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ARTICLE

Fishery collapse, recovery, and the cryptic decline of wild salmon on a major California river

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Abstract: Fall-run Chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento–San Joaquin River system form the backbone of California's salmon fishery and are heavily subsidized through hatchery production. Identifying temporal trends in the relative contribution of hatchery- versus wild-spawned salmon is vital for assessing the status and resiliency of wild salmon populations. Here, we reconstructed the proportion of hatchery fish on natural spawning grounds in the Feather River, a major tributary to the Sacramento River, using strontium isotope ($^{87}Sr/^{86}Sr$) ratios of otoliths collected during carcass surveys from 2002 to 2010. Our results show that prior to the 2007–2008 salmon stock collapse, 55%–67% of in-river spawners were of hatchery origin; however, hatchery contributions increased drastically (89%) in 2010 following the collapse. Data from a recent hatchery marking program corroborate our results, showing that hatchery fish continued to dominate (~90%) in 2011–2012. Though the rebound in abundance of salmon in the Feather River suggests recovery of the stock postcollapse, our otolith chemistry data document a persistent decline of wild spawners, likely leading to the erosion of locally adapted Feather River salmon populations.

Résumé : Les saumons quinnats (*Oncorhynchus tshawytscha*) à migration automnale du réseau du fleuve Sacramento et de la rivière San Joaquin forment l'épine dorsale de la pêche aux saumons en Californie et sont fortement soutenus par la production en alevinières. La détermination des tendances dans le temps des apports relatifs de saumons issus d'alevinières et de saumons nés dans la nature est cruciale pour évaluer l'état et la résilience des populations de saumons sauvages. Nous avons reconstitué la proportion de poissons issus d'alevinières dans des aires de frai naturelles dans la rivière Feather, un important affluent du fleuve Sacramento, en utilisant les rapports d'isotopes de strontium ($^{87}Sr/^{86}Sr$) d'otolites prélevés durant des relevés de carcasses de 2002 à 2010. Les résultats montrent que, avant l'effondrement des stocks de saumons de 2007–2008, de 55 % à 67 % des frayeurs dans la rivière provenaient d'alevinières; toutefois, l'apport d'alevinières a connu une augmentation très marquée (89 %) en 2010 dans la foulée de l'effondrement. Les données tirées d'une campagne récente de marquage en alevinière corroborent ces résultats, démontrant que les poissons issus d'alevinières sont toujours prédominants (~90 %) en 2011–2012. Si la remontée de l'abondance des saumons dans la rivière Feather semble indiquer un rétablissement du stock à la suite de l'effondrement, nos données sur la chimie des otolites documentent un déclin soutenu des géniteurs sauvages, qui mène vraisemblablement à l'érosion des populations de saumons adaptées aux conditions locales de la rivière Feather. [Traduit par la Rédaction]

Introduction

The Sacramento–San Joaquin River system in California's Central Valley (CV) is the foundation of California's water supply, providing water for approximately 35 million residents and supporting a multibillion dollar agriculture industry, and is home to the southernmost spawning runs of Chinook salmon (*Oncorhynchus tshawytscha*) in the Northern Hemisphere (Fisher 1994; Yoshiyama et al. 1998; Moyle 2002; Williams 2006). Chinook salmon populations have persisted in California's highly variable Mediterranean climate by exhibiting a diverse portfolio, expressed as distinct run types (spring, fall, late-fall, winter) and plastic life history strategies (Yoshiyama et al. 1998; Hilborn et al. 2003; Williams 2006), which buffers population abundance against stochastic environmental variability. However, habitat loss and degradation, water diversions, fish harvest, and the construction of dams, which blocked large areas (>80%) of spawning habitat and rearing grounds, have resulted in population decline threatening the long-term survival of salmon in the CV (Yoshiyama et al. 2000, 2001). Spring- and winter-run Chinook salmon are listed as threatened and endangered, respectively, under the federal Endangered Species Act (NMFS 1999, 2005), while fall–late-fall-run salmon are considered species of concern and are targeted for harvest in the ocean fishery.

Hatcheries were built along CV tributaries to mitigate for dam construction and habitat loss, and many salmon populations in the CV are heavily subsidized by hatchery production (HSRG 2012, 2014; Palmer-Zwahlen and Kormos 2015). Fall-run Chinook salmon from the Sacramento–San Joaquin River system form the backbone of California's ocean salmon fishery, contributing sub-

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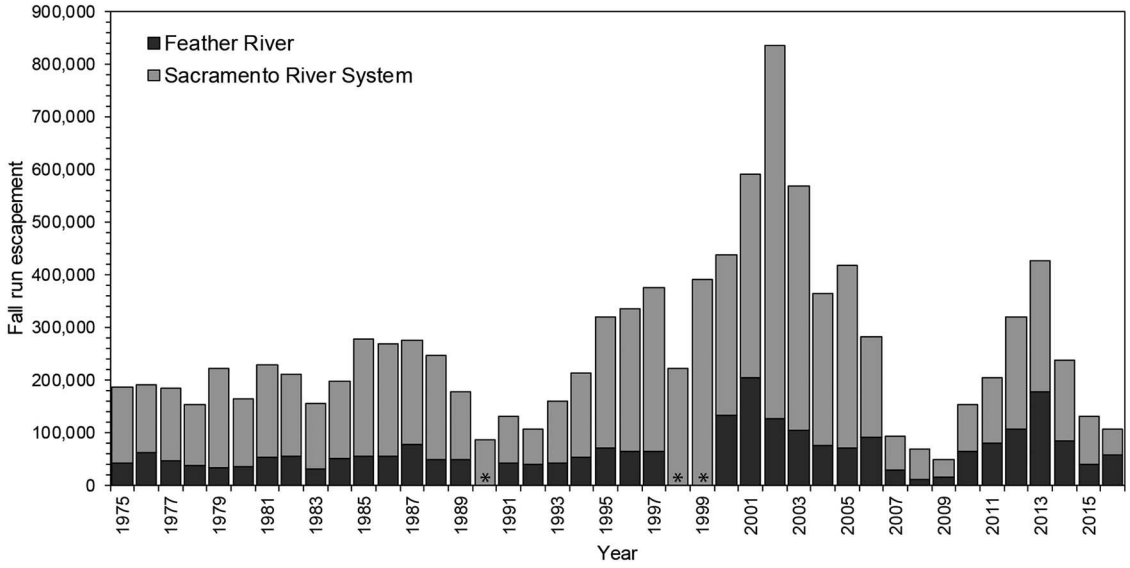
Fig. 1. Fall-run escapement estimates for the Sacramento River System (grey) and the Feather River (hatchery and in-river spawning population; black) from 1975 to 2016. Data from GrandTab2017.04.07, California Central Valley Chinook Population Database Report. An asterisk (*) indicates that there is no in-river escapement data available for 1990, 1998, and 1999 for the Feather River.



stantially to the fisheries off Oregon and Washington (Lindley et al. 2009; Satterthwaite et al. 2015), and are an integral part of the present and past culture in this region (Yoshiyama et al. 1998). However, wild stocks in several California rivers are now dominated by hatchery fish (Barnett-Johnson et al. 2007; Johnson et al. 2012; Quiñones and Moyle 2014), potentially eroding the long-term resiliency of wild, locally adapted populations by disrupting selection for heritable traits that improve lifetime reproductive success in variable environments.

