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Strontium isotopes reveal ephemeral streams used for spawning and rearing by an imperilled potamodromous cyprinid Clear Lake hitch *Lavinia exilicauda chi*

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Abstract. Identification of habitats responsible for the successful production and recruitment of rare migratory species is a challenge in conservation biology. Here, a tool was developed to assess life stage linkages for the threatened potamodromous cyprinid Clear Lake hitch *Lavinia exilicauda chi*. Clear Lake hitch undertake migrations from Clear Lake (Lake County, CA, USA) into ephemeral tributary streams for spawning. An aqueous isoscape of strontium isotopic ratios ($^{87}Sr/^{86}Sr$) was constructed for Clear Lake and its watershed to trace natal origins and migration histories of adult recruits. Aqueous $^{87}Sr/^{86}Sr$ differentiated Clear Lake from 8 of 10 key tributaries and clustered into 5 strontium isotope groups (SIGs) with 100% classification success. Otolith $^{87}Sr/^{86}Sr$ showed all five groups contributed variably to the population. The age at which juveniles migrated from natal streams to Clear Lake ranged from 11 to 152 days (mean $\pm$ s.d., 43 ± 34 days) and was positively associated with the permanency of natal habitat. This information can be used by resource managers to develop conservation actions for Clear Lake hitch. This study demonstrates the utility of strontium isotopes in otoliths as a tool to identify important freshwater habitats occupied over the lifespan of an individual that would otherwise be challenging or impossible to trace with other methods.[A]

Additional keywords: intermittent, isoscape, LA-MC-ICP-MS, laser ablation–multicollector–inductively coupled plasma–mass spectrometry, migration, potamodromy, threatened species.

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Introduction

Effective conservation of threatened or endangered species fundamentally requires knowledge of the habitats that contribute to production and recruitment. Determining productive habitats for highly mobile species, such as migratory fishes with life cycles that span heterogeneous environments, is particularly challenging. For example, directly observing and tracking individuals and their survival from birth to adulthood across diverse environments over time is often not feasible. An increasingly common approach to dealing with this challenge is to reconstruct life histories of individual fish that have successfully recruited into a population of interest through the use of natural tags (Kennedy *et al.* 2000; Walther and Limburg 2012; Brennan *et al.* 2015*a*; Johnson *et al.* 2016). In particular, isotope ratios of strontium ($^{87}Sr/^{86}Sr$) present in the otoliths of fishes closely resemble those present in the aqueous environment and provide a reliable and powerful approach to reconstruct the life history of individuals (Hobbs *et al.* 2005; Barnett-Johnson *et al.* 2008; Walther and Thorrold 2009; Sturrock *et al.* 2015).

Most California's native freshwater fishes are imperilled (Moyle *et al.* 2011, 2015). Low abundance levels, diverse geographic ranges and complex life histories pose considerable challenges to the conservation of the native endemic fish fauna. One example is the potamodromous Clear Lake hitch *Lavinia exilicauda chi*, an imperilled cyprinid endemic to a single freshwater lake (Clear Lake, Lake County, CA, USA). Historically highly abundant and a staple food for the Pomo tribes of the region, Clear Lake hitch abundance is believed to have declined 100-fold from historical levels (California Department of Fish and Wildlife 2014). Clear Lake hitch is presently listed as a

