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Tracking natal origins of salmon using isotopes, otoliths, and landscape geology

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Abstract

The inability to identify natal origins (i.e., individual rivers and hatcheries) of adult Pacific salmon in the ocean has impeded our understanding of their ocean ecology and the management of mixed-stock fisheries. Strontium isotope ($^{87}Sr:^{86}Sr$) ratios recorded in otoliths of fall-run Chinook salmon (*Oncorhynchus tshawytscha*) from all major natural and hatchery spawning sites in the California Central Valley can be used as natural tags to identify natal origins with high accuracy (82%) and improved when additional otolith markers identified fish to hatchery (98%) or naturally spawned (94%) sources. A spatial baseline of $^{87}Sr:^{86}Sr$ signatures was developed by targeting $^{87}Sr:^{86}Sr$ within juvenile portions of otoliths accreted in natal streams and hatcheries using laser ablation and a multicollector inductively coupled plasma mass spectrometer. The availability and analyses of known-origin coded wire tagged adults provides a rare test of this technique to reconstruct early life-histories of adults (90% correct classification). By quantifying the area of watershed influenced by granitic rocks using hydrologic and geologic data layers, we explained 94% of the geographic variability in $^{87}Sr:^{86}Sr$ in salmon otoliths. Creating a spatial map in geographic information systems relating landscape geology to Sr isotopes is a useful framework for evaluating the efficacy of Sr isotopes to track the natal origin and movement of salmonids in freshwater, estuarine, and marine environments to better understand how processes occurring in these habitats influence the growth, survival, and reproductive success of anadromous fishes.

One of the most challenging aspects of understanding population structure and connectivity for migratory species is identifying the natal origins of individuals across broad geographic areas where populations potentially mix. The use of isotopes and the development of spatial maps of isotopic variation (isoscapes) to track migrations have advanced our knowledge of population structure and feeding ecology in terrestrial taxa (reviewed in Hobson 1999; Hobson and Wassenaar 2008). Fewer empirical examples or isoscapes exist in aquatic systems, despite the fundamental role that connectivity plays in understanding the demography of populations. Such information and tools would extend our understanding of spatial mechanisms of population persistence for marine and anadromous fishes and aid in determining critical aquatic habitats (e.g., nurseries, tributaries) for reproduction, survival, and growth of endangered species and those targeted by fisheries.

Chinook salmon (*Oncorhynchus tshawytscha*) from the California Central Valley (CCV) make significant contributions to fisheries along the west coast of North America largely because of hatchery supplementation of the fall-run (Barnett-Johnson et al. 2007). Like many formerly abundant Chinook salmon stocks (e.g., Columbia River, Klamath-Trinity River), freshwater populations of CCV Chinook salmon vary in their extinction risks under the U.S. Endangered Species Act. All four runs of wild (naturally spawned) Chinook salmon in the CCV are listed as endangered (winter run), threatened (spring run), or are candidates (fall and late-fall run; Fisher 1994). Fall-run CCV Chinook salmon alone constitute 85–95% of the ocean salmon landings in California, resulting in US$56

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million in state income annually (Pacific Fisheries Management Council (PFMC) 2006). Thus, understanding the relative contributions of individual natal sources (i.e., individual rivers and hatcheries) to the CCV fall population is critical to understanding key sources that may be contributing disproportionately to its persistence. Currently, no traditional tagging methods (e.g., physical or genetic) are sufficient to identify natal sources for Chinook salmon from the CCV (Banks et al. 2000).

Tracking natal sources is important in understanding the status and trends of declining stocks and has prompted a search for ''ideal'' population tags for fisheries applications (Ward and Grewe 1994; Thorrold et al. 2002; Cadrin et al. 2005). The chemical compositions of fish earbones (i.e., otoliths) are becoming regularly employed as tools to address questions of natal origins (Swearer et al. 1999; Campana and Thorrold 2001; Brown 2006). This technique is predicated on differences in otolith chemistry among natal locations and can function as a tag whether the underlying mechanisms for elemental differences are identified (Thorrold et al. 2001; Gillanders 2002; Warner et al. 2005). Results of these site-specific applications are compelling, but often ignore processes acting at different spatial scales that drive the among-site chemical variation in marine or freshwater environments. Without a mechanistic understanding of how environmental characteristics relate to otolith chemistries and a quantitative framework that spatially maps the important environmental properties, one is limited to documenting site-specific patterns.

Strontium isotope ($^{87}Sr:^{86}Sr$) ratios in otoliths have proven useful in identifying natal freshwater habitats (Kennedy et al. 1997; Ingram and Weber 1999; Hobbs et al. 2005), tracking small-scale movement patterns (Kennedy et al. 2000) and chronicling the timing of migration between marine and freshwater environments (Koch et al. 1992; Bacon et al. 2004; McCulloch et al. 2005). Several characteristics of Sr isotopes make them ideal spatial markers for characterizing natal sources: Sr readily substitutes for Ca in calcified structures like otoliths and can be recovered from discrete growth increments deposited throughout the life of a fish; Sr isotope ratios in watersheds and fish tissues are controlled by the age and composition of rocks comprising individual watersheds and have been found to be stable across years (Kennedy et al. 2000), although seasonal variation has been reported in some systems (Semhi et al. 2000); unlike stable isotopes and trace element concentrations, there is no evidence that Sr isotopes dissolved in water are altered by biotic (trophic; Blum et al. 2000) or abiotic processes when they are incorporated in otoliths (Ingram and Weber 1999; Kennedy et al. 2000). There is recent evidence that fractionation of the stable isotopes of Sr ($^{88}Sr:^{86}Sr$) may be temperature dependent in biogenic carbonates (e.g., during coral growth), but this potential source of fractionation is accounted for in mass-bias corrections for $^{87}Sr:^{86}Sr$ reported in most studies (Fietzke and Eisenhauer 2006). $^{87}Sr:^{86}Sr$ ratios vary in nature because ^{87}Sr is produced through the radioactive decay of ^{87}Rb (half-life = 4.9×10^{10} yr; Faure, 1977). As a result, older rocks or rocks that have higher Rb concentrations (e.g., granites) tend to have more radiogenic (i.e., higher) $^{87}Sr:^{86}Sr$ ratios.

