Contribution of hatchery and natural origin Chinook salmon to the Lower Yuba River

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CONTRIBUTION OF HATCHERY AND NATURAL ORIGIN CHINOOK SALMON TO THE LOWER YUBA RIVER

ABSTRACT

Recovery of self-sustaining populations of wild salmon is a primary goal for many conservation programs. Connectivity patterns across time and space are key to understanding the demographic and genetic boundaries of a population. The impact of immigrants on local population dynamics and fitness are largely unknown, and straying rates remain largely unquantified. Here, we used otolith ("earstone") Sr isotopes in adult Chinook salmon returning to the Yuba River in 2009 to determine the relative contributions of fish that were produced and returned to the Yuba River *vs.* produced in other rivers or hatcheries that strayed to the Yuba River to spawn. We observed considerable variation in otolith Sr profiles during early freshwater rearing, indicating that the surviving adults had used a diverse array of habitats and outmigration timings as juveniles. One "profile type" was characterized by a high and stable otolith core value, indicating egg development in isotopically heavy water, but which dropped to isotopically distinct values immediately after emergence, suggesting early movements and extended rearing in habitats isotopically distinct from the Yuba mainstem. This "step" was prevalent in the adult sample (38%), so had a significant impact on our natal assignments; however, we are confident that it is Yuba-diagnostic as the only plausible explanation is that egg development occurred in isotopically heavy water (of which the Yuba is the only conceivable option). Also, we have only ever seen this "profile type" in known-origin fish from the Yuba River and never from any other Central Valley tributaries or hatcheries. Otolith thermal mark analyses further strengthened our inferences, and water sampling revealed locations of potential rearing habitats in the watershed, based on isotopic values matching those observed in some of the otolith profiles. Our data indicated that the proportion of wild Yuba fish in the 2009 escapement was 57% (48-66%), with 43% (34-52%) comprised of strays from the Feather River and the Feather, Mokelumne and Merced River Hatcheries. Of the known phenotypic spring run fish in the 2009 sample, 50% had originated in and returned to the Yuba River.

BACKGROUND

Chinook salmon (*Oncorhynchus tshawytscha*) display strong natal homing behavior, resulting in reproductively-isolated populations with distributions differing across time and (or) space. Environmental heterogeneity drives local adaptation as well as phenotypic and behavioral plasticity, resulting in complex life histories that vary across micro (among streams) to macro (among continents) scales (Taylor 1991). This biocomplexity has enabled Chinook salmon to exploit a vast range of habitats and environmental regimes (Yoshiyama et al. 2001, Lindley et al. 2007) and is thought to contribute to their long-term persistence by providing a buffering 'portfolio effect' (Hilborn et al. 2003, Schindler et al. 2010). An important component of

Chinook salmon life history diversity lies in the timing that they migrate to and from freshwater as adults and juveniles, respectively. The California Central Valley (CCV) contains some of the most diverse salmon life histories in the world, hosting four distinct 'runs' (spring, fall, late-fall and winter), distinguished by the season in which the adults return to spawn. However, CCV salmon populations have undergone dramatic declines (Yoshiyama et al. 2000) and all runs are currently listed as threatened, endangered or species of concern (NOAA 2004, 2005). More than 70% of spawning habitats have been lost or degraded as a result of dam construction, water diversions and mining activities (Moyle 1994, Yoshiyama et al. 2001). Such anthropogenic pressures are intensified by extreme hydroclimatic variability, with the CCV representing the southernmost reaches of the species range and often subjected to extended periods of drought (Healey 1991). Historically, spring-run were the most abundant Chinook salmon run in the CCV, with escapement in the Sacramento River estimated at around half a million spawners per year (Yoshiyama et al. 2001). Spring-run salmon typically hold over the warm summer months, ascending to higher elevations to make use of the cool, snow-fed streams in the slopes of the Sierra Nevada. However, large-scale dam construction has prevented upstream passage and many spring run populations have now been extirpated (Yoshiyama et al. 2001). Currently, spring-run are listed as Threatened under the Endangered Species Act (NOAA 2005) and the projected reductions in snow pack caused by climate change are likely to make it increasingly difficult to meet their necessary habitat requirements in the region (DWR 2010). Fall run are now numerically dominant, but populations are heavily reliant on hatchery supplementation (Barnett-Johnson et al. 2007, Johnson et al. 2012, Kormos et al. 2012).

The extent to which hatchery-produced fish are functioning to sustain CCV salmon populations, and the long-term fitness implications of their extensive straying rates within- and among-basins are not fully understood (Johnson et al. 2012, Kormos et al. 2012). However, increasingly synchronized population dynamics among CCV rivers and basins have indicated a weak portfolio effect that has deteriorated in the past few decades (Carlson and Satterthwaite 2011). The ecological impacts of hatchery propagation have received less attention than the genetic implications, largely due to the methodological difficulties in distinguishing among runs and hatchery *vs.* wild salmon. Until the Constant Fractional Marking Program (CFM) was initiated in the region in 2007, low and inconsistent numbers of fall-run hatchery Chinook salmon were marked ("adclipped") and coded-wire tagged (CWT). Since Brood Year 2006, the CFM has ensured that $\geq$25% of fall-run releases are marked and tagged, resulting in the recovery of nearly 27,000 CWTs from the 2010 escapement (Kormos et al. 2012). Prior to this point, the contribution of hatchery fish to the CCV escapement was estimated from the limited and variable numbers of CWT returns, resulting in significant caveats and error propagation (Mesick in review). Recent advances in techniques using chemical markers recorded in biomineralised tissues provide rare opportunity to retrospectively "geolocate" individual fish in time and space (Campana and Thorrold 2001). Given their incremental growth and metabolically inert nature, otoliths ("earbones") represent a unique "natural tag" for reconstructing provenance and movement

patterns of individual fish (Sturrock et al. 2012a). As with all natural tags, their presence in all subject animals results in a relatively low-cost marker given that every capture represents a 'recapture'. The technique relies on differences in the physicochemical environment producing a distinct and reproducible "chemical fingerprint" in the otolith. In the CCV, strontium isotopes ($^{87}Sr/^{86}Sr$) are ideal markers because the water signature varies among many of the rivers due to variations in bedrock geology (Barnett-Johnson et al. 2008). Ambient isotopic signatures are stable across years (Kennedy et al. 2000) and do not undergo significant biological fractionation (Blum et al. 2000), and are thus faithfully recorded in the otoliths of Chinook salmon (Kennedy et al. 1997, Ingram and Weber 1999, Kennedy et al. 2002, Barnett-Johnson et al. 2008). Otolith $^{87}Sr/^{86}Sr$ values can therefore be used to reconstruct origin, as well as time- and age-resolved movements as salmon migrate through the freshwater and estuarine environments (Ingram and Weber 1999, Barnett-Johnson et al. 2008).

Here, we measured $^{87}Sr/^{86}Sr$ signatures in the otoliths of adults from the 2009 Yuba River escapement to determine the contribution of hatchery *vs.* natural origin Chinook salmon spawning in the lower Yuba River. Historically, there was an established spring run salmon population in the Yuba River (Yoshiyama 2001), so in addition, we examined phenotypically spring-running fish in the Yuba River to determine whether they were strays, or had originated in and returned to the Yuba River.

STUDY AREA

The Yuba River (herein, termed the Yuba) is a large tributary of the Feather River in the Sacramento basin of the CCV. The watershed drains 3,468 km^2 (1,339 $miles^2$) and originates in the high elevations of the Sierra Nevada Mountains. The lower Yuba is fed by the North, Middle, and South Yuba Rivers, which converge upstream of Englebright Dam. The lower Yuba provides spawning habitat for spring-, fall-, and late fall-run Chinook salmon, with Englebright Dam representing the upstream barrier to salmon migration. Yuba salmonid populations have been adversely affected by a variety of anthropogenic activities, including mining, dam construction and water diversions. These activities have impacted available spawning and rearing habitat through modified flow regimes, reduced water quality, unsuitable water temperatures, and physical loss of habitat such as spawning gravel substrates and riparian cover.

METHODS

SAMPLE COLLECTION

Adult otoliths were collected from post-spawned Chinook salmon during the 2009 CDFW carcass surveys. Most carcasses were observed in reaches around Parks Bar, downstream of Englebright Dam (Fig. 1). A subset of otoliths (n = 103, 49-106.5cm FL, sampled 8th September 2009 to 5th January 2010) were selected randomly for the current study. Included in this sample were six adults that had been floy tagged when they had passed Daguerre Dam in May 2009 ("early returning"; Table 1).

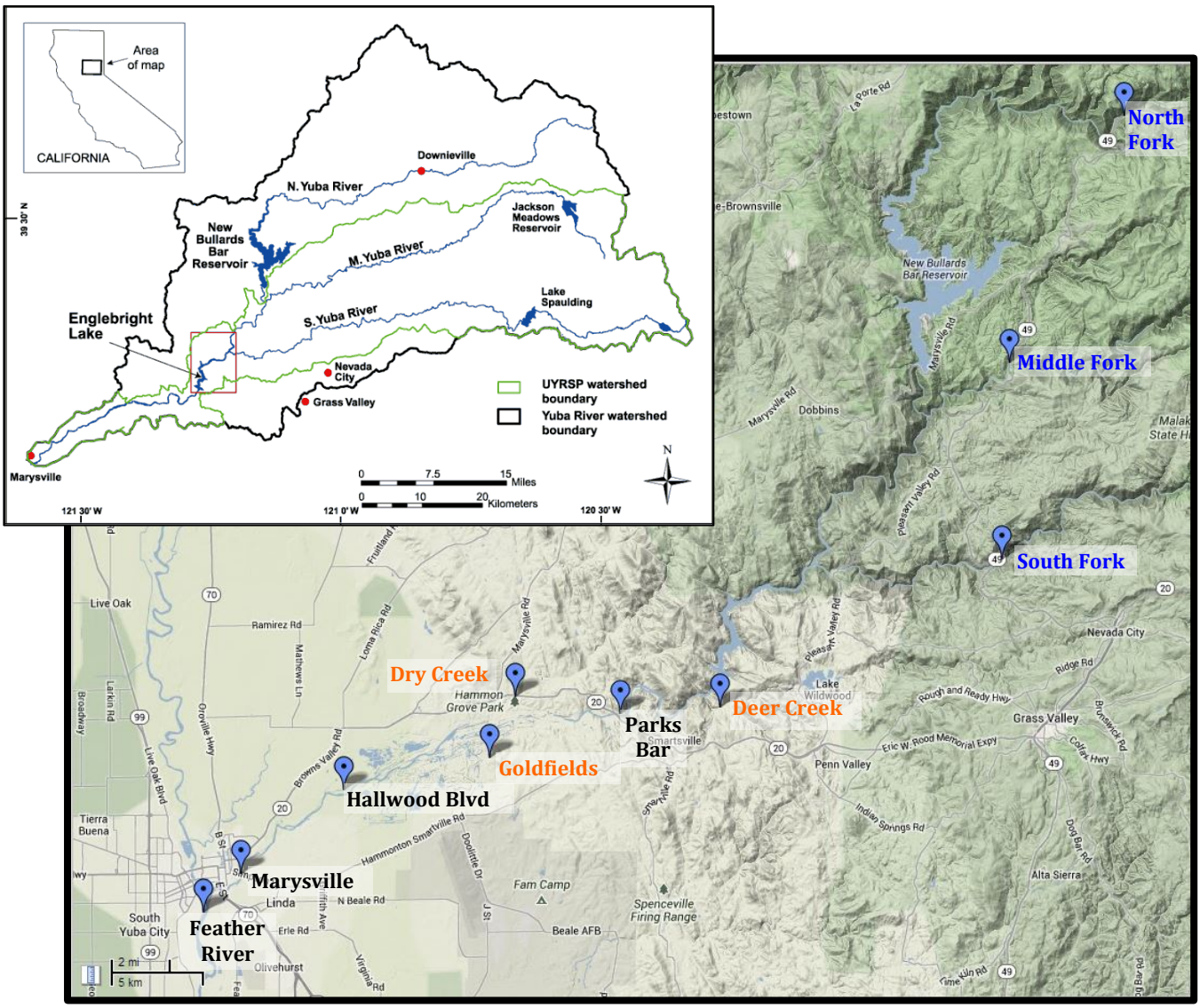

Fig. 1 Map to show study area and water collection sites (blue pointers) in the Yuba and Feather Rivers sampled in March and(or) May 2013. Mainstem sites are labeled black, lower Yuba River tributaries are labeled orange, and upper river forks above Englebright Dam (the upstream migration barrier to salmon) are labeled blue. The rotary screw trap site used to sample emigrating juvenile salmon was located at Hallwood Boulevard.