[A]Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

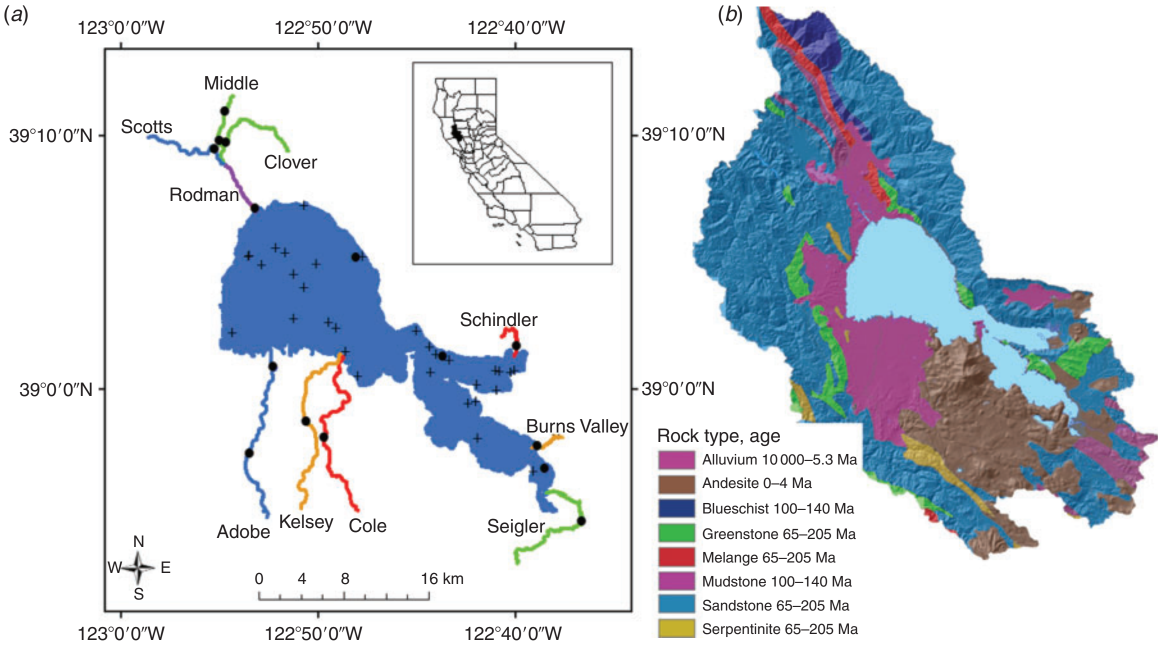

Fig. 1. (*a*) Map of Clear Lake and streams showing sites where water (closed circles) and fish (crosses) were collected. Colours represent strontium isotope groups (SIG) based on aggregations of non-overlapping $^{87}Sr/^{86}Sr$ values given in Table 1: SIG 1, red; SIG 2, orange; SIG 3, blue; SIG 4, purple; SIG 5, green. Readers are referred to Table 1 for the range of $^{87}Sr/^{86}Sr$ values corresponding to each SIG. Inset, map of the counties of California with Lake County highlighted as the filled polygon. (*b*) Geological map showing the primary rock types in the Clear Lake watershed. Original map and data are available from the County of Lake, California, USA (http://www.lakecountyca.gov/Assets/Departments/WaterResources/Clear+Lake+Integrated+Watershed+Management+Plan/09+Plate+2+Clear+Lake+Watershed+Geology.pdf, accessed 21 March 2019).

threatened species under the *California Endangered Species Act* and has been petitioned for listing under the *USA Endangered Species Act*.

Adult Clear Lake hitch ascend Clear Lake's ephemeral streams during the spring to spawn. Adult migration, spawning, embryo incubation, larval development and juvenile emigration all occur during a short time window during the spring season when dry stream beds become temporarily inundated from seasonal rains (Moyle 2002). Modification and loss of stream spawning habitat are thought to be important elements driving the decline of Clear Lake hitch (California Department of Fish and Wildlife 2014). Thus, identifying the relative importance of individual streams to the production and recruitment of Clear Lake hitch is important for the development of management and conservation strategies.

The goal of this study was to determine the relative importance of natal habitats and early life migration histories (i.e. the age at which individuals migrated from natal habitats to Clear Lake) that have contributed to the production and recruitment into the adult population of Clear Lake hitch. The approach involved the application of isotope ratios of strontium ($^{87}Sr/^{86}Sr$) as natural tags to reconstruct early life histories of individual fish. First, an aqueous isoscape of $^{87}Sr/^{86}Sr$ of Clear Lake and its watershed was developed to generate a baseline map of available habitat. Next, the $^{87}Sr/^{86}Sr$ values in the early life portion of adult otoliths for individuals collected throughout Clear Lake were compared to the isoscape to identify natal origins and early life migration histories.

Materials and methods

Study area

Clear Lake is located in central California, ~100 km north of San Francisco Bay (Fig. 1). It is the largest natural freshwater lake completely within California. At full capacity, Clear Lake has a surface area of ~17 700 ha and a total volume of $\sim 1.4 \times 10^9$ m^3. Clear Lake is fed by several intermittent streams situated around its perimeter (Fig. 1). The streams are typically dry, except during short periods of time in spring when they become inundated from seasonal rains associated with the local Mediterranean climate. Flow in most of the streams is not measured. Kelsey Creek is the only stream presently instrumented for flow measurements near its confluence with Clear Lake. Kelsey Creek is one of the larger streams and had a maximum mean monthly streamflow from 2011 to 2017 that ranged from 1.6 to 24.7 m^3 s^{-1} (mean ± s.d., 11.1 ± 7.6 m^3 s^{-1}; data are freely available from the California Department of Water Resources at http://cdec.water.ca.gov/dynamicapp/staMeta?station_id=KCK, accessed 15 November 2018). The regional landscape has a diverse volcanic geological history (Hearn *et al.* 1995). Dominant rock types vary broadly across the watershed and include alluvium, andesite, blueschist, greenstone, melange, mudstone, sandstone and serpentinite (Fig. 1; Lake County, Division of Water Resources 2010). Collectively, the aforementioned factors contributed to the hypothesis that there would be sufficient variation in $^{87}Sr/^{86}Sr$ across the watershed to facilitate provenance research by otolith chemistry.

Table 1. Information on site, location, date collected, mean (±2 s.e.) $^{87}Sr/^{86}Sr$ ratios and strontium isotope group (SIG) assignment for all water samples

