather River Hatchery and high numbers of hatchery origin fish are observed on the natural spawning grounds (often around 50% of total escapement;

e.g., Palmer-Zwahlen et al., 2019), leading to likely introgression between hatchery and natural origin fish (Lindley et al., 2004). The Yuba River was also a focal point during the Goldrush in the 1850s, with entire mountainsides removed by hydraulic mining. Then, in the 1900s, two major dams (Englebright and Daguerre Point) were built that blocked access to 70% of historic upstream habitats (Yoshiyama et al., 2001). Today, the mine tailings are still visible along its lower reaches and the flows are heavily managed, but considerable habitat restoration is now being carried out to improve spawning and rearing opportunities along the lower reaches (<https://yubariver.org/projects/>). The extent to which this large-scale habitat loss, flow modification, and hatchery introgression have affected intraspecific diversity in Yuba River salmon is unclear. In particular, questions remain about whether a self-sustaining spring-run population exists today and/or whether recent restoration efforts have had any impact on growth rates, survival, and life-history diversity. Here, we use a multi-method approach to identify and create a modern-day baseline of in-river “biodiversity” based on the diversity of genotypes, return ages, emigration sizes, and juvenile growth rates observed in natural-origin Yuba River Chinook salmon. Given the large interannual variation in flows and temperatures typical of California's Mediterranean climate, we targeted cohorts characterized by low and high flows to maximize the opportunity to capture the full range of phenotypic traits, and also to explore direct influences of the environment on demographically important factors such as size and growth. Specifically, we identified Yuba River origin fish and then analyzed interannual variation in (1) genotype frequencies, focusing on the GREB1L locus, (2) juvenile migratory phenotype frequencies, focusing on the size and age at which they outmigrated from the Yuba River, and (3) juvenile growth rates during natal and non-natal rearing.

2 | MATERIALS AND METHODS

2.1 | Study system

This study focuses on CCV fall- and spring-run Chinook salmon population from the Yuba River. In this watershed both runs coexist, and although spring-run Chinook salmon adults return to spawn in the spring, they spend the summer months in the natal reaches before spawning in the fall, creating a temporal overlap between spring- and fall-run spawners. Moreover, while historically fall- and spring-run Chinook salmon spawning grounds were spatially separated, the construction of Englebright dam blocked access to the higher elevation spawning habitat used by spring-run, leading to a spatial overlap of spawning reaches for these two runs today. Furthermore, the nearby Feather River Hatchery produces both spring- and fall-run juveniles that frequently spawn in the Yuba River (and while 100% of their spring-run production are externally marked by an adipose fin clip, 75% of their fall-run are released unmarked). Consequently, a combination of genetic and geochemical analyses is required to identify both the natal origin and run type of unmarked fish.

2.2 | Sample selection

A total of 448 otolith samples and 439 genetic (fin clip) samples were analyzed for this project (Table 1 and Figure S1). All samples were collected from adult Chinook salmon carcasses in the spawning reaches of the Yuba River. Generally, carcasses with intact adipose fins were selected given that Central Valley hatcheries mark (adipose fin clip and coded wire tag [CWT]) 25% of fall-run production and 100% of known spring-run production, and we were primarily interested in the life-history characteristics of natural origin fish. Otoliths, scales, and fin clips were taken in the field and stored dry. The 2009, 2010, and 2019 samples were randomly selected throughout the river reach. For some of the 2009 and 2010 samples, 2- and 3-year-olds were selected, respectively, to target the driest year in the time series (outmigration year 2008) to bookend the effects of hydrologic variation on habitat use and growth. These samples were excluded from the adult age distribution analysis. The 2011 and 2018 samples were selected to target potential spring-run, by focusing on the upper river reaches and spawning timing before November. However, given the paucity of samples where both otoliths and fin clips were present, the geographic and date ranges were extended for 2018. For 2020, the only available fin-clip samples were from November to January (Figure S1). Given this spatiotemporal selectivity, some caution should be applied when interpreting the phenotype and genotype fractions from escapement years 2011, 2018, and 2020 (dominant outmigration years 2009, 2016, and 2018; Table 1). Finally, of the unmarked fish sampled in 2009–2011, six had been tagged externally between May 13 and June 24 (i.e. known phenotypic spring-run), their otoliths extracted during the fall carcass survey, and their origin identified using otolith strontium isotopes.

To link juvenile fish experience to local flow conditions, we used the Sacramento Water Index and the California Department of Water Resource water-year classification for each outmigration year (<https://cdec.water.ca.gov/>). This index provides an indication of the amount of surface water in the Sacramento River basin during a given season (from October to July). It is calculated based on surface runoff in million-acre feet from the Sacramento River and its larger

tributaries (Feather River, Yuba River, and American River). The water year classifications are based on this index, with ranges equivalent to C = critical <5.4, D = dry >5.4–6.5, BN = below normal >6.5–7.8, AN = above normal >7.8–9.2, and W = wet >9.). As spring- and fall-run salmon in the CCV spawn in the fall and typically migrate to sea in the spring (subyearlings) or fall (yearlings), the water year classifications incorporate the full juvenile experience from incubation to outmigration for both run types.

2.3 | Genetic analyses

Genetic analyses were carried out using fin clips (Table 1), following the methods of Hugentobler et al. (2024). In brief, DNA was extracted from fins using the DNeasy® Blood and Tissue extraction kit (Qiagen). We then assigned samples to genotypes at the run-timing associated GREB1L locus using 16 SNPs spread throughout the gene and genotyped using Fluidigm SNPtype assays (Hugentobler et al., 2024; Prince et al., 2017; Thompson et al., 2019). Individuals that are homozygous for the early-running allele are spring- or winter-running fish, those that are homozygous for the late-running allele are fall- or late-fall-running fish. Additionally, individuals can be heterozygous, meaning they have one copy of the early-running allele and one copy of the late-running allele. The phenotypic run-timing of these fish is more uncertain in the Central Valley, although preliminary work suggests they may display an intermediate spawn timing (Hugentobler et al., 2024). In other systems, individuals that are heterozygous at GREB1L have also been shown to have intermediate-run timing, returning to spawn in the period between spring- and fall-running fish (Thompson et al., 2019).

2.4 | Otolith sample preparation

Adult Chinook salmon sagittal otoliths were cleaned of any adhering tissues and rinsed with deionized ultrapure water. The samples were stored dry before being mounted onto glass rounds using Crystalbond

TABLE 1 Analyzed otolith and genetic samples by return year.

Return year	Dominant outmigration year	Dominant outmigration water year type	Dominant outmigration Sacramento Water Index	Otolith samples	Genetic samples
2009	2007	Dry	6.2	103	36
2010	2008	Critical	5.4	127	36
2011	2009	Dry	5.5	44	155
2018	2016	Below normal	7.1	15	17
2019	2017	Wet	14.9	116	64
2020	2018	Below normal	7.2	43	131
Total samples				448	439

Note: Overview of dominant juvenile outmigration year and corresponding environmental conditions (Sacramento Water Year, freshwater outflow, and Sacramento Water Index). The dominant outmigration year assumes a 3-year-old fish and was used to select the samples. For subsequent analyses all samples are assigned to their actual outmigration year based on individual age estimates.

(509) resin. Otoliths were prepared for age and geochemical analyses following established methods at the Center for Watershed Sciences, UC Davis (Johnson et al., 2016). Briefly, otoliths were ground on both sides on the sagittal plane using 600 and 1500 grit wet/dry sandpaper to expose the primordia and surrounding microstructure. The surfaces were then polished using 3 and 1 μm Al_2O_3 lapping films. Finished samples were mounted to a 1-cm square glass pedestal using Gorilla Glue™.