Sr isotopes show great possibilities for many applications in fisheries science, yet studies of geochemical markers rely on extensive site-specific analyses to determine whether isotopic values are distinct among populations of interest. Because $^{87}Sr:^{86}Sr$ are controlled by geologic processes and high resolution hydrologic and geologic data layers are readily accessible in geographic information systems (GIS), we sought to quantify rock composition of watersheds on various spatial scales. By placing spatial variation in Sr isotope ratios in the context of bedrock geology, a mechanistic and quantitative framework can be developed to determine how particular rock types contribute to patterns of $^{87}Sr:^{86}Sr$ variability in watersheds and otoliths. Developing these geologic models across systems will assist in evaluating whether general characteristics in geology emerge in explaining $^{87}Sr:^{86}Sr$ variability in otoliths and aid in forecasting the efficacy of Sr isotopes as natural tags.

We build upon recent studies using $^{87}Sr:^{86}Sr$ variations in otoliths to identify natal environments and link Sr isotope variation in otoliths to watershed lithology using GIS hydrologic and geologic data layers (Kennedy et al. 1997; Ingram and Weber 1999; Douglas et al. 2002). Results to date do not provide a clear answer as to whether Sr isotopes can be employed to discriminate at spatial scales important to managing ocean populations, much less provide a quantitative framework to explain isotope variation in otoliths. The objectives of this study were to assess the utility of Sr isotopes as natural tags for mixed-stock fisheries applications by evaluating the following essential criteria using otoliths from Chinook salmon from the CCV as a model system: (1) watershed geology (age and/or rock composition) should vary at the spatial scale of interest (among rivers in this case), (2) all potential natal sources contributing to the fishery should differ significantly in $^{87}Sr:^{86}Sr$ values in otoliths such that individuals can be classified to origin with high accuracy, (3) natal origin of adults should be reconstructed through analysis of $^{87}Sr:^{86}Sr$ in the juvenile portion of adult otoliths with accurate methods conducive for large sample sizes, (4) geologic properties of watersheds should be quantified to understand the mechanisms contributing to spatial variation in otolith $^{87}Sr:^{86}Sr$ values.

Methods

Our approach to exploring the use of Sr isotopes and geographic patterns of geology to identify the natal sources of Chinook salmon was to first establish a baseline of $^{87}Sr:^{86}Sr$ ratios in the otoliths of juveniles collected from each natal source. We then assessed the accuracy of the baseline by reconstructing the natal origins of known-origin adults. Finally, we examined the geographic variation in $^{87}Sr:^{86}Sr$ ratios in terms of watershed geologic characteristics and provide a useful framework to aid in developing general geologic models across watersheds.

Study system—The watershed of the Sacramento–San Joaquin river system drains 163,000 km^2 or 40% of

California's land mass into the San Francisco Estuary (Fig. 1; Conomos et al. 1985). Fall-run Chinook salmon spawn in rivers and tributaries off the mainstem Sacramento River and San Joaquin River along the valley floor (Fisher 1994). The geochemistry of the water in the lower portion of the rivers where juveniles rear in the wild is derived from weathering of rocks within the entire upstream watershed. The northern Sacramento River watershed receives freshwater input from the southern extent of the Cascade Mountain Range, which is composed largely of Cenozoic volcanic rock (California Division of Mines and Geology, 2000; Fig. 1). The southern Sacramento and San Joaquin Rivers drain the Sierra Nevada Mountains, which generally is older Mesozoic granitic material (Blum et al. 1994; California Division of Mines and Geology 2000; Fig. 1). In the CCV both age and rock type act in concert (e.g., granites are both older and have higher initial Rb concentrations) to produce a general meridional gradient in Central Valley rivers from low $^{87}Sr:^{86}Sr$ values in the north to higher $^{87}Sr:^{86}Sr$ in the south (Ingram and Weber 1999). Previous strontium isotopic measurements of bedrock and stream waters within the Sacramento–San Joaquin system report significant differences between the two drainages and among individual tributaries (Kistler and Peterman 1973; Ingram and Weber 1999).

Natal source $^{87}Sr:^{86}Sr$ ratios—To develop a baseline of $^{87}Sr:^{86}Sr$ ratios across natal sources, fall-run juvenile CCV Chinook salmon were sampled from all five hatcheries and nine naturally spawning (wild) populations between 1999 and 2003 to include all major sources of juveniles (Fig. 1). Any unsampled rivers in the CCV did not have significant numbers of fall-run Chinook salmon (PFMC 2006). Wild juveniles were collected from streams with rotary screw traps operated by the California Department of Fish and Game, East Bay Municipal Utility District, Department of Water Resources, or S.P. Cramer and Associates. All wild juveniles were collected on rivers without supplementation or before releases of hatchery fish into rivers. Sagittal otoliths were extracted, washed, and stored in dry vials before cleaning and mounting. The left otolith was soaked for 6 hours in 30% Suprapur H_2O_2 to remove organic material. The right otolith was used if the left otolith was composed of the vaterite form of calcium carbonate. Otoliths were then double-rinsed in ultrafiltered water, triple-washed in 0.01 mol L^{-1} HNO_3, and double-rinsed again in ultrafiltered water.