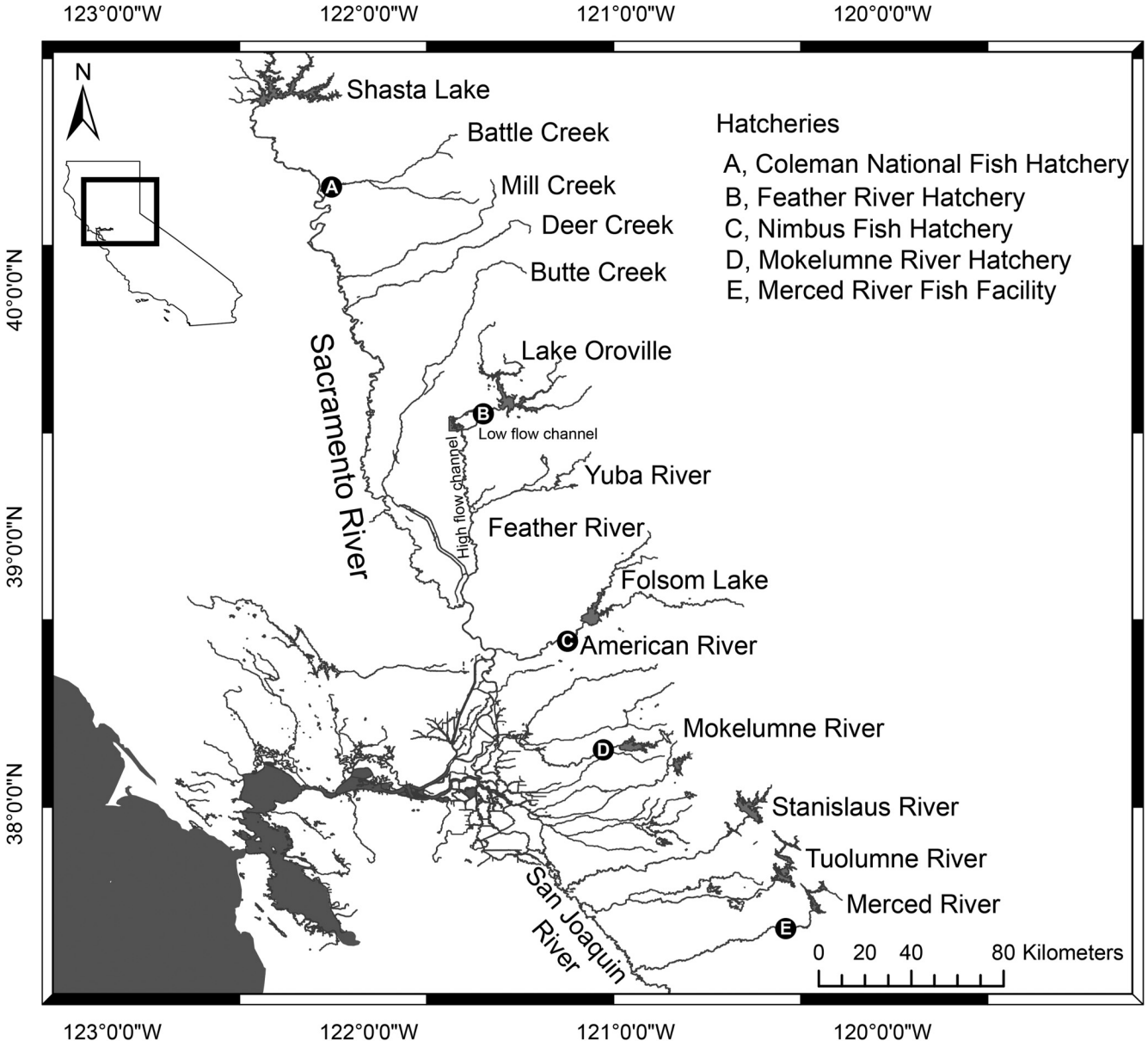
In 2007, record low numbers of adult salmon returned to the CV (Fig. 1), and forecasted low escapement resulted in the closure of the commercial ocean fishery off the coast of California and Oregon in 2008 and 2009 for the first time in over 100 years, causing major economic impact (Schwarzenegger 2008; Michael 2010). While the proximate cause of this stock collapse was attributed to low food availability in the coastal ocean in spring 2005 and 2006 (Lindley et al. 2009), the effect of hatchery practices likely contributed to a weakened CV salmon portfolio through increasing synchrony in fall-run population dynamics, further exacerbating the impact of climatic variability (Satterthwaite and Carlson 2015). After 2009, Chinook salmon fall-run escapement numbers rebounded, suggesting a quick and successful recovery of the salmon stock, before the decreases in 2014 and 2015 that were potentially linked to the recent prolonged drought period (Dettinger and Cayan 2014). Owing to the continued declines in wild salmon abundance, lack of hatchery management reform, and impending climate change, the fate of wild salmon in California are in jeopardy, and extinction in the wild is deemed likely if drastic management actions are not taken (Katz et al. 2012; Franks and Lackey 2015; Moyle et al. 2017).

Effective management, monitoring, and status assessment of wild salmon populations require reliable estimates of hatchery fish abundance on the natural spawning grounds (Araki et al. 2008; HSRG 2012, 2014; Christie et al. 2014; Quiñones et al. 2014). However, only recently have hatchery fish been consistently physically marked (adipose fin clip) and tagged (coded wire tags) in California rivers (Lindley et al. 2007; HSRG 2014). The California Constant Fractional Marking Program (CFM) began marking 25% of fall-run hatchery releases in 2007, providing a method to estimate hatchery contributions to natural spawning grounds since 2010 (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015). The results of the CFM program showed that most CV rivers have a high contribution of hatchery-origin fish in their natural spawning grounds, particularly those co-located with hatcheries, such as the Feather River (Palmer-Zwahlen and Kormos 2013). However, the CFM data cannot provide estimates prior to 2010 and thus does not inform stock composition prior to and during the salmon stock collapse. Without such estimates, it is impossible to quantify trends in the abundance of natural-origin fish (Johnson et al. 2012) or to evaluate population extinction risk (Lindley et al. 2007; Katz et al. 2012). Ultimately, understanding the extent of gene flow between hatchery- and natural-origin spawners is critical, since the influence of too many hatchery adults can reduce the fitness of subsequent generations in the wild (Waples 1991; McGinnity et al. 2003; Araki et al. 2008; Christie et al. 2014).

A variety of methods have been used to discriminate between hatchery- and natural-origin salmonids, including physical tags (Palmer-Zwahlen and Kormos 2015), genetics (Hauser et al. 2006), otolith microstructure (Barnett-Johnson et al. 2007), and otolith chemistry (Johnson et al. 2012, 2016). Otoliths (i.e., ear stones) consist of calcium carbonate and are found in the inner ear of bony fishes. They are metabolically inert and accrete continuously, producing a unique record of fish age and growth. Chemical elements from the environment are incorporated into the otolith, resulting in a chemical composition that can reflect the habitat occupied during deposition (Campana 1999). Strontium (Sr) is readily substituted for calcium in the mineral lattice, resulting in element concentrations and isotope ratios ($^{87}Sr/^{86}Sr$) that reflect environmental abundances and are frequently used to reconstruct individual movements (Rooker et al. 2001; Walther and Limburg 2012). In the CV, $^{87}Sr/^{86}Sr$ can be a powerful natural tag of fish origin, because the water $^{87}Sr/^{86}Sr$ isotope ratios vary among many of the salmon-producing rivers and hatcheries (Ingram and Weber 1999; Barnett-Johnson et al. 2008; Sturrock et al. 2015).

Here, we use otolith $^{87}Sr/^{86}Sr$ isotope ratios to identify natal origin of adult Chinook salmon spawning in the Feather River to determine the annual contribution of hatchery-produced fish to escapement years 2002–2010, encompassing the years of stock collapse and recovery. We refer to individuals that reared in the river as wild fish and fish that reared in the hatchery as hatchery fish, independent of their parental or genetic origin. Furthermore, we focused only on phenotypic fall-run salmon, defined as returning to in-river spawning grounds after 1 September, and did not examine the genetic run identity of these fish.

Fig. 2. Overview map of the study region and the hatcheries producing Chinook salmon. The Feather River is further divided into the High Flow and Low Flow channels. Data from the National Hydrography Dataset, US Geological Survey.



Materials and methods

The Feather River

The Feather River Basin is located in the foothills of the western Sierra Nevada (Fig. 2). The basin is a major contributor to the California State Water Project, and Lake Oroville, created by the completion of Oroville Dam in 1967, plays an important role in flood management, water storage, water quality, power generation, and recreation. The Fish Barrier Dam represents the uppermost barrier to upstream fish migration, as well as the location of the fish ladder entering the Feather River Hatchery (FRH). In addition to the main hatchery, there is an annex hatchery located along Highway 99, about 2 km south of Oroville Dam Blvd., with warmer water temperatures that provide opportunities for increased growth rates.

The Feather River Hatchery is one of the largest producers of CV Chinook salmon, supporting both spring- and fall-run populations (Fisher 1994; Yoshiyama et al. 1998). Historically, spring-run salmon returned from the ocean in spring–early summer and then held over summer and spawned in the uppermost reaches of small tributaries to the Feather River, while fall-run fish returned later in the fall and spawned in the lower foothill reaches of the mainstem river. Spawning for both populations is concentrated in approximately 12 river kilometres below Oroville Dam (Mercer and Kurth 2014). Hatchery broodstock management has attempted to separate the two runs; however, considerable mixing has occurred, resulting in substantial genetic introgression (Clemento et al. 2014; Meek et al. 2016*b*), and spring-run fish have hybridized with fall-run fish, resulting in overlapping run timings and frequent examples of "run-switching" between parents and offspring (Sommer et al. 2001).

The FRH maintains an integrated hatchery program resulting in considerable mixing of hatchery and wild fish in the fall-run hatchery broodstock and in-river spawning population (Williamson and May 2005; HSRG 2012). To reduce in-river mortality during seaward migration, juveniles produced by the FRH (and many other hatcheries in the CV) are trucked directly to San Pablo Bay

Table 1. Number of otoliths sampled and analyzed by recovery location (High Flow and Low Flow channels).

