Information to Aid the Listing Decision and Critical Habitat Designation of the Clear Lake Hitch: Identifying Spawning Habitats, Population Structure, and Habitat Associations

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Photographs and Video Clips of Clear Lake Hitch (*Lavinia exilicauda chi*): U.S. Geological Survey data release, [https://doi.org/10.5066/P908NFFL](https://doi.org/10.5066/P908NFFL)

Trace element concentration data for Clear Lake and selected tributaries: Seigler Creek, Burns Valley Creek, Cole Creek, Kelsey Creek, Adobe Creek, Rodman Slough, Schindler Creek, and Middle Creek. Hyperlink to retrieve the data from the National Water Information System (NWIS) database: [https://nwis.waterdata.usgs.gov/nwis/qwdata?multiple_site_no=390511122480401%390948122545901%2C3907072531101%2C390511122480401%2C390118122433801%2C390140122395401%2C390053122521401%2C3858431225303501%2C385803122493901%2C385444122363801%2C38574512235201&group_key=NONE&sitefile_output_format=html_table&column_name=agency_cd&column_name=site_no&column_name=station_nm&inventory_output=0&rdb_inventory_output=file&TZoutput=0&pm_cd_compare=Greater%20than&radio_parm_cds=all_parm_cds&format=html_table&qw_attributes=0&qw_sample_wide=wide&rdb_qw_attributes=0&date_format=YYYY-MM-DD&rdb_compression=file&list_of_search_criteria=multiple_site_no](https://nwis.waterdata.usgs.gov/nwis/qwdata?multiple_site_no=390511122480401%390948122545901%2C3907072531101%2C390511122480401%2C390118122433801%2C390140122395401%2C390053122521401%2C3858431225303501%2C385803122493901%2C385444122363801%2C38574512235201&group_key=NONE&sitefile_output_format=html_table&column_name=agency_cd&column_name=site_no&column_name=station_nm&inventory_output=0&rdb_inventory_output=file&TZoutput=0&pm_cd_compare=Greater%20than&radio_parm_cds=all_parm_cds&format=html_table&qw_attributes=0&qw_sample_wide=wide&rdb_qw_attributes=0&date_format=YYYY-MM-DD&rdb_compression=file&list_of_search_criteria=multiple_site_no)
Preliminary Results on the Status, Distribution and Habitat of Clear Lake Hitch in Summer 2017 and 2018

Elements of this report will be put into a manuscript intended to be submitted to the journal Ecology of Freshwater Fish.

Introduction

The Clear Lake Hitch *Lavinia exilicauda chi* is an imperiled fish species that is endemic to Clear Lake, Lake County, California. It is listed as a threatened species under the California Endangered Species Act and has been petitioned for listing under the U.S. Endangered Species Act. Formerly highly abundant and a staple food for the Pomo tribes of the Clear Lake region, abundance is believed to have declined 100-fold. Major threats to Clear Lake Hitch are presently thought to include (1) loss of spawning habitat through changes in land and water use along the lake’s tributaries, (2) loss of nursery areas from alterations of the lakeshore, and (3) predation and competition from alien fishes.

Clear Lake Hitch exhibit a potamodromous life history (migration from one location to another entirely within freshwater) in that adults ascend low-gradient tributary streams for spawning. Annual spawning migrations from Clear Lake to tributary streams resemble small-scale salmon runs. Spawning migrations usually occur in response to heavy spring rains, from mid-February through May at water temperatures of about 14-18°C. The embryos hatch and become free-swimming larvae in approximately fourteen days. Larvae move downstream to Clear Lake before stream flows reside. Within Clear Lake, larvae are thought to remain near shore and preferably rear in stands of tules as they grow into juveniles. Juveniles are thought to occur in shallow littoral habitats and adults are thought to probably occupy offshore habitats until they begin spawning migrations. Adults grow to almost 400 cm in length and 6-7 years of age.
The objectives of this study were to determine the status, distribution, and habitat occupied by Clear Lake Hitch in Clear Lake. The purpose of generating this information was to fill information gaps on basic Clear Lake Hitch ecology that are needed to conserve and manage the species.