Otoliths were mounted sulcus side up on microscope slides and polished using Al_2O_3 lapping paper until daily increments in the juvenile portion of the otolith were revealed (Barnett-Johnson 2007). Otoliths were transferred and grouped onto clean petrographic slides, randomized by source location and sampled using $60 \times 500 \times 80$ μm (W $\times$ L $\times$ D) laser tracks in the ventral region along the longest axis parallel to daily increments (5 μm increment^{-1}; ~12 days) where the plane of growth exhibits the least curvature (Barnett-Johnson et al. 2005). We measured $^{87}Sr:^{86}Sr$ in the region of the otolith accreted while in the natal tributary or hatchery, but after yolk absorption and before

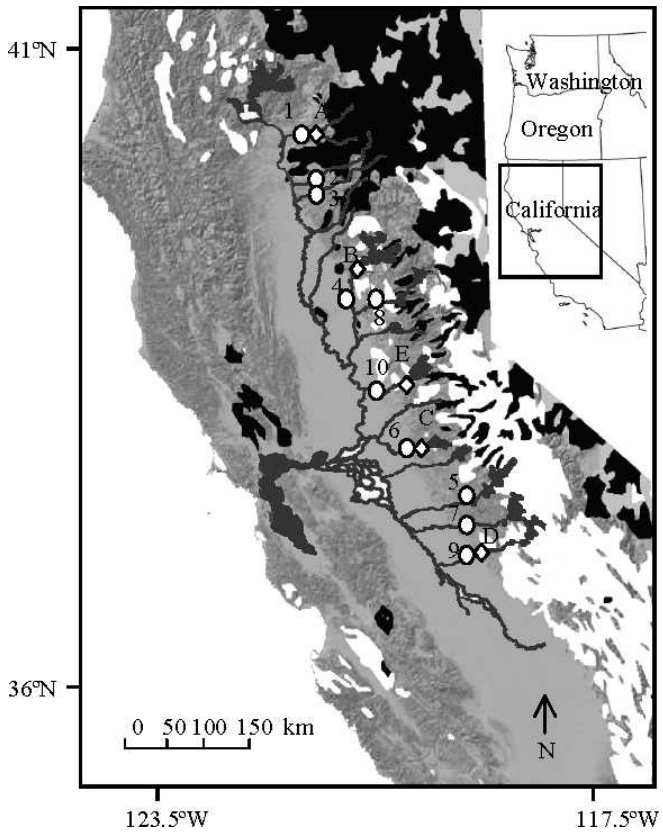

Fig. 1. Geographic locations and watershed geology where juvenile Chinook salmon were collected in rivers (open circles) and hatcheries (open diamonds) between 1999 and 2003 corresponding to populations listed in Table 1. Volcanic rocks (black) dominate the Cascade Mountain range to the north, whereas older granitic rocks (white) are widespread along the western slope of the Sierra Nevada mountain range producing a general north-to-south gradient in rock type and age.

outmigration (~250 μm from primordia). This region was just distal to the dark band diagnostic of the onset of exogenous feeding (Barnett-Johnson et al. 2007). Isolating this region is particularly important when characterizing natal $^{87}Sr:^{86}Sr$ values, because the prefeeding value reflects Sr derived from both marine (maternally inherited) and natal river sources (Bacon et al. 2005).

We used a New Wave UP213nm Laser (LA) and ThermoFinnigan Neptune multicollector inductively coupled plasma mass spectrometer (MC-ICPMS) with specific instrument, laser, and interference corrections described in Ramos et al. (2004) as applied to otoliths (Barnett-Johnson et al. 2005). Thirty ratios, each integrated for 8 seconds, were measured for each laser track and used to estimate within-run precision (2 $\times$ standard error $\pm$ 0.00004). Although there are several potential interferences on Sr isotopes in carbonates, including Ca dimers, Ca argides, and doubly-charged Er and Yb, only Rb and Kr affected the accuracy and precisions of $^{87}Sr:^{86}Sr$ (Barnett-Johnson et al. 2005). We accounted for the effects of ^{84}Kr and ^{86}Kr present in the Ar gas by subtracting on-peak baselines ($<$1 mV ^{83}Kr), measured before firing the laser from measured beam intensities. To correct for ^{87}Rb, we used

the measured $^{86}Sr:^{88}Sr$ and natural $^{85}Rb:^{87}Rb$ value to calculate a mass bias uncorrected $^{85}Rb:^{87}Rb$ ratio and the measured ^{85}Rb intensity to calculate and remove any ^{87}Rb contributions to measured ^{87}Sr intensities. $^{87}Sr:^{86}Sr$ ratios were then normalized to $^{88}Sr:^{86}Sr = 0.1194$ to account for any natural or machine-induced fractionation. External precisions (reproducibility) of $^{87}Sr:^{86}Sr$ measurements in otoliths using LA-MC-ICPMS were 0.00003–0.00009 (2 SD; Barnett-Johnson et al. 2005).

Development of natal source $^{87}Sr:^{86}Sr$ baselines—Hatchery and wild-origin Chinook salmon from the same sources as in this study can be identified with high accuracy (91%) using diagnostic differences in otolith microstructure (Barnett-Johnson et al. 2007). Therefore, two baselines of natal source $^{87}Sr:^{86}Sr$ signatures were developed and evaluated. The full model includes $^{87}Sr:^{86}Sr$ values for all hatcheries and wild tributaries together to determine the utility of Sr isotopes alone to identify fish to origin. The separate model evaluates $^{87}Sr:^{86}Sr$ values for fish rearing in rivers and hatcheries as two independent groups. Sr isotope ratios among natal sources were compared using analysis of variance (ANOVA) with post-hoc pairwise comparisons, Tukey's honestly significant difference (HSD), to determine whether there were significant differences in the means in isotopic signatures among sources. Sr isotope values met the assumptions of normality for ANOVA and were robust against violations of homogeneity of variances observed for hatchery fish.

A single-factor linear discriminant function analysis (DFA) with jackknife resampling was conducted to determine whether $^{87}Sr:^{86}Sr$ values could be used to correctly classify individual fish to natal origin (SAS version 8, SAS Institute). A linear function was used to estimate the variance-covariance matrix response and was applied across all sites. Jackknife resampling used the same data set to generate and evaluate the discriminant function by calculating the function (in this case mean $^{87}Sr:^{86}Sr$ for each natal source) with $n - 1$ observations, classifying the one observation omitted to the source with the closest mean and then repeating the procedure for all n observations. Prior probability of group membership was assumed to be equal for all DFAs. Further performance evaluation of the discriminant functions were conducted using Cohen's kappa, a statistic that provides a method of calculating the chance-corrected percentage of agreement between actual and predicted group classification. Values of kappa range from 0 to 1, with 0 indicating the DFA resulted in no improvement over chance and 1 indicating perfect agreement (Titus et al. 1984).