2.5 | Age reconstructions

Otolith- (2011, 2018, and 2020) and scale- (2009, 2010, 2019) based age reconstructions were carried out for 435 fish to match them to outmigration year, excluding 13 samples that had no available scales or otoliths that could be consistently aged by experienced age readers. These 13 samples were excluded from all subsequent analyses.

Otolith-derived annual ages were determined in the sagittal plane on the dorsal lobe. Bands were counted as a sequence of winter (translucent) and summer bands (opaque). Characteristic checks produced at hatching (hatch check), onset of exogenous feeding (exogenous feed check), and smoltification (smolt check) were also identified. Age precision was tested using three independent age readers that had been trained on known-age fish following established methods (Campana, 2001). The results were evaluated using the FSA package (Ogle, 2016) in R and we found overall good agreement among readers (percentage agreement = 94%, average coefficient of variation = 1.5, average percentage error = 1.1, readers = 2, $n = 124$). For fish with age disagreements, ages were assigned based on majority vote if at least two secondary readers agreed, otherwise the fish was removed from the dataset (<1% of samples). Age read accuracy was generally high based on blind analysis of known age coded wire tagged (CWT) fish (percentage agreement = 95%, average coefficient of variation = 1.2, average percentage error = 0.9, $n = 23$).

Annual ages were also determined using scales mounted and imaged by the CDFW Santa Rosa office. A scale annulus was defined as a region of closely spaced circuli that included crossing over and discontinuous circuli (Anderson et al., 2022). Scale readers were trained using a random sample of known aged CWT marked hatchery fish from the CCV Chinook salmon fall-run stock. Total age was estimated by counting the number of winter annuli present in the scale (usually assessing three scales per fish) and adding an additional year for the year spent in freshwater during egg incubation and rearing. Following training, age read accuracy (percentage agreement between estimated and known age from CWT data) was 81% ($n = 78$). Where available, scale reads carried out by the expert readers in the Santa Rosa office were used ($n = 231$ from return years 2009 and 2010). Scale reads for fish that returned in 2019 were read by two independent readers. Among-reader agreement was 80% ($n = 116$), disagreeing ages were all within 1 year of each other, and a single age was agreed on via re-aging and discussion of the images.

2.6 | Otolith geochemical analysis

We measured strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) at the University of California-Davis Interdisciplinary Center for Plasma Mass Spectrometry following established protocols (Sturrock et al., 2015; Willmes et al., 2021) using a Nd:YAG 213 nm laser (New Wave Research UP213) coupled to a Nu Plasma HR MC-ICP-MS (Nu032). All ablations were done at 10 Hz frequency and $\sim 5\text{--}15\text{ J}/\text{cm}^2$ photon output and we applied a normalization for mass bias ($^{86}\text{Sr}/^{88}\text{Sr} = 0.1194$), ^{87}Rb interference correction, and on-peak subtraction for ^{86}Kr . Samples were analyzed in two different instrument configurations. For the samples from 2009, 2010, and 2019 a line of laser spots with a diameter of 40 μm , a dwell time of 35 s, and a spacing of 40 μm was placed from the core to the dorsal edge, and spot distances were measured using the same standardized 90° transect used for growth analyses. Marine carbonate in-house reference materials ('UCD Vermeij Mollusk' and *O. tshawytscha* otoliths) were analyzed periodically to monitor instrument bias and drift. The deviation of the marine portion of *O. tshawytscha* otoliths (mean of three spots at the start and end of every slide) from the global average $^{87}\text{Sr}/^{86}\text{Sr}$ value of modern seawater of 0.70918 (Mokadem et al., 2015) was used to correct $^{87}\text{Sr}/^{86}\text{Sr}$ values of the samples from the same slide. Prior to any corrections, the reference materials produced a mean $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.70923 ± 0.00030 (mean \pm 2SD, $n = 226$), within 1SD of the global marine value of 0.70918. For the 2011, 2018, and 2020 samples a continuous laser line with a diameter of 40 μm and moving 5 $\mu\text{m}/\text{s}$ was ablated from the ventral edge, across the core, and to the dorsal edge. For data reduction we used IsoFishR (Willmes, Ransom, et al., 2018) and applied a five-point average to the raw data collected by the mass spectrometer with an integration time of 0.2 s, resulting in one datapoint per second. Outliers were removed based on a 20-point moving interquartile range (IQR) criterion. Finally, a thin plate spline ($k = 200$) with generalized cross-validation to optimize the effective degrees of freedom using the mgcv package in R (Wood, 2017) was applied to the data to create a continuous profile for each fish, resolved to the same standardized 90° transect used for spot analyses and increment reads. The accuracy and reproducibility of the line profiles were evaluated using a modern marine otolith from a white seabass (*Atractoscion nobilis*) collected offshore of Baja California, which showed average values of 0.70916 ± 0.00010 (mean \pm 2SD, $n = 63$), in good agreement with the global average $^{87}\text{Sr}/^{86}\text{Sr}$ value of modern seawater of 0.70918.

2.7 | Natal assignments

To reconstruct natal origins for individual samples from otoliths we identified the natal region in the strontium isotope profiles based on the period immediately following the exogenous feeding check (assumed to represent the point at which the maternal yolk has been depleted and the fry is emerging from the gravel; Barnett-Johnson et al., 2007) and calculated the mean $^{87}\text{Sr}/^{86}\text{Sr}$ natal value. The start

of the natal period was identified by visual inspection of the otolith section and the $^{87}\text{Sr}/^{86}\text{Sr}$ time-series, and indicated by a microstructural and isotopic breakpoint indicative of yolk depletion, typically at around 200 μm from the core along the dorsal radius. Then we used the established $^{87}\text{Sr}/^{86}\text{Sr}$ baseline for Central Valley rivers (Barnett-Johnson et al., 2008; Ingram & Weber, 1999; Phillis et al., 2018; Sturrock et al., 2015; Willmes, Hobbs, et al., 2018) to classify the natal origins of each fish to the individual river level using a classification and regression tree (CART) approach. For return years prior to 2018, we constrained the baseline data to only the Sacramento River watershed, while for later years we also included the Mokelumne River hatchery as a potential source (Figure S2). This decision was based on the negligible occurrence of out-of-basin strays in the CWT data prior to 2018, but a considerable increase since then in Mokelumne River hatchery strays (Dean & Lindley, 2023; Kormos et al., 2012; Letvin et al., 2021a,b; Palmer-Zwahlen & Kormos, 2013). Data were resampled to 30 samples per source, with replacement, and then split into training (80%) and test (20%) data and a bagging (bootstrap aggregating) ensemble algorithm was used (500 trees, 10-fold cross-validation) to improve the stability and accuracy of the decision tree using the CARET package (Kuhn, 2008). For the model constrained to the Sacramento River watershed, this approach resulted in classification accuracy of 95% (CI 87%–99%, kappa = 95%) as evaluated on the test data. For the model including the Mokelumne River hatchery classification accuracy was 94% (CI 86%–98%, kappa = 94%). In both models all Yuba River origin samples were correctly classified (Table S1). When the natal origin of a fish could not be assigned to a single natal source with high classification confidence ($\geq 75\%$) we combined the best natal matches until they reached $\geq 75\%$ classification confidence to create a combined natal origin. Fish assigned to hatcheries that less frequently stray into the Yuba River (Coleman National Fish hatchery and Nimbus fish hatchery), or where the assignment to FRH or MOH was with similar probabilities, were grouped as aggregated hatchery strays for data visualization (AHS). Fish with uncertain assignments between a wild or hatchery source were labeled as “unclassified” as we could not discern their origin. Finally, fish coming from the Thermolito Rearing Annex were grouped together with Feather River Hatchery fish given that both groups of fish begin their life in that hatchery.