Site	Latitude	Longitude	Date	$^{87}Sr/^{86}Sr$ ratio	±2 s.e.	SIG
Cole Creek	38°58′03.45″	−122°49′39.25″	05 Apr 2017	0.704 99	0.000 01	1
Schindler Creek	39°01′40.43″	−122°39′54.21″	05 Apr 2017	0.705 00	0.000 01	1
Schindler Creek	39°01′40.43″	−122°39′54.21″	15 May 2017	0.705 05	0.000 01	1
Cole Creek	38°58′03.45″	−122°49′39.25″	11 May 2017	0.705 08	0.000 01	1
Seigler Creek[A]	38°54′44.43″	−122°36′38.23″	28 Mar 2018	0.705 22	0.000 01	1
Cole Creek	38°58′03.45″	−122°49′39.25″	28 Mar 2018	0.705 24	0.000 01	1
Burns Valley Creek	38°57′44.51″	−122°38′52.29″	11 May 2017	0.705 50	0.000 01	2
Kelsey Creek[B]	38°58′43.01″	−122°50′35.15″	05 Apr 2017	0.705 51	0.000 01	2
Kelsey Creek[B]	38°58′43.01″	−122°50′35.15″	05 Apr 2017	0.705 53	0.000 01	2
Burns Valley Creek	38°57′44.51″	−122°38′52.29″	05 Apr 2017	0.705 56	0.000 01	2
Kelsey Creek	38°58′43.01″	−122°50′35.15″	28 Mar 2018	0.705 63	0.000 01	2
Kelsey Creek	38°58′43.01″	−122°50′35.15″	11 May 2017	0.705 66	0.000 06	2
Clear Lake, lower	38°56′50.01″	−122°38′30.44″	02 May 2018	0.705 83	0.000 01	3
Clear Lake, lower	38°56′50.01″	−122°38′30.44″	11 May 2017	0.705 86	0.000 01	3
Scotts Creek	39°09′28.05″	−122°55′14.92″	05 April 2018	0.705 87	0.000 01	3
Clear Lake, lower	38°56′50.01″	−122°38′30.44″	05 Apr 2017	0.705 88	0.000 01	3
Clear Lake, middle	39°01′17.54″	−122°43′38.25″	02 May 2018	0.705 89	0.000 01	3
Adobe Creek, upper	38°57′26.60″	−122°53′27.49″	28 Mar 2018	0.705 90	0.000 01	3
Clear Lake, middle	39°01′17.54″	−122°43′38.25″	15 May 2017	0.705 90	0.000 01	3
Clear Lake, middle[C]	39°01′17.54″	−122°43′38.25″	05 Apr 2017	0.705 91	0.000 01	3
Clear Lake, upper[D]	39°05′10.99″	−122°48′04.01″	02 May 2018	0.705 92	0.000 01	3
Clear Lake, upper[D]	39°05′10.99″	−122°48′04.01″	02 May 2018	0.705 92	0.000 01	3
Clear Lake, middle[C]	39°01′17.54″	−122°43′38.25″	05 Apr 2017	0.705 92	0.000 01	3
Clear Lake, upper	39°05′10.99″	−122°48′04.01″	11 May 2017	0.705 92	0.000 01	3
Clear Lake, upper	39°05′10.99″	−122°48′04.01″	05 Apr 2017	0.705 93	0.000 01	3
Adobe Creek, lower	39°00′52.69″	−122°52′14.37″	05 Apr 2017	0.705 94	0.000 01	3
Adobe Creek, lower	39°00′52.69″	−122°52′14.37″	11 May 2017	0.705 95	0.000 01	3
Adobe Creek, lower	39°00′52.69″	−122°52′14.37″	28 Mar 2018	0.705 97	0.000 01	3
Rodman Slough	39°07′07.12″	−122°53′10.58″	28 Mar 2018	0.706 21	0.000 01	4
Rodman Slough[E]	39°07′07.12″	−122°53′10.58″	11 May 2017	0.706 22	0.000 01	4
Rodman Slough[E]	39°07′07.12″	−122°53′10.58″	11 May 2017	0.706 23	0.000 01	4
Rodman Slough	39°07′07.12″	−122°53′10.58″	05 Apr 2017	0.706 28	0.000 01	4
Middle Creek, upper	39°10′57.28″	−122°54′42.48″	28 Mar 2018	0.706 71	0.000 01	5
Middle Creek, lower	39°09′48.4″	−122°54′58.6″	24 May 2017	0.706 77	0.000 01	5
Seigler Creek	38°54′44.43″	−122°36′38.23″	05 Apr 2017	0.706 78	0.000 01	5
Seigler Creek	38°54′44.43″	−122°36′38.23″	11 May 2017	0.706 78	0.000 01	5
Clover Creek	39°09′43.89″	−122°54′38.25″	28 Mar 2018	0.706 99	0.000 01	5

[A]Unusual observation (see Discussion for explanation).
[B]Paired field duplicate.
[C]Paired laboratory duplicate.
[D]Paired laboratory duplicate.
[E]Paired field duplicate.

Take of Clear Lake hitch for this study was permitted under a Scientific Collection Permit (SC-3602) and an associated Memorandum of Understanding issued by the California Department of Fish and Wildlife.

Isoscape development

To develop an aqueous $^{87}Sr/^{86}Sr$ isoscape, water samples were collected in 2017 and 2018 within Clear Lake and its 10 most significant tributaries thought to support Clear Lake hitch spawning (Moyle 2002), with any unsampled streams unlikely to contribute meaningfully to the population. Samples were collected at 3 sites within the lake (1 each in the upper, middle and lower geographic regions) and at a total of 12 sites across the following 10 tributary streams: Schindler, Burns Valley, Seigler, Cole, Kelsey, Adobe, Scotts, Clover and Middle creeks and Rodman Slough; Fig. 1; Table 1). Water collections were made during the spring coincident with the presence of Clear Lake hitch in streams for spawning and larval or juvenile rearing (Table 1). Water was collected at each site by sterile syringes and passed through 0.45-μm filters into acid-washed 150-mL polyethylene containers using traditional triple-rinse clean-chemistry protocols and stored in a refrigerator before analysis (Barnett-Johnson *et al.* 2005, 2007). Field blanks and paired field and laboratory duplicate samples were analysed to confirm $^{87}Sr/^{86}Sr$ reproducibility (Table 1).

Water samples were analysed with a Nu Plasma HR multiple-collection double-focusing plasma-source mass spectrometer (multicollector–inductively coupled plasma–mass spectrometry, MC-ICP-MS; Nu Instruments, Wrexham, UK). Samples were purified through a specific ion-exchange resin (Sr Resin; Eichrom Technologies, Lisle, IL, USA) in a Class 100 clean laboratory facility (PicoTrace, Bovenden, Germany). After being reconstituted in ultrapure sub-boiling double-distilled 2% nitric acid, the purified samples were introduced into the Nu Plasma with a desolvating nebuliser system (DSN-100, MkII; Nu Instruments) with a 0.1-mL min^{-1} uptake (227.5 kPa with 700-mm capillary) quartz MicroMist nebuliser (Glass Expansion, Melbourne, Vic., Australia). Instrument sensitivity typically ranges from 500 to 1000 V per ppm Sr. Ratios include 50–60 data points and each data point integrates Faraday signals for 10 s. Baselines were measured for 30 s by electrostatic analyser (ESA) deflection. The NIST SRM 987 standard (0.71034; National Institute of Standards and Technology, Gaithersburg, MD, USA) was used as a reference to normalise measured values and to establish measurement accuracy and precision (Moore *et al.* 1982). The standard was measured approximately every six samples and produced a mean ($\pm$s.d.) $^{87}Sr/^{86}Sr$ value of $0.710\,16 \pm 0.000\,01$ ($n = 9$).