Reconstructing natal origins in adults—The accuracy of this technique in reconstructing the $^{87}Sr:^{86}Sr$ ratios in the natal portion of adult otoliths was tested through collection and analysis of adults of known hatchery origin, identified by the presence of clipped adipose fins and coded wire tags (CWTs), upon returning to spawn at five hatcheries in 2002. CWTs were extracted and read by U.S. Fish and Wildlife Service and California Department of Fish and Game staff to identify the hatchery of origin and year of release as subyearlings (1998–2000). Otolith preparation and isotope measurements were identical to juveniles described above. Adults were analyzed without prior knowledge of their origin and were used as an independent test of the robustness of the separate model to correctly classify hatchery adults to natal origin.

Geologic variability across watersheds—To quantify the variability in surficial geology within study area watersheds, we used ArcInfo 8.2 (ESRI) to intersect two GIS data layers, including a modified version of the GIS Data for the Geologic Map of California (California Division of Mines and Geology 2000) and a modified version of the California Interagency Watershed Map, CalWater 2.2 (California Department of Forestry and Fire Protection 1999). The CalWater 2.2 hydrologic data layer consists of a mix of hydrologic and administrative boundaries to define planning watershed units. This data layer was edited to remove administrative boundaries, where they existed, and were replaced with hydrologic boundaries interpreted from 30-meter digital elevation models and stream networks, including the National Hydrography Dataset (United States Geological Survey and United States Environmental Protection Agency 2001; Lindley et al. 2006). The geologic data layer was modified by adding a field to the polygon attribute table for aggregate geologic type. A look-up table was constructed of geologic types and corresponding aggregate geologic types based on general characteristics of age and rock types that likely reflect patterns of Sr geochemistry (Barnett-Johnson 2007). The new attribute field was populated using the "lookup" command in ArcInfo that classified rock types into four aggregate groups referred to as granitic, volcanic, young sedimentary, or old sedimentary. The intersection of these two layers yielded a new geologic-watershed data layer. To evaluate the variability in geologic characteristics across watersheds, polygons from this new data layer were grouped by study area watershed, and summary statistics were calculated for aggregate geologic type (Table 1).

GIS geologic and isotopic model—A multiple regression was conducted to determine whether the geologic composition in watersheds (i.e., percent aggregate type) could be used to explain the variability in Sr isotopes across wild sources and thus begin to produce a general predictive model. Percent aggregate geological type (e.g., volcanic, granitic, young sedimentary, and old sedimentary) for each watershed was calculated by dividing the area of aggregate type by watershed area and tested for colinearity (Table 1). The American River watershed (AME; Table 1) is composed of older Paleozoic undivided sedimentary rock, which likely contributes to its atypical geochemistry ($^{87}Sr:^{86}Sr$ higher than the ocean value) relative to the surrounding rocks in the CCV (Ingram and Weber 1999). Due to this unique feature of the watershed, two regression models, including and excluding AME, were evaluated.

Results

Natal source $^{87}Sr:^{86}Sr$ ratios—$^{87}Sr:^{86}Sr$ values were significantly different across all natal sources (full model,

Table 1. Area of aggregate geology derived by GIS hydrology and geology analyses for watersheds and measured isotopic values.

Map reference No., river (code)	Area 1,000 km² (proportion of watershed by rock type; %)					$^{87}Sr:^{86}Sr$ (SE)		Year
	Granitic	Volcanic	Young Sedimentary	Old Sedimentary	Watershed			
1. Battle Creek (BAT)	0 (0)	839 (88)	115 (12)	2 (0)	956	0.703864	(0.000056)	1999
& hatchery (CNH)[A]						0.705306	(0.000094)	2002
2. Deer Creek (DEE)	0 (0)	536 (95)	24 (4)	3 (0)	563	0.704115	(0.000013)	2002
3. Mill (MIL)	0 (0)	332 (97)	4 (1)	5 (1)	342	0.704112	(0.000010)	2002
Butte Creek*	121 (6)	592 (29)	1,322 (64)	32 (2)	2,069	0.704810		2002
4. Feather (FEA) &	4,548 (44)	3,186 (31)	2,007 (20)	289 (3)	10,281	0.706278	(0.000011)	2002
hatchery (FEH)[B]						0.707078	(0.000048)	2002
5. Stanislaus (STA)	1,733 (61)	718 (25)	276 (10)	97 (3)	2,843	0.706870	(0.000035)	2002
6. Mokelumne (MOK)	1,122 (61)	341 (19)	698 (16)	28 (2)	1,843	0.706891	(0.000012)	2002
& hatchery (MOH)[C]						0.707486	(0.000032)	2002
7. Tuolumne (TUO)	3,464 (79)	218 (5)	542 (12)	121 (3)	4,409	0.707392	(0.000102)	2003
8. Yuba (YUB)	2,619 (74)	600 (17)	208 (6)	54 (2)	3,524	0.708151	(0.000044)	2002
9. Merced (MER) &	2,446 (75)	1 (0)	601 (19)	165 (5)	3,245	0.708492	(0.000007)	2003
hatchery (MEH)[D]						0.708611	(0.000011)	2002
10. American (AME) &	3,064 (60)	978 (19)	348 (7)	607 (12)	5,086	0.710249	(0.000019)	1999
hatchery (NIH)[E]						0.709741	(0.000022)	2002

Natal sources ordered by increasing $^{87}Sr:^{86}Sr$ measured in wild fish otoliths. Superscript letters for hatchery locations correspond with letters on Fig. 1: A, Coleman National Fish Hatchery; B, Feather River Fish Hatchery; C Mokelumne River Fish Hatchery; D, Merced River Fish Hatchery; E, Nimbus River Fish Hatchery.

*$^{87}Sr:^{86}Sr$ value from water samples (Ingram and Weber 1999) used for watershed analysis because of the availability of isotopic data for the river but the absence of fall-run Chinook salmon present.