2.8 | Escapement expansions

We estimated the total number of Yuba River origin fish based on the otolith geochemical analyses and the escapement data from the Vaki Riverwatcher (Poxon & Bratovich, 2020). The Vaki Riverwatcher provides data on the total escapement and proportion of fish with a clipped adipose fin (representing coded wire tagged hatchery fish) and includes only fish above Daguerre Point Dam. We first estimated the proportion of Yuba River origin fish based on our otolith analyses and then applied that proportion to the escapement numbers of unmarked fish.

2.9 | Size at emigration

The size that Yuba River origin fish had outmigrated from the natal river as juveniles was reconstructed using $^{87}\text{Sr}/^{86}\text{Sr}$ profiles, specifically, the otolith distance from the core to when $^{87}\text{Sr}/^{86}\text{Sr}$ values first deviated higher or lower than the range of values measured in the Yuba River mainstem below Englebright Dam (0.70756–0.70885) based on the Central Valley strontium isoscape. Otolith distances were measured along a standardized 90° transect (Barnett-Johnson et al., 2007) and used to classify migratory phenotypes using the cut-offs and fork-length (FL) conversion equation in Sturrock et al. (2020) that was built using fall-run juveniles only (equation based on otolith radius on the dorsal axis (R) measured in microns: $\text{FL} = \text{if } (R < 264, 0.01334R + 30, \text{else}[0.15989R - 8.6892])$). FL cutoffs: fry ≤ 55 mm, parr > 55 to 75 mm, smolts > 75 mm, yearlings > 110 mm; Table S2). Size- and age-at-natal exit are highly correlated in these early life stages and thus small outmigrants tend to leave the natal river early, around February, and smolt migrants tend to leave late, around May, while yearlings tend to leave the following fall (Williams, 2006).

2.10 | Otolith daily growth rate analysis

Juvenile daily growth rates during freshwater residence were estimated for Yuba River origin Chinook salmon randomly sampled from outmigration years characterized by the most extreme flow conditions (low flow = 2007–2008 and high flow = 2017). Specifically, we estimated daily increment widths for 33 fish from wet year 2017, representing $n = 17$ and $n = 16$ fish randomly selected from fry and non-fry migrants, respectively, and 37 fish from low flow years, representing $n = 20$ fry migrants randomly selected from 2008, and $n = 8$ and $n = 9$ non-fry migrants randomly selected from 2007 and 2008, respectively. Note that we needed to include some 2007 fish as there were so few non-fry migrants that returned from the critically dry year 2008. Overall, of the fish analyzed, 47 were female, and 23 were male. The dorsal axis of each otolith was imaged at 200 \times magnification using a Q imaging digital camera (MicroPublisher 5.0 RTV) mounted to an Olympus BX60 microscope using ImagePro Premier. The daily increment widths were measured along a standardized 90° transect (Barnett-Johnson et al., 2007) from the exogenous feeding check (representing emergence from the gravel) to when that individual had left freshwater, determined via otolith $^{87}\text{Sr}/^{86}\text{Sr}$ (Figure S3). Confidence in increment reads was assessed among two otolith readers and otoliths identified as outliers or with low confidence in increment reads were re-measured.

We used mixed-effects generalized additive models (GAMMs) (“mgcv” package; Wood [2017]) to compare growth rates between habitats (natal; Yuba, vs. non-natal; anywhere not in the mainstem Yuba River, i.e. including Feather and Sacramento Rivers, potentially Yolo and Sutter Bypasses, and freshwater Delta), sexes, and high (2017) vs. low (2007, 2008) flows. To standardize growth comparisons, we isolated days 20–100 from all fish and only included increments deposited in natal (non-fry migrants) and non-natal (fry migrants) habitats for a given individual (Figure S4). Days < 20 were

excluded given that this is when most fry migrants were transitioning among habitats (Figure S4) and days >100 were excluded as this was when many chronologies ended, and beyond this age there was little natal rearing in any year. We modeled daily growth rates using restricted maximum likelihood (REML) and a smooth term ($k = 10$) with a random effect of fish ID to account for ontogenetic and individual trends (after Coleman et al., 2022). For the fixed effects we included sex and an interaction between flow (high/low) and rearing habitat (natal/non-natal). Finally, we added a penalty term in the smoothness selection procedure (Marra & Wood, 2012) to effectively exclude unimportant predictors, and tested and corrected for autocorrelation using the 'itsadug' package (van Rij et al., 2022). To statistically compare growth rates among each habitat-flow type combination, we used Tukey's pairwise comparisons ('emmeans' package; Lenth, 2021). All statistical analyses were carried out in R 4.2.3 (R Core Team, 2023).

3 | RESULTS

3.1 | Genotype diversity

To investigate the genotypic diversity of Yuba River origin fish, we first screened the sample for hatchery and natural origin strays using otolith

geochemistry. Overall, based on otolith geochemistry, Yuba River origin fish represented 7%–73% of the spawners in the six escapement years examined (Table 2), with the rest being strays, mostly from nearby Feather River hatchery, and from 2018 onwards also from the Moke-lumne River hatchery (Figure S5). Genotypic run assignments were made for 135 Yuba River origin fish, in which we identified all three GREB1L genotypes—homozygous early, heterozygous, and homozygous late (Figure 2). Homozygous late-running individuals were generally the most common (mean across years = 52%), but homozygous early-running fish ranged from 14% (2020) to 50% (2011) and were observed in all years (mean across years = 30%) (Table S3). For years with random sampling and larger sample sizes of genotyped individuals (2009, 2010, 2019) we estimated the total number of Yuba origin fish with different GREB1L designations based on the VAKI river escapement estimates and marked fish rates (Table 3). These expansions suggested 631, 732, and 380 Yuba-origin spring-run spawners for escapement years 2009, 2010, and 2019, respectively. The total number of spring-run in the Yuba River is potentially higher, as our expanded estimates only account for fish passing Daguerre Point Dam (excluding fish spawning in the lower river).

While fin clips – and thus GREB1L genotypes – were unavailable for the six fish that were tagged in spring (i.e., known phenotypic spring-run), previous work has shown strong relationships between genotype and phenotype (Hugentobler et al., 2024), and of these six

TABLE 2 Expanded numbers of Yuba origin fish for the study time series.

Escapement year	Total escapement	Proportion adipose fin clipped	Marked escapement	Unmarked escapement	Yuba origin escapement proportion	Total Yuba origin escapement
2009	4558	0.17	757	3801	0.73	2761
2010	6384	0.40	2541	3843	0.53	2027
2011	7756	0.22	1737	6019	0.29	1739
2018	3060	0.38	1175	1885	0.07	126
2019	2691	0.19	506	2185	0.63	1375
2020	3868	0.16	607	3261	0.28	910

Note: The total escapement and proportion of fish with a clipped adipose fin (representing coded wire tagged hatchery fish) was obtained from Vaki Riverwatcher data (Poxon & Bratovich, 2020) and includes only fish above Daguerre Point Dam.