	Population estimates			Analyzed otoliths			Proportion of population sampled by otoliths		
Year	High Flow	Low Flow	Total	High Flow	Low Flow	Total	High Flow	Low Flow	Total
2002	34 125	71 038	105 163	41	70	111	0.15	0.12	0.13
2003	37 643	52 303	89 946	41	54	95	0.11	0.10	0.11
2004	17 113	37 058	54 171	35	64	99	0.24	0.17	0.19
2005	12 583	36 577	49 160	33	70	103	0.27	0.19	0.21
2006	16 990	59 424	76 414	23	49	72	0.14	0.08	0.09
2007	876	21 033	21 909	33	76	109	3.78	0.36	0.50
2008	297	5 642	5 939	27	62	89	9.09	1.10	1.50
2009	223	4 624	4 847	7	38	45	3.14	0.80	0.91
2010	2 201	42 713	44 914	4	28	32	0.18	0.07	0.07

Note: Population estimates are from GrandTab2017.04.07, California Central Valley Chinook Population Database Report and California Department of Water Resources (unpublished data, contact Jason.Kindopp@water.ca.gov).

and acclimatized in net pens prior to release. Since 2000, FRH has released 80%–100% of its fall-run production directly into the San Francisco Estuary or Bay (Huber and Carlson 2015). Because of a lack of olfactory imprinting during juvenile emigration, juveniles that are trucked stray disproportionately as adults to other rivers, resulting in increased gene flow among salmon populations (Palmer-Zwahlen and Kormos 2013, 2015; Huber and Carlson 2015; Meek et al. 2016*a*). Hatchery fish are also released over a relatively short time window, leading to reduced diversity in emigration phenology and increased risk of mismatch with optimal ocean conditions (Satterthwaite et al. 2014; Huber and Carlson 2015).

Otolith collection

Otoliths were collected from postspawned Chinook salmon between 2002 and 2010 as part of the annual carcass survey. For this survey, the Feather River is divided into 40 stream sections, each section corresponding to a single riffle–pool complex. The Low Flow Channel includes the Feather River from the Fish Barrier Dam to the Thermalito Outlet, and the High Flow Channel extends from the Thermalito Outlet downstream to the Gridley Bridge (Fig. 2). Otoliths were collected from a total of 50 fish per week, among 10 river sections randomly selected each week, five in the Low Flow Channel and five in the High Flow Channel. To ensure that these fish are representative of the overall population, the first five salmon carcasses, irrespective of size, sex, and presence or lack of adipose fin, were sampled within each of these randomly selected locations. This stratification of the river into sections ensures that the entire river's spawning grounds are surveyed equally (Table 1).

From this set of collected fish, a subset (n = 755) was selected for otolith analysis in proportion to fish abundances in the High Flow and Low Flow channels for each year. However, this was not possible for all years, leading to an uneven sample distribution between the High Flow and Low Flow channels. We used the escapement estimates for each recovery location as a weighting factors to incorporate this variation in subsampling into our estimations of hatchery and wild contributions to the overall escapement. In addition to these stratified samples, fish with coded wire tags (CWT, n = 110) were randomly selected and used to validate the otolith isotope assignments (natal origins).

Otolith sample preparation

Sagittal otoliths were extracted from each fish, cleaned, dried, labeled, and transferred to the Department of Wildlife, Fish, and Conservation Biology, University of California Davis. Otoliths were mounted in Epocure (Buehler Scientific) epoxy resin and thin-sectioned with an Isomet diamond cutting saw in the transverse plane. Thin sections were adhered to glass microscope slides with Crystal Bond thermoplastic resin (Crystalbond 509, Ted Pella Inc., Redding, California), sanded to the core on both sides with 1200–2000 grit sandpaper, and polished with 0.3 μm alumina and a polishing cloth, following methods from Wells et al. (2003). Digital images of otoliths were taken at 6× magnification on a CH30 Olympus compound microscope. Otoliths sections were washed with 1 mol·L^{-1} chemical grade nitric acid for 5 to 10 s, rinsed in an ultrasonic water bath for 5 min, and dried under a class 100 laminar flow hood.

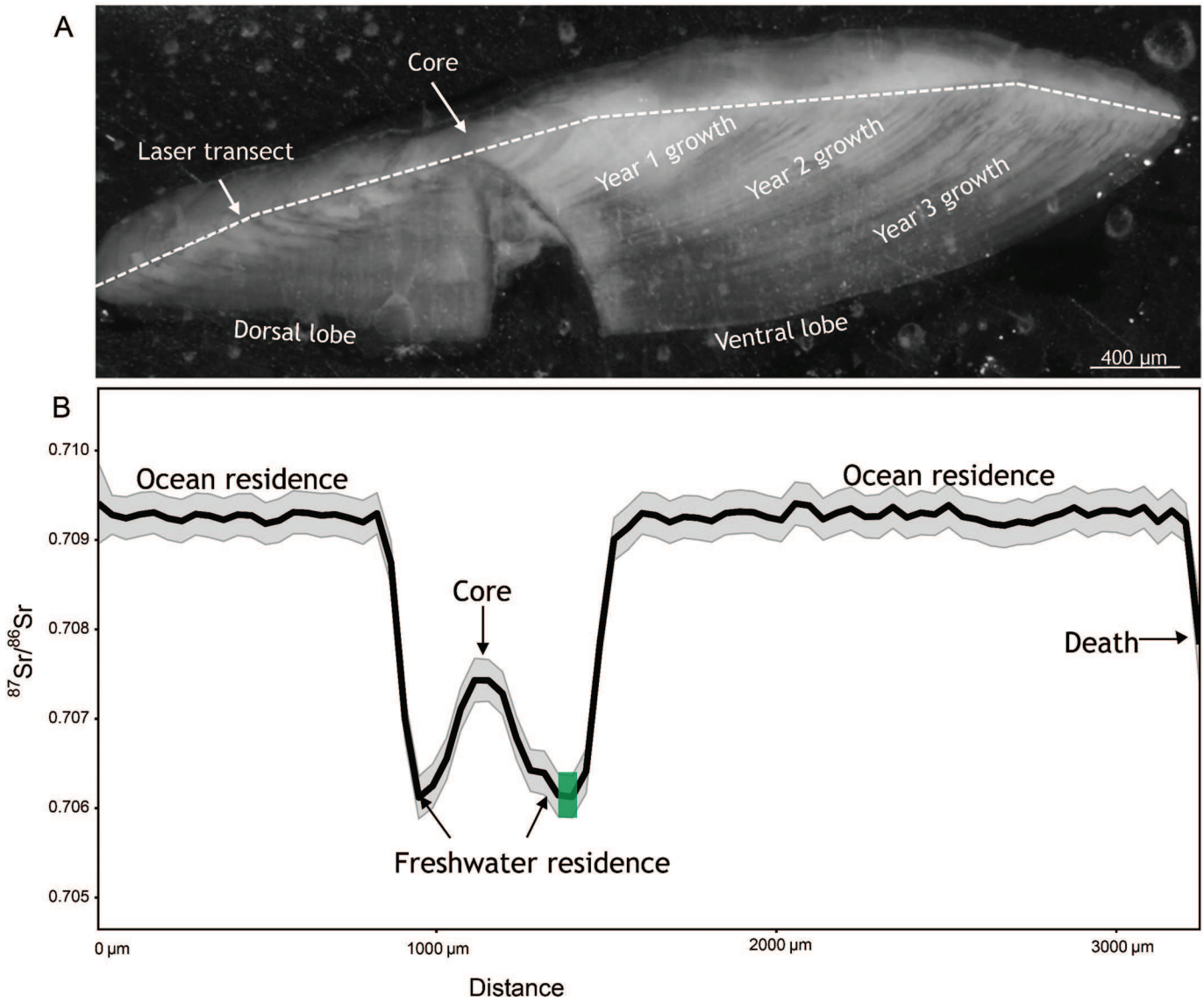
Otolith aging

Otoliths contain a unique time series of opaque and translucent bands that are deposited on a daily and seasonal basis in response to photoperiod, temperature, diet, and endogenous rhythms (Neilson and Geen 1982; Campana and Neilson 1985). On adult otoliths, an opaque zone followed by a translucent zone (Fig. 3) represents 1 year of otolith growth (Welch et al. 1993). Annual ages were estimated from digital images along the transverse plane of the ventral lobe (Fig. 3), counting the summer bands. We used the transverse section instead of the sagittal preparation typically used for juvenile habitat use and growth reconstructions (Woodson et al. 2013; Sturrock et al. 2015) to preserve the outer rings in the convex adult otoliths. Otoliths that were completely vateritic, or broken along the ventral lobe by the sanding process, were not aged. Ages were validated by comparing age counts with those of hatchery fish with physical tag information and known age (n = 74) and between two age readers following the methods proposed by Campana (2001) and using the FSA package (Ogle 2018) in R (R Core Team 2017). All fish were aged as either 2-, 3-, 4-, or 5-year-olds, consistent with the currently understood life history of the species (Fisher 1994).