Methods

Study design and data collection

Prior to this research very little was known about the distribution and habitat of Clear Lake Hitch in Clear Lake. Given the lack of knowledge to help guide this study, a stratified random study design was implemented to sample Clear Lake Hitch to collect the data necessary to address the study objectives. Sampling sites were stratified across the three major regions of Clear Lake (upper lake, middle lake and lower lake) to ensure all regions of the lake were sampled, with effort (number of samples) approximately proportional to the surface area of each region (Figure 1). Sampling for Clear Lake Hitch was conducted with experimental, multi-mesh monofilament gill nets because they permitted a consistent, standardized approach to sampling age-1+ individuals throughout Clear Lake. Other types of net sampling, whether it be passive (e.g., fyke nets) or active (e.g., trawls), or other methods such as electrofishing, could potentially have been effective in certain habitats or for certain life stages but not universally applicable across all life stages and available habitats (e.g., nearshore, offshore, shallow, deep). Sampling took place in early summer of 2017 (26-30 June and 17-21 July) and 2018 (11-15 and 18-22 June), a time period when Clear Lake Hitch distribution is constrained to Clear Lake and is not influenced by behavior associated with reproduction, and when water temperatures are cool relative to late summer to minimize handling stress associated with sampling.

Two types of experimental gill nets were used in this study. One was configured for demersal sampling and the other for surface sampling. The only physical difference between the two nets was that the height of the demersal net was 1.8 m while the height of the surface net was 3.6 m. Both gill
nets measured 45.7 m in length and had five equal length panels of 38 mm, 51 mm, 64 mm, 76 mm and 
89 mm stretched mesh. Mesh sizes were selected to attempt to effectively sample all sizes/ages of age-
1+ Clear Lake Hitch based upon prior experience with closely-related native minnows in the nearby 
Sacramento-San Joaquin Delta. Short-duration (average = 40 minutes, standard deviation = 13) gill net 
deployments comprised individual samples in this study. Short-duration deployments were conducted 
to minimize stress, injury and mortality to Clear Lake Hitch and other fishes encountered. Sampling was 
conducted during the day, generally starting around the dawn crepuscular period and ending in the late 
afternoon. Sites were established randomly with GIS software and were located in the field with GPS. 
At least two gill nets were deployed at each random site in attempt to survey the full extent of habitable 
area. At offshore sites, one surface and one or two demersal gill nets were deployed in attempt to 
sample as much of the vertical water column as possible. At nearshore sites one demersal gill net was 
deployed perpendicular to the shoreline and one gill net was deployed ~300 m from shore. Depending 
on water depth the second net was either surface or demersal to ensure the majority of the water 
column was sampled. Gill net deployments associated with a single random site were typically set > 300 
m apart from each other to ensure that each deployment represented a single independent sample. 
Aside from a small subset of individuals retained for otolith studies (see manuscript included with this 
report), Clear Lake Hitch collected in this study were measured for standard length (SL) and weight, 
marked with a passive integrated transponder (PIT) tag and released alive. No tagged fish were 
recovered in the course of the study, lending support to the assumption that each gill net deployment 
represented an independent random sample of the population and could be treated as such in statistical 
analyses.

Selected water quality parameters were measured with each individual gill net deployment. 

Water temperature (°C), dissolved oxygen concentration (mg/L), turbidity (NTU), chlorophyll
fluorescence (μg/L) and pH were measured at the location and depth of each gill net. Water depth was measured at the two ends and midpoint of each gill net deployment with a commercial sonar unit.

All data collected by this study have been published on ScienceBase, USGS’ open-source data repository platform, and are publicly available here: http://doi.org/10.5066/P9A03O16

Data analysis

The water quality data were summarized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, surface, bottom) and inspected for patterns. The data were also processed with GIS software to create two-dimensional interpolation maps of water temperature and dissolved oxygen concentration conditions at the surface and bottom of Clear Lake in 2017 and 2018.