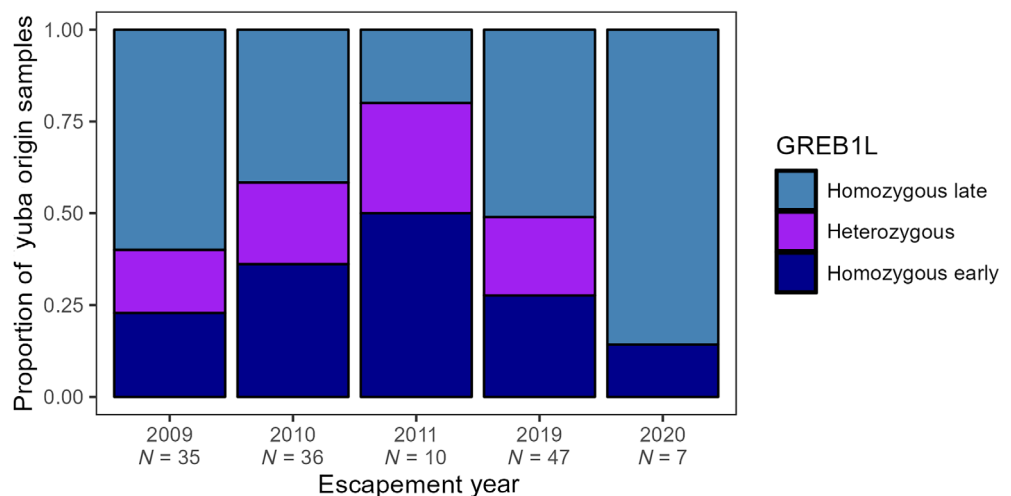


FIGURE 2 Genotypic assignments for Yuba River origin fish using the GREB1L locus for run timing, separated by escapement year. Note that earlier spawning fish were preferentially analyzed from escapement years 2011 and 2020, so caution should be applied to interpreting the frequencies from these 2 years.

TABLE 3 Expanded numbers of Yuba origin fish for each genotype per year (2009, 2010, 2019)

Year	Ad clipped	Total escapement	Marked escapement	Unmarked escapement	Yuba river natal origin proportion	Yuba river origin escapement	GREB1L	GREB1L proportion	Yuba river origin escapement by Greb1L
2009	0.17	4558	757	3801	0.73	2761	Homozygous early	0.23	631
2009	0.17	4558	757	3801	0.73	2761	Heterozygous	0.17	473
2009	0.17	4558	757	3801	0.73	2761	Homozygous late	0.60	1657
2010	0.40	6384	2541	3843	0.53	2027	Homozygous early	0.36	732
2010	0.40	6384	2541	3843	0.53	2027	Heterozygous	0.22	451
2010	0.40	6384	2541	3843	0.53	2027	Homozygous late	0.42	845
2019	0.19	2691	506	2185	0.63	1375	Homozygous early	0.28	380
2019	0.19	2691	506	2185	0.63	1375	Heterozygous	0.21	293
2019	0.19	2691	506	2185	0.63	1375	Homozygous late	0.51	702

Note: The total escapement and proportion of fish with a clipped adipose fin (representing coded wire tagged hatchery fish) was obtained from Vaki Riverwatcher data (Poxon & Bratovich, 2020) and includes only fish above Daguerre Point Dam.

TABLE 4 Results of the age reconstructions from otoliths and scales.

Natal origin	Sex	Age proportion by sex			n
		2	3	4	
YUB	F	0.10	0.74	0.16	93
YUB	M	0.10	0.75	0.16	63
FRH	F	0.11	0.76	0.14	37
FRH	M	0.32	0.40	0.28	25
MOH	F	0.03	0.62	0.34	29
MOH	M	0.50	0.17	0.33	12
FEA	F	0.13	0.88	NA	8
FEA	M	NA	1.00	NA	3
AHS	F	NA	0.75	0.25	4
AHS	M	0.40	0.40	0.20	5
Unclassified	M	0.43	0.43	0.14	7
All origins	M + F	0.19	0.67	0.14	286

Abbreviations: YUB, Yuba River; FRH, Feather River Hatchery; MOH, Mokelumne River Hatchery; FEA, Feather River; AHS, aggregated hatchery strays (strays assigned to any of the other Central Valley hatcheries or to MOH and FRH with similar probability). Fish that could not reliably be classified as either wild or hatchery origin are labelled as "Unclassified".

fish, half were identified as having been born in the Yuba River 2–4 years earlier.

3.2 | Phenotype diversity

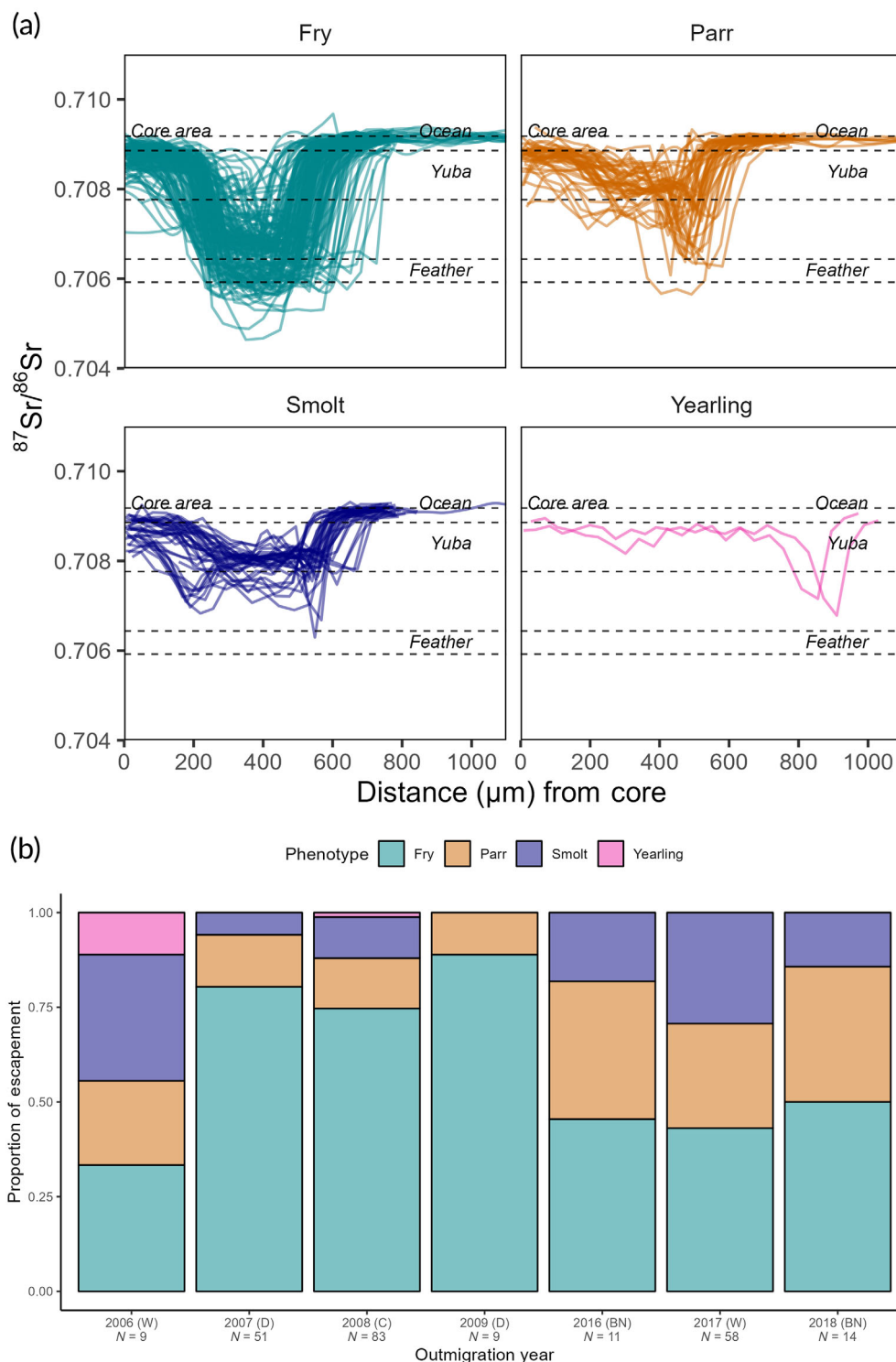
To link the returning adults to the flow conditions they had experienced in the Yuba River during juvenile rearing and outmigration, we

determined age-at-return for every individual. All fish returned at age 2–4 years old (Table S4). Focusing on age distributions for the years with random sampling ($n = 286$ fish; Table 4), the natural origin fish had a higher tendency to return at age 3 (means for both sexes: 74% Yuba River, 94% Feather River) than the Feather River Hatchery (58%) and Mokelumne River Hatchery (40%). Feather and Mokelumne River Hatcheries produced three to five times more age-2 male returns than either wild source, but also approximately two times more age-4 males compared to Yuba origin males (Table 4).