Table 1 collection details of "early returning" floy tagged fish included in the otolith isotopic analyses. Two individuals were coded wire tagged (CWT) fish from the Feather River Hatchery (FEH)

Sample ID	Floy tag no.	Floy tag insert date	CWT run	CWT code	Brood year	Age	Hatchery source
YR093009-001	022 (nonfresh)	5/20/09	Spring	062337	2006	4	FEH
YR100609-012	039 (nonfresh)	5/25/09		no cwt			
YR100609-043	14	5/18/09	Spring	062337	2006	4	FEH
YR101309-521	042 (nonfresh)	5/25/09		no cwt			
ROV1	7	5/13/09		no cwt			
ROV2	28	5/21/09		no cwt			

To create a strontium isoscape (Hobson et al. 2010) for reconstructing natal origin of returning adults, juvenile otoliths were analyzed from salmon collected in rotary screw traps (RST) and hatcheries around the CCV. New otolith samples and previously-published water data (Ingram and Weber 1999) were added to the existing isotopic baseline (Barnett-Johnson et al. 2008) to improve its long-term relevance.

OTOLITH MICROCHEMISTRY

BACKGROUND

Initial findings from the current study were presented at the annual 2011 Yuba River Symposium. Results suggested greater than expected Sr isotopic variation within the natal rearing portion (c. 250-450μm from the core, equivalent to c. 30-50mm FL) of otoliths from Yuba-collected adults. We first learned of this variation when known-origin Feather River Hatchery (FEH) fish were incorrectly classified in a 'blind' test as having originated from the Mokelumne River Hatchery (MOH). We reported this project challenge to the Program in May 2012 and proposed a solution for further exploring these results.

The isotopic variation in the natal region of the otolith also influenced the interpretation of the proportion of Yuba River spawners that may have originated from other sources. We expanded the study and analyzed a broader suite of known-origin juveniles from the FEH encompassing several different years in an attempt to better characterize this variation. Known-origin juveniles from FEH and the Yuba (Barnett-Johnson et al. 2008) were re-analyzed using full life history transects across the entire otolith, and additional juveniles from the Yuba River rotary screw trap (RST) were also analyzed. In the adult otoliths, full life history transects from the egg (otolith core) to ocean entry were carried out, consisting of a ~ 20 spot "Sr profile" for each otolith, rather than the original project design of 3 targeted spots in the natal region. This new approach proved enlightening into the sources and mechanisms of our initial misclassifications.

OTOLITH PREPARATION & STRONTIUM ISOTOPE ANALYSES

Otolith strontium isotopic ratios ($^{87}Sr/^{86}Sr$) were determined using the methods of Barnett-Johnson et al. (2005). In brief, otoliths were rinsed 2-3 times with deionized water and cleaned of adhering tissue. Once dry, otoliths were stored in clean microcentrifuge tubes then mounted in Crystalbond™ resin and polished (600 grit, 1500 grit, then 3 μm lapping film) until the primordia were exposed. Isotopic analyses were carried out on a Nu Plasma HR (Nu Instruments, Inc.) double-focusing, plasma-source multiple collector mass spectrometer (MC-ICPMS) equipped with fixed detectors, interfaced with a Nd:YAG 213 nm laser (New Wave Research) at the UC Davis Interdisciplinary Center for Plasma Mass Spectrometry. Contrasting with the line transects used to establish natal signatures of tributaries in the CCV (Barnett-Johnson et al. 2005, Barnett-Johnson et al. 2008) spot analyses were used to prevent cross-contamination of ablated material and to allow coupling of chemical data with discrete microstructural features. Depending on instrument performance and sample thickness, a 40-55μm laser beam diameter was used (roughly equivalent to 10-14 days of growth) with pulse rate of 10-20 Hz at 65-70% power and a dwell time of 25-35 seconds. Helium was

used as the carrier gas to improve sensitivity and was mixed with argon before reaching the plasma source. Gas blank and background signals were monitored following sample changes and measured for 30 s prior to each batch of spot analyses. A modern coral sample was analyzed at the start of each analytical session and the outer (marine) portion of adult salmon otoliths analyzed between every otolith. The measured $^{87}Sr/^{86}Sr$ ratio was normalized to $^{86}Sr/^{88}Sr = 0.1194$ and to maximize accuracy, batches of unknowns were corrected to the global $^{87}Sr/^{86}Sr$ value (0.70918) by correcting to the mean of three spot analyses on the marine portion of an adult salmon otolith analyzed immediately afterwards.

A standardized 90° transect was used for $^{87}Sr/^{86}Sr$ and otolith radius measurements, from the post-rostrum primordia towards the dorsal edge (after Barnett-Johnson et al. 2007). In the juvenile otoliths, the transect was terminated at the otolith edge to ensure analysis of the most recently deposited material in order to characterize the full natal signature. In the adult otoliths, initially, three spot analyses were carried out just after the exogenous feeding check (c.250µm from the core), but following unexpected patterns and spurious results (see Results), full life history transects were carried out, comprising 20-spot transects to a distance of c.1000µm (c. 40cm FL) to ensure inclusion of the full freshwater outmigration period (Fig. 2).

Strontium isoscape & Natal assignment of spawning adults

The natal $^{87}Sr/^{86}Sr$ signature was determined from otolith material deposited immediately after onset of exogenous feeding (~250µm from the core, see Barnett-Johnson et al. 2005). Material deposited prior to this point can exhibit an elevated signature due to the influence of maternally-derived strontium from the yolk, which is often formed while the mother is in the ocean (Fig. 2). Our strontium isoscape (updated from Barnett-Johnson et al. 2008) included juvenile otolith samples and water samples from all potential natal sources in the CCV, with many sites sampled across multiple years and hydrologic regimes.

We used linear discriminant function analysis (LDFA) to classify adults to natal location based on otolith $^{87}Sr/^{86}Sr$ ratios. Our ability to assign individuals to their correct natal source was assessed using jackknifed cross-validation assignment of known-origin samples within the $^{87}Sr/^{86}Sr$ baseline (MYSTAT 12.02), and through blind assignment of coded wire tagged (CWT) adult salmon (n=20). We applied prior probabilities to the FEH (0.6) and Yuba (0.28), based on the straying rates reported by the Constant Fractional Marking Program for the 2010 Yuba escapement (CFMP; Kormos et al. 2012), using the estimated proportions of FEH strays (spring and fall run combined) and "natural" fish. All other sites were assigned equal priors.

To achieve the most accurate point estimate of the proportion of fish originating from hatcheries, we used Laplace's procedure (Laplace 1812). This approach has been determined to be more robust than dividing the number assigned to hatchery-origin by the total number of fish in the sample (Agresti and Coull 1998). The 95% confidence interval (CI) for the population is governed by binomial statistics and was calculated using the Adjusted Wald estimate modified for small sample sizes (Lewis and Sauro 2006).

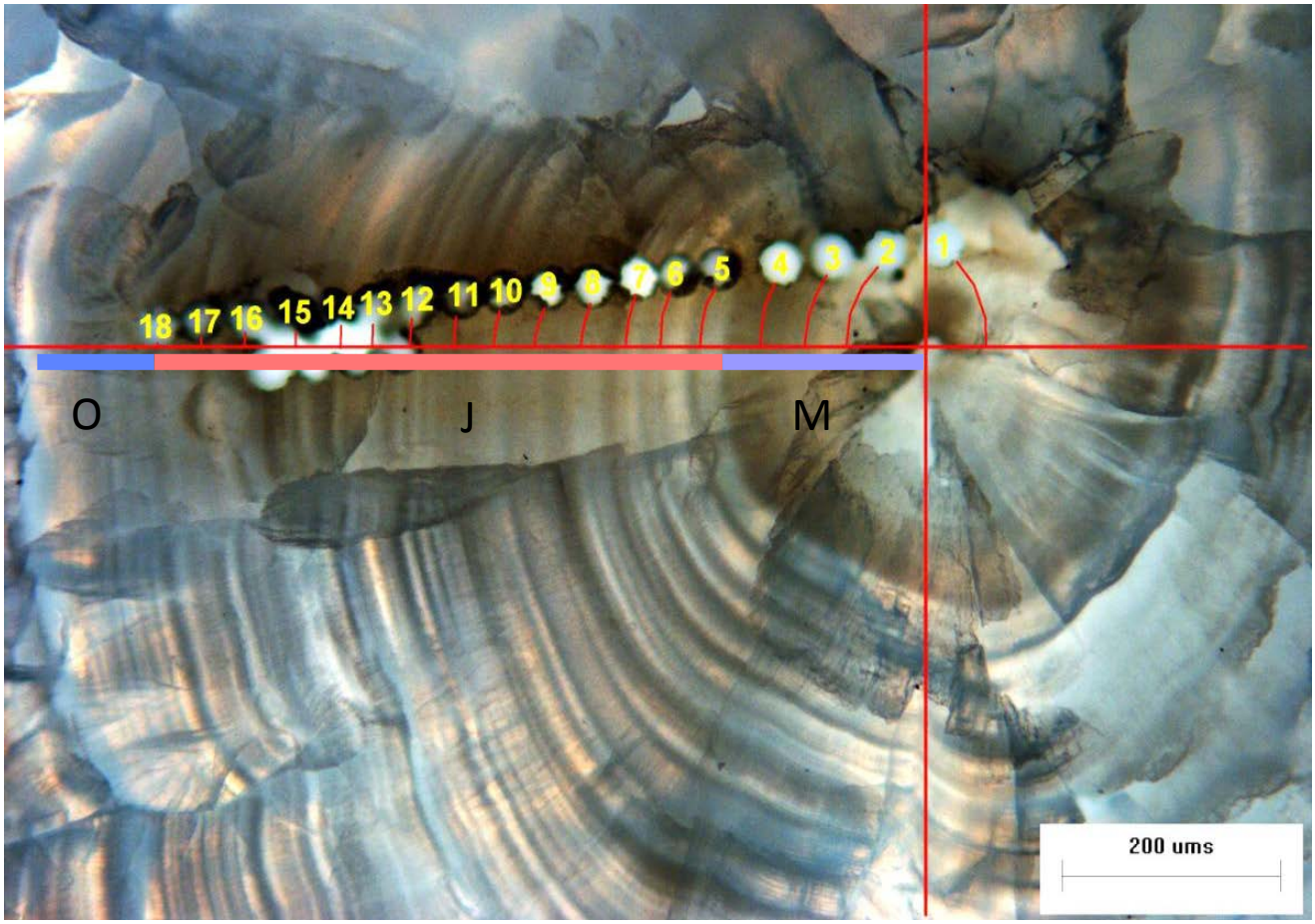

Fig. 2 A typical $^{87}Sr/^{86}Sr$ transect showing laser ablation pits (numbered) across an adult otolith, from the core (crosshairs) to ocean entry, used to reconstruct freshwater habitat use. The major life history stages are labeled: maternal (M), juvenile (J) and ocean (O). "Maternal" represents the period when the juvenile fed on maternally-derived yolk, with the exogenous feeding check (here, c. 220µm from the core) representing the point at which the juvenile emerged from the gravel and began exogenous feeding. Natal origin assignments are usually carried out using the otolith $^{87}Sr/^{86}Sr$ of material deposited beyond this point, where the isotopic signature has equilibrated with the ambient water and food sources. Note the 'respots' at positions 12.5-15.5 carried out to more accurately reconstruct habitat transitions.