The effectiveness of the gill nets employed in this study as a tool for obtaining meaningful, representative samples of Clear Lake Hitch was assessed by examining mesh size-selectivity. This was done by constructing log-linear models implemented in the ‘gillnetfunctions’ package in the R statistical. Size-selectivity retention curves for each gill net mesh size were fit based on fish SL grouped into 10-mm increments. The resulting curves were inspected to determine if there was any bias with gill net sampling with respect to the size of fish captured.

Clear Lake Hitch catch data were aggregated into life stage. For this analysis, individuals > 175 mm SL were considered adults and individuals < 175 mm SL were considered juveniles. Count data for each life stage in each sample were standardized by the duration (number of minutes) of each gill net deployment to generate a catch-per-unit-effort (CPUE) and summarized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, surface, bottom) and inspected for patterns. Juvenile and adult CPUE data were also mapped on Clear Lake for visual interpretation using GIS software.
Generalized additive models (GAMs) were constructed to determine if Clear Lake Hitch abundance was associated with any of the measured water quality variables. GAMs are nonparametric extensions of generalized linear models useful for describing non-linear relationships between variables. They are data-driven and do not presuppose a particular functional relationship between variables; smoothers characterize the empirical relationships between predictor and response variables. The GAMs were constructed with the ‘mgcv’ package in the R statistical computing environment. Relatively simple models were constructed for juveniles and adults separately. The count data were highly zero-inflated (Figure 2) so the GAMs were fit using a negative binomial distribution with thin plate spline smoothing functions. Gamma was set to 1.4 in attempt to help avoid over fitting the models to the data. Models were constructed in a backwards step-wise manner. Initially, a full model was built for each life stage that included the log of all measured water quality variables as independent variables, counts of Clear Lake Hitch as the response variable, and sampling effort (gill net set duration in minutes) as an offset. Any non-significant (P < 0.05) variables were removed, and new models were constructed until only significant variables remained in a model. It should be emphasized that these models be considered simple, preliminary examinations of relationships between Clear Lake Hitch abundance and water quality variables; a much more rigorous examination will be conducted in a future analysis.

Results and Discussion

A total of 504 samples (gill net sets and corresponding water quality measurements) were collected during the study (Figure 1; Table 1). Average water temperature was 25 °C (standard deviation = 2) in 2017 and 22 °C (standard deviation = 1) in 2018. In general, water temperature was lowest in bottom samples and warmest in surface and shore samples (Figure 3), with substantial among- and within-regional variability (Figure 4).
Average dissolved oxygen concentration was 7 mg/L (standard deviation = 4) in 2017 and 7 mg/L (standard deviation = 3) in 2018. In general, dissolved oxygen concentration was lowest in bottom samples and highest in surface and shore samples (Figure 5), with substantial among- and within-region variability (Figure 6). Hypoxia was prevalent, especially in bottom samples, in both 2017 and 2018 (Figure 6).

Average turbidity was 12 NTU (standard deviation = 15) in 2017 and 3 NTU (standard deviation = 3) in 2018. In general, dissolved oxygen concentration was highest in surface samples (shore and surface) and lowest in bottom samples (Figure 7). Overall, turbidity values were higher and more variable in 2017 compared to 2018 (Figure 7).

Average chlorophyll fluorescence was 6 μg/L (standard deviation = 6) in 2017 and 9 μg/L (standard deviation = 6) in 2018. In general, chlorophyll fluorescence values were highly spatio-temporally variable (Figure 8).

Average pH was 9 (standard deviation = 1) in 2017 and 8 (standard deviation = 1) in 2018. In general, pH values were highest in surface samples (shore and surface) and lowest in bottom samples (Figure 9). Overall, pH values were higher and more variable in 2017 compared to 2018 (Figure 9).