We then determined juvenile migratory phenotypes for all Yuba River origin fish with corresponding age data ($n = 235$). Strontium isotope profiles revealed a variety of different strategies and extensive non-natal rearing downstream of the Yuba River (Figure 3a). In general, fry migrants left the Yuba River almost immediately after emergence (median size at natal exit = 252 μm otolith radius, equivalent to 33 mm FL; median age for the subset with increment reads = 8 days post-emergence). Fry migrants then reared in downstream freshwater habitats until going out to sea at a similar size to the other subyearling phenotypes (Figure 3a). Parr and smolt migrants typically spent around 2–4 months rearing in the natal river before moving downstream in spring (median size at natal exit: 453 μm and 64 mm FL vs. 534 μm and 77 mm FL, respectively; median age for the subset with increment reads = 70 and 99 days post-emergence, respectively). Conversely, yearlings spent the entire summer in the Yuba River before emigrating the following fall (median size and age at natal exit = 795 μm and 118 mm FL, and 229 days post-emergence), however we only observed two fish that represented the rare yearling phenotype.

Overall, fry were the most commonly represented phenotype, averaging 59% of Yuba-origin returns per year (range = 33%–89%; Figure 3b). The three GREB1L genotypes exhibited clear temporal separation in the carcass sampling dates (range = September 21 to December 15), but no relationship with juvenile outmigration

FIGURE 3 (a) Strontium isotope profiles for Yuba River origin Chinook salmon faceted by the four different juvenile migratory phenotypes. The mean global ocean value (0.70918) and the range of isotopic values observed in the Yuba and Feather Rivers are shown by dashed lines. (b) Phenotype frequencies for Yuba River origin fish by outmigration year and water year type, based on the Sacramento Water Index: C, critical; D, dry; BN, below normal; W, wet.



phenotypes (Figure 4). Interestingly, the only yearlings successfully genotyped ($n = 2$) were both homozygous late, suggesting they were fall-run rather than spring-run Chinook salmon, and both carcasses were found late in the spawning season (Figure 4).

There was a correlation in fry vs. non-fry frequencies among years that appeared to be associated with the flow conditions experienced during outmigration (Figure 5a). In general, later migrating juveniles (>55 mm FL comprising parr, smolts, and yearlings) returned at higher rates when outmigration flows were higher, accounting for

57%–67% of the returning adults from wet years (2006, 2017) vs. 11%–20% from dry and critical outmigration years (2007–2009) (Figure 5 and Table S5).

3.3 | Growth diversity

Otolith increment widths exhibited an ontogenetic trend with age, showing a general increase in fish growth rate from emergence to a

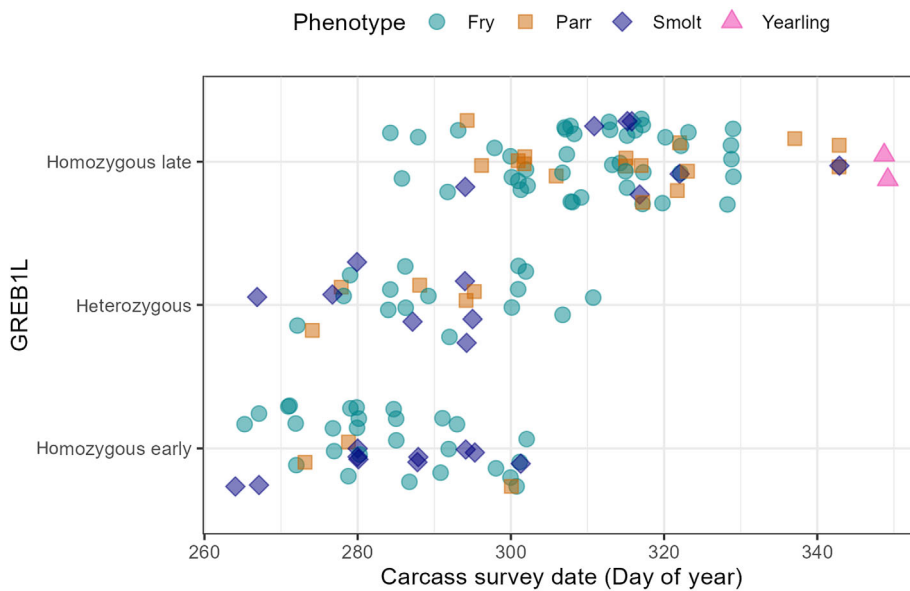


FIGURE 4 Sampling dates for all fish, separated on the y axis by GREB1L genotype and colored by their outmigration phenotype identified using otolith strontium isotopes.

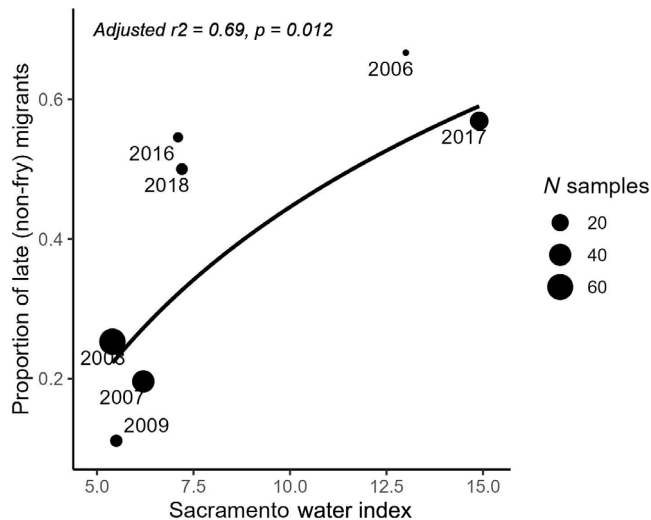


FIGURE 5 Relationship between the Sacramento Water Index and the fraction of Yuba-origin adults that left the natal river as a late migrant (>55 mm FL, i.e. parr, smolt or yearling), fitted with a logistic curve weighted by the number of samples (circle size). Labels represent outmigration year.

peak growth rate typically at about 60–90 days post-emergence (Figure 6a). The exception was among wet year late migrants, whose growth rates continued to increase throughout their period of freshwater residence. Generally, peak growth was highest in early fry migrants that reared non-natally downstream, particularly around February to March (days 55–70) of low flow years 2007–2008. However, fish in low flow years also exhibited rapid declines in growth towards the end of the season, exhibiting the lowest growth rates observed around April to June (days 90–150; Figure 6a). Late migrants in high flow year 2017 showed increasing growth through the season, reaching peak growth rates from day 90 onwards (Figure 6a).