Otolith Sr isotopic analysis

For laser ablation, otoliths were remounted on petrographic glass slides, with 20 individual otoliths per slide. $^{87}Sr/^{86}Sr$ isotope ratios were measured at the University of California Davis Interdisciplinary Center for Plasma Mass Spectrometry. For the in situ Sr isotope analysis, an Nd:YAG 213 nm laser (New Wave Research UP213) was coupled to a Nu Plasma HR MC-ICP-MS (Nu032). A laser beam of 55 μm diameter was traversed across the otolith from the core to the edge at 10 μm·s^{-1}, with the laser pulsing at 10 Hz frequency and 5–15 J·cm^{-2} photon output. The $^{87}Sr/^{86}Sr$ isotope ratio was normalized for instrumental mass discrimination by monitoring the $^{86}Sr/^{88}Sr$ isotope ratio (assuming $^{86}Sr/^{88}Sr$ = 0.1194), and ^{87}Rb was corrected by monitoring the ^{85}Rb signal. Krypton interference originating in the argon supply (^{86}Kr) was subtracted using the on peak zero method before each analysis. Kr contribution was monitored throughout the analyses, as increasing amounts of Kr would lead to an increased uncertainty of the individual measurement. Operating conditions and reproducibility of standards on the LA-MC-ICP-MS were evaluated using a modern marine coral from the South China Sea and a modern marine otolith from a white seabass (*Atractoscion nobilis*) collected offshore of Baja California. Replicate analyses for the coral yielded a mean (±2σ) $^{87}Sr/^{86}Sr$ isotope ratio of 0.70921 ± 0.00008 (n = 61) and for the

Fig. 3. (A) Image of a transverse section of an adult otolith in transmitted light, showing growth increments used to estimate ages as well as the laser trajectory (white dotted line) from the strontium isotopic analysis. (B) Corresponding $^{87}Sr/^{86}Sr$ isotope profile with a loess smooth (span = 0.1) applied; grey bands represent the 95% confidence intervals. Green box indicates the approximate region used for the natal origin assignment. [Colour online.]



otolith of 0.70919 ± 0.00003 (n = 63). These values are in good agreement with the mean modern $^{87}Sr/^{86}Sr$ isotope value of seawater, 0.70918 (McArthur et al. 2001).

Baseline Sr isotope data

The $^{87}Sr/^{86}Sr$ isotope ratio baseline for the Sacramento River System was compiled from published data (Ingram et al. 1999; Barnett-Johnson et al. 2008; Sturrock et al. 2015) and newly collected water and otolith samples of known origin from five locations along the Feather River, from the FRH, and from the Thermalito Annex.

Water samples were collected at base flow conditions during the fall of 2013, in the direct flow of water using 50 mL polypropylene tubes, acidified with 1 mol·L^{-1} nitric acid and filtered with a 0.45 µm filter. The samples were transported to a class 100 clean room facility at the UC Davis Interdisciplinary Center for Plasma Mass Spectrometry. An aliquot of each water sample was made at a volume totaling approximately 1 µg of Sr. This volume was evaporated to dryness in an acid-leached polytetrafluoroethylene (Teflon) vial on a hotplate, and Sr was isolated from all other aqueous constituents by selective ion exchange chromatography (Horwitz et al. 1992). Sr separates were reconstituted in 2% HNO_3 and introduced in the MC-ICP-MS (Nu Plasma HR) using a desolvating nebulizer introduction system (Nu Instruments DSN-100). $^{87}Sr/^{86}Sr$ data were internally normalized by the measured $^{86}Sr/^{88}Sr$ ratio (assuming $^{86}Sr/^{88}Sr = 0.1194$). ^{85}Rubidium was monitored to correct for ^{87}Rb if present, but all were well below the Rb correction threshold due to the selective ion exchange chromatography beforehand. $^{84}Sr/^{86}Sr$ was monitored to estimate the $^{84}Kr/^{86}Kr$ isotope ratio. ^{86}Kr was subtracted until the $^{84}Sr/^{88}Sr$ ratio equalled the canonical value of 0.006755, while iterating the mass-bias correction. Procedural blank was measured and contributed <0.002% of total Sr processed per sample. Replicated analyses of NIST SRM 987 were conducted every six samples, normalizing for instrument drift over the course of the day and for analytical artifacts among sessions. An in-house modern marine coral standard was processed in parallel with water samples and

resulted in a mean (2σ) $^{87}Sr/^{86}Sr$ isotope ratio of 0.70918 ± 0.00002 (n = 8).

Sr isotope ratios from the natal region of hatchery-reared otoliths (Fig. 3) were analyzed by LA-MC-ICP-MS, following the same protocols as the samples collected from the spawning grounds, to determine the range of isotope ratios indicative of rearing in the FRH. We examined otoliths from 10 fall-run Chinook salmon reared at the Feather River's main hatchery facility in two raceways collected on 19 April 2012 and ranging in fork length from 43 to 78 mm and 10 fish reared at the Thermalito Annex from two raceways removed on 19 March 2012 and ranging in fork length from 88 to 90 mm.

Natal origin assignments

To assign natal origin, the otolith material deposited immediately following onset of exogenous feeding (i.e., with no isotopic influence of the maternal yolk) was visually identified in the Sr isotope profile and matched to the distance from the otolith core (typically ~250 μm). The mean $^{87}Sr/^{86}Sr$ isotopic ratio for this natal portion of the profile (Fig. 3) was then assigned to a source location by matching it to the established Sr isotopic baseline for the Sacramento River System (Ingram and Weber 1999; Barnett-Johnson et al. 2008) using single-factor quadratic discriminant function analysis (QDFA) in R (R Core Team 2017). We used the quadratic function instead of a linear function because it relaxes the assumption that all the variances of the $^{87}Sr/^{86}Sr$ values from groups are the same. There are some $^{87}Sr/^{86}Sr$ overlaps between natal sources in the San Joaquin and Sacramento basins (particularly Mokelumne versus Feather River Hatcheries and Merced versus Yuba rivers; Sturrock et al. 2015), which could result in strays from the San Joaquin basin potentially being misclassified by our Sacramento-focused QDFA. However, given the large production differences among basins, San Joaquin origin strays have little numerical effect, with the combined contribution of Merced and Mokelumne Hatchery strays to the Feather River and FRH escapements being <1% in 2010–2012 (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015). Given that CV hatchery fish are likely to stray at much higher rates than natural-origin fish due to the extensive trucking program, we assumed that the potential error rate attributable to misclassified San Joaquin origin strays was below 1%. We made no attempt to adjust prior probabilities in the QDFA based on annual hatchery production estimates.

Otolith subsample sizes among weekly surveys and channel strata were too small to calculate proportion of hatchery fish at fine spatial and temporal scales; therefore, samples were pooled by survey year retaining the stratification by High Flow and Low Flow channels. To provide a robust estimate of the proportion of hatchery-origin fish on the spawning grounds, we estimated the mean and standard deviation using bootstrapping with 1000 iterations and sample sizes equal to the number of otoliths collected in each channel for each year. The annual contribution and number of hatchery-origin fish on the spawning grounds was estimated by expanding the bootstrapped mean proportion by the escapement estimates in the High Flow and Low Flow channels for each year. The accuracy of our hatchery classifications was evaluated using otoliths of known hatchery origin (n = 110) that were included in the sample set without prior decoding of their origin.

Emigration timing

To investigate the difference in timing of ocean entry of wild- and hatchery-origin fish, we compared fall-run hatchery release data from Huber and Carlson (2015) with catch data from the USFWS Chipps Island Midwater Trawl Survey. The hatchery release data were filtered to include only fall-run FRH-produced fish that were released into San Pablo Bay from 2002 to 2012 and normalized for each day of the year by the total number of fish released that year. Chipps Island Survey data was filtered to include only fall-run sized, unmarked fish captured in 2002–2012 and then normalized for each Julian day using catch per unit effort and total catch for that year. Note that the latter will therefore include unmarked hatchery fish released upstream of Chipps Island, for example from the Coleman National Fish Hatchery (75% unmarked), and thus likely represents a lower estimate for the true emigration timing variability of wild fish. This allows us to compare emigration timing irrespective of differences in interannual abundance.

Results

Ages

Otolith annual band counts provided a reliable determination of fish age. Otolith age estimates of known-age fish showed high accuracy: 92% (n = 74). Fish incorrectly aged were ±1 year of known age, 5% were estimated to be 1 year older, and 3% were estimated to be 1 year younger than their known age. Age estimations between the two age readers across all otoliths (n = 755) reached an agreement of 92% (ACV = 1.771, APE = 1.252). This level of agreement between readers is comparable to that of other otolith aging studies (Flain and Glova 1988; Murray 1994; Secor et al. 1995). Of the individuals aged, 6.1%, 68.6%, 24.6%, and 0.7% were estimated as 2-, 3-, 4-, and 5-year-old fish, respectively. This age distribution was similar to age class distribution estimates for the Feather River (Grover and Kormos 2008). Similarly, of the CWT retrieved from fish at FRH from 2002 through 2007, 15.58% were 2-year-olds, 56.07% were 3-year-olds, 28.23% were 4-year-olds, and 0.13% were 5-year-olds (Mesick et al. 2009).

Natal origins

The baseline $^{87}Sr/^{86}Sr$ isotope ratios for the Sacramento River System varied significantly between different rivers and hatcheries (Fig. 4; Table 2). Using QDFA, we achieved an overall classification success rate of 96%, providing a robust baseline to determine the natal origins of Chinook salmon in this river system. Furthermore, 95% of known-origin (CWT) fish were correctly assigned to the FRH (Table 3). Classification success rate varied by collection year, ranging from 75% in 2002 to 100% in 2006, 2009, and 2010.