TRANSGENERATIONAL RUN ASSIGNMENT USING OTOLITH CORE CHEMISTRY

The water chemistry at the location in which female salmon produce their eggs and undergo vitellogenesis greatly influences the core chemistry of their progeny (Fig. 3). As spring-running females largely produce the egg yolk while holding in the river over summer, the otolith primordia of their progeny tend to reflect the signature of the natal river (Miller and Kent 2009). Conversely, fall running females tend to produce their eggs in the ocean, and the core chemistry of their progeny reflects the elevated marine $^{87}Sr/^{86}Sr$ signature. Progeny of fall-run parents show this elevated marine $^{87}Sr/^{86}Sr$ in the core and a systematic depletion of $^{87}Sr/^{86}Sr$ which converges to the natal river $^{87}Sr/^{86}Sr$ value upon complete yolk absorption. So long as the river is isotopically distinct from marine values and spring running fish hold in the river for a sufficient length of time, it can be possible to use otolith core $^{87}Sr/^{86}Sr$ to distinguish individuals born of fall- or spring-run parents (Miller and Kent 2009). In the CCV, with the exceptions of the Yuba, Merced and

American Rivers, the salmon rivers have lower $^{87}Sr/^{86}Sr$ signatures than the mean ocean value of 0.70918 (Barnett-Johnson et al. 2008), resulting in a potential otolith marker to discriminate salmon produced by spring or fall-running parents. Here, we used FEH-origin CWT fish (n=33 from escapement 2009-10) of known run-type (1) to test for a difference in primordia $^{87}Sr/^{86}Sr$ signatures between fish born of spring- and fall-run parents, and (2) to use these data to train an LDFA to predict run type for samples of unknown run and origin. Note that this analysis was only carried out on individuals assigned to sites other than the Yuba, Merced and American Rivers and the Merced and Nimbus hatcheries, given the isotopic differential between ocean and natal river necessary for the technique to be effective.

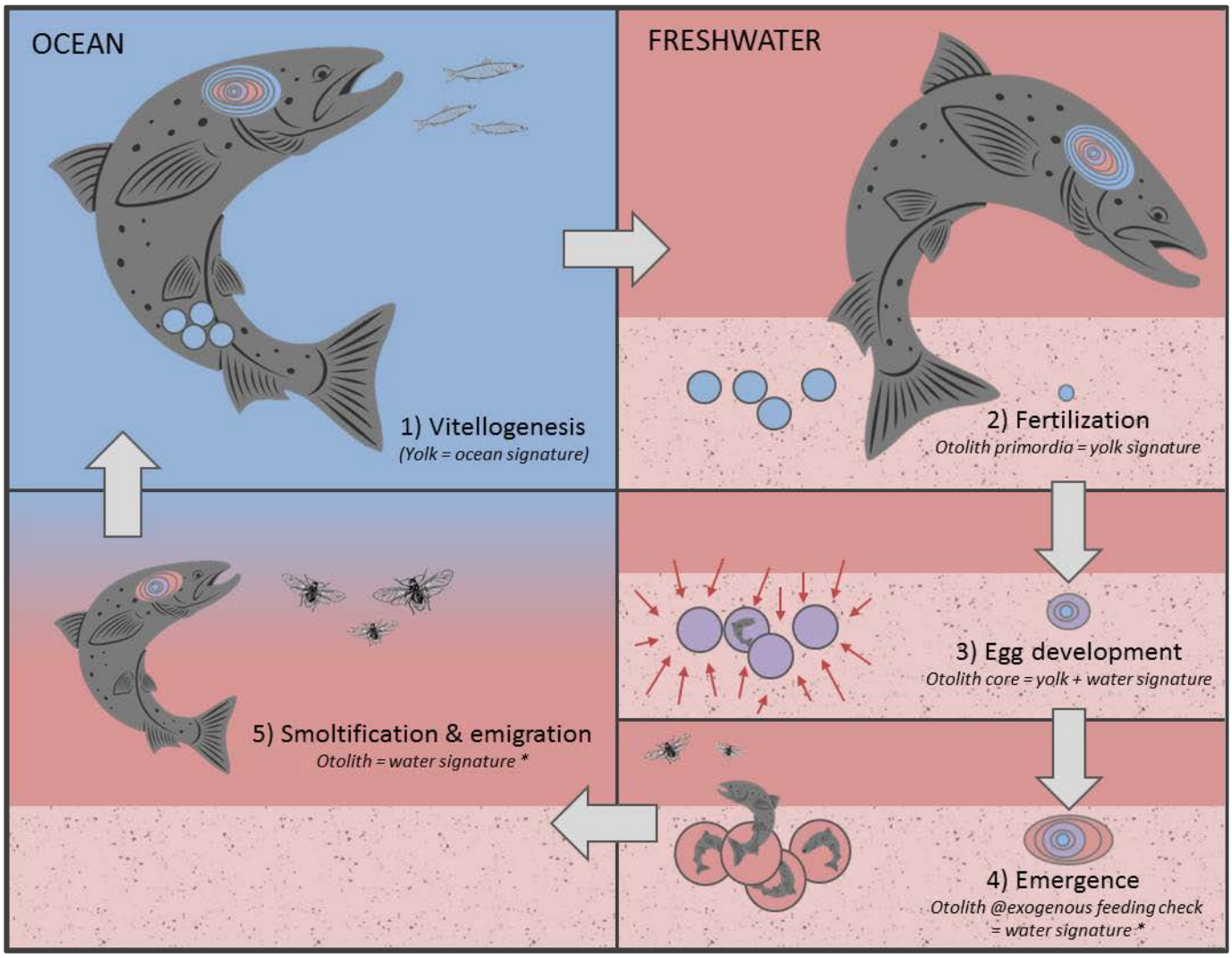

Fig. 3 Schematic to explain the patterns in otolith core chemistry typically exhibited by fall-run Chinook salmon (not to scale). The primordia exhibits a marine signature due to the maternally-derived yolk (1-2), which gradually equilibrates with the ambient water (3) until the yolk is used up and the fish is feeding exogenously (4). * Note that under natural conditions, the food web tends to reflect the isotopic composition of the local water source, but hatchery fish are fed a marine-based diet, resulting in natal otolith signatures (post-emergence) that reflect a mixture of water + dietary inputs.

OTOLITH THERMAL MARK ANALYSES

Otolith thermal marking (OTM) has been carried out at Feather River Hatchery (FEH) since 2005. Marks are race and brood year specific, and created through manipulation of rearing water temperatures (Cavallo et al. 2009). The unusual isotopic profiles exhibited by some of the adults in the Yuba River escapement (see Results) meant that additional verification of natal origin was sought, so a subsample of otoliths (n=12 of which 5 were known-origin FEH adults based on CWT records) were re-prepared to maximize clarity of core increments, and the images sent to experts at FEH for blind, independent thermal mark analysis.

WATER ISOTOPIC ANALYSES

To provide further information on the patterns in otolith chemistry observed in the current study, water samples were collected from 10 sites on March 12th and 13th 2013 (Fig. 1). All sites except the Goldfields and the three forks were sampled again on May 11th 2013. Water was collected in 60ml syringes and immediately filtered (0.45µm) into acid-washed 150ml Nalgene bottles. Procedural blanks were collected in the same manner using MQ water. Samples were stored at 4^{o}C in the dark until analysis (within 4 months).

Water samples were first purified using Sr-specific resin then analyzed for $^{87}Sr/^{86}Sr$ ratios using the same MC-ICPMS system described above. Samples were introduced to the MC-ICPMS using a desolvating nebulizer system (DSN-100) and a 0.1mL/min quartz nebulizer. Instrument sensitivity typically ranged from 160 - 400 V/ppm Sr. Baselines were measured for 30 s by ESA deflection. Ratios comprise approx. 50 data points, each integrated for 5 s. The software excludes outliers (~95% confidence) in real time. NIST SRM 987 (strontium carbonate reference material) was analyzed every six analyses and used to correct sample based on the TIMS literature value of 0.710249 (Housh and McMahon 2000, Christian et al. 2011).

RESULTS

SR PROFILES FROM KNOWN-ORIGIN FISH

Before examining otoliths from adults of unknown-origin, it is useful to familiarize oneself with Sr profiles from known (and relevant) sources. The most likely sources of strays to the Yuba River escapement (based on geography and/or known straying patterns) include the Feather River Hatchery [FEH] and associated Thermalito Rearing Annex [THE], the Coleman National Fish Hatchery [CNH] and the Feather River [FEA]. Figure 4 illustrates typical isotope profiles of juveniles captured in their natal river or strays of known-origin based on CWT records. Most Yuba-origin juveniles exhibited profiles similar to Fig 4A (93%; Appendix 1), but one (Fig. 4B) exhibited a sharp drop in isotopic signature at 325µm from the core (c.43mm FL) implying that it reared somewhere in the Yuba that is fed by water isotopically distinct from the mainstem before its capture in the Yuba RST.

It is also important to understand the processes governing $^{87}Sr/^{86}Sr$ in the core of juvenile salmon. As indicated by the schematic in Figure 3, the otolith primordia of salmon produced by fall-run parents tend to exhibit a marine isotopic signature (~0.70918) because the yolk was produced while the mother was feeding in the ocean. As the eggs develop in the gravel, they gradually equilibrate with the ambient water until the fry emerge and feed exogenously. After this point, the otolith $^{87}Sr/^{86}Sr$ signature reflects the signature of the water body (and diet) experienced by the fish. Most of the CCV rivers are characterized by lower $^{87}Sr/^{86}Sr$ signatures than the ocean, resulting in a gradual decrease in otolith $^{87}Sr/^{86}Sr$ values from primordia to emergence (e.g. Fig 4C-H).