A GAMM analysis focusing on the earlier part of the season when there was high representation of individuals and limited among-

habitat movement (20–100 days), indicated a significant effect of flow (high vs. low) and habitat (natal vs. non-natal) on otolith increment widths, after accounting for temporal autocorrelation in the chronologies and the ontogenetic trend in growth. No effect of sex was detected ($p > 0.05$). The model explained about half of the observed variation (deviance explained 47.9%; Table 5). Post hoc pairwise comparisons indicated significantly higher growth rates during non-natal rearing in low flow years compared with natal rearing in either low or high flow years (Figure 6b and Table 5).

4 | DISCUSSION

Monitoring changes in intraspecific biodiversity is crucial for species management and recovery and requires using a broad toolbox approach and sampling the population(s) at appropriate time frames across a range of environmental conditions. Spring-run Chinook salmon used to be highly abundant and the foundation of the commercial salmon fishery in California, but have experienced drastic declines over the last century (Yoshiyama et al., 1998, 2000). The current status of spring-run in the Yuba River is uncertain due to the potential dependency on and introgression with straying Feather River hatchery origin fish (Lindley et al., 2004, 2007). Here, we combined genetics and biochronologies to investigate three key aspects of intraspecific diversity of Yuba River origin fish: (1) adult migration phenotypes, (2) juvenile migratory phenotype frequencies, focusing on the size and age at which they outmigrated from the Yuba River, and (3) juvenile growth diversity during natal and non-natal rearing.

4.1 | Adult migration diversity

Our combined otolith and genetic analyses show that 7%–73% of adults spawning in the Yuba River had been born on the Yuba River,

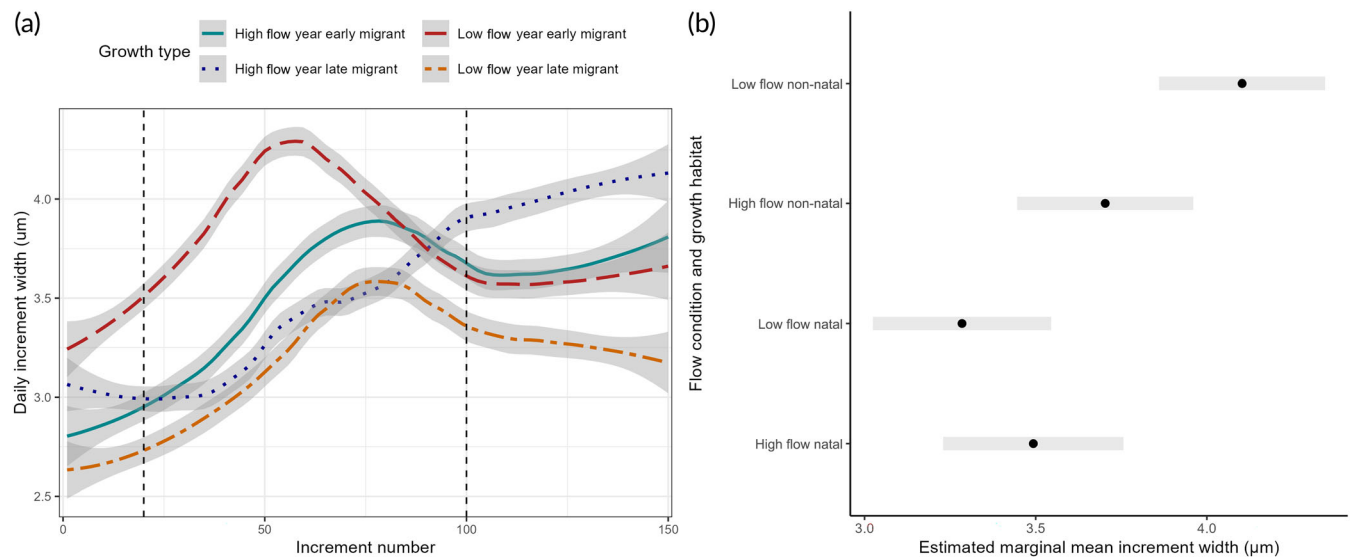


FIGURE 6 (a) Juvenile salmon growth rates from emergence (day zero) to around freshwater exit (which varies by individual, but can extend to day 150, which would be approximately June 1 assuming an emergence day of January 1). Data are separated into early (fry) and late (parr/smolts/yearlings) migrants that emigrated in low (2007–2008) vs. high (2017) flow years, fitted with a LOESS smoother (span = 0.3) ± standard error (gray area). Dashed vertical lines show the period isolated for the GMM given that this is the period when most individuals remained in a single rearing habitat. (b) Mean increment widths for juvenile salmon rearing in natal vs. non-natal habitats (days 20–100), in low (2007–2008) vs. high (2017) flow years, after accounting for temporal autocorrelation in the increment data.

TABLE 5 Post hoc pairwise comparisons from a GMM comparing natal vs. non-natal growth in low (2007–2008) vs. high (2017) flow years, derived from the estimated marginal mean daily otolith increment widths during the first 100 days post-emergence.

Pairwise comparison	Estimate	SE	t ratio	p value
High flow natal – low flow natal	0.21	0.18	1.15094	0.65787
High flow natal – (high flow non-natal)	–0.21	0.18	–1.17895	0.64021
High flow natal – (low flow non-natal)	–0.61	0.17	–3.54405	0.00225
Low flow natal – (high flow non-natal)	–0.42	0.18	–2.35135	0.08688
Low flow natal – (low flow non-natal)	–0.82	0.17	–4.75790	0.00001
(High flow non-natal) – (low flow non-natal)	–0.40	0.17	–2.39075	0.07896

Note: p values use a Tukey adjustment. Results are averaged over the levels of sex.

and that Yuba River origin fish display both spring- and fall-run phenotypes and genotypes. Homozygous late-running fish (fall-run) were generally most common, but homozygous early-running fish (spring-run) were present in all years, demonstrating that the Yuba River supports a population of wild-produced spring-run individuals. Our results also show there are a number of GREB1L heterozygous individuals in the Yuba River. This presence of heterozygous fish may be due to introgression between the runs from artificially compressed spawning habitat availability resulting from dam construction and/or due to the influence of the Feather River Hatchery, which has artificially mixed the two runs in the hatchery in the past. Future work is needed to further evaluate the role of heterozygous fish in the CCV Chinook portfolio, but other studies suggest that these fish may have an intermediate run timing, which could lead to future habitat-phenotypic mismatches (Thompson et al., 2019; Hugentobler et al., 2024). Our data – along with those presented in Hugentobler et al. (2024) – suggest that the Yuba River consistently produces spring-running fish every year. Across years, an average of 30% of post-

spawned Yuba-origin adults exhibited a homozygous early-running genotype, and in years with larger sample sizes and random sampling strategies (escapement years 2009, 2010, and 2019), the fraction of spring-running genotypes was fairly consistent (23%, 36%, and 28%, respectively).

Whether or not the progeny of Yuba River spring-run origin adults are returning at high enough rates to result in positive population growth needs to be monitored and assessed. Importantly, Yuba-origin spring-run adults often outnumbered spring-run returns to Mill and Deer Creeks, which are often considered to be the last of the wild spring-run. In the three years with reliable sample sizes, encompassing a full decade of returns (2009, 2010, 2019), the number of Yuba-origin spring-run spawners above Daguerre Point Dam was estimated here to be 631, 732, and 380 individuals, respectively. In contrast, the number of spring-run Chinook salmon estimated to have spawned in Mill and Deer Creeks in 2009, 2010, and 2019 was 237, 482, and 180 (Mill Creek) and 213, 262, and 585 (Deer Creek), respectively (Johnson et al., 2023). While all these populations are still exhibiting

lower abundances than Butte Creek (estimates of 989, 1661, and 3867, respectively; Johnson et al., 2023), it may be that the threatened spring-run ESU has more strongholds than previously thought. Using a toolbox approach (e.g., reintroduction programs, functional flows, and habitat restoration) and monitoring changes in abundance and phenotypic diversity across a range of populations will be critical for Central Valley spring-run recovery. Indeed, proposals are already in place to reintroduce spring-run Chinook salmon into the upper Yuba River watershed, where these fish have been extirpated since the construction of Englebright Dam (NMFS, 2014, 2022).