ANOVA, $F_{14,123} = 1{,}503$, $p < 0.001$) and among hatcheries (ANOVA, $F_{4,50} = 819$, $p < 0.001$) and rivers (ANOVA, $F_{9,73} = 2{,}999$, $p < 0.001$) for the separate model. Pairwise comparisons using the separate model showed all individual hatcheries (HSD, df = 50, $p < 0.001$) and rivers (HSD, df = 73, $p < 0.005$) were significantly different from one another, with the exception of juvenile salmon from Deer (DEE) and Mill (MIL) Creeks, which had overlapping $^{87}Sr:^{86}Sr$ values (natal location codes referenced in Table 1). The full model showed that all 104 pairwise comparisons were significantly different (HSD, df = 123, $p < 0.005$), with the exception of five comparisons (Battle Creek [BAT] with DEE and MIL; DEE and MIL, Feather River Hatchery [FEH], and Mokelumne River [MOK]; and Mokelumne River Hatchery [MOH] and Tuolumne River [TUO]; Table 1).

DFA indicated that 98% of hatchery juveniles ($n = 55$) and the majority of wild juveniles could be correctly assigned to natal origin using the separate model (Fig. 2). For four of the five hatcheries, 100% of juveniles were correctly classified to hatchery of origin, with one individual from the FEH misclassified as originating from Coleman National Fish Hatchery ([CNH] Fig. 3). The chance-corrected Cohen kappa value was 98% for hatchery juvenile classifications, with 95% confidence intervals (CIs) estimated as 93% to 100%. All individuals from 4 of the 10 rivers were correctly assigned to origin (AME, MOK, Feather River [FEA], and Merced River [MER]), with one individual misclassified for three rivers (TUO, Stanislaus [STA], and Yuba [YUB]). Fish from BAT, DEE, and MIL had lower classification success (78%, 63%, and 40%), respectively. Overall chance-corrected performance of wild classification was 0.83 (Cohen kappa value, CI = 0.72–0.90).

DFA for the full model resulted in 100% of hatchery and 100% of wild juveniles from 7 of the 15 natal sources being correctly classified. All individual fish were similarly assigned between both the full and separate model, with the exception of a few individuals originating from five different sources whose classifications were improved by the separate model. Using the full model, accuracy decreased for CNH, FEH, MOK, STA, and TUO from

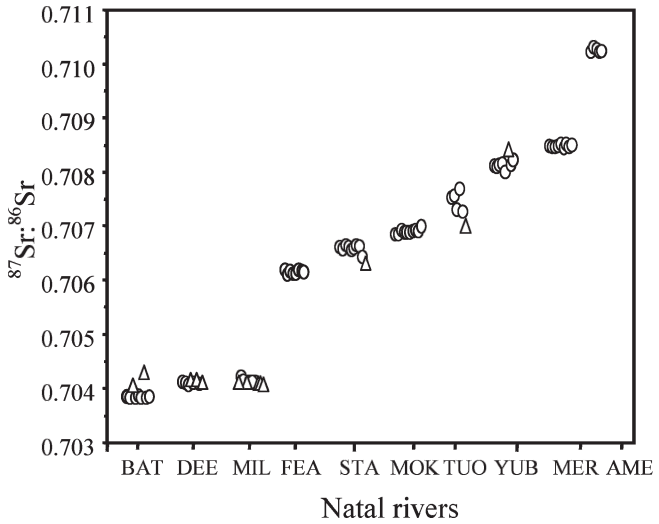

Fig. 2. Natal river $^{87}Sr:^{86}Sr$ values in otoliths from wild juvenile Chinook salmon correctly classified (open circles) and misclassified (open triangles) to river of origin using a discriminant function. All pairwise comparisons are significantly different (Tukey's HSD, $p < 0.001$), with the exception of DEE and MIL. Natal river codes correspond to populations in the California Central Valley listed in Table 1.

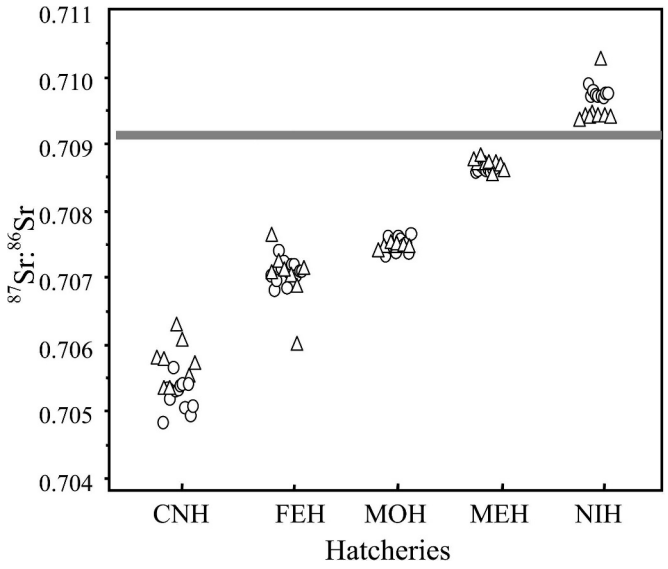

Fig. 3. Sr isotopes $^{87}Sr:^{86}Sr$ in the juvenile growth portion of known-origin adult otoliths (open triangles) analyzed without knowledge of hatchery of origin and plotted with respective baseline values for hatchery juveniles (open circles). The solid grey line shows the marine carbonate shell standard (line thickness ±2 SE; global marine value).