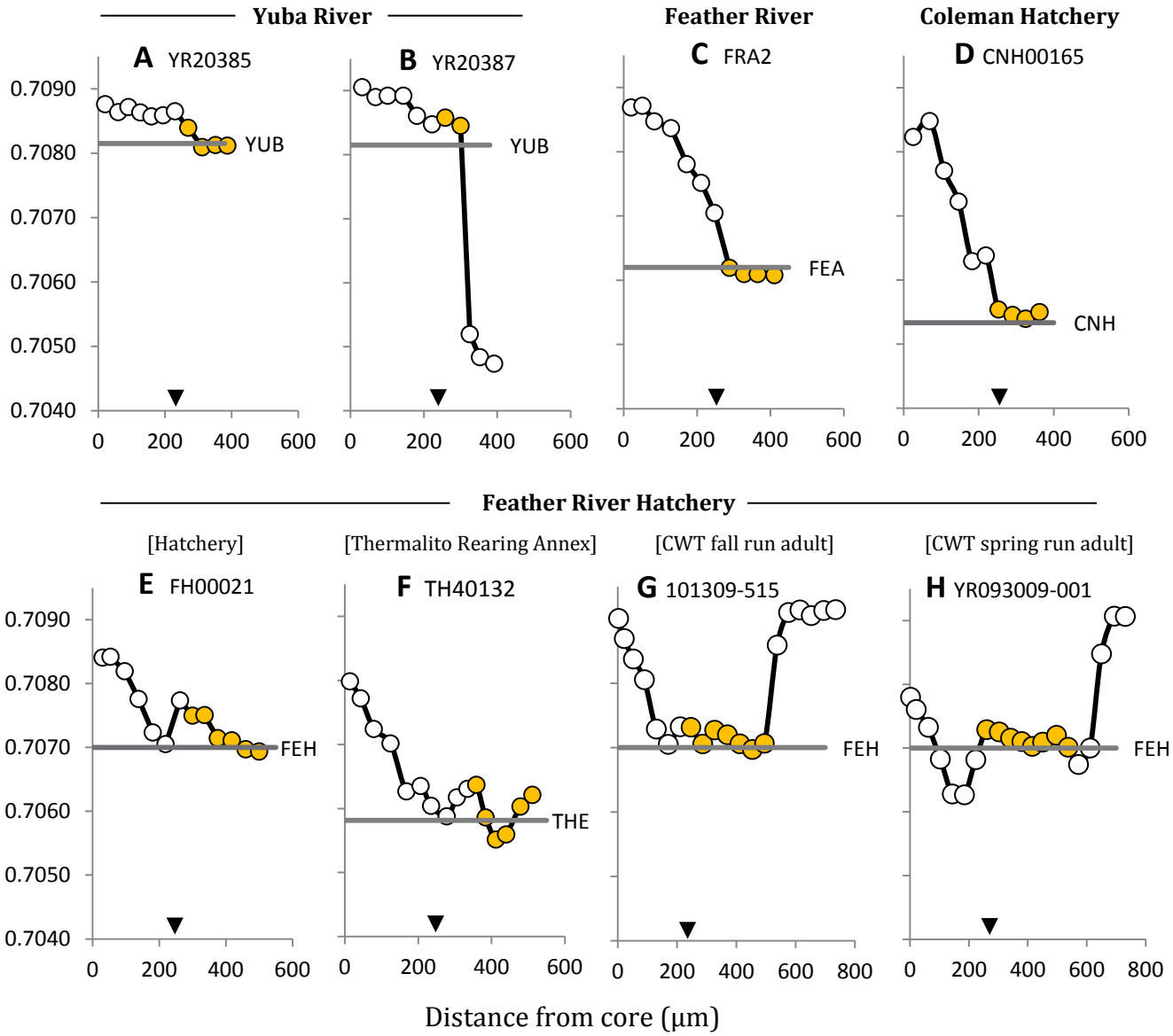

Fig. 4 Otolith $^{87}Sr/^{86}Sr$ profiles for known-origin Chinook salmon from natal sources relevant to the current project. Mean natal values for the entire isoscape are displayed (grey lines), along with the analyses that would be averaged and used to assign natal origin (orange spots) and the size at emergence (arrow). Plots A to F represent juveniles captured in river or from the hatchery. Plots G&H represent CWT marked fall and spring run adults from the Feather River Hatchery. Note that all profiles apart from A&B have dropped below the mean Yuba value (0.70815) well before emergence.

SUCCESS OF LDFA FOR NATAL ORIGIN ASSIGNMENT

The LDFA correctly classified 100% of known-origin CWT fish from the Feather River Hatchery (FEH, n = 20). None of these known-origin hatchery fish exhibited the "step" profile type. Within the isoscape, known-origin juveniles from the most likely sources in the Sacramento basin (Fig. 4; Kormos et al. 2012) were correctly classified using jack-knife resampling in 95% (Yuba, YUB), 97% (FEH), 88% (Feather River, FEA), 80% (Thermalito Annex, THE) and 69% (Coleman Fish Facility, CNH) of cases (Table 2). The LDFA also performed well at classifying other sites in the Sacramento watershed (62-100% correct), but performed poorly at classifying the rivers and hatcheries in the San Joaquin basin (0-29% correct; Table 2).

Table 2 Classification counts (actual rows by predicted columns) and percentage correct for known-origin juveniles or water samples by weighted linear discriminant function analysis and jackknife resampling, used to predict natal origin of adults of captured in the 2009 Yuba River escapement. Key sites for the current project are highlighted (shaded and in bold): Yuba (YUB) and Feather (FEA) Rivers, Coleman (CNH) and Feather River (FEH) Hatcheries, and Thermalito Rearing Annex (THE; part of the FEH facility). Other site codes include Battle (BAT), Deer (DEE), Mill (MIL) and Butte (BUT) Creeks; Stanislaus (STA), Mokelumne (MOK), Tuolumne (TUO), Merced (MER) and American (AME) Rivers; Mokelumne (MOH), Merced (MEH) and Nimbus (NIH) Hatcheries.

	BAT	DEE	MIL	BUT	**CNH**	**THE**	**FEA**	STA	MOK	**FEH**	MOH	TUO	**YUB**	MER	MEH	NIH	AME	**% correct**
BAT	7	1	1	0	**0**	**0**	**0**	0	0	**0**	0	0	**0**	0	0	0	0	78
DEE	0	8	5	0	**0**	**0**	**0**	0	0	**0**	0	0	**0**	0	0	0	0	62
MIL	0	3	7	0	**0**	**0**	**0**	0	0	**0**	0	0	**0**	0	0	0	0	70
BUT	0	0	0	5	**0**	**0**	**0**	0	0	**0**	0	0	**0**	0	0	0	0	100
CNH	**0**	**0**	**0**	**2**	**9**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**69**
THE	**0**	**0**	**0**	**0**	**0**	**4**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**80**
FEA	**0**	**0**	**0**	**0**	**0**	**1**	**22**	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**88**
STA	0	0	0	0	**0**	**0**	**1**	7	0	**16**	0	0	**0**	0	0	0	0	29
MOK	0	0	0	0	**0**	**0**	**0**	0	0	**18**	0	0	**0**	0	0	0	0	0
FEH	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**31**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**97**
MOH	0	0	0	0	**0**	**0**	**0**	0	0	**12**	0	7	**1**	0	0	0	0	0
TUO	0	0	0	0	**0**	**0**	**0**	0	0	**25**	0	9	**21**	0	0	0	0	16
YUB	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**18**	**0**	**0**	**0**	**0**	**95**
MER	0	0	0	0	**0**	**0**	**0**	0	0	**0**	0	0	**12**	0	1	0	0	0
MEH	0	0	0	0	**0**	**0**	**0**	0	0	**0**	0	0	**11**	0	4	0	0	27
NIH	0	0	0	0	**0**	**0**	**0**	0	0	**0**	0	0	**0**	0	0	9	0	100
AME	0	0	0	0	**0**	**0**	**0**	0	0	**0**	0	0	**0**	0	0	0	5	100

SUCCESS OF LDFA FOR TRANSGENERATIONAL RUN ASSIGNMENT

As hypothesized, progeny of known fall-run Chinook salmon from the FEH exhibited significantly higher core $^{87}Sr/^{86}Sr$ values than those born of spring-running parents (averages of 0.70846 ± 0.0001 SE *vs.* 0.70789 ± 0.00005 respectively; $F_{1,32} = 26.8$, $p<0.0001$; Fig. 5). These differences resulted in predicted

maternal run time being accurate in 85% of cases based on CWT records from 33 tagged adults (combining escapement years 2009-2011), using an LDFA with equal priors and jack-knife resampling (Table 3).

Table 3 Classification counts (actual rows by predicted columns) for CWT assigned fall and spring run Chinook salmon from the Feather River Hatchery based on $^{87}Sr/^{86}Sr$ values in the otolith primordia

CWT run designation	Fall	Spring	% correct
Fall	6	1	86%
Spring	4	22	85%
Total	10	23	85%

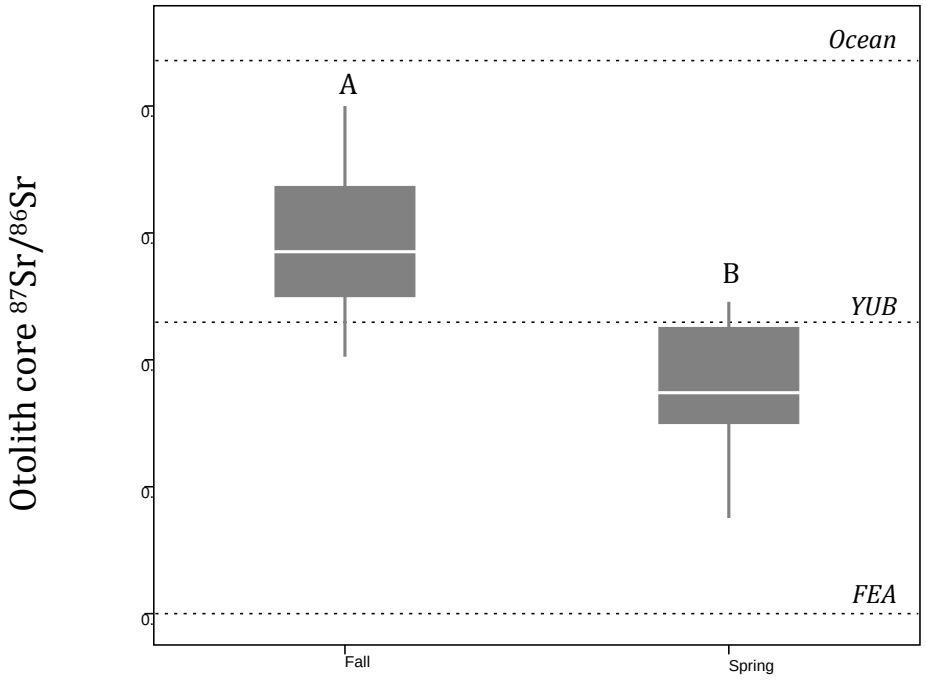

Fig. 5 Boxplot (median ± interquartile range) showing the difference in otolith core $^{87}Sr/^{86}Sr$ values of adults from the Feather River Hatchery born of fall (n = 7) and spring (n=26) run designated parents, as indicated by CWT records. Boxes not joined by the same letter are significantly different from each another ($p<0.05$, Tukey's Test). The mean value for the Yuba (YUB) and Feather (FEA) Rivers and ocean are indicated by dashed reference lines.

VARIATION IN OTOLITH ISOTOPIC PROFILES OF ADULTS CAPTURED IN THE YUBA RIVER

ADULT OTOLITH PROFILES OF YUBA-ORIGIN FISH

In the adults captured in the Yuba River 2009 escapement, 57% (95% CI = 48-66%) were classified as Yuba origin and 43% (34-52%) were classified as strays from other rivers and hatcheries. Unexpectedly, only 9% of the adults exhibited the typical otolith Sr profile for a fish that had originated in - and reared in - the Yuba prior to outmigration (profile type 1; Table 4, Fig. 6A-C). For these fish, the mean isotopic signature of the otolith natal region (post-emergence and post-exogenous feeding) was assigned to the Yuba and the profile exhibited a clear inflection point when the fish had emigrated through the isotopically lighter waters

of the Feather River (0.7062), Sacramento River (0.7058) and Delta (0.7060-0.7064). Another 8% of adults exhibited the same profile, only missing the inflection point (type 2; Fig. 6D). These were interpreted to have migrated to the ocean faster than the resolution of our spot analyses (equivalent to c.10-14 days of growth). A smaller proportion of adults (3%) exhibited mean isotopic values that were assigned to the Yuba, but reared for extended periods in locations other than the mainstem ("Habitat X"; type 3, Fig, 6E-F).