An isoscape of the available habitat was developed based on non-overlapping $^{87}Sr/^{86}Sr$ values. First, to determine the resolution of the isoscape, a single-factor linear discriminant function analysis (DFA) was conducted using $^{87}Sr/^{86}Sr$ values for individual habitats (SAS ver. 9.4, SAS Institute, Cary, NC, USA). Prior probability of group membership was assumed to be equal. The posterior probabilities of the strength of habitat assignments were evaluated and a new DFA model was developed that grouped sites with overlapping $^{87}Sr/^{86}Sr$ values into strontium isotope groups (SIG; *sensu* Brennan *et al.* 2015*a*). A linear function was used to estimate the variance–covariance matrix response and was applied across all five SIGs. Jack-knife resampling used the same dataset to generate and evaluate the discriminant function by calculating the function (in this case the mean $^{87}Sr/^{86}Sr$ for each SIG) with $n - 1$ observations, classifying the one observation omitted to the SIG with the closest mean and then repeating the procedure for all observations.

Natal source and migration history reconstruction with natural tags

Otoliths examined in the present study were from randomly sampled individual Clear Lake hitch that recruited into the adult population in Clear Lake. The individuals were collected in the course of a broad study examining the distribution and habitat associations of Clear Lake hitch within Clear Lake. Sampling occurred in two separate week-long efforts that took place in June and July 2017. Collections during each sampling event were made using experimental gill nets deployed at randomised sites (Fig. 1). The protected status of Clear Lake hitch under the *California Endangered Species Act* constrained the number of individuals that could be retained and killed for scientific study to 45 individuals.

Lapilli otoliths were extracted from fish, rinsed in deionised water to remove any attached organic tissue and allowed to air dry before storage. Dry otoliths were individually mounted on glass microscope slides in an epoxy (West Systems 105, Bay City, MI, USA), sectioned in the frontal plane with a diamond saw and polished to the core with 0.3-μm lapping film to expose the juvenile core and what appeared to be daily growth bands.

Fish age in days was estimated as the number of increments observed following the onset of an obvious check that was consistently observed among fish and interpreted as the first feeding check. Daily increments were measured within the first year along the longest axis using a compound microscope (BX60; Olympus, Center Valley, PA, USA) at a magnification of 200×, a camera (Q-Imaging MicroPublisher, ver. 6, Surry, BC, Canada) and image analysis software (ImagePro Premier, Rockville, MD, USA) as per established techniques (Barnett-Johnson *et al.* 2007). The mean ($\pm$s.d.) distance of the first feeding check from the otolith primordium was 72.2 ± 6.3 μm. Larval Clear Lake hitch may be up to ~2 weeks old after hatch at the onset of exogenous feeding because Swift (1965) observed that the yolk sac was fully absorbed at 13 days after hatch in larvae reared at 16°C.

Strontium isotope composition in otoliths was measured with an MC-ICPMS interfaced with a Nd : YAG 213-nm laser (New Wave Research UP213, Fremont, CA, USA) as per established techniques (Barnett-Johnson *et al.* 2005). Briefly, a transect of spots was ablated along the longest axis from the core to the perimeter of the otoliths. The distance (μm) of each spot to the primordium was measured. Spot ablations were made with a laser spot diameter of 40 μm and 40 μm apart at 60% laser power, a dwell time of 25 s and a 10-Hz laser pulse repetition rate. Mean ($\pm$s.d.) voltage values for ^{88}Sr during analyses were 3.298 ± 0.699 V. Helium was used as a carrier gas in the sample chamber to maximise sensitivity and minimise sample deposition at the ablation site. Ablated otolith powder material was then carried from the sample cell with additional argon to the plasma source. Gas blank and background signals were monitored until ^{84}Kr and ^{86}Kr decayed and stabilised after the sample change (i.e. exposing the sample cell to the air) and were measured for 30 s. These background measurements were blank subtracted from the measured signals before sample ablation. The $^{86}Sr/^{88}Sr$ value of 0.1194 was used to correct for instrumental fractionation. Peak intensities for ^{88}Sr, ^{87}Sr, ^{86}Sr, ^{85}Rb and ^{84}Sr were measured simultaneously. Peak ^{85}Rb was monitored to correct for any ^{87}Rb interference on ^{87}Sr, which was negligible. An in-house marine otolith standard, an otolith from the marine fish *Atractoscion nobilis*, was used as a marine standard (0.70918; Faure and Mensing 2005) to normalise measured values and to establish measurement accuracy and precision because there is no recognised otolith standard commercially available. Thirty-nine analyses of the standard conducted throughout the otolith analysis process produced a mean ($\pm$s.d.) $^{87}Sr/^{86}Sr$ value of $0.709\,04 \pm 0.000\,08$, which was normalised and used to correct the measured $^{87}Sr/^{86}Sr$ in the samples.