A total of 577 Clear Lake Hitch were captured in 130 (25%) of the 504 gill net samples. A random subsample of 44 individuals were retained for otolith analyses (see manuscript included with this report) and all other individuals were measured for standard length (SL) and weight, marked with a passive integrated transponder (PIT) tag and released alive. Clear Lake Hitch was the 5th most abundant species collected in 2017 (N = 280) and the most abundant species collected in 2018 (N = 297; Table 2). The apparent high abundance of Clear Lake Hitch relative to other species encountered in the samples was probably in part a function of the type of sampling gear employed and time of year sampled but was nonetheless an unexpected finding.
Gill net effectiveness, as assessed by the selectivity curves generated from log-linear models, indicated that individual mesh sizes were selective for particular size ranges of individuals but as a group all mesh sizes together effectively sampled all size ranges of age-1+ Clear Lake Hitch (Figure 10). These results suggest that the gill nets used in this study successfully captured representative samples of the Clear Lake Hitch population.

There was a substantial difference in the size distribution of Clear Lake Hitch collected in 2017 versus 2018 (Figure 11). In 2017, the majority of fish were juveniles less than approximately 175 mm SL. That same cohort of fish appeared to make up the majority if the catch a year later in 2018. These data suggest that a relatively strong year class was produced in 2015 which presently dominates the overall population. Curiously, very few juveniles were observed in 2018 (Figures 12 and 13), suggesting a poor year class was produced in 2016 or that survival of the 2016 cohort to 2018 was poor. There was a large fish kill that occurred in Clear Lake between the 2017 and 2018 sampling events which may possibly have contributed to this observation, although there are no available data to directly affirm or dispute such a linkage. Approximately equal sampling effort among years and the retention selectivity information on the gill nets presented above suggest that the result was not caused by any bias associated with effort or sampling gear. Additional years of data will be needed to further assess the strength of individual year classes.

Average juvenile Clear Lake Hitch CPUE was 0.017 (standard deviation = 0.047) in 2017 and 0.001 (standard deviation = 0.01) in 2018. In general, juvenile Clear Lake Hitch CPUE was highest in shore samples (Figure 12) and was substantially higher in 2017 compared to 2018 (Figure 13). The near absence of juvenile Clear Lake Hitch in 2018 was an unexpected finding and might have resulted from the factors mentioned in the previous paragraph.

Average adult Clear Lake Hitch CPUE was 0.007 (standard deviation = 0.022) in 2017 and 0.024 (standard deviation = 0.101) in 2018. In general, adult Clear Lake Hitch CPUE was more broadly
distributed among bottom, shore and surface samples (Figures 14 and 15). Interestingly, adult CPUE in bottom samples was much higher in 2018 compared to 2017 when dissolved oxygen concentration conditions were more suitable for the lake bottom to be occupied (Figure 14).

The final GAM fitted for juvenile Clear Lake Hitch included all five measured water quality variables - water temperature, dissolved oxygen concentration, turbidity, chlorophyll fluorescence, and pH - as significant independent variables and explained 90% of the deviance (variation) in juvenile Clear Lake Hitch CPUE (Table 3). Juvenile Clear Lake Hitch CPUE was positively linearly related to water temperature, turbidity, and dissolved oxygen concentration, and negatively linearly related to pH (Figure 15). These relationships also reflect the fact there is some correlation among the independent variables that needs to be addressed in future analyses. The relationship to chlorophyll fluorescence was essentially flat except that there was an association of low CPUE with low Chlorophyll fluorescence (Figure 16). Please note that this model should be considered an initial, exploratory analysis into the relationships between fish abundance and water quality variables.

The final GAM fitted for adult Clear Lake Hitch included dissolved oxygen concentration, turbidity, chlorophyll fluorescence, and pH as significant independent variables and explained 89% of the deviance (variation) in adult Clear Lake Hitch CPUE (Table 4). Adult Clear Lake Hitch CPUE was negatively linearly related to chlorophyll fluorescence and pH, and positively linearly related to dissolved oxygen concentration (Figure 16). The relationship with turbidity was less clear and appeared to be generally positive, albeit with high variability (Figure 17). These relationships also reflect the fact there is some correlation among the independent variables that needs to be addressed in future analyses. Please note that this model should be considered an initial, exploratory analysis into the relationships between fish abundance and water quality variables.
Table 1. Total number of gill net samples collected by year and region.