The more spring-run populations that exist across the freshwater habitat mosaic (Stanford et al., 2005), the stronger the portfolio effect should be (Cordoleani et al., 2024; Schindler et al., 2010). However, it is important to note some caution as the Yuba River is still heavily influenced – and potentially numerically supported in low return years – by strays from the Feather River Hatchery, increasing the potential for introgression between hatchery and natural origin fish of both run types (Lindley et al., 2004). Future modeling efforts should explore the trade-offs between numerical supplementation by hatcheries and potential demographic rescue (e.g., following drought) vs. potential negative fitness impacts from introgression between hatchery and wild stocks. Indeed, while our otolith natal assignments were performed on unmarked fish only (thus excluding Feather River Hatchery spring-run), the Constant Fractional Marking Program shows that, for escapement years 2010 and 2019, c. 33% and c. 6% of Yuba River spawners (representing c. 2106 and c. 196 individuals) were Feather River Hatchery spring-run origin and c. 35% and c. 50% of spawners were Feather River Hatchery fall-run (representing c. 4584 and c. 1354 individuals, respectively). Such large influxes of hatchery fish each year could mean that a large fraction of our ‘Yuba origin spring-run’ could be the direct offspring of Feather River Hatchery spring-run fish spawning in the Yuba River. While there is concern that hatchery-produced salmon exhibit lower fitness than their wild counterparts in natural settings (Araki et al., 2008; McConnell et al., 2018), some reintroduction efforts have effectively used hatchery-origin fish to reestablish locally adapted salmon populations without the continued reliance on hatchery supplementation (Nuetzel et al., 2023). To support locally adapted spring-run populations on the Yuba River, it may be necessary to reduce the proportion of hatchery origin spawners in the river to achieve a proportionate natural influence (PNI) of 0.5, as per the guidance of the California Hatchery Scientific Review Group (HSRG, 2012).

4.2 | Outmigration strategies across different flow conditions

We found that returning adults were represented by a wide variety of juvenile migratory phenotypes, with fry migrants being by far the most common (33%–89% of returns per escapement year). This differs from the fry contribution rates on the Stanislaus River (5%–23% per year; Sturrock et al. 2020), which is in the warmer and more water scarce San Joaquin basin. The Stanislaus River also drains into the southern Delta, which is highly degraded and home to some of

the largest water diversions and predator hotspots in the system (Michel et al., 2020). Conversely, the Yuba River drains into the lower Feather River and its fry migrants can rear in a mosaic of different habitats, including the Feather River and its adjacent tributaries such as Bear Creek, as well as remnant floodplain on the Sutter Bypass, which is known to support rapid salmon growth (Cordoleani et al., 2022). In the returning adults we also observed the parr and smolt life histories in high numbers, but only a negligible number of yearlings ($n = 2$). This contrasts to Mill and Deer Creeks, where the yearling phenotype was the most common, particularly following drought years (Cordoleani et al., 2021). The rarity of yearlings on the Yuba River was surprising, given that temperature modeling suggests suitable over-summer temperatures below those of the Englebright dam (Cordoleani et al., 2021). It may be that the habitat characteristics of the lower Yuba River (e.g., prey availability) might be insufficient to support juveniles over the summer months, or that the modeling in Cordoleani et al. (2021), which was based on a mean monthly stream temperature model, averaged out temperature spikes in summer months that would be lethal to an over-summering juvenile salmon. In Butte Creek, another spring-run producing river lacking access to high elevation habitat, yearlings were also very rare among the adult returns (Cordoleani et al., 2024).

Interestingly, we found no relationship between adult genetic run timing and their juvenile outmigration phenotype. While fall-run salmon can produce yearlings if suitable temperatures can be found on the valley floor, it is typically a more common strategy among spring-running fish given their increased propensity to use higher elevation, cooler spawning habitats if available (Lindley et al., 2007). However, both yearlings identified in this study were associated with the homozygous late-run timing GREB1L allele, suggesting that they were fall-run fish.

The years included in this study were specifically targeted to encompass a variety of hydrologic conditions (both at outmigration and return) to create a more realistic contemporary “biodiversity baseline” from which to compare future metrics to, and to assess whether outmigration strategies and growth varied with streamflow. While we focused on flow as it is the easier metric to measure, it is important to note that flow and temperature are highly correlated, and both play important roles in shaping juvenile salmon phenotypes. Specifically, flow and temperature – both their absolute values and changes through time – can represent important migratory cues for juvenile salmonids (Sturrock et al., 2020) and also play a critical role in determining juvenile survival in this system (Michel, 2019; Sturrock et al., 2015). While there are many examples of studies showing increases in fry expression (the fraction of juvenile production that leaves the natal river at sizes <55 mm FL) at higher flows (Apgar et al., 2021; Sturrock et al., 2015, 2020), including some rotary screw trap data from the Yuba River itself (Yuba Accord RMT, 2013), the otolith data suggested that the percentage of fry migrants in the returning adults (i.e., the survivors) was negatively correlated with streamflow. Indeed, the fraction of parr and smolt outmigrants was more than two times higher in the adults that returned from cooler, wetter outmigration years (mean = 57% of the returns from outmigration cohorts 2006, 2016, 2017 and 2018 vs. mean = 19% from 2007,

2008 and 2009). While we do not have screw trap data for the Yuba River for many of the years in this study - so cannot determine whether this trend results reflect expression vs. post-migration selection - our hypothesis is that this difference reflects time-selective processes, with high temperatures through the migratory corridor in spring and summer hypothesized to disproportionately select against late non-fry migrants in drier years. Indeed, smolt survival rates through the freshwater Sacramento-San Joaquin River Delta are often extremely low in late spring and summer of low flow years, where poor water quality, high temperatures, low food availability, and warm-adapted introduced predators cause high levels of mortality (Buchanan et al., 2018; Nobriga et al., 2021; Sturrock et al., 2022).

4.3 | Juvenile growth rate diversity

Juvenile growth rates were generally faster for early outmigrants that reared in non-natal habitats. The entire Central Valley has experienced widespread anthropogenic alteration, particularly substantial losses of wetlands and floodplain habitats which are so important to juvenile salmonids (Cloern et al., 2021; Coleman et al., 2022; Jeffres et al., 2008). The lower Yuba River has been particularly impacted by historical gold mining and its legacy effects, the construction of multiple large dams and the associated flow modifications, and disconnection from its floodplains and the associated food production benefits (Cordoleani et al., 2022; Yoshiyama et al., 1998). While the river is now undergoing significant habitat restoration, aiming to enhance habitat complexity and increase the amount and access to off-channel habitats (<https://www.yubawater.org/404/Yuba-River-Habitat-Restoration-Agreement>), these efforts had not started when the fish studied here were present as juveniles in the river. As such, these data should provide a useful baseline from which to assess whether salmon growth rates and in-river residence times show the expected increases in years post-restoration. Importantly, however, abundance and density-dependent processes should always be considered, given that high levels of crowding and competition can significantly impair juvenile salmon growth, even in productive rearing conditions (Lindeman et al., 2015).