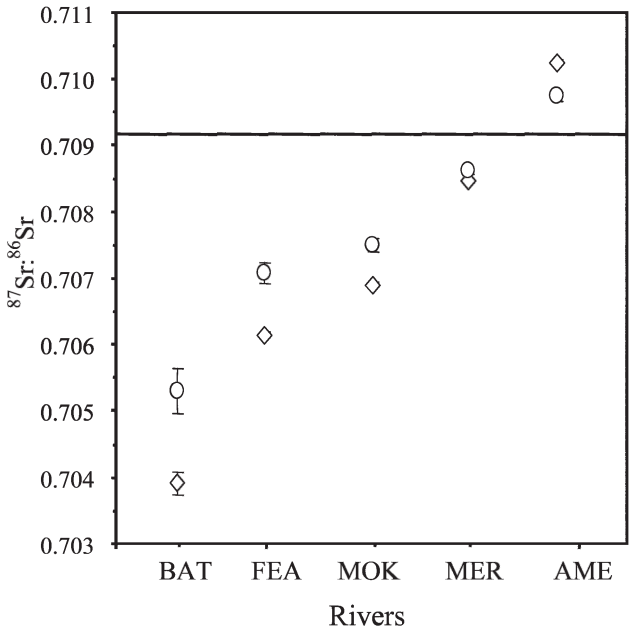

Fig. 4. Sr isotope values for hatchery (open circles) and wild (open diamond) fish co-located on the same rivers with all sources below the global marine $^{87}Sr:^{86}Sr$ value (solid line) except sources on the American River. Note: Error bars ± 1 within-group standard deviation are smaller than the symbol for some sites. Wild and hatchery pairs referenced by river in Table 1.

100% to 92%, 92% to 69%, 100% to 73%, 100% to 90%, and 83% to 33%, respectively. However, the Cohen kappa values between the separate and full models were similar, with the full model yielding 0.82 with 95% CI of 0.75–0.89.

Hatchery vs. wild $^{87}Sr:^{86}Sr$ values—Hatchery and wild fish from the same rivers had significantly different otolith $^{87}Sr:^{86}Sr$ values, with hatchery fish exhibiting more within-site variability (Fig. 4). Natal source isotopic values for all hatchery fish were closer to the global marine value than wild fish.

Reconstructing natal origins in adults—Hatchery adults were correctly assigned to hatchery of origin with 90% accuracy using $^{87}Sr:^{86}Sr$ values from hatchery juveniles as a training-set, an improvement over the full model (80%; Fig. 3). All hatchery adults from three of the five hatcheries (MOH, Merced River Fish Hatchery [MEH], Nimbus Fish Hatchery [NIH]) were correctly classified, with one CNH adult misclassified as originating from FEH, and one FEH misclassified to CNH and MOH. Whereas most CWT adult $^{87}Sr:^{86}Sr$ values closely matched their respective juvenile signatures, adults from NIH did not overlap the juvenile values, although they were classified with 100% accuracy because their $^{87}Sr:^{86}Sr$ values aligned closest to that of juveniles from NIH (Fig. 3).

GIS geologic and isotopic model—The geologic compositions of watersheds are highly variable in the CCV because of the influence of the differing geomorphology of the Cascade Mountain Range and the Sierra Nevada Mountains. Summary statistics of the area of aggregate rock types vary across watersheds, establishing a foundation for isotopic differences (Table 1). Rock composition within watersheds explained the variability in Sr isotopes observed in wild fish from those rivers. Watersheds with the lowest (0%) granite (BAT, DEE, MIL) had less radiogenic (lower) isotopic values, whereas watersheds like YUB and MER, with ~75% of their watersheds composed of granitic rock types, had substantially higher $^{87}Sr:^{86}Sr$ values. The percent of granitic rock alone explained 94% of the $^{87}Sr:^{86}Sr$ values in otoliths when AME was removed from the analysis because of its anomalous geochemistry (Fig. 5). When AME was included, the percent of granitic and old sedimentary rocks were retained in the stepwise multiple regression, and both contributed independently to the model explaining 96% of the variability in $^{87}Sr:^{86}Sr$ across CCV watersheds, an improvement over using granitic rock alone (73%; Fig. 5).

Discussion

Natal source $^{87}Sr:^{86}Sr$ ratios—$^{87}Sr:^{86}Sr$ values were significantly different among natal sources and produced accurate classifications for individuals at the majority of source locations. Classification success was better for the separate model where hatchery and wild sources were considered separately than for the full model, although overall Cohen kappa values were only marginally different. This result is not surprising as overlap among $^{87}Sr:^{86}Sr$ values becomes more likely as the number of sources increases (i.e., 14 sources in the full model and 5 and 9 in the separate models). Juveniles from adjacent rivers MIL and DEE had similar isotopic values, as their natal streams are within watersheds with virtually identical rock compo-

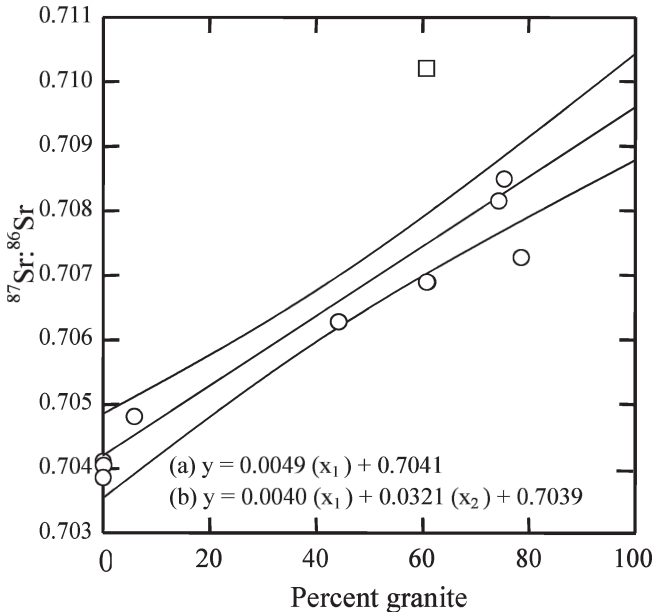

Fig. 5. Regression plot using watershed composition to explain $^{87}Sr:^{86}Sr$ values in otoliths of wild juveniles collected in corresponding rivers including AME (open square; $^{87}Sr:^{86}Sr$ = 0.710249). Regression equations (a) exclude AME (r^2 = 0.94) and (b) include AME with an additional variable (x_2 = percent old sedimentary aggregate type) retained in the multiple regression (r^2 = 0.96).