<table>
<thead>
<tr>
<th>Year</th>
<th>Lower Lake</th>
<th>Middle Lake</th>
<th>Upper Lake</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>2017</td>
<td>76</td>
<td>85</td>
<td>100</td>
<td>261</td>
</tr>
<tr>
<td>2018</td>
<td>79</td>
<td>62</td>
<td>102</td>
<td>243</td>
</tr>
<tr>
<td>Total</td>
<td>155</td>
<td>147</td>
<td>202</td>
<td>504</td>
</tr>
</tbody>
</table>
Table 2. Total number of individual fish species collected in 2017 and 2018. Asterisks indicate native species.

<table>
<thead>
<tr>
<th>Species</th>
<th>2017</th>
<th>2018</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Threadfin Shad <em>Dorosoma petenense</em></td>
<td>3,293</td>
<td>23</td>
<td>3,316</td>
</tr>
<tr>
<td>Black Crappie <em>Pomoxis nigromaculatus</em></td>
<td>490</td>
<td>236</td>
<td>726</td>
</tr>
<tr>
<td>*Clear Lake Hitch <em>Lavinia exilicauda chi</em></td>
<td>280</td>
<td>297</td>
<td>577</td>
</tr>
<tr>
<td>Channel Catfish <em>Ictalurus punctatus</em></td>
<td>333</td>
<td>226</td>
<td>559</td>
</tr>
<tr>
<td>Largemouth Bass <em>Micropterus salmoides</em></td>
<td>359</td>
<td>83</td>
<td>442</td>
</tr>
<tr>
<td>Bluegill Sunfish <em>Lepomis macrochirus</em></td>
<td>162</td>
<td>36</td>
<td>198</td>
</tr>
<tr>
<td>*Tule Perch <em>Hysterocarpus traskii</em></td>
<td>135</td>
<td>29</td>
<td>164</td>
</tr>
<tr>
<td>Redear Sunfish <em>Lepomis microlophus</em></td>
<td>52</td>
<td>14</td>
<td>66</td>
</tr>
<tr>
<td>*Sacramento Sucker <em>Catostomus occidentalis</em></td>
<td>22</td>
<td>23</td>
<td>45</td>
</tr>
<tr>
<td>*Sacramento Blackfish <em>Orthodon microlepidotus</em></td>
<td>30</td>
<td>12</td>
<td>42</td>
</tr>
<tr>
<td>White Catfish <em>Ameiurus catus</em></td>
<td>17</td>
<td>5</td>
<td>22</td>
</tr>
<tr>
<td>Common Carp <em>Cyprinus carpio</em></td>
<td>7</td>
<td>10</td>
<td>17</td>
</tr>
<tr>
<td>Brown Bullhead <em>Ameiurus nebulosis</em></td>
<td>8</td>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>Unidentified sunfish <em>Lepomis spp.</em></td>
<td>3</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Sockeye salmon/Kokanee <em>Oncorhynchus nerka</em></td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Black Bullhead <em>Ameriurus melas</em></td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>5,193</td>
<td>1,005</td>
<td>6,198</td>
</tr>
</tbody>
</table>
Table 3. Output for the final generalized additive model fitted to relate the abundance of juvenile Clear Lake Hitch to water quality variables. Please note that this model should be considered an initial, exploratory analysis into the relationships between fish abundance and water quality variables.

**Family: Negative Binomial(0.017)**
**Link function: log**

**Formula:**
\[ \text{Juv} \sim s(\log(\text{Temperature}), \text{bs} = \text{"tp"}) + s(\log(\text{Turbidity}), \text{bs} = \text{"tp"}) + s(\log(\text{Chlorophyll}), \text{bs} = \text{"tp"}) + s(\log(\text{DO} \_ \text{concentration}), \text{bs} = \text{"tp"}) + s(\log(\text{pH}), \text{bs} = \text{"tp"}) \]

**Parametric coefficients:**

| Estimate | Std. Error | z value | Pr(>|z|) |
|----------|------------|---------|----------|
| (Intercept) | -40.498 | 0.554 | -73.1 | <2e-16 *** |

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**Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1**