Sr isotope profiles from the core to the edge of otoliths for 755 individuals revealed distinct patterns in natal origins and life histories (Fig. 5). All otoliths examined reached $^{87}Sr/^{86}Sr$ isotope ratios equivalent to the global ocean value 0.70918 (McArthur et al. 2001) prior to the first annual band, indicating that all individuals had entered the ocean in their first year of life. Each otolith was classified based on its natal origin, escapement year, and recovery location (Table 4). A majority of fish were classified as FRH fish (n = 373), with a small contribution from the Thermalito Annex (n = 15) or as wild fish from the Feather River (n = 292). The remaining fish were classified as strays within the Sacramento River System, most originating from the Yuba River (n = 32) and the Nimbus Fish Hatchery (n = 35) on the American River, with minor contributions from the Coleman National Fish Hatchery (n = 6) and the Northern Tributaries (n = 2). The relatively large presence of Yuba River strays is likely explained by the fact that the Feather–Yuba confluence is only about 40 river miles (1 mile = 1.609 km) downstream from the FRH, with well-documented exchange occurring between the two tributaries (Yuba Accord RMT 2013).

Changes in spawning composition over time

The proportion of hatchery- and wild-origin fish varied throughout the time series (2002–2010; Fig. 6; Table 5). Since stray fish are included in the overall CFM estimates of hatchery and wild contributions in the CV, we combined them with the FRH- or wild-origin fish, based on their natal assignment (hatchery strays or wild strays).

The contribution of hatchery origin fish on the Feather River spawning grounds before the stock collapse (2002–2006) varied from 55% ± 7% (±1σ) to 67% ± 9% (±1σ) (Fig. 6). During the collapse (2007–2008), the proportion of hatchery fish decreased to 40% ± 7% (±1σ) in 2008. After the collapse (2009), the contribution of hatchery

Fig. 4. Boxplot showing the $^{87}Sr/^{86}Sr$ isotope ratios of natal sources in the Sacramento River System assumed to potentially contribute to the Feather River escapement. Note that the northern tributaries (Upper Sacramento, Mill Creek, Deer Creek, Battle Creek, Butte Creek) were combined and treated as a single source. The acronyms are NT (northern tributaries), CNH (Coleman National Fish Hatchery), THE (Thermalito Annex), FEA (Feather River), FRH (Feather River Hatchery), YUB (Yuba River), NIH (American River Nimbus Fish Hatchery), AME (American River). [Colour online.]

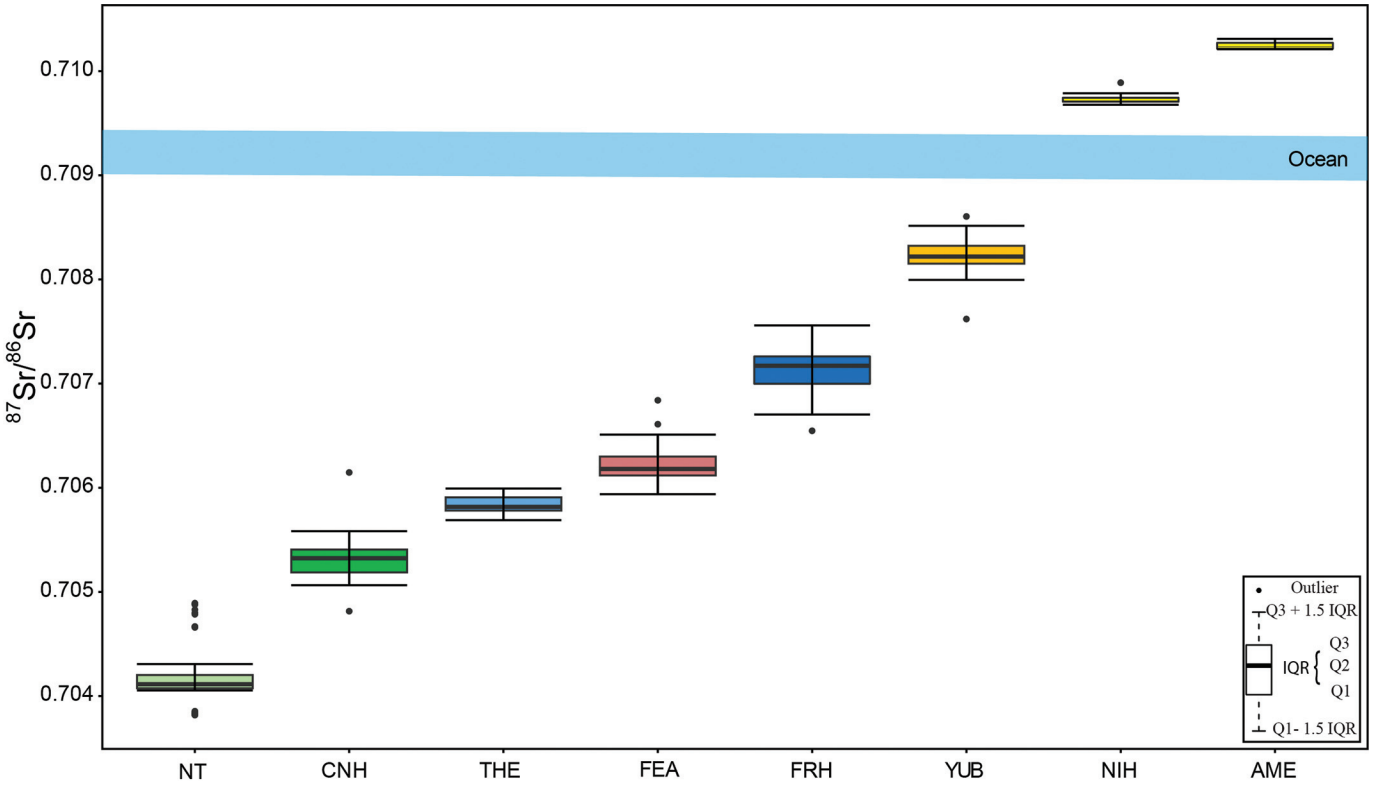


Table 2. Summary statistics for the baseline $^{87}Sr/^{86}Sr$ isotope ratios for the Sacramento River System.

	Northern tributaries	Coleman National Fish Hatchery	Feather River	Feather River Fish Hatchery	Thermalito Annex	Yuba River	Nimbus Fish Hatchery	American River
Min.	0.70382	0.70481	0.70594	0.70655	0.70569	0.70762	0.70968	0.71021
Q_1	0.70407	0.70519	0.70612	0.70700	0.70578	0.70815	0.70971	0.71022
Median	0.70411	0.70532	0.70618	0.70717	0.70582	0.70822	0.70971	0.71023
Mean	0.70421	0.70533	0.70623	0.70712	0.70584	0.70823	0.70974	0.71025
Q_2	0.70420	0.70541	0.70630	0.70726	0.70591	0.70832	0.70975	0.71027
Max.	0.70489	0.70615	0.70684	0.70756	0.70599	0.70861	0.70989	0.71031
n	41	13	31	37	10	19	9	5

Note: Data from Ingram and Weber (1999), Barnett-Johnson et al. (2008), Sturrock et al. (2015), and this study.

Table 3. Classification success rate of known-origin (coded wire tags, CWT) Feather River Hatchery fish using quadratic discriminant function analysis and the Sacramento River basin $^{87}Sr/^{86}Sr$ isotope baseline.

		Assigned to		
Collection year	No. of fish with CWT	Hatchery	River	Correct assignment (%)
2002	8	6	2	75
2003	7	6	1	86
2004	8	7	1	88
2005	16	15	1	94
2006	6	6	0	100
2007	11	10	1	91
2008	—	—	—	—
2009	5	5	0	100
2010	49	49	0	100
Total	110	104	6	95