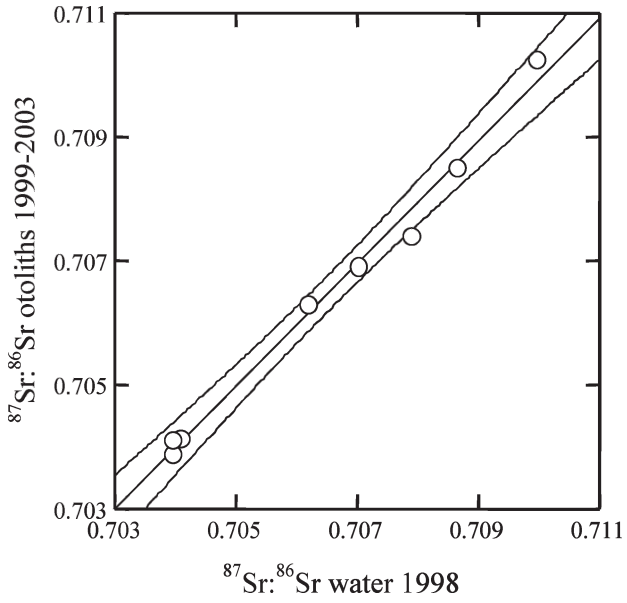

Fig. 6. Inter-annual variability in $^{87}Sr:^{86}Sr$ in the California Central Valley expressed by a regression of $^{87}Sr:^{86}Sr$ values in water collected in 1998 (reported in Ingram and Weber 1999) and $^{87}Sr:^{86}Sr$ values in wild juvenile otoliths collected in 1999, 2002, or 2003 in this study (r^2 = 0.99). Water and otolith samples were collected from corresponding rivers during the same season. The slope of this line (0.99) approximates a 1 : 1 relationship.

sitions (i.e., 95% volcanic and 0% granitic vs. 97% volcanic and 0% granitic) and are heavily influenced by the geology of Lassen Volcano. Other watersheds that had similar percent of granitic rock values had similar $^{87}Sr:^{86}Sr$ values, but were measurably different in $^{87}Sr:^{86}Sr$ using LA-MC-ICPMS, likely because of the differences in the abundance of the other rock types, high Sr isotope measurement precisions, and low within-site Sr isotope variability (Table 1).

Some wild rivers had individual fish that had $^{87}Sr:^{86}Sr$ more similar to neighboring rivers than the mean $^{87}Sr:^{86}Sr$ from the river from which they were collected. This could reflect true variability in $^{87}Sr:^{86}Sr$ at a given river or perhaps movement of juveniles into non-natal rivers before collection. Kennedy et al. (2000) employed the deviation in river $^{87}Sr:^{86}Sr$ values to identify movers. For example, two individual fish collected in BAT had $^{87}Sr:^{86}Sr$ values similar to those of MIL and DEE. Based on the low variability of the $^{87}Sr:^{86}Sr$ values for other fish from BAT and many other rivers, it is possible that these two fish moved as juveniles from their natal rivers (MIL/DEE) into BAT (~40 km upstream) before collection.

Small variations in Sr isotope ratios in watersheds and fish tissues have been found across years and seasons (Kennedy et al. 2000; Semhi et al. 2000). The extent to which temporal variation (either seasonal or annual) compromises classification success is a function of the amount of variation in $^{87}Sr:^{86}Sr$ with time vs. among locations. $^{87}Sr:^{86}Sr$ values in the natal portion of wild juvenile otoliths in our study were similar to values of the water from the same tributaries in different years reported by Ingram and Weber 1999. Water values collected in 1998 explained 99% of the variation in $^{87}Sr:^{86}Sr$ in otoliths from juveniles collected in 1999–2003 during the same season, confirming the relative stability of $^{87}Sr:^{86}Sr$ as spatial markers in the CCV (Fig. 6). The slope of the relationship was close to 1 (0.99; Fig. 6).

Hatchery vs. wild $^{87}Sr:^{86}Sr$ values—$^{87}Sr:^{86}Sr$ values for hatchery and wild fish otoliths from the same rivers were significantly different (Fig. 4, Table 1). Previous research by Koch et al. (1992) first documented different $^{87}Sr:^{86}Sr$ in hatchery salmon calcified structures (vertebrae) relative to source water, attributing this deviation to potential remobilization of Sr during marine growth after initial vertebrae formation. Using non-exchangeable calcified tissues (e.g., otoliths), Ingram and Weber (1999) and Kennedy et al. (2002) documented the same deviation toward marine $^{87}Sr:^{86}Sr$ values for hatchery salmon and implicated two sources of marine Sr: (1) hatchery feed, which is derived from marine fish, or (2) yolk with maternally-inherited marine Sr values (due to vitellogenesis occurring in the ocean). We isolated the natal growth portion of both hatchery and wild fish and removed the influence of prefeeding values. Hatchery fish had $^{87}Sr:^{86}Sr$ values closer to the global marine value than wild fish and thus support the influence of hatchery feed as the likely mechanism for isotopic differences (Fig. 4, Table 1). Because AME and NIH differ from all other hatchery and wild pairs in that their $^{87}Sr:^{86}Sr$ values fall above the global ocean value, the less radiogenic isotopic value of NIH hatchery fish and more radiogenic values for AME wild fish (a reversal in trend from other hatchery and wild

pairs) is further support of the effect of hatchery feed and marine $^{87}Sr:^{86}Sr$ on otolith isotopic values (Fig. 4).

Variability in $^{87}Sr:^{86}Sr$ values in hatchery fish decreased as mean $^{87}Sr:^{86}Sr$ values approached the marine value, whereas variability remained similar among wild sources (Fig. 4; Table 1). The trend observed in hatchery fish indicates mixing between isotopically different sources (marine food vs. natal water) with the greatest variability for fish from CNH, whose two Sr sources are most isotopically distant. Variability remained similar for wild fish because their prey and water Sr sources are likely to be isotopically identical. The variability in $^{87}Sr:^{86}Sr$ within hatcheries may be due to differences in metabolic or feeding rates of individual fish causing variation in assimilating Sr from food sources vs. water or changes in hatchery practices. Although Kennedy et al. (2000) suggest food contributes significant amounts of Sr to the otoliths of freshwater salmonids, their experimental design does not isolate whether the pathway is truly through direct ingestion of food or indirectly via dissolved food in the water. Nonetheless, excess feed with marine Sr likely plays a role either directly or indirectly in the observed variability in our hatchery fish otoliths. Sr concentrations in seawater are higher than in most rivers, and therefore $^{87}Sr:^{86}Sr$ in hatchery feed may have a greater influence on fish whose river concentrations are lower.