**Approximate significance of smooth terms:**

<table>
<thead>
<tr>
<th>edf</th>
<th>Ref.df</th>
<th>Chi.sq</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>s(log(Temperature))</td>
<td>1.001</td>
<td>1.001</td>
<td>4.532</td>
</tr>
<tr>
<td>s(log(Turbidity))</td>
<td>2.358</td>
<td>2.979</td>
<td>15.098</td>
</tr>
<tr>
<td>s(log(Chlorophyll))</td>
<td>6.744</td>
<td>7.828</td>
<td>35.113</td>
</tr>
<tr>
<td>s(log(DO_concentration))</td>
<td>3.085</td>
<td>3.893</td>
<td>148.411</td>
</tr>
<tr>
<td>s(log(pH))</td>
<td>3.091</td>
<td>3.944</td>
<td>25.357</td>
</tr>
</tbody>
</table>

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**Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1**

**R-sq.(adj) = -3e+65**  **Deviance explained = 90.1%**

**-REML = 398.69**  **Scale est. = 1**  **n = 504**
Table 4. Output for the generalized additive model fitted to relate the abundance of adult Clear Lake Hitch to water quality variables. Please note that this model should be considered an initial, exploratory analysis into the relationships between fish abundance and water quality variables.

**Family**: Negative Binomial(0.022)  
**Link function**: log

**Formula**:  
Adult ~ s(log(Turbidity), bs = "tp") + s(log(chlorophyll), bs = "tp") + s(log(DO_concentration), bs = "tp") + s(log(pH), bs = "tp")

**Parametric coefficients**:

| Estimate | Std. Error | z value | Pr(>|z|)  |
|----------|------------|---------|-----------|
| (Intercept) | -38.6242 | 0.7966 | -48.49 | <2e-16 *** |

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**Signif. codes**: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

**Approximate significance of smooth terms**:

<table>
<thead>
<tr>
<th>edf</th>
<th>Ref.df</th>
<th>Chi.sq</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>s(log(Turbidity))</td>
<td>6.473</td>
<td>7.045</td>
<td>170.99</td>
</tr>
<tr>
<td>s(log(chlorophyll))</td>
<td>1.000</td>
<td>1.000</td>
<td>28.00</td>
</tr>
<tr>
<td>s(log(DO_concentration))</td>
<td>4.263</td>
<td>5.332</td>
<td>65.73</td>
</tr>
<tr>
<td>s(log(pH))</td>
<td>7.611</td>
<td>8.546</td>
<td>72.22</td>
</tr>
</tbody>
</table>

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**Signif. codes**: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