Natal habitat assignments were based on $^{87}Sr/^{86}Sr$ values for ablation spots situated <70 μm from the otolith primordium, which corresponds to the period of life from otolith formation, hatch and first feeding. Assignments were made by using the aqueous $^{87}Sr/^{86}Sr$ DFA to classify adults into SIGs. Early life migration histories are defined here as the age in days that an individual migrated from its natal stream habitat to Clear Lake. This can also be interpreted as the amount of time individuals reared in natal habitat before entering Clear Lake. Age at entry to Clear Lake was determined by inspection of the time series of

$^{87}Sr/^{86}Sr$ values across ontogeny for each individual. The distance of each ablation point from the otolith primordium was converted to an estimated age based on predictions made by linear regression models of age–distance for each individual on data generated in the otolith increment analyses. Age at lake entry was defined as the predicted age for the first ablation spot in which otolith $^{87}Sr/^{86}Sr$ values overlapped those of the aqueous $^{87}Sr/^{86}Sr$ values for Clear Lake. The average daily increment after exogenous feeding in Clear Lake hitch is ~8 µm wide. Therefore, the 40-µm beam integrates $^{87}Sr/^{86}Sr$ values over ~5–7 days of fish growth. All original otolith and standard data are available in a supplementary data file accessible at https://doi.org/10.5066/P9IX7L5V.

Results

Isoscape

In all, 37 water samples were analysed for $^{87}Sr/^{86}Sr$ to develop the isoscape that ranged across habitat values from 0.70499 to 0.70699 (Table 1). Mean $^{87}Sr/^{86}Sr$ values were used per sampling event when duplicate samples were collected and analysed to assess analytical precision. The results of the initial DFA based on the resolution of individual habitats resulted in low classification strength for habitats with overlapping $^{87}Sr/^{86}Sr$ values. The results from the initial DFA were used to identify SIGs with non-overlapping $^{87}Sr/^{86}Sr$ values and 100% correct classification (Fig. 2). Aqueous $^{87}Sr/^{86}Sr$ values differentiated Clear Lake from 8 of the 10 tributaries examined and clustered into 5 fully distinct (non-overlapping values) SIGs (Table 1; Fig. 2). Aqueous $^{87}Sr/^{86}Sr$ values for SIG 1 ranged from 0.70499 to 0.70524 and included Cole Creek and Schindler Creek (see the Discussion for an explanation of the omission of the 2018 $^{87}Sr/^{86}Sr$ value for Seigler Creek for the fish examined in this study). Aqueous $^{87}Sr/^{86}Sr$ values for SIG 2 ranged from 0.70550 to 0.70566 and included Kelsey Creek and Burns Valley Creek. Aqueous $^{87}Sr/^{86}Sr$ values for SIG 3 ranged from 0.70583 to 0.70597 and included Adobe Creek, Scotts Creek and Clear Lake. Aqueous $^{87}Sr/^{86}Sr$ values for SIG 4 ranged from 0.70621 to 0.70628 and included Rodman Slough. Aqueous $^{87}Sr/^{86}Sr$ values for SIG 5 ranged from 0.70671 to 0.70699 and included Seigler Creek, Middle Creek and Clover Creek.

Natal sources and migration histories

The 45 individual Clear Lake hitch collected for otolith analyses ranged in size from 125 to 310 mm standard length (mean ± s.d., 192 ± 58 mm). Based upon the size–age relationships in Geary and Moyle (1980), the estimated ages of the individual fish ranged from 2 to 5+ years old.

Most adults were assigned to individual SIGs with high classification strength (Table 2). In fact, 40 of 44 fish assigned to SIGs with >90% classification strength. Most adults originated from habitats in SIG 3 (57%), SIG 2 (18%) and SIG 4 (18%), with lower contributions from SIG 1 (2%) and SIG 5 (5%). Age in days at lake entry across all individuals assigned to SIGs 1, 2, 4 and 5 ranged from 11 to 152 (mean ± s.d., 43 ± 34 days; Figs 4, 5). Note that SIG 3 is omitted because streams in this group cannot be differentiated from Clear Lake. The single fish assigned to SIG 1 entered Clear Lake 16 days after first feeding. Ages at lake entry for the eight individuals assigned to SIG 2 were 11, 21, 21, 24, 25, 29, 31 and 42 days. Ages at lake entry for the six individuals assigned to SIG 4 were 11, 37, 52, 62, 102 and 152 days. Ages at lake entry for the two individuals assigned to SIG 5 were 41 and 43 days.

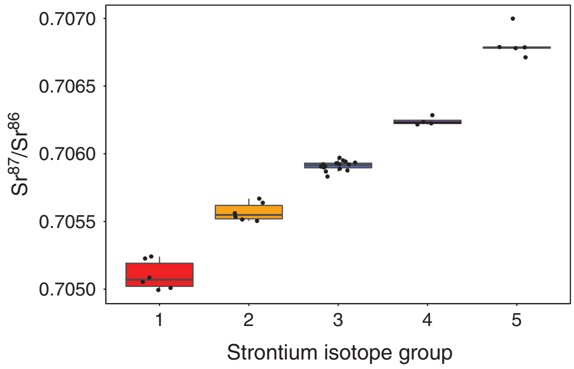

Fig. 2. Boxplot representation of all aqueous $^{87}Sr/^{86}Sr$ values from Table 1 aggregated into five non-overlapping strontium isotope groups. Boxes show the median (horizontal line) and 25 and 75% quantiles. Points show individual values with some horizontal jitter added to minimise superimposition to improve visualisation. SIG colours match Fig. 1.

Discussion

Assessing spatiotemporal variation of aqueous $^{87}Sr/^{86}Sr$ is fundamental for applications of provenance or migration studies of fishes (Elsdon *et al.* 2008; Hobson *et al.* 2010; Brennan *et al.* 2015*a*, 2015*b*). In this study, $^{87}Sr/^{86}Sr$ values underlying the isoscape were spatially stable within and among hydrologically diverse years (representative flow data from Kelsey Creek are available from http://cdec.water.ca.gov/dynamicapp/staMeta?station_id=KCK, accessed 15 November 2018). There was no overlap of $^{87}Sr/^{86}Sr$ values among SIGs in the waters sampled, but there was some evidence in the otolith data to suggest that there may have been unsampled habitats. Alternatively, it is also possible that the SIGs would have exhibited a broader range of values had they been developed based on otolith $^{87}Sr/^{86}Sr$ of known-origin individuals rather than water $^{87}Sr/^{86}Sr$. The $^{87}Sr/^{86}Sr$ habitat signatures appear to be insensitive, at least at the level of resolution required for otolith $^{87}Sr/^{86}Sr$ application, to the dynamic seasonal hydrology of the watershed and the resulting flow variability within and among streams. These factors provide a strong foundation for the development of the isoscape and for the application of otolith $^{87}Sr/^{86}Sr$ to be used as a tracer of Clear Lake hitch life history.