Reconstructing natal origins in adults—Many studies using otolith microchemistry develop baselines using juveniles collected from known origins and assume that natal signatures can be reconstructed in adults. This has rarely been tested due to the lack of known-origin adults in most systems. The presence of adults of known hatchery origin provided us this rare opportunity. The correct identification of 37 of the 40 CWT adults to their hatchery of origin demonstrates the utility of this technique in applications to adults. Most adult $^{87}Sr:^{86}Sr$ values (from the juvenile portion of the otolith) closely match those of juveniles from the same natal source from different years. Adults from NIH are the exception, with most adults having significantly lower ratios than juveniles. This deviation is likely because of the anomalous geochemistry of the AME watershed, which is spatially heterogeneous, and may be more sensitive than other source locations to inter-annual variability in precipitation and discharge that would change the weathering patterns of the bedrocks contributing to dissolved strontium loads (Grosbois et al. 2000). However, for utility as a natal marker, all adults from NIH were correctly classified because their $^{87}Sr:^{86}Sr$ values aligned closest to that of juveniles from NIH.

Applications to adult fish have been hindered largely by methodological constraints in isolating juvenile-origin material for $^{87}Sr:^{86}Sr$ measurements in numerous adults. Analyses of water or vertebrae enable baseline measurements of $^{87}Sr:^{86}Sr$, but are of limited utility in systems with hatchery supplementation or for reconstructing natal origins in adults (Ingram and Weber 1999; Kennedy et al. 2002). A juvenile baseline of natal sources can be developed using whole otolith dissolution with traditional solution-based analysis using a thermal ionization mass spectrometer (Ingram and Weber 1999), but this technique may obscure natal $^{87}Sr:^{86}Sr$ values because of the disproportionate prefeeding (marine Sr) influence in smaller otoliths (<0.4 mg, Barnett-Johnson 2007). Subsequent analyses of adult otoliths then require isolating and collecting the juvenile portion for solution-based analyses, which can introduce additional challenges (Brown 2006). Spatial analysis using LA-MC-ICPMS enables rapid and accurate measurements of $^{87}Sr:^{86}Sr$ in juvenile and adult otoliths, which is vital when linking these two life-history stages.

GIS geologic and isotopic model—$^{87}Sr:^{86}Sr$ measurements in otoliths followed a general trend of lower ratios in tributaries in the northern, younger volcanic basins of the Sacramento River drainage and higher ratios in the southern granitic basins of the San Joaquin, although the spatial extent of granitic rock types in watersheds was a better predictor of $^{87}Sr:^{86}Sr$ than latitude (Table 1; Fig. 5). Wild juveniles from AME and hatchery fish from NIH are located on the same river and are conspicuous exceptions to the north-to-south trend, recording high $^{87}Sr:^{86}Sr$ values (0.70974 and 0.71025) at the center of the latitudinal gradient. This has previously been attributed to several branches of the American River flowing through large areas of undivided Paleozoic metasedimentary rocks (classified in this study as old sedimentary aggregate), which have higher than ocean $^{87}Sr:^{86}Sr$ values (Ingram and Weber 1999; California Division of Mines and Geology 2000).

With improved understanding of environmental and/or biological sources contributing to variations in otolith microchemistry, spatial maps at the correct temporal scales can be constructed to track fish movement in aquatic systems (Harrington et al. 1998; Warner et al. 2005). The GIS hydrologic and geologic data layers provide quantitative tools to aid in understanding the mechanisms of Sr variability in watersheds and otoliths as an alternative to previous qualitative interpretations (Kennedy et al. 1997; Ingram and Weber 1999; Douglas et al. 2002). Our regression-based approach can be used across watersheds to evaluate whether general characteristics in geology emerge in explaining $^{87}Sr:^{86}Sr$ variability in otoliths. In the CCV, granitic rock aggregate is a proxy for high $^{87}Sr:^{86}Sr$ values. By aggregating rock types to reflect Sr geochemistry, percent of granitic rocks explained 94% of the variability in isotopic values. In a further cluster analysis, we determined that the similarity of rock composition in river catchments using the non-aggregated data layer in GIS supported the relationships we found among sites with our empirical measurements (California Division of Mines and Geology 2000). These results suggest that GIS geologic and hydrologic analyses of watersheds may be useful in evaluating which sites may be most similar in their Sr isotopic values before collection of empirical data and guide field sampling designs. This approach may be particularly valuable in large watersheds where only a subset of values can be empirically sampled (e.g., Great Lakes) or where only a subset has been measured (e.g., Connecticut River). Identifying similarity in lithology among sampled and unsampled sites within a watershed

could provide a likelihood estimate that an individual may have originated from an unsampled source. It should be emphasized that Sr isotopes exhibit low within-population variability and therefore some sites with relatively similar geology may still be distinguishable.

Sr isotopes recorded in otoliths from all major wild and hatchery spawning sites of the fall-run Chinook salmon in the CCV can be used to successfully identify natal origin with high accuracy, a prerequisite for quantifying the relative contribution of natal sources in a mixed ocean fishery. In particular, the availability and analyses of known-origin coded, wire-tagged adults provided a rare opportunity to confirm the success of our methods in reconstructing the early life-histories of adults. Sr isotopic variation in watersheds and otoliths is determined by geologic characteristics. Thus, the use of national and state GIS geologic and hydrologic data layers can be employed to quantify the scale of variation in rocks and to explore this variation relative to fish movement to guide research efforts. Sr isotopes combined with quantitative information about landscape geology can be used to track the natal origin and movement of salmonids in freshwater, estuarine, and marine environments to better understand how processes occurring in these habitats influence the growth, survival, and reproductive success of anadromous fishes.

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