**R-sq.(adj) = -9.99e+61**  
**Deviance explained = 89.3%**  
**-REML = 519.5**  
**Scale est. = 1**  
**n = 504**
Figure 1. Map of Clear Lake showing gill net sampling sites. Color shading is water depth generated from interpolation of depth values measured at each sample site.
Figure 2. Histogram representation of the number Clear Lake Hitch collected in samples. The vertical axis is the count of samples that had the number of Clear Lake Hitch shown on the horizontal axis. Across both years, most samples (75%) collected zero Clear Lake Hitch, indicating the sample data are highly zero-inflated.
Figure 3. Water temperature values observed at each sampling site organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface).
Figure 4. Water temperature values observed at each sampling site organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface). Note that ranges of temperature are unique to each plot.
Figure 5. Dissolved oxygen concentration values observed at each sampling site organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface).
Figure 6. Dissolved oxygen concentration values observed at each sampling site organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface). Note that ranges of dissolved oxygen concentration are unique to each plot.
Figure 7. Turbidity values observed at each sampling site organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface).
Figure 8. Chlorophyll concentration values observed at each sampling site organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface).
Figure 9. Values of pH observed at each sampling site organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface).
Figure 10. Retention curves generated from log-linear models showing the relative selectivity of gill net mesh size across Clear Lake Hitch standard length. Mesh sizes are: black = 38 mm, red = 51 mm, green = 64 mm, purple = 76 mm, and blue = 89 mm. The curves demonstrate that any single mesh size is biased for a particular size group of Clear Lake Hitch but when used together, as with the experimental gill nets used in this study, they are effective at capturing the full size range of Clear Lake Hitch.
Figure 11. Length-frequency histograms showing the size-structure of Clear Lake Hitch collected in 2017 and 2018.
Figure 12. Boxplot representation of juvenile catch per unit effort (CPUE) organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface). Zero values have been excluded from the plot to improve visual interpretation.
Figure 13. Map of juvenile Clear Lake Hitch catch per unit effort (CPUE) (x100) organized by year (2017, 2018).
Figure 14. Boxplot representation of adult catch per unit effort (CPUE) organized by year (2017, 2018), region (upper lake, middle lake, lower lake) and location (shore, bottom, surface). Note that the bottom panel is the same as the top except that vertical axis of the bottom panel has been constrained to improve visualization of the major patterns. Zero values have been excluded from the plot to improve visual interpretation.
Figure 15. Map of adult Clear Lake Hitch catch per unit effort (CPUE) (x100) organized by year (2017, 2018).
Figure 16. Plots showing the relationships between the abundance of juvenile Clear Lake Hitch and water quality variables. Individual plots show fitted smooths and 95% confidence intervals for partial responses from generalized additive models. The vertical axis units are centered on zero and the number in the label is the estimated degrees of freedom of the smooth. Please note that this model should be considered an initial, exploratory analysis into the relationships between fish abundance and water quality variables.
Figure 17. Plots showing the relationships between the abundance of adult Clear Lake Hitch and water quality variables. Individual plots show fitted smooths and 95% confidence intervals for partial responses from generalized additive models. The vertical axis units are centered on zero and the number in the label is the estimated degrees of freedom of the smooth. Please note that this model should be considered an initial, exploratory analysis into the relationships between fish abundance and water quality variables.
Strontium isotopes reveal ephemeral streams used for spawning and rearing by an imperiled 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, California, USA) into ephemeral tributary streams for spawning. An aqueous isoscape of strontium isotopic ratios \(^{87}\text{Sr}/^{86}\text{Sr}\) was constructed for Clear Lake and its watershed to trace natal origins and migration histories of adult recruits. Aqueous \(^{87}\text{Sr}/^{86}\text{Sr}\) differentiated Clear Lake from 8 of 10 key tributaries and clustered into five Strontium Isotope Groups (SIGs) with 100% classification success. Otolith \(^{87}\text{Sr}/^{86}\text{Sr}\) showed all five groups contributed variably to the population. The age that juveniles migrated from natal streams to Clear Lake ranged from 11 to 152 days (average = 43; standard deviation = 34) 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.

Introduction

Effective conservation of threatened or endangered species fundamentally requires knowledge of the habitats which contribute to production and recruitment. Determining productive habitats for highly mobile species, such as migratory fishes with life cycles that span heterogenous 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; Johnson et al. 2016). In particular, isotopic ratios of strontium ($^{87}\text{Sr}/^{86}\text{Sr}$) present in the otoliths of fishes closely resembles that present in the aqueous environment and provides 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).

The majority of California’s native freshwater fishes are imperiled (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 imperiled cyprinid endemic to a single freshwater Lake (Clear Lake, Lake County). 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 [CDFW] 2014). Clear Lake Hitch is presently listed as a threatened species under the California Endangered Species Act and has been petitioned for listing under the U.S. 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 (CDFW 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 isotopic 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, USA, approximately 100 km north of San Francisco Bay (Fig. 1). It is the largest natural freshwater lake completely within California. At full capacity, it has a surface area of approximately 17,700 ha and a total volume of approximately 1.4 billion 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 winter and/or 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. It is one of the larger streams and had a maximum average monthly streamflow from 2011 to 2017 that ranged from 1.6 to 24.7 m$^3$/sec (average = 11.1, standard deviation = 7.6; data are freely available from the California Department of Water Resources at:
The regional landscape has a diverse volcanic geological history (Hearn et al. 1995). Dominate 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). The collective aforementioned factors contributed to the hypothesis that there would be sufficient variation in $^{87}\text{Sr}/^{86}\text{Sr}$ across the watershed to facilitate provenance research via otolith chemistry.