Natural and human-induced disturbances to stream channels and exposure to new sediment sources may affect aqueous $^{87}Sr/^{86}Sr$ signals. Such appeared to be the case in this study following a significant amount of construction and placement of out-of-basin fill material into Seigler Creek for Clear Lake hitch habitat and passage restoration in the summer dry season of 2017. This habitat alteration appeared to cause a meaningful change in $^{87}Sr/^{86}Sr$ values and SIG assignments in 2018 (0.70523; SIG 1) compared with those observed before the construction activity in 2017 (0.70679 and 0.70679; SIG 5). This change in aqueous $^{87}Sr/^{86}Sr$ did not affect the results of this

Table 2. Summary natal habitat assignment data for individual Clear Lake hitch

Data shown are the number of ablation spots within 70 µm of the otolith core (*N*), mean $^{87}Sr/^{86}Sr$ ratio and its s.e., strontium isotope group (SIG) assignment and classification strength reported as a posterior probability (%) of assignment to the SIG. Note that numerical identification codes for each individual are the same as those in Fig. 3

Individual	*N*	$^{87}Sr/^{86}Sr$	s.e.	SIG	Posterior probability (%)
1	5	0.706 62	0.000 08	5	100
2	3	0.705 68	0.000 10	2	99
3	4	0.706 25	0.000 05	4	100
4	4	0.706 00	0.000 05	3	99
5	1	0.706 07	–	3	67
6	3	0.705 90	0.00 001	3	100
8	4	0.705 93	0.00 002	3	100
9	4	0.706 34	0.00 003	4	100
10	2	0.705 80	0.000 01	3	98
11	4	0.705 74	0.000 03	2	68
12	4	0.705 99	0.000 08	3	100
13	3	0.705 93	0.000 17	3	100
14	3	0.705 35	0.000 12	2	90
15	4	0.706 49	0.000 08	4	99
16	3	0.706 72	0.000 05	5	100
17	2	0.705 79	0.000 08	3	95
18	4	0.706 05	0.000 09	3	91
19	3	0.705 81	0.000 03	3	99
20	3	0.705 92	0.000 05	3	100
21	3	0.705 89	0.000 11	3	100
22	3	0.705 76	0.000 05	3	70
23	3	0.706 32	0.000 09	4	100
24	4	0.705 83	0.000 02	3	100
25	3	0.706 16	0.000 04	4	100
26	4	0.705 97	0.000 01	3	100
27	2	0.705 85	0.000 07	3	100
28	3	0.706 32	0.000 03	4	100
29	3	0.705 88	0.000 05	3	100
30	3	0.706 41	0.000 05	4	100
31	3	0.706 28	0.000 07	4	100
32	3	0.705 92	0.000 03	3	100
33	3	0.705 90	0.000 03	3	100
34	2	0.705 93	0.000 03	3	100
35	4	0.706 01	0.000 02	3	99
36	3	0.705 63	0.000 05	2	100
37	4	0.705 39	0.000 06	2	100
39	3	0.705 90	0.000 05	3	100
40	3	0.705 91	0.000 02	3	100
41	4	0.705 20	0.000 02	1	100
42	3	0.705 65	0.000 04	2	100
43	3	0.705 70	0.000 06	2	97
44	3	0.705 93	0.000 04	3	100
45	1	0.705 48	–	2	100
46	2	0.706 07	0.000 17	3	64

study because fish assigned to SIGs were born and captured before the construction activity. Therefore, preconstruction $^{87}Sr/^{86}Sr$ values for Seigler Creek were used as the relevant $^{87}Sr/^{86}Sr$ stream signature for adult cohorts in this study. The observation nonetheless underscores the value of monitoring baseline $^{87}Sr/^{86}Sr$ values spatially and temporally in systems undergoing significant streambed habitat alterations.

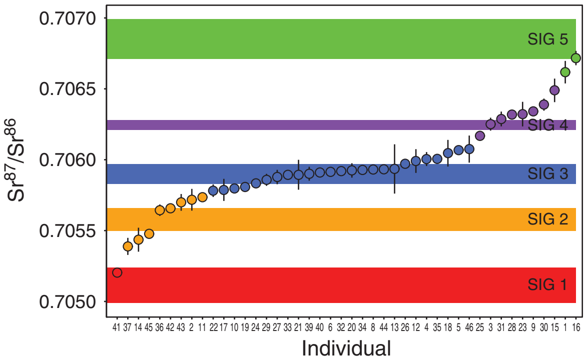

Fig. 3. Plot showing the correspondence between aqueous strontium isotope groups (SIGs) and otolith SIG assignments. The vertical spreads of the horizontal bands are the ranges of $^{87}Sr/^{86}Sr$ values for each aqueous SIG based on the data in Table 1. Points are the mean (±s.e.) otolith $^{87}Sr/^{86}Sr$ values for ablation spots <70 µm from the primordium for each individual fish examined. Point labels on the horizontal axis are the identification codes of the individuals examined. SIG colours match Fig. 1. Note that numerical identification codes for each individual are the same as those in Table 2.