The fourth profile type was highly prevalent (38% of adults), featuring a "step" not seen previously in CCV salmon otoliths (Fig. 6G-I). This profile type was typical of Yuba-origin fish through the core area (stable $^{87}Sr/^{86}Sr$ values around the Yuba mean value of 0.70815), but suddenly dropped to non-Yuba mainstem values at the point of emergence. Using our typical method for natal assignment (LDFA analysis of the mean $^{87}Sr/^{86}Sr$ value of otolith material deposited post-emergence) these fish were classified as non-Yuba; however - to the best of our knowledge - there is no mechanism by which this pattern could arise unless the eggs had undergone vitellogenesis in a female holding in isotopically heavy freshwater. There are three possible candidates for this in the CCV: the American, Merced and Yuba Rivers. The American River is isotopically heavier than seawater, resulting in increasing isotopic values through the core area; however the observed trend was either stable or slightly decreasing, ruling this river out. Given that the shift consistently coincided with emergence (c.250 µm = c.30mm FL) we could rule out Merced Hatchery strays, as they do not release fish at such small sizes. We also ruled out Merced River strays as this river produces low numbers of natural returns (Sturrock et al. 2012b) and straying of wild salmon is uncommon among basins (Quinn 1997). As such, we interpreted the pattern as Yuba-diagnostic, with the "step" representing migration or displacement from the Yuba mainstem soon after emergence, followed by rearing in isotopically distinct water ("Habitat X"). Profiles were given a "step" score (excluding those that reared in the Yuba [profile types 1 and 2] or Merced River Hatchery because their natal signatures are so similar to ocean that it conceals patterns in the core) of 1 (otolith $^{87}Sr/^{86}Sr \geq 0.7080$ until emergence followed by a sharp decline, e.g. Fig. 6E-I) or 0 (gradual decrease in otolith $^{87}Sr/^{86}Sr$ from primordia to emergence, e.g. Fig. 4C-H). Individuals scored 1 were classified as Yuba-origin. Some individuals exhibited a "step" well after emergence and were assigned to the Yuba using both the "LDFA" and the "step scoring" methods (e.g. Fig. 6E-F). In Table 4 these individuals are classified under "profile type 3".

Table 4 Description and frequency of 'profile types' among adults classified as Yuba (YUB) origin fish.

Profile Type	Description	Origin	Rearing location	N	Proportion of all adults (n=103)
1	DFA predicted YUB; typical profile	YUB	YUB	9	9%
2	DFA predicted YUB but no 'dip' representing outmigration through FEA, SAC and Delta	YUB	YUB	8	8%
3	DFA predicted YUB, but profile indicated extended rearing at site(s) other than YUB mainstem	YUB	"Habitat X"	3	3%
4	DFA did not predict YUB (i.e. extended rearing at site(s) other than YUB mainstem), but "step" profiles imply eggs were deposited in the YUB.	YUB	"Habitat X"	39	38%

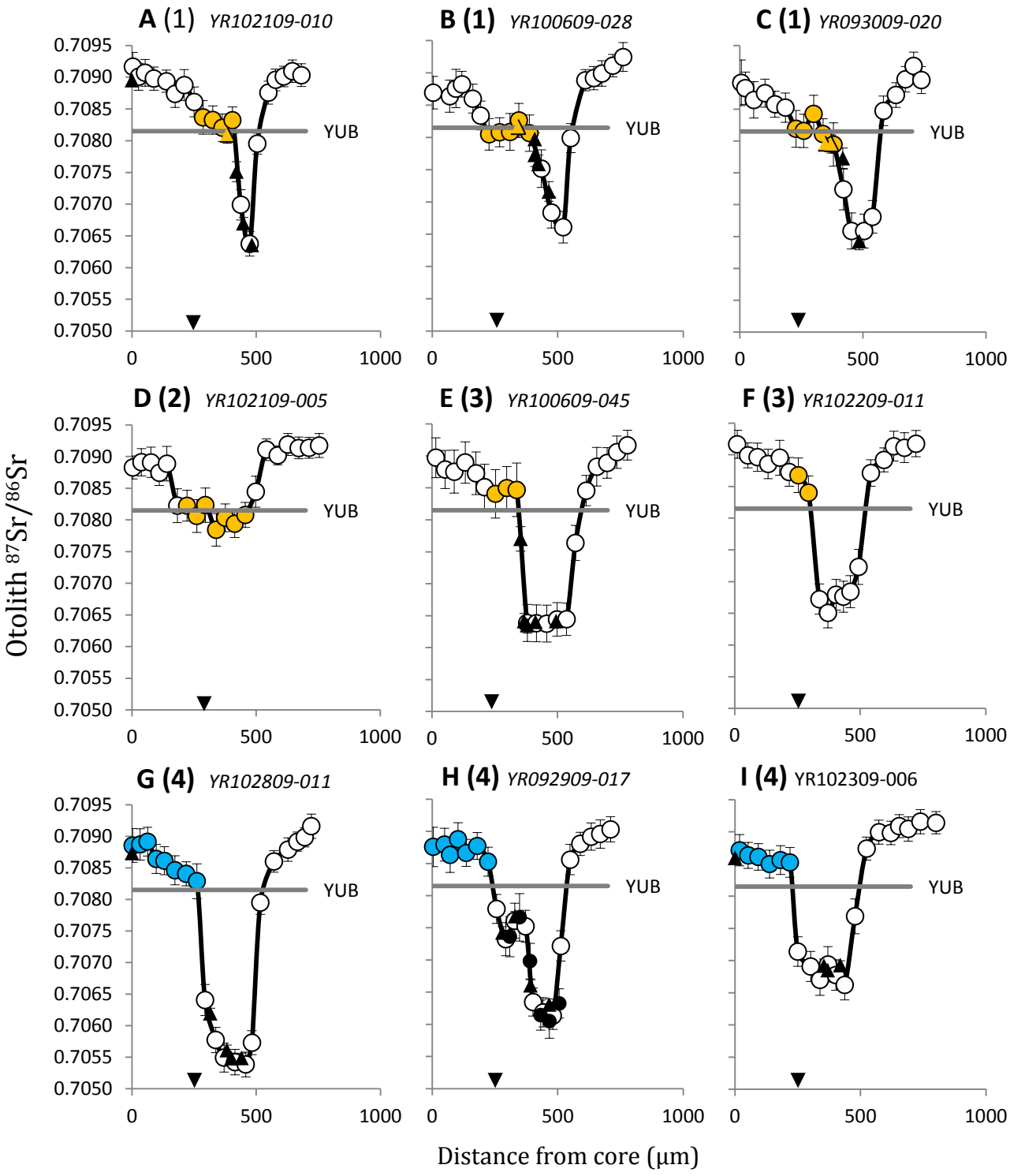

Fig. 6 Examples of otolith $^{87}Sr/^{86}Sr$ profiles (types 1-4: labeled in parentheses, described in Table 4) for adults captured in the Yuba (YUB) in 2009 and classified as YUB-origin. The profiles represent egg (otolith core) to ocean entry (mean value = 0.70918). The typical size at emergence is indicated by an arrow and the mean signature of the mainstem YUB indicated by a grey line. The mean signature of otolith material deposited immediately post-emergence is typically used to assign natal origin (orange spots, plots A-F), but for individuals exhibiting a "step profile" the high and stable core chemistry was also interpreted as YUB-diagnostic (blue spots, plots G-I). This "step" pattern has not been observed in salmon from other rivers in the Central Valley, and implies downstream movement immediately post-emergence and rearing in isotopically lighter water. The original Sr data (filled triangles) provided only a snapshot of the underlying variation, resulting in misclassifications of natal origin and the project extension to carry out full life history transects.

OTOLITH ISOTOPIC PROFILES & NATAL ORIGIN OF EARLY RETURNING FISH

Of the six early-returning fish to the Yuba with recovered floy tags and otoliths (Table 1), 50% were classified as FEH spring run (Fig. 7A-C) and 50% as YUB-origin (maternal run time unknown; Fig. 7D-F). Of the three fish assigned to the FEH, two were confirmed by CWT records (Fig. 7A & B). Of the three fish assigned to the Yuba, one was classified according to the traditional "LDFA method" (Fig. 7D), and the other two by their "step" profiles (Fig. 7E & F), with the elevated and stable core value reflecting their origin in the isotopically heavy waters of the Yuba. Note that if we had interpreted these two fish (Fig. 7 E & F) as strays to the Yuba, the elevated isotopic signature in their primordia would have indicated that their mothers were both fall run and they had both strayed and switched run types. This is certainly not impossible, but within such a small sample size it would be fairly unusual.