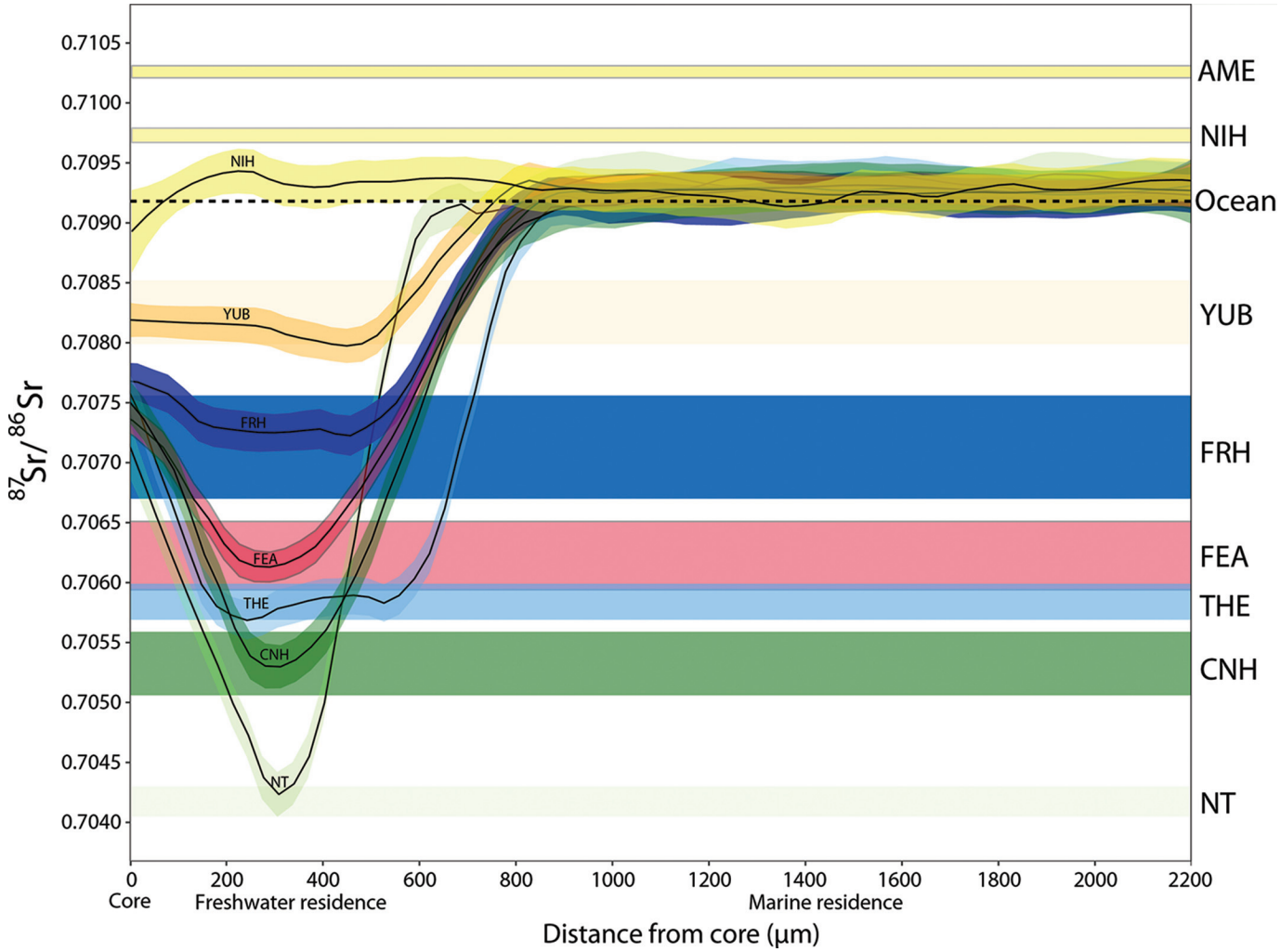
fish increased rapidly to 89% ± 8% (±1σ) in 2010 and, according to CFM data, remained at 90% for 2011–2012 (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015).

For 2010, both CFM and microchemistry data are available, with CFM estimates yielding 78% hatchery fish and otolith estimates 89% ± 8% (±1σ). However, CFM data from 2010 is thought to underestimate the proportion of hatchery fish due to problems in the identification of hatchery fish from decayed carcasses (Mohr and Satterthwaite 2013). Given the directionality of bias in the CFM estimate, the otolith microchemistry and CFM estimates appear compatible.

Emigration timing

During this time series (2002–2012), Feather River fall-run hatchery fish were almost exclusively (~95%) trucked and released directly into San Pablo Bay (Huber and Carlson 2015). The timings of the hatchery fish releases overlap within their interquartile range with the timing of wild emigration, suggesting that most of the fish enter the ocean at a similar time. However, the

Fig. 5. Example otolith $^{87}Sr/^{86}Sr$ isotope profiles of Chinook salmon with different natal origins. The cores show an influence of the marine strontium isotopic signature, indicating that the parents of these fish matured in the ocean and that this marine signature was incorporated into the organism prior to hatching, typical for fall-run Chinook salmon. Shaded bars are the $^{87}Sr/^{86}Sr$ isotope ranges of the different freshwater source regions from Fig. 4. The acronyms are NT (northern tributaries), CNH (Coleman National Fish Hatchery), THE (Thermalito Annex), FEA (Feather River), FRH (Feather River Hatchery), YUB (Yuba River), NIH (American River Nimbus Fish Hatchery), AME (American River). No fish were classified as American River natal origin. [Colour online.]



variance of the wild emigrating fish is larger, with both earlier and later emigrants, than the hatchery releases, which occur over a shorter time period (Fig. 7).

Discussion

Identifying the contribution of hatchery-origin fish to a population is essential for assessing the status, fitness, and resilience of locally adapted wild salmon populations (Lindley et al. 2007; Williams et al. 2016). Numerous studies have documented reduced fitness (Araki et al. 2008; Christie et al. 2014) and loss of diversity (portfolio) in populations with supplementation from hatchery-reared fish, causing overall reduced resilience (Schindler et al. 2010). In this study, otolith Sr isotope analysis was highly successful in identifying natal origin and discerning hatchery from wild origins of Chinook salmon in the Feather River. Combining our otolith-based approach with CFM data allowed us to reconstruct an 11-year record of hatchery contributions to the in-river escapement. Temporal trends in the contribution of hatchery- and wild-origin fish in our time series document an increase in the proportion of hatchery-origin fish on the natural spawning grounds after the salmon stock collapse (Figs. 6 and 8). This substantial change in the proportion of hatchery fish was likely the result of relatively stable hatchery production from the small numbers of returning fish during stock collapse and either poor production or survival of wild offspring in-river during the 2007–2009 drought (DWR 2010).

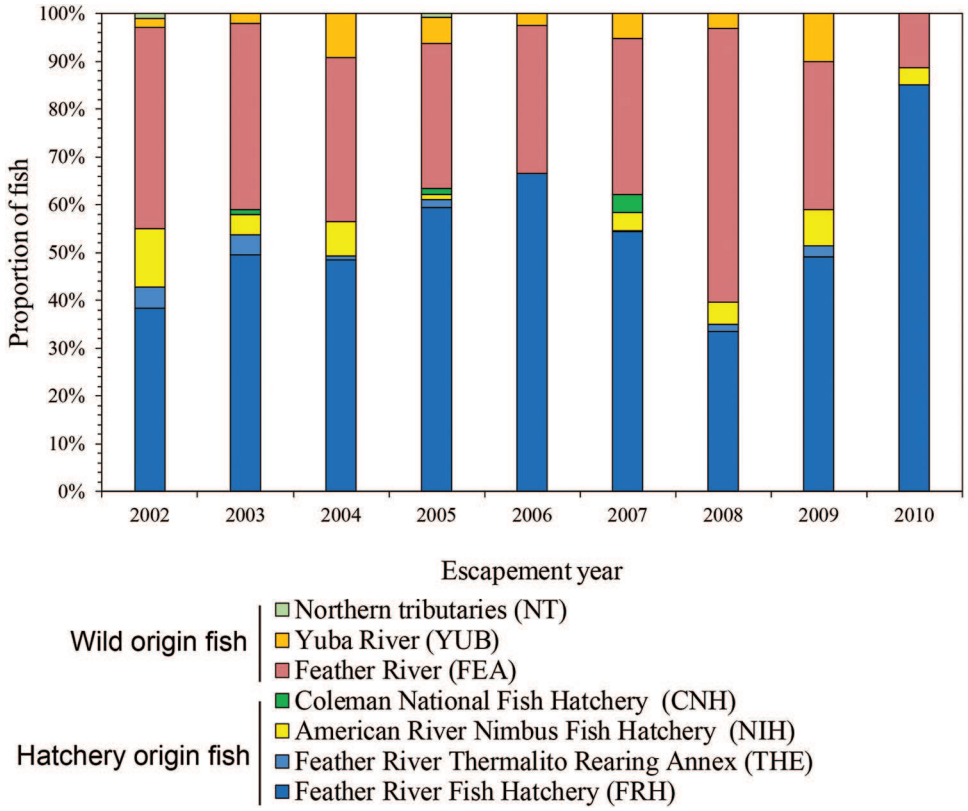
The proximate cause of the 2007–2009 salmon stock collapse has been attributed to poor ocean conditions and food availability in the ocean after emigration (Lindley et al. 2009; Wells et al. 2016). Ocean conditions off the Californian coast are highly variable, with wind patterns driving the intensity and timing of coastal upwelling, influencing food production and survival of young salmon during ocean entry (Mantua et al. 1997; Satterthwaite et al. 2014; Sabal et al. 2016; Wells et al. 2016). Hatchery-produced smolts entering the ocean in 2005 and 2006 experienced weakly upwelled ocean conditions with variable timing of the spring transition (Lindley et al. 2009), which led to elevated ocean mortality and decline in hatchery contributions and stock abundance on the Feather River in 2008 (Huber and Carlson 2015). Meanwhile, wild fish exhibited a broader ocean arrival window during emigration (Fig. 7), increasing the odds that at least part of the population would be matched with optimal feeding opportunities

Table 4. Number of otoliths by escapement year and recovery location classified to their natal origin.