Given that low flow years are typically associated with less off-channel habitat and prey production (Cordoleani et al., 2022), it was unexpected to see significantly higher growth in non-natal habitats in low flow years. However, it is important to note that this model only compared salmon growth rates during days 20 to 100 post-emergence (typically January to March), when warmer winter temperatures can be highly conducive to salmon growth, especially when the Sutter Bypass is inundated and potentially providing prey subsidies to the tributaries downstream (Cordoleani et al., 2022; Sturrock et al., 2022). Importantly, however, this "treatment" (low flow, non-natal rearing) also exhibited the largest and most rapid declines in growth later in the season, presumably as a result of elevated temperatures, reduced water quality, and reduced prey availability (Sturrock et al., 2022). Increased metabolic rates among many warm-adapted, introduced piscivores present in the Delta (Nobriga et al., 2021) also likely resulted in additional

stress and reduced feeding rates later in the outmigration season. Interestingly, growth rates were fastest later in the season for the high flow year, particularly for the late migrating smolts. Note that most of the non-fry migrants left the Yuba River around day 100 (Figure S3), so the continually rising growth rates among these fish in high flow year 2017 were likely primarily explained by conditions experienced downstream of the Yuba River. Indeed, it is likely that the large-scale inundation of the Sutter Bypass in 2017 resulted in excellent rearing conditions downstream as temperatures started to rise (Cordoleani et al., 2022).

4.4 | Population and age compositions

While straying is a natural phenomenon among salmonids and is critical to establish populations in new habitats and increase genetic diversity, elevated straying rates of hatchery fish can reduce local adaptation and cause domestication selection (Araki et al., 2008). In the Central Valley, background straying levels of hatchery-produced Chinook salmon are typically 10% when the smolts are released directly from the hatchery (0.3%–9.1%; Sturrock et al., 2019), and are likely lower among wild individuals (e.g., <3.2% in the Lewis River in Washington; McIsaac (1990) and 0–6.7% [mean = 2.42%] for summer Chinook from the upper Columbia River; Pearsons & O'Connor, 2020). However, in this study, over 50% of the spawners on the Yuba River were strays, primarily from the nearby Feather River hatchery. Similar levels of straying have been observed in other systems (Westley et al., 2013) and are frequently even higher across the California Central Valley (Johnson et al., 2012; Sturrock et al., 2019). The variation we observed in natal contribution rates among years is likely due to variation in the abundance and survival of natural vs. hatchery origin juveniles caused by interannual differences in hydroclimatic regime (Michel, 2019; Sturrock et al., 2015) and hatchery practices (Huber & Carlson, 2015; Sturrock et al., 2019). In the Central Valley, trucking of millions of hatchery smolts direct to the San Francisco Estuary is particularly common during droughts and augments the survival advantage of hatchery fish even further by bypassing the dangerous journey through the Delta (Buchanan et al., 2018; Sturrock et al., 2022). Also, by disrupting their olfactory map, trucking results in abnormally high straying rates of hatchery fish (Sturrock et al., 2019). These factors likely explain the high fraction of strays observed in return year 2018, which primarily represents outmigrants from drought years 2015 and 2016, when survival rates of naturally migrating fish was almost certainly very low and when hatchery smolts were trucked, on average, 295 and 107 river kilometers (rkm) downstream of their natal hatchery, respectively (Sturrock et al., 2019). Conversely, the highest fraction of Yuba-origin returns was observed in return year 2019, which primarily represents outmigrants from wet year 2017, when survival of naturally migrating fish was likely high and hatchery smolts were generally released on site (mean trucking distance = 49 rkm, median = 0 rkm; Sturrock et al., 2019). Furthermore, fall 2019 was also wet, providing natural "attraction flows" that likely increased homing rates for all populations (Del Real & Saldate, 2014; Sturrock et al., 2019).

Salmon mature and return to spawn at different ages, and this age diversity is important for promoting population resilience and stability (Munsch et al., 2022; Price et al., 2021; Schindler et al., 2010), particularly in the face of extreme events such as droughts (Carvalho et al., 2023). Here, otolith- and scale-based age reconstructions showed that the Yuba River origin fish were heavily dominated by 3-year-olds, followed by 4-year-olds. This is typical for naturally reproducing Chinook salmon populations in the Central Valley (Satterthwaite et al., 2023; Sturrock et al., 2020), although it is important to recognize that the fraction of 4-year-olds would be naturally lower given their exposure to an extra year of natural and fishing mortality in the ocean (Chen et al., 2023). No 5-year-old fish were observed in this dataset, and these are generally found to be exceedingly rare throughout the Sacramento River watersheds (Satterthwaite et al., 2023; Sturrock et al., 2020; Willmes, Hobbs, et al., 2018). Here, Feather and Mokolumne River Hatchery males were about three to five times more likely to return age 2 than natural origin fish, which is frequently observed across ESUs, species, and systems (Chen et al., 2023), and typically explained by higher growth in the hatchery environment leading to earlier maturation (Ford et al., 2012; Milot et al., 2013). Unlike the results for winter-run salmon (Chen et al., 2023), Feather and Mokolumne River Hatchery males were also about two times as likely to return at age 4 than Yuba origin males. Given that older fish tend to be larger and fecundity increases nonlinearly with fish size (e.g., Barneche et al., 2018), if this were a common phenomenon across populations and sexes, this could lead to even higher levels of introgression between hatchery and wild populations.

4.5 | Conclusions

Our findings highlight the benefits of applying complementary analytical methods to quantify intraspecific biodiversity. By integrating otolith geochemistry, otolith microstructure, and genetics, we were able to reconstruct salmon origin, movement patterns, growth rates, and run timing. The results show the importance of life-history diversity in Yuba River salmon and suggest that this watershed may play a more prominent role in the future of the threatened spring-run ESU than previously thought. The data also provide a baseline from which to evaluate the impacts of restoration efforts and climate change. Overall, while it is generally agreed that maintaining intraspecific biodiversity is key to increasing resilience and productivity in an increasingly unpredictable climate, we have historically lacked the tools to monitor it at appropriate resolution or frequency (Roches et al., 2021). With the range of methods now at our disposal, it is essential we identify explicit diversity targets (alongside the more traditional abundance-focused goals) in restoration and management actions, and to monitor changes in relevant parameters through time. This will allow us to assess the effectiveness of conservation actions, to identify early warning signs of collapse, and to promote the stability of ecosystem services in an increasing uncertain environment (Greene et al., 2010; Johnson et al., 2014; Roches et al., 2021).

AUTHOR CONTRIBUTIONS

Conceptualization: A.M.S., M.W., N.S.O., and M.H.M. Methodology: M.W., A.M.S., S.H., G.W., K.E., and M.H.M. Investigation: A.M.S., M.W., F.C., S.H., and M.H.M. Visualization: M.W., A.M.S., F.C., and S.H. Supervision: R.C.J., M.H.M., and E.P.P. Writing—original draft: All authors. Writing—review & editing: All authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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ORCID

Malte Willmes  <https://orcid.org/0000-0001-8734-5324>

Anna M. Sturrock  <https://orcid.org/0000-0001-9423-9845>

Flora Cordoleani  <https://orcid.org/0000-0002-6017-2678>

Sara Hugentobler  <https://orcid.org/0000-0003-1239-7909>

Mariah H. Meek  <https://orcid.org/0000-0002-3219-4888>

George Whitman  <https://orcid.org/0000-0002-0701-0282>

Eric P. Palkovacs  <https://orcid.org/0000-0002-5496-7263>

Natalie J. Stauffer-Olsen  <https://orcid.org/0000-0003-1535-5691>

Rachel C. Johnson  <https://orcid.org/0000-0002-0278-7826>

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SUPPORTING INFORMATION

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