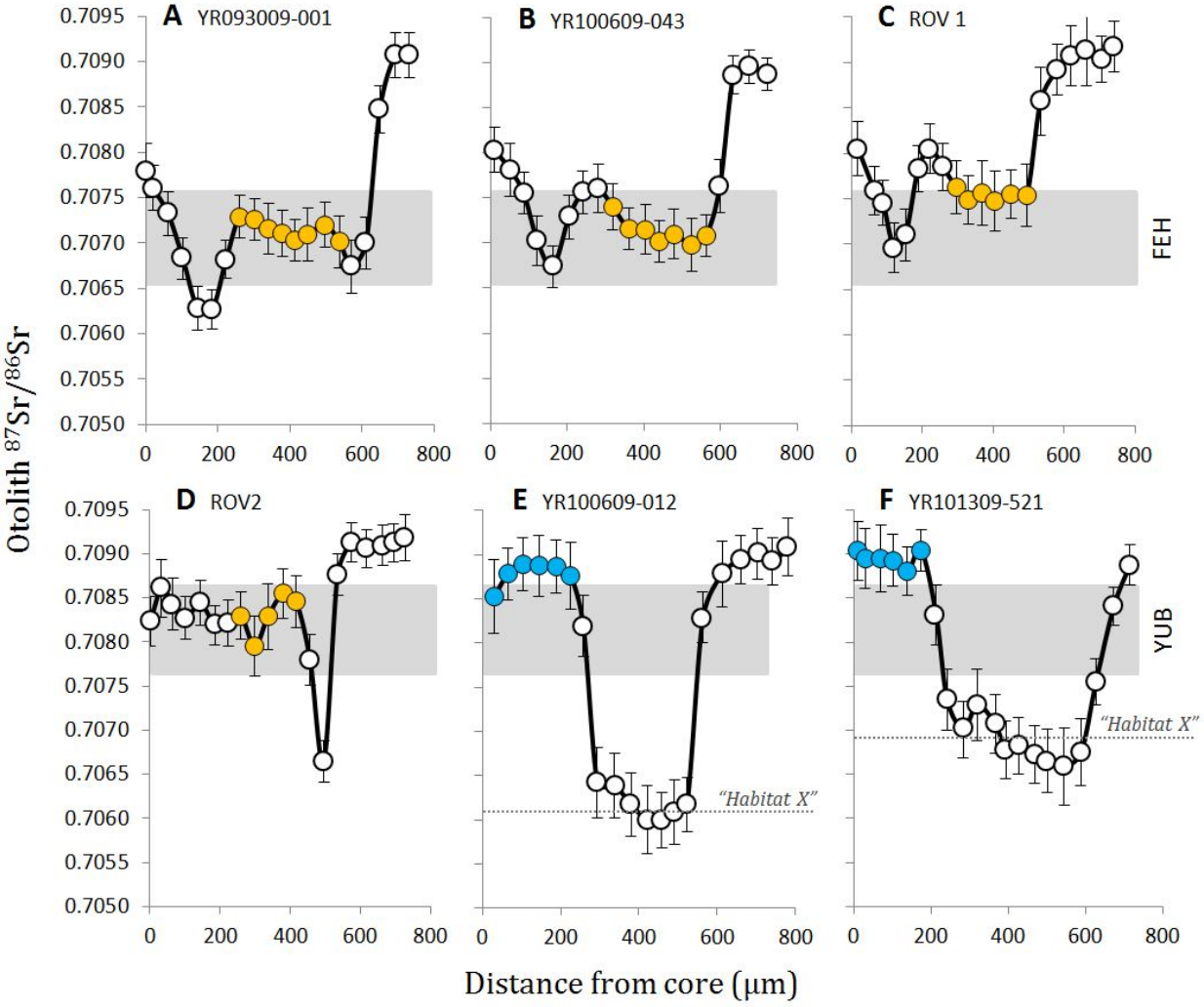

Fig. 7 Otolith $^{87}Sr/^{86}Sr$ profiles for six early returning adults that were floy tagged as they passed Daguerre Dam in the Yuba River, May 13-25th 2009. These transects reflect juvenile life history from egg (otolith core) to ocean entry (mean ocean value = 0.70918). Fish A-C were classified as spring run FEH (range of values in isoscape indicated by shaded area) based on the low primordia value and natal signature (orange spots). Fish D-F were classified as YUB-origin (range of values in isoscape indicated by shaded area), based on their natal (orange spots) or core (blue spots) isotopic values, with profiles E and F implying extended rearing in water isotopically distinct from the Yuba mainstem ("Habitat X").

NATAL ORIGIN OF ALL FISH IN THE YUBA 2009 ESCAPEMENT

The proportion of natural origin fish within the Yuba River 2009 escapement was estimated at 57% (95% CI =48-66%), with 43% (34-52%) classified as strays from the FEH (35%), FEA (5%), MEH (5%) and MOH (1%) (Table 5). Of the 20 CWT fish included blind within the sample, all were correctly classified to FEH and 85% were correctly classified as fall or spring run. The maternal run time of the three misclassified fish was corrected according to their CWT records before their inclusion in Table 5. One individual assigned to the FEH was *post hoc* reassigned to the Mokelumne Hatchery (MOH), as it exhibited a very stable profile throughout the rearing period (a phenomenon never observed in known-origin FEH fish, e.g. Fig. 4). We were confident of this reassignment as its mean natal isotopic signature was assigned to the MOH using an LDFA with equal priors, and we were aware that our weighted LDFA had poor capability at classifying known-origin MOH fish (Table 2). Also, one individual identified as having reared in the Thermalito Rearing Annex (THE) was also predicted to have been born of spring-running parents based on the isotopic composition of its primordia. However, the posterior probability of the prediction was similar for both run types (0.52 *vs.* 0.48), and the THE is used only for fall run juveniles from the FEH, so this individual was *post hoc* re-assigned as fall run before its inclusion in Table 5.

Table 5 Natal assignments and parental run timing of adult Chinook salmon from the Yuba River 2009 escapement based on otolith Sr isotopes. Site codes: Yuba (YUB) and Feather (FEA) Rivers, the Feather (FEH), Mokelumne (MOH) and Merced (MEH) River Hatcheries, and the Thermalito Rearing Annex (THE), part of the FEH facility. "Habitat X" represents rearing habitat(s) isotopically distinct from the mainstem Yuba.

Origin	**Parental run timing**	**Rearing location**	**N**	**%**	
YUB	n/a †	YUB	17	17%	57% wild
		"Habitat X"	42	41%	
FEA	Fall	FEA	5	5%	43% strays
FEH	Fall	FEH	11	11%	
	Spring	FEH	20	19%	
	Fall	THE	5	5%	
MOH	Fall	MOH	1	1%	
MEH	n/a †	MEH	2	2%	
TOTAL			**103**		

† River isotopic signature too similar to global ocean (0.70918) to use primordia to predict maternal run time

INVESTIGATIONS INTO THE "STEP"

Given the uniqueness of the "step" profile within the CCV and yet its prevalence in the current dataset, further investigations were carried out to try to understand the mechanism and confirm that these were indeed fish from the Yuba and not strays. We were particularly concerned that they might be strays from the Feather River Hatchery (FEH), given that straying from the FEH is common (Kormos et al. 2012) and the natal ('rearing') region of "step profiles" occasionally resembled mean FEH isotopic values (e.g. Fig. 6I). Otolith thermal mark (OTM) analyses were carried out to see if any individuals with the "step" were assigned to the FEH using an entirely different approach, and trends in return size and date were compared between fish exhibiting step *vs.* non-step profiles.

OTOLITH THERMAL MARK ANALYSES

OTM analyses correctly identified all CWT-fish as FEH-origin (n=5). Of four fish exhibiting "step profiles" that dropped to rearing signatures resembling the mean FEH value (e.g. Fig. 6I), one was classified as "not from FEH", and the other three were deemed "ambiguous" due to otolith preparation or image quality. Of three fish exhibiting "step" profiles that dropped to rearing signatures resembling the mean Feather River (FEA) value (e.g. Fig. 6E & H), two were classified as "not from FEH", while one was classified as "FEH spring run". This latter classification was for the individual presented in Figure 6E, and was deemed incorrect given that (1) the high core isotopic value extends to a distance of 337µm (c. 45mm FL; well after emergence), resulting in it being assigned by the LDFA to the Yuba, (2) the rearing signature was too low for the FEH (closer to the Feather River), (3) the "step" pattern has never been observed in known-origin FEH spring or fall run fish, (4) there was no associated CWT, and all FEH spring run fish are meant to be marked, and (5) the high isotopic value at the core implies either that the fish was born in isotopically heavy water (i.e. not the FEH) or that the eggs were produced in the ocean, i.e. fall-run (Fig. 3).

These OTM data, combined with (1) the absence of the "step" profile in any known-origin fish from any other river or hatchery, (2) the presence of a similar "step" in a juvenile captured in the Yuba RST (Fig. 4B), and (3) our knowledge of the mechanisms governing otolith core chemistry in Chinook salmon (Fig, 3), strengthened our confidence in our interpretation of the pattern being Yuba-diagnostic, with the sharp decline at emergence representing migration or displacement from the Yuba mainstem and rearing in isotopically distinct water ("Habitat X").

TRENDS IN SIZE AND DATE AT RETURN

Individuals exhibiting the "step profile" were significantly larger ($F_{1,79} = 13.53$, $p = 0.0004$) and returned to the Yuba significantly later ($Chi^2 = 4.64$, $df = 1$, $p = 0.0312$, Wilcoxon Rank Sums Test) than fish with no "step" in their otolith Sr profile (Fig. 8).

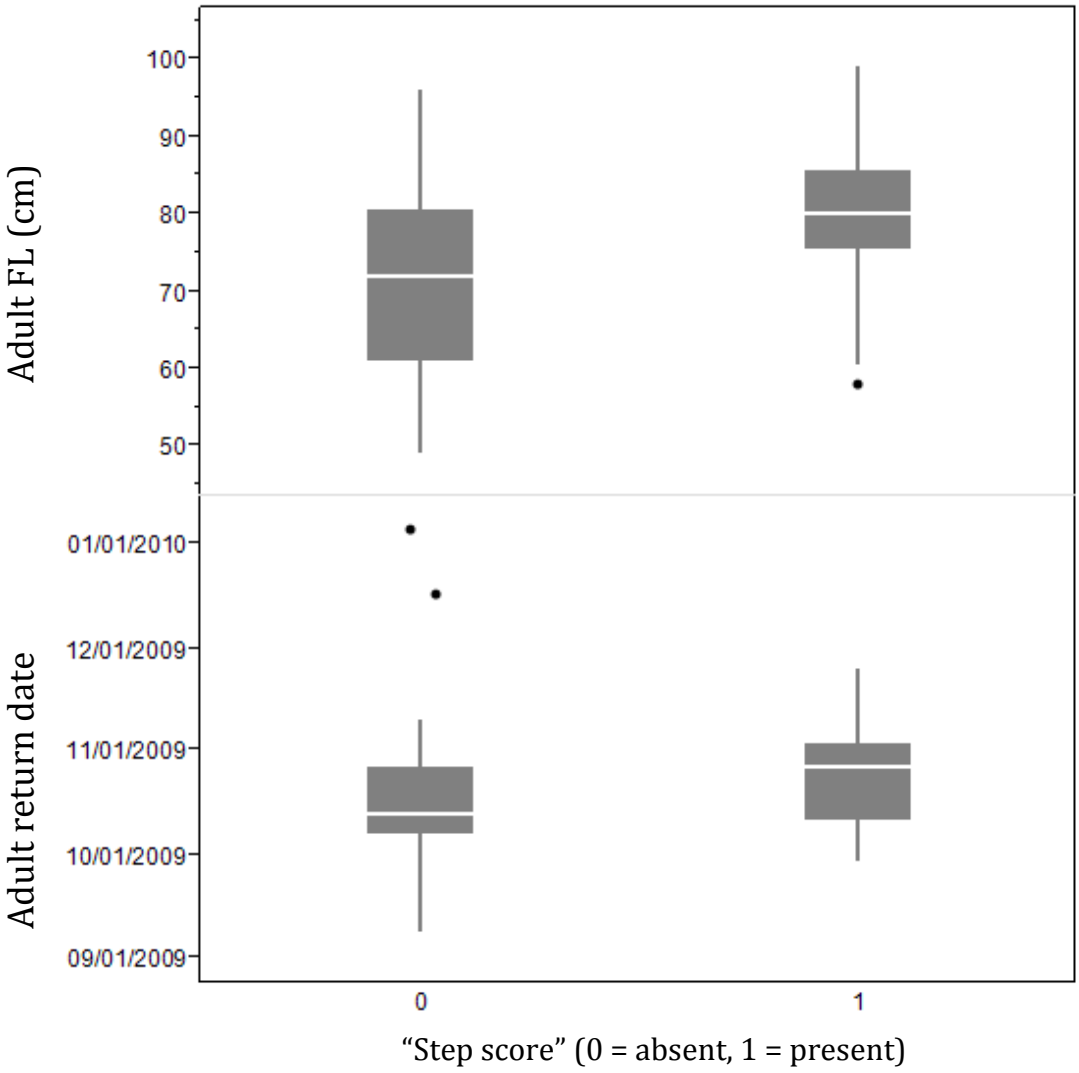

Fig. 8 Boxplot (median ± 25th to 75th percentiles) to show difference in fork length (FL) and return date of adults in the 2009 Yuba River escapement whose otoliths were assigned a "step score" of 0 (a gradual decrease in core isotopic value to rearing signatures) or 1 (extended and stable elevated core value followed by a sharp decline to rearing signatures).