		Hatchery-origin fish (otolith *n*)					Wild-origin fish (otolith *n*)		Total (otolith *n*)	
Escapement year	Recovery location	FRH	THE	NIH	CNH	FEA	YUB	NT	Hatchery	Wild
2002	High Flow	18	2	2	—	19	—	—	22	19
	Low Flow	25	3	11	—	28	2	1	39	31
2003	High Flow	18	3	2	1	17	—	—	24	17
	Low Flow	29	1	2	—	20	2	—	32	22
2004	High Flow	17	1	2	—	12	3	—	20	15
	Low Flow	31	—	5	—	22	6	—	36	28
2005	High Flow	12	1	—	—	16	3	1	13	20
	Low Flow	47	1	1	1	17	3	—	50	20
2006	High Flow	13	—	—	—	9	1	—	13	10
	Low Flow	34	—	—	—	14	1	—	34	15
2007	High Flow	11	1	—	1	19	1	—	13	20
	Low Flow	42	—	3	3	24	4	—	48	28
2008	High Flow	7	—	—	—	20	—	—	7	20
	Low Flow	21	1	3	—	35	2	—	25	37
2009	High Flow	2	—	—	—	5	—	—	2	5
	Low Flow	19	1	3	—	11	4	—	23	15
2010	High Flow	3	—	—	—	1	—	—	3	1
	Low Flow	24	—	1	—	3	—	—	25	3

Note: The northern tributaries (Upper Sacramento, Mill Creek, Deer Creek, Battle Creek, Butte Creek) were combined and treated as a single source. The acronyms are NT (northern tributaries), CNH (Coleman National Fish Hatchery), THE (Thermalito Annex), FEA (Feather River), FRH (Feather River Hatchery), YUB (Yuba River), and NIH (American River Nimbus Fish Hatchery).

Fig. 6. Time series of the proportions of fall-run Chinook salmon on the Feather River assigned to each of the seven natal habitats. No fish were assigned to the American River. [Colour online.]



(Wells et al. 2016). We hypothesize that this diversity in outmigration timing may have led to the observed increase in the wild component of the 2008 returns. However, even with this apparent difference in the resiliency of hatchery and wild populations, all populations declined precipitously during this period. Thus, the population collapse can be attributed to poor ocean survival for both hatchery- and wild-origin smolts from the 2005 and 2006 emigration years (Lindley et al. 2009).

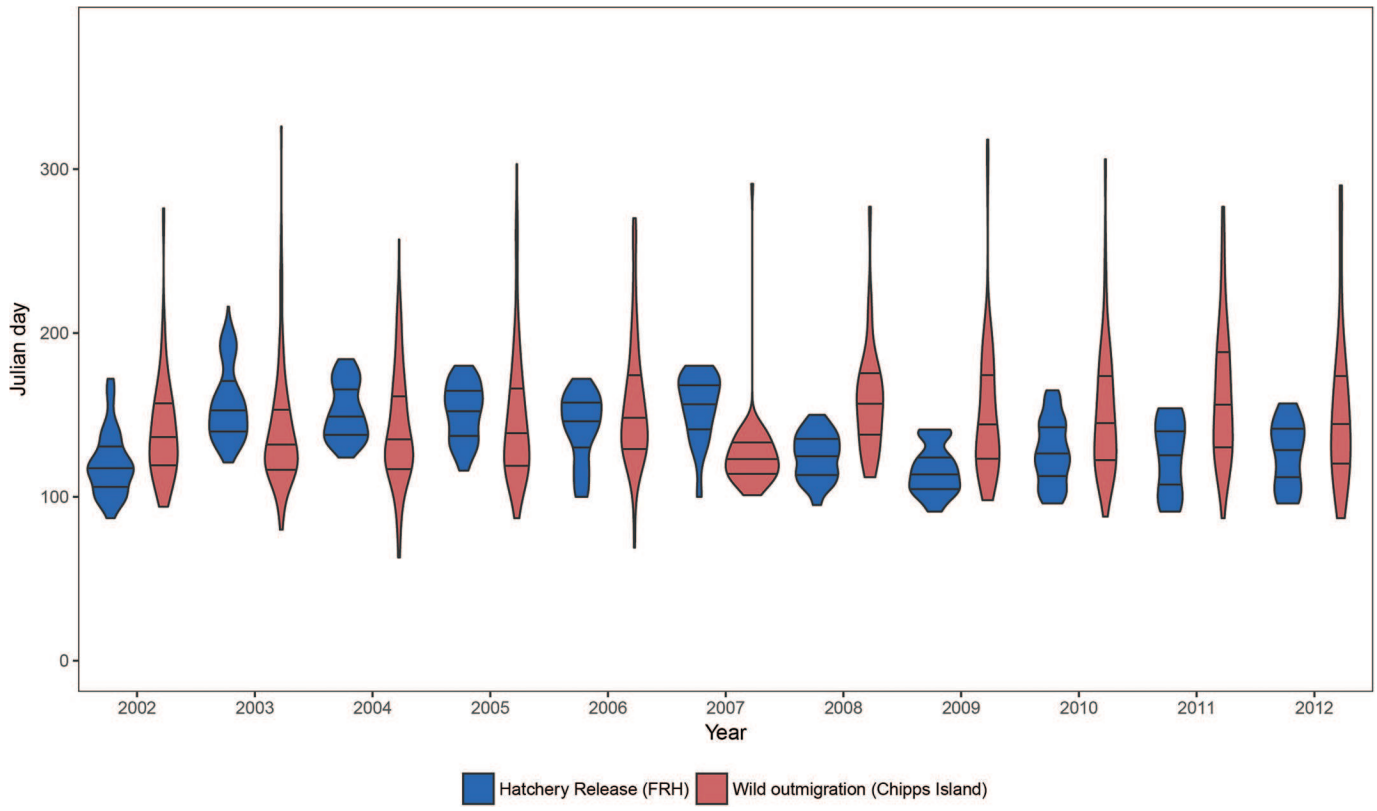
Total escapement to the Feather River and the Sacramento Valley increased rapidly from 2009 to 2013 (Fig. 8), reaching near prestock collapse abundances in just 3 years. Our analysis showed that ~90% of these fish returning to the Feather River were of

Table 5. Contributions of hatchery origin fish on the Feather River spawning grounds from 2002 to 2010.

Escapement year	Recover location	Population estimate	Hatchery origin (%)	Hatchery origin (1σ)	Hatchery fish (*n*)	Hatchery fish (1σ)	Combined hatchery origin (% ± 1σ)	Combined hatchery fish (*n* ± 1σ)
2002	High Flow	34 125	54	8	18 348	2 700		
2002	Low Flow	71 038	56	6	39 508	4 295	55±7	57 863±7 106
2003	High Flow	37 643	59	8	22 115	2 951		
2003	Low Flow	52 303	59	7	31 014	3 506	59±7	53 127±6 483
2004	High Flow	17 113	57	8	9 781	1 451		
2004	Low Flow	37 058	56	6	20 748	2 239	56±7	30 505±3 700
2005	High Flow	12 583	39	9	4 923	1 078		
2005	Low Flow	36 577	71	6	26 118	2 034	63±15	31 117±7 576
2006	High Flow	16 990	56	10	9 578	1 753		
2006	Low Flow	59 424	70	6	41 317	3 853	67±9	50 930±7 075
2007	High Flow	876	40	8	347	72		
2007	Low Flow	21 033	62	5	13 011	1 134	61±7	13 358±1 544
2008	High Flow	297	26	9	78	25		
2008	Low Flow	5 642	40	6	2 269	357	40±7	2 347±424
2009	High Flow	223	28	17	63	39		
2009	Low Flow	4 624	60	8	2 777	376	59±11	2 841±532
2010	High Flow	2 201	75	22	1 650	473		
2010	Low Flow	42 713	89	6	38 152	2 494	89±8	39 802±3 613