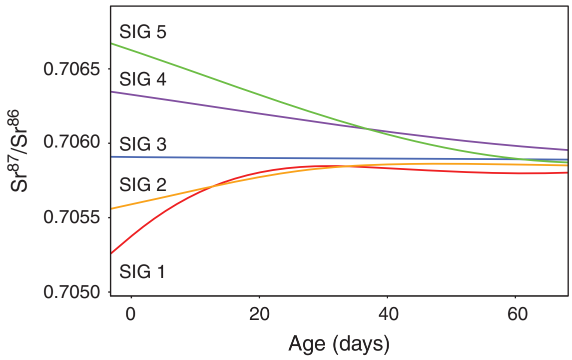

Fig. 4. Plot showing loess smooths with standard error confidence bands fitted to otolith $^{87}Sr/^{86}Sr$ values by age for all individuals across each strontium isotope group (SIG). Note that age-0 corresponds to the first feeding check; ablation spots before the first feeding check cause the models to initiate before age-0. SIG colours match Fig. 1.

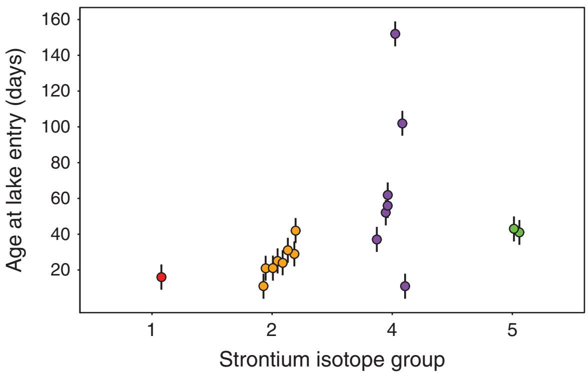

Fig. 5. Estimated age of individual Clear Lake hitch at the time at they were estimated to have entered Clear Lake for each stontium isotope group (SIG). Error bars represent a period of ±7 days, which is the approximate duration of time encompassed by the laser ablation spots. Note that some slight jitter was imposed on the points to minimise superimposition to improve visualisation. SIG 3 is not shown because streams in this group cannot be differentiated from Clear Lake. SIG colours match Fig. 1.

Natal habitat assignments generated in this study indicated that Clear Lake hitch spawned in a diversity of habitats. These included flowing streams situated around the lake, low- to zero-velocity stream confluences with Clear Lake such as Rodman Slough and possibly even the main body of Clear Lake itself. Although it is not possible to fully differentiate Clear Lake from all its tributaries using $^{87}Sr/^{86}Sr$, circumstantial evidence suggests that within-lake spawning may be more prevalent than previously thought, especially during droughts. First, a meaningful proportion of individuals appeared to have been produced in Rodman Slough (SIG 4), the physical habitat of which resembles a permanent backwater cove of Clear Lake rather than that of an ephemeral stream. Second, Clear Lake, together with Adobe Creek and Scotts Creek, was a member of SIG 3, which contained the majority (58%) of natal assignments. Adobe Creek is a well known spawning location, but Scotts Creek is thought to support fewer fish. Indeed, Adobe Creek and Clear Lake are the sources of individuals assigned to SIG 3 in this study because no individuals in this group exhibited $^{87}Sr/^{86}Sr$ signatures of SIG 4 (Rodman Slough), which they would have had to occupy in a migration from Scotts Creek to Clear Lake. This assumes that individuals would have spent sufficient time in Rodman Slough to adopt its signature. It seems unlikely that Adobe Creek alone would have been the sole contributor to the high overall proportion of fish assigned to SIG 3. These facts suggest indirectly that Clear Lake hitch may possibly use Clear Lake and the mouths of its tributary streams for spawning more so than previously thought, especially during drought conditions such as those experienced in the region for several years leading up to this study, as observed by Kimsey (1960). It is also possible that classification into SIG 3 could be overestimated because of the limitation of this tool in detecting small fish from tributaries that could have migrated very quickly to Clear Lake to rear. The development of additional markers to separate Clear Lake from Adobe Creek would be needed to fully differentiate lake and stream production of Clear Lake hitch.

Although the SIG assignments typically included multiple potential source habitats, in many cases it is possible to identify the likely primary contributors to production and adult recruitment. For example, Cole Creek and Kelsey Creek are likely primary sources of individuals assigned to SIG 1 and SIG 2 respectively. This is because the other members of these groups (Schindler Creek for SIG 1 and Burns Valley Creek for SIG 2) are much smaller, less stable habitats that are thought to support minimal and infrequent spawning. As evidence of this, Schindler Creek and Burns Valley Creek were dry for most of 2018, including when water sampling occurred. Adobe Creek and Clear Lake are the likely primary sources of individuals assigned to SIG 3 for the reasons stated above. Rodman Slough is the sole member of SIG 4. Middle Creek, Clover Creek and Seigler Creek may have both meaningfully contributed to SIG 5 because they are well known spawning locations and benefitted from the development of additional markers to differentiate these two habitats from each other.

Additional elemental markers such as Sr, Ba, Mg and Mn may assist in resolving individual habitats currently aggregated to SIGs. For example, water samples collected from a subset of the locations indicate that the inclusion of Sr/Ca and Ba/Ca to the classification model can resolve differences between sites within SIG groups with 100% classification success (data publicly available at: https://tinyurl.com/y4gg7kjv, accessed 21 March 2019). Clear Lake appears to have significantly lower Ba/Ca than Adobe Creek, allowing for 100% correct classification between these two sites with the inclusion of $^{87}Sr/^{86}Sr$, Sr/Ca and Ba/Ca in the classification model. In addition, Cole Creek has significantly lower Sr/Ca and higher Ba/Ca than Schindler Creek, resulting in 100% differentiation between the two sites within SIG 1. Lastly, Kelsey Creek has significantly higher Sr/Ca and Ba/Ca than Burns Valley Creek, the two sites within SIG 2. Although the inclusion of additional markers shows promise in providing finer-scale resolution, the lack of biological fractionation of $^{87}Sr/^{86}Sr$ and the heterogeneity observed among SIGs that is temporally stable is at a sufficient scale to be management-relevant in this system. A more significant sampling effort would be necessary to quantify the variability in Sr/Ca and Ba/Ca in the intermittent streams seasonally and annually, and any fractionation between water and otoliths, to be meaningfully applied to fish that can be $>$5 years of age.