The three most prevalent "types" of step profile in the current dataset are displayed in Figures 6 and 7. These show extended rearing in non-Yuba locations, which were collectively dubbed "Habitat X", but are in fact represented by at least three isotopically distinct water bodies with signatures around 0.7055 (say, "Habitat X"; e.g. Fig. 6G), 0.7063 ("Habitat Y"; e.g. Fig. 6E & H, Fig. 7E) and 0.7070 ("Habitat Z"; e.g. Fig. 6F & I, Fig. 7F). Potential sites that might represent or contribute water to these habitats were investigated via water sampling throughout the Yuba watershed (Fig. 2).

In the area of the mainstem Yuba available to migrating salmon (Parks Bar, Hallwood Boulevard and Marysville), water $^{87}Sr/^{86}Sr$ values gradually decreased with increasing distance downstream, but were all within or marginally higher than the range used to build the Sr isoscape (derived from juveniles captured in the Yuba RST in 2002). Of the three major upstream sources to the Yuba (cut off to migrating salmon by Engelbright Dam), the Middle Fork was the most isotopically similar to the Lower Yuba, while the North and South Forks were >0.002 higher (Fig. 9). The isotopic signature of the Feather River (FEA) water immediately downstream of the Yuba was >0.002 lower than the Yuba mainstem, and typical of the range used in the isoscape (derived from juveniles and water samples collected in the FEA in 1997-1998, 2000 and 2002). It was also typical of the "Habitat Y" signature (~0.7063) and it was deemed likely that a number of these Yuba-origin fish had been swept downstream and reared for many weeks in the FEA (e.g. Fig. 6E & H, Fig. 7E). The tributaries that feed the upper reaches of the Lower Yuba (Deer and Dry Creeks) exhibited isotopic values >0.003 lower than the mainstem Yuba and >0.001 lower than the FEA (Fig. 9). The signature of Deer Creek was typical of the rearing signature of "Habitat X" (~0.7055) and deemed likely to be another potential rearing location of newly emerged salmon (e.g. Fig. 6G). The lightest isotopic signature we measured was in Dry Creek (average of 0.70468), which may have represented the rearing location of the single known-origin Yuba juvenile with a "step profile" just before it was captured in the Yuba RST (Fig. 4B; final measured value of 0.70473). The gold fields canal upstream of the RST site exhibited an isotopic value intermediary between the Yuba and FEA (0.70782), but this is consistently higher than our "Habitat Z" signature (~ 0.7070) so is unlikely to be the water source or habitat region used by fish exhibiting this particular profile type (e.g. Fig. 6F & I, Fig. 7F). It is important to note that the mixing zones between water bodies, e.g. around the confluence between the Yuba River and Dry Creek could also create the intermediary isotopic signatures of "Habitat Y" and "Habitat Z".

Paired water samples collected in March and May 2013 were highly correlated (R^2 = 0.999, Fig. 10), but samples collected in May 2013 had a significantly higher isotopic value (mean difference = 0.00009, t = 3.12, df =5, p = 0.0263). Importantly, this isotopic difference was negligible compared with among-site differences (Fig. 9).

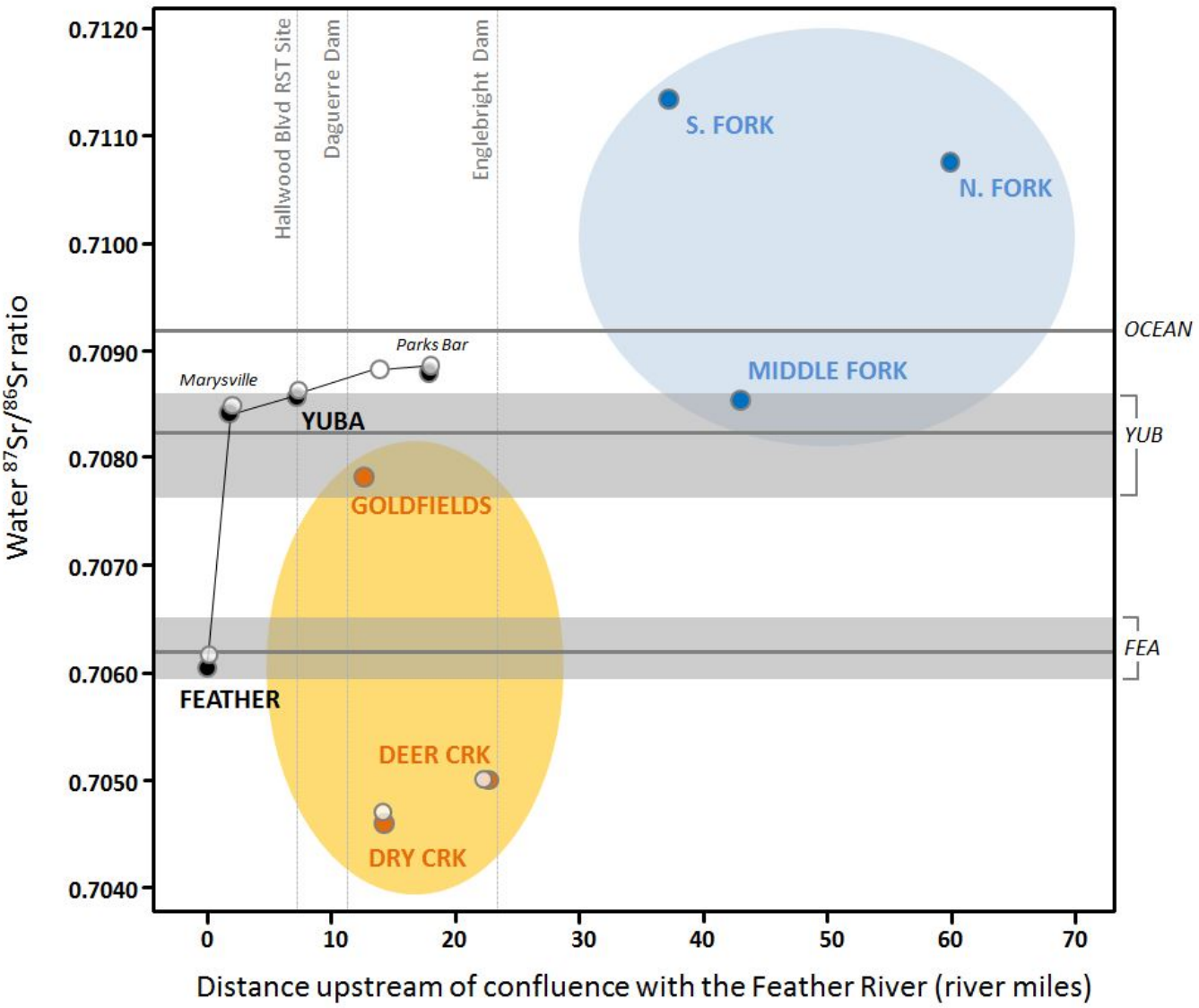

Fig. 9 Water $^{87}Sr/^{86}Sr$ values for sites around the Yuba (YUB) watershed, sampled March 12-13th 2013 (filled circles, n=10) and May 11th 2013 (white transparent circles, n=7). Sampling sites are labeled (Fig. 1) and plotted by distance from the Feather River (FEA) confluence. Vertical reference lines indicate distance to the RST site at Hallwood Boulevard (juvenile sampling), Daguerre Dam (VAKI Riverwatcher) and Englebright Dam (upstream barrier to migrating salmon). Solid reference lines indicate mean (± range where available) $^{87}Sr/^{86}Sr$ values for global ocean, YUB (based on juvenile otoliths sampled in 2002) and FEA (based on water and juvenile otoliths sampled 1997-98, 2000, 2002).

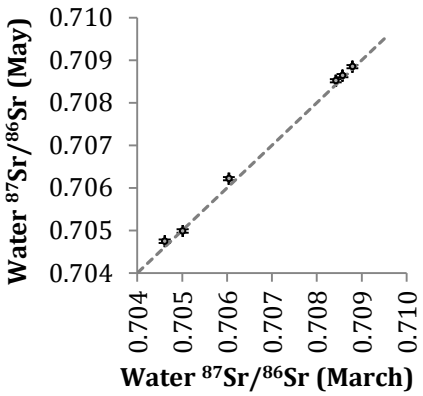

Fig. 10 Strontium isotopic values (±2SD) of paired water samples collected in the Yuba-Feather watershed on March 12-13th and May 11th 2013 (R^2 = 0.999). The 1:1 relationship is displayed (dashed line).

DISCUSSION

Our results indicate that the proportion of wild fish returning to the Yuba River in 2009 was 57% (48-66%), which is considerably higher than the rates indicated by the CFMP the following year (29%, which would have also included non-hatchery strays; Kormos et al. 2012). Of the fish known to have returned to the Yuba in spring 2009 (n=6), 50% were Yuba-origin returns and 50% from the Feather River Hatchery (FEH). In order to gain absolute confidence in our assignments, a more detailed understanding of the "step profile" is required, as it was so commonly observed that it had a significant impact on our estimates (Table 4). However, given the data currently available to us, we are confident that the "step" is Yuba-diagnostic, as the only conceivable explanation for the elevated and stable $^{87}Sr/^{86}Sr$ values through the core area is that egg development occurred in isotopically heavy water (of which the Yuba is the only plausible option within the CCV). Our confidence is strengthened by the following observations: (1) we have never seen a "step" in any known-origin fish from other CCV tributaries or hatcheries (including 264 juveniles and 86 CWT fish across a nine year sampling period), (2) the only "step" ever observed in a known-origin fish was from the Yuba (Fig. 4B), (3) otolith thermal mark analyses (carried out blind) did not definitively assign Feather Hatchery origin to any of the individuals with a "step profile", and (4) we have identified a plausible mechanism and potential rearing habitats for (most of) the profile types. Data gaps that will further inform our interpretation include continued water and juvenile sampling to identify the rearing location represented by "Habitat Z" (~ 0.7070; e.g. Fig. 6F & I, Fig. 7F), which overlaps with the FEH signature and thus causes the most concern. We would also like to analyze known-origin FEH, CNH, THE and FEA fish (juveniles and/or CWT adults) from the 2006 outmigration cohort (brood year 2005) as our current FEH collection only covers the 2007 and 2008 cohorts, and known-origin CNH, THE and FEA fish from outmigration years 2007-08.

Fry are generally perceived to have poor survivorship, however the prevalence of the "step profile" in our dataset suggests that migration or displacement of newly emerged fry can be successful. But why was the "step" so common in the 2009 escapement (38% of the returns) yet so rare in the juvenile RST sample captured in 2002 (7%)? Many of the individuals exhibiting a "step" appeared to have reared in the Feather River ("Habitat Y"; e.g. Fig. 6E & H, Fig. 7E), which is downstream of the Yuba RST site and thus would not be represented in our juvenile collection. Also, given that fry are relatively poor swimmers, the rapid movements implied by the "step" were deemed likely to coincide with high flow events, so we hypothesize that they will be primarily exhibited by individuals born in wetter years. The juveniles sampled from the RST were collected July 2002, a dry water year type (WYT), while the outmigration cohorts contributing to the 2009 escapement include 2006 (4 yr olds; wet WYT), 2007 (5 yr olds; dry WYT) and 2008 (2 yr olds; critical WYT). The 2005-06 winter flows were extremely high (e.g. 84,200 cfs on 12/31/05 near Marysville) and accompanied by considerable floodplain inundation and large pulses of fry outmigrants (25-40mm FL; Massa and Campos 2006). As such, we hypothesize that "step profiles" will be primarily exhibited by 4 year old fish

within the 2009 escapement. While we currently do not have age data accompanying our otolith samples, individuals exhibiting a "step profile" were on average larger and later returning; trends which are typically exhibited by older fish.