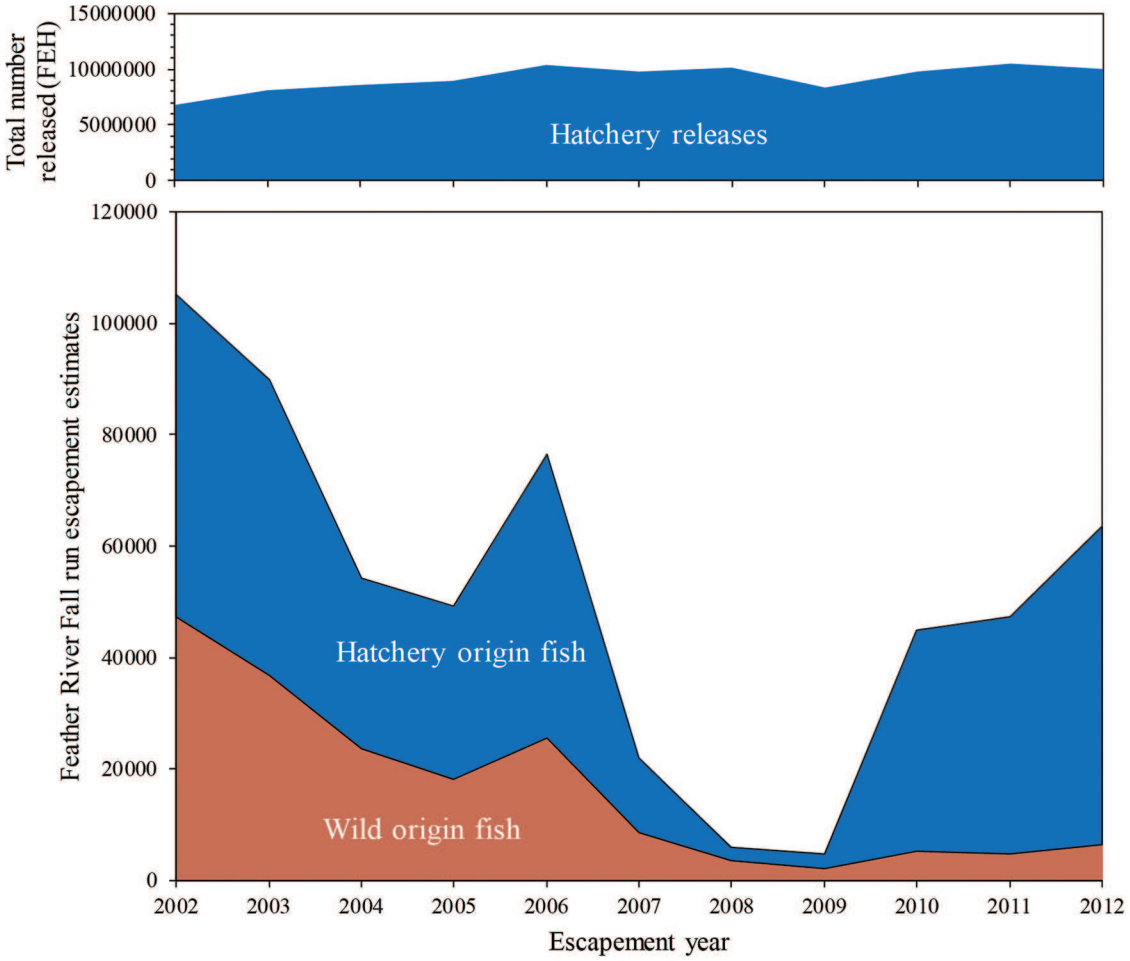
Note: Population estimates from GrandTab2017.04.07, California Central Valley Chinook Population Database Report, and California Department of Water Resources (unpublished data, contact Jason.Kindopp@water.ca.gov). Mean values and standard deviation (1σ) were calculated using bootstrapping for each recovery location (High Flow and Low Flow channels) and then expanded by the population estimate and combined for each year.

Fig. 7. Timing of ocean entry of fish released from the Feather River hatchery (blue) and wild out-migrating (red) from 2002 to 2010. The area of each violin represents the proportion of fish out-migrating at that Julian day and is normalized to the total abundance of outmigrants for that year. The black lines represent the interquartile range (first to third quantiles). Hatchery release data for the Feather River Hatchery (FRH) are from Huber and Carlson (2015). Data for "wild" (unmarked) fall-run sized outmigrants are from the USFWS Chipps Island Midwater Trawl. [Colour online.]



hatchery origin. This could in part be attributed to hatchery fish benefitting from improved ocean conditions as well the fishery closure, showing that hatchery and fishery management actions were highly effective at recovering fish stocks following the stock collapse. During this period, FRH release practices were relatively unchanged, with comparable numbers of juveniles produced and trucked directly to the bay relative to escapement (Fig. 8) (Huber and Carlson 2015). Wild populations likely take longer to recover from stock collapse because their population dynamics are reliant on spawning stock size more so than that of the hatchery. Fur-

Fig. 8. Feather River fall-run in-river escapement estimates split between hatchery- (blue) and wild-origin (red) fish based on otolith (2002–2010) and California Constant Fractional Marking Program (CFM) data (2011–2012). The time of the salmon stock collapse (2007–2009) is marked by low escapement numbers. Top panel shows the relative stability of hatchery releases over the time series. Escapement data are taken from the GrandTab2016.04.11, California Central Valley Chinook Population Database Report, and hatchery releases numbers are from Huber and Carlson (2015). [Colour online.]



thermore, wild populations are subject to high early life mortality during emigration from CV rivers, which is exacerbated by periods of low-flow conditions during droughts (Zeug et al. 2014). In-river spawner abundance was greatly reduced during the stock collapse (J. Kindopp, unpublished data, Jason.Kindopp@water.ca.gov), which coincided with a period of drought in California (2007–2009), and their offspring likely experienced high mortality. Continued monitoring of proportion of hatchery-origin fish as part of this time series will be critical to determine the extent to which the observed pattern represents a fundamental shift towards hatchery dominance. The overwhelming presence of hatchery-origin adults on the spawning grounds would suggest that fall-run Chinook on the Feather River may now be dependent on hatchery fish. Thus, while management strategies for population supplementation of salmon have been successful, they may also facilitate synchronization of hatchery and wild populations (Satterthwaite and Carlson 2015), eroding their resilience to ocean and climate variability.

The dominance of hatchery fish on the Feather River spawning grounds in recent years suggests that interbreeding of hatchery and wild fish is likely and pervasive, particularly given that we did not consider cross-generational hatchery influence (treating all juveniles produced in-river as "wild", independent of parental origin). This is supported by unusually high hatchery contributions on most natural spawning grounds in the CV (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015) and a lack of genetic structuring in fall-run CV Chinook salmon, both hatchery and "wild" (Williamson and May 2005). This introgression of hatchery- and wild-origin fish may have reduced fitness (Araki et al. 2008) and weakened the Chinook salmon population portfolio, increasing synchrony among populations and eroding life history diversity and resilience (Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015). Given the environmental variability inherent to California and predictions of increased frequency of extreme events with future climate change (Cloern et al. 2011; Dettinger et al. 2011), loss of phenotypic diversity could have serious impacts on salmon stock resilience, increasing ecological and economic uncertainty.

The dominance of hatchery-origin fish is not limited to the Feather River. For example, 90% of in-river spawners on the Mokelumne River in 2004 were classified as hatchery fish (Johnson et al. 2012), and CFM data indicate high hatchery contributions (~80%–90%) to natural spawning grounds on Battle Creek, the Merced River, and the Stanislaus River (Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013, 2015). Furthermore, the majority of the ocean fishery is supported by hatcheries, with 90% of the fishery supported by hatchery fish in 2001 (Barnett-Johnson et al. 2007). There is a growing concern that salmon populations in the CV of California are becoming dependent upon hatchery supplementation, a conservation status recently identified as "mitigated extinction"

(Baumsteiger and Moyle 2017). Further studies are needed basin-wide to better understand the role that hatcheries may be playing in "reseeding" in-river populations, masking their declines, and (or) depressing natural production.

It is likely that a number of factors have resulted in hatchery fish effectively replacing wild stocks in the CV, including high and sustained smolt production, largely independent of spawner abundance and freshwater conditions (Huber and Carlson 2015), increased straying rates of trucked fish onto natural spawning grounds (Palmer-Zwahlen and Kormos 2013, 2015), and inflated survival of hatchery smolts as a result of their larger size and the reduction in freshwater mortality for trucked individuals. Such management practices have synchronized the CV salmon stock complex, contributing to a weakened portfolio (Carlson and Satterthwaite 2011; Huber and Carlson 2015; Satterthwaite and Carlson 2015), increased genetic homogenization, and potentially reduced population productivity (Williamson and May 2005). Owing to the reliance on hatchery fish and the high synchrony among the hatcheries in the CV, salmon stock collapses are likely in the future, and compensating for these collapses by increasing hatchery salmon production is likely to prove ineffective (Lindley et al. 2009). We recommend implementation of hatchery practices designed to promote population diversity, such as varying the timing, size, and location of releases to facilitate greater expression of life history diversity in this region and, in turn, its productivity and resiliency (Greene et al. 2010). Moving forward, to reduce the vulnerability of the fishery to over-reliance on hatchery fish and reduce overall extinction risk to wild CV fall-run Chinook salmon, production hatcheries could implement practices that (*i*) reduce domestication selection through balanced gene flow between hatchery- and natural-origin fish in hatchery broodstock and in rivers (HSRG 2014), (*ii*) minimize the numbers of hatchery-origin fish interbreeding with wild fish on spawning grounds, and (*iii*) reduce straying of hatchery adults to support local adaptation in natural salmon populations. CV salmon are at a critical juncture, with many populations close to extinction and facing an increasingly volatile climatic future (Greene et al. 2010; Cloern et al. 2011). Hatcheries can play a key role in the recovery of wild stocks, supplementing the fishery, and the reestablishment of natural areas, but only with cautious and appropriate management.

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