Little is known about female hitch reproduction, including the timing of vitellogenesis or how long females spend in tributaries before spawning. Interestingly, the pre-exogenous portion of the adult otolith, typically associated with maternal influence ($<$70 μm) showed the most distinct $^{87}Sr/^{86}Sr$ values from Clear Lake $^{87}Sr/^{86}Sr$ values and best matched the aqueous isoscape (Fig. 4). The inference that can be made is that females ripen eggs while in the streams before spawning and that the juveniles are experiencing the same $^{87}Sr/^{86}Sr$ values from the natal water and maternal yolk during otolith formation. An alternative hypothesis that can explain our data is that the otolith core $^{87}Sr/^{86}Sr$ values in progeny are influenced more by water $^{87}Sr/^{86}Sr$ in the habitat than $^{87}Sr/^{86}Sr$ contribution from females (if vitellogenesis occurred in Clear Lake before spawning). In either case, our data support the use of data from the core to 70 μm in characterising their juvenile experience, because only tributary $^{87}Sr/^{86}Sr$ values could generate the observed data.

Most adults showed strong assignments to SIGs using $^{87}Sr/^{86}Sr$ alone with 95% posterior probability of membership to the assigned SIG. However, a few ($n = 4$) individuals had $^{87}Sr/^{86}Sr$ values that were intermediate to those in the SIG water baseline. This could be because of the temporal resolution of the laser sampling (beam size 40 μm) relative to juvenile movements that could integrate $^{87}Sr/^{86}Sr$ values in the otolith from different $^{87}Sr/^{86}Sr$ sources. It is also possible that there is an uncharacterised habitat, or some interannual variability not accounted for in the water baseline. Alternatively, there may be variation in maturation timing and habitat location where females ripen eggs before spawning that could create additional variation in otolith core $^{87}Sr/^{86}Sr$ values. Some or all of these factors could affect the classification strength of the few individuals, but do not appear to be common enough to affect the majority of classifications.

Age at lake entry provides an estimate of how long individual fish reared in streams before migrating into Clear Lake. There was a general pattern whereby age at lake entry was positively associated with permanency of wetted habitat. This was demonstrated as younger ages at lake entry in SIG 1 and

SIG 2, which include smaller ephemeral streams, and older ages at lake entry in SIG 4 and SIG 5, which are composed of the permanently wetted Rodman Slough and its ephemeral tributary Middle Creek. The older ages at lake entry for SIG 4 and SIG 5 indicate that juvenile Clear Lake hitch will rear in habitats such as Rodman Slough for substantial periods of time (up to 152 days observed in this study) before migrating into the main body of Clear Lake. Conceivably, longer rearing durations may lead to a larger size at lake entry, which may potentially have fitness benefits, such as increased lake survival. This would be similar to observations of migratory salmonids where size at key outmigration thresholds is positively associated with survival (Holtby *et al.* 1990; Zabel and Achord 2004; Woodson *et al.* 2013). Presumably individuals born in the ephemeral streams migrate to Clear Lake when natal habitats are no longer hospitable, yet variation in age at lake entry suggests other factors are also in play. Given that a variety of physical, biological and social factors are known to drive salmonid outmigration from natal habitats (Quinn 2011; Zeug *et al.* 2014; Sturrock *et al.* 2015), further study on Clear Lake hitch is warranted because it is likely to generate information useful for guiding stream habitat restoration. It should be noted that our analysis is likely an overestimate of the duration of stream rearing based on the temporal resolution of the beam size, isotopic equilibrium once fish enter an isotopically different environment and variation in individual growth rates, which all limit using otoliths to infer time-dependent movements. However, given this method was used for each fish, it is still a robust proxy for comparing among-individual patterns of lake entry.

This study demonstrated the utility of natural tags to identify important habitats occupied over the lifespan of an individual that would otherwise be challenging or impossible to trace. Specifically, it is possible to reconstruct short-term occupation of seasonally ephemeral habitats by fishes based on otolith $^{87}Sr/^{86}Sr$. In a generally similar application, Chen *et al.* (2017) were able to discriminate spawning rivers of Lake Erie walleye *Sander vitreus* using bulk otolith strontium (Sr/Ca) despite brief rearing durations of larvae. These results generate new opportunities for the study and conservation of a diversity of fishes, including imperilled species such as the Clear Lake hitch or important sportfish such as the walleye. For example, with Clear Lake hitch it is now technically possible to determine the relative importance of specific natal habitats and migration histories contributing to production and, by extension, the contribution of habitats supporting commercial or subsistence fisheries should they be re-established. As an example of the broad applicability of such an approach, Johnson *et al.* (2016) determined the relative importance of natal habitats and life histories contributing to Chinook salmon *Oncorhynchus tshawytscha* caught in fisheries by using otolith $^{87}Sr/^{86}Sr$. Brennan *et al.* (2015*a*) and Padilla *et al.* (2015) have also done similar work with coastal fisheries. With additional years of data to develop a time series for Clear Lake hitch or other species, this approach can potentially be used to provide insights into the differential effects of droughts on individual stream productivity or as a monitoring tool to assess the effectiveness of restoration activities intended to influence the quantity or quality of spawning habitats in specific streams.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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