There are a number of possible reasons why the ratio of wild *vs.* hatchery fish was so much higher in 2009 compared with 2010 (Kormos et al. 2012), including improved survival of wild fish in the outmigration cohorts contributing to the 2009 escapement. We hypothesize that the high flows of winter and spring 2006 created large areas of suitable rearing habitat within the Yuba and its tributaries, as well as in downstream habitats, resulting in the diversification of habitats and promoting a greater range of salmon life histories. Such biocomplexity is believed to promote persistence by providing a buffering 'portfolio effect' to the population or stock complex (Hilborn et al. 2003, Schindler et al. 2010). Higher flows stimulate and facilitate dispersal of juvenile salmon while controlling water temperatures and increasing floodplain inundation. Floodplains are dynamic and productive habitats (Bellmore et al. 2013) that can convey significant growth and survival benefits to juvenile salmon (Sommer et al. 2001). As such, higher flows are thought to increase habitat availability, quality and diversity, augmenting the carrying capacity of the watershed (Burns 1971) and reducing density dependent mortality of rearing fish (Achord et al. 2003). In the Stanislaus River in San Joaquin basin, fry contributions to the surviving adults was significantly higher under wetter outmigration conditions (Sturrock et al. submitted), so it is certainly possible that fry survival was unusually high in the unusually wet year of 2006, as inferred by the prevalence of the "step profile" in our dataset. A second possibility for the differences in the hatchery *vs.* wild contributions to the 2009 and 2010 Yuba escapements may involve interannual differences in hatchery practices. The FEH is the most common source of strays to the Yuba, and the hatchery released approximately 1 million fewer juveniles in 2007 (BY 2006: 11,869,375) compared with 2008 (BY 2007: 12,824,381) (Ryon Kurth pers. comm), which represent the dominant age class (3 yr olds; Fisher 1994) for escapement years 2009 and 2010, respectively. Finally, a third potential explanation could include interannual differences in flow management. Recent analyses have indicated that the YUB:FEA flow ratio (combined with relatively lower YUB temperatures) is positively correlated with the number of adclipped salmon that pass Daguerre Point Dam four weeks later (Yuba Accord RMT 2013). In other words, one would expect greater straying rates when the YUB:FEA flow ratio is higher. We did a cursory analysis of "attraction flows" (YUB:FEA flow ratio) for 2009 and 2010 using the same datasets as the M&E Interim Report (Marysville Gage, CDEC station "MRY", USGS station 11421000 in the lower Yuba River *vs.* Gridley Gage in the lower Feather River, CDEC station "GRL", USGS station 11407150), and attraction flows were generally higher in April to July 2010 (Fig. 11). This would imply that the greater straying rates of spring running fish in 2010 might be explained by flow regime, and given its four week lag time, the considerable flow difference in June 2010 may have also induced greater straying rates among the earlier returning fall-run fish.

With such high mixing rates between the Feather and Yuba River populations, it has been stated that phenotypic spring run salmon on the Yuba represent "introgressive hybridization of larger Feather-Yuba river populations, partly comprised of hatchery-origin fish" (Yuba Accord RMT 2013). As such, there has been increasing discussion about recognizing the Feather-Yuba populations as a single stock. The high levels of exchange indicated by the abundance of adclipped fish passing Daguerre Dam (Yuba Accord RMT 2013) and the CWT records analyzed by CFMP (Kormos et al. 2012) were confirmed by the results of the current study, however, 50% of the phenotypic spring-run salmon in the 2009 dataset were born in, and returned to, the Yuba River. This implies that the survival of Yuba River spring-run juveniles is high enough that they are detectable in the adult population on the Yuba River and that the Yuba River has habitat and hydrologic conditions capable of contributing successful natural spring-run to the population. With further hatchery and flow management it may be possible to further reduce straying rates and hybridization between the two populations. Local adaptation and asynchrony among populations is thought to be crucial for increasing stability in adult returns, and allowing the stock-complex to deal with unexpected perturbations (Hilborn et al. 2003).

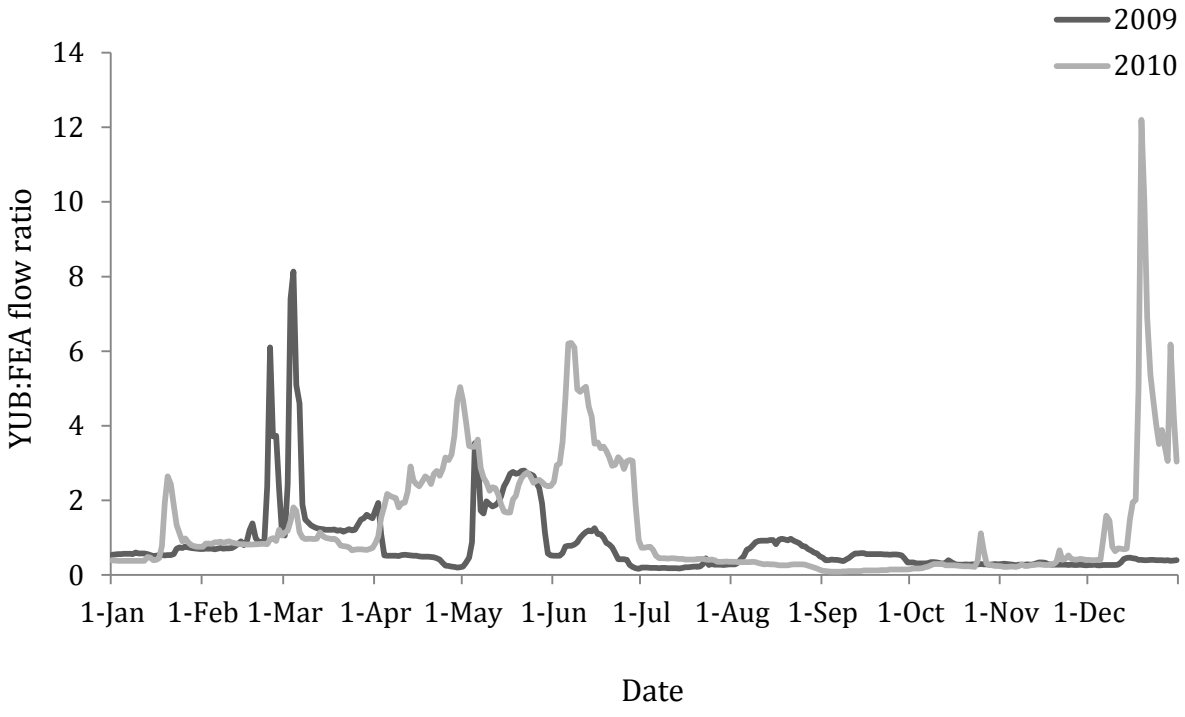

Fig. 11 "Attraction flows" to the Yuba River in 2009 (dark line) and 2010 (pale line), indicated by the ratio of Yuba River to Feather River River (YUB:FEA) daily mean flows (Marysville Gage, CDEC station "MRY", USGS station 11421000 *vs.* Gridley Gage, CDEC station "GRL", USGS station 11407150).

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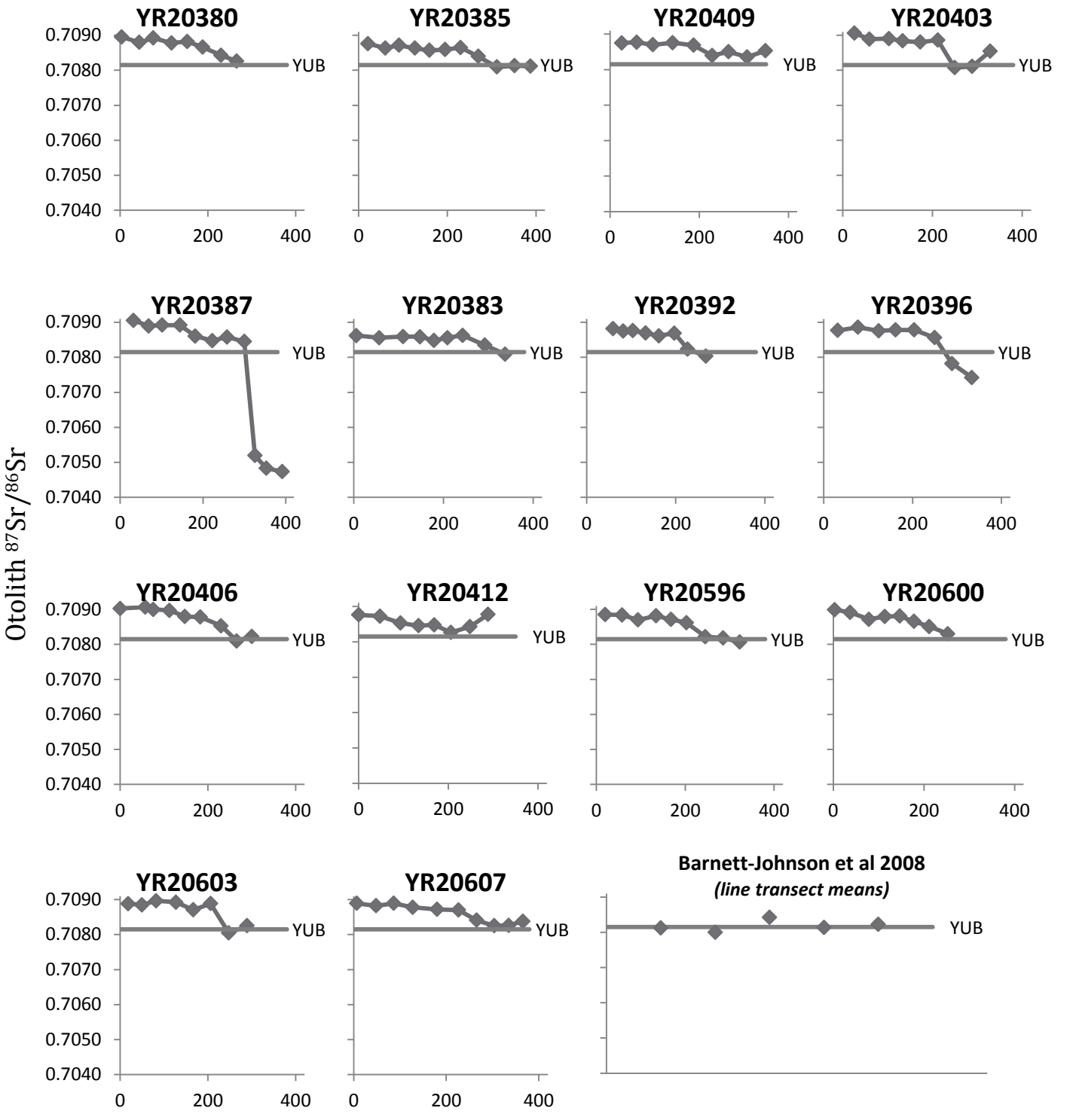
APPENDIX 1

Otolith $^{87}Sr/^{86}Sr$ life history profiles for 14 juveniles from the Yuba River (YUB; mean natal value indicated by solid line), and mean natal values for five additional Yuba-origin juveniles (from Barnett-Johnson et al. 2008). Juveniles were captured in rotary screw traps near Hallwood Boulevard, so assumed to have been born in the Yuba River. These transects reflect early life history from egg (otolith core), through juvenile rearing, to just before outmigration from the Yuba River. Note the clear departure from the mean YUB natal value for YR20387 and YR20396.



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