**Isoscape development**

To develop an aqueous $^{87}\text{Sr}/^{86}\text{Sr}$ 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 (one 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/juvenile rearing (Table 1). Water was collected at each site via sterile syringes and passed through 0.45µm filters into acid-washed 150 ml polyethylene containers using traditional triple rinse clean-chemistry protocols and stored in a refrigerator prior to analysis (Barnett-Johnson et al. 2005, 2007). Field blanks and paired field and laboratory duplicate samples were analyzed to confirm $^{87}\text{Sr}/^{86}\text{Sr}$ reproducibility (Table 1).

Water samples were analyzed with a Nu Plasma HR multiple-collection, double-focusing, plasma-source mass spectrometer (MC-ICPMS; Nu Instruments, Inc.). Samples were purified through a specific ion-exchange resin, Sr Resin (Eichrom Technologies, Inc.), in a class 100 clean lab facility (PicoTrace, GmbH). After being reconstituted in ultrapure sub-boiling double-distilled 2% nitric acid, the purified samples were introduced into the Nu Plasma with a desolvating nebulizer system (DSN-100,
MkII) with a 0.1mL/min uptake (33 psi with 700mm capillary) quartz MicroMist nebulizer (Glass Expansion, Inc.). Instrument sensitivity typically ranges from 500 - 1000 V/ppm Sr. Ratios include 50-60 data points and each data point integrates faraday signals for 10 seconds. Baselines were measured for 30 seconds by electrostatic analyzer (ESA) deflection. The NIST SRM 987 standard (0.71034) was used as a reference to normalize measured values and to establish measurement accuracy and precision (Moore et al. 1982). The standard was measured approximately every 6 samples and produced a mean $^{87}\text{Sr} / ^{86}\text{Sr}$ value of 0.71016 with a standard deviation of 0.00001 (N=9).

An isoscape of the available habitat was developed based on non-overlapping $^{87}\text{Sr} / ^{86}\text{Sr}$ values. First, to determine the resolution of the isoscape, a single factor linear discriminant function analysis (DFA) was conducted using $^{87}\text{Sr} / ^{86}\text{Sr}$ values for individual habitats (SAS version 9.4, SAS Institute). 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 $^{87}\text{Sr} / ^{86}\text{Sr}$ values into strontium isotope groups (SIG; sensu Brennan et al. 2015). A linear function was used to estimate the variance-covariance matrix response and was applied across all 5 SIGs. Jackknife resampling used the same data set to generate and evaluate the discriminant function by calculating the function (in this case the mean $^{87}\text{Sr} / ^{86}\text{Sr}$ 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 this 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 randomized 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 sacrificed for scientific study to 45 individuals.

Lapilli otoliths were extracted from fish, rinsed in deionized water to remove any attached organic tissue and allowed to air dry prior to storage. Dry otoliths were individually mounted on glass microscope slides in an epoxy (West systems 105), 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 (Olympus BX60) at 200x magnification, camera (Q-Imaging MicroPublisher 6) and image analysis software (ImagePro Premier) per established techniques (Barnett-Johnson et al. 2007). The average distance (µm) of the first feeding check from the otolith primordium was 72.2 µm (standard deviation = 6.3). Larval Clear Lake Hitch may be up to approximately 2 weeks old post hatch at the onset of exogenous feeding as Swift (1965) observed that the yolk sac was fully absorbed at 13 days post hatch in larvae reared at 16 °C.

Strontium isotopic composition in otoliths was measured with a MC-ICPMS interfaced with a Nd: YAG 213-nm laser (New Wave Research UP213) 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, dwell time of 25 seconds, and a 10-Hz laser pulse repetition rate. Average voltage values for 88Sr during analyses was 3.298 with a standard deviation of 0.699. Helium was used as a carrier gas in the sample chamber to maximize sensitivity and minimize 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 stabilized after the sample change (i.e., exposing sample cell to the air) and were measured for 30 s. These background measurements were blank subtracted from the measured signals prior to 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 normalize measured values and to establish measurement accuracy and precision since there is no recognized otolith standard commercially-available. Thirty-nine analyses of the standard conducted throughout the otolith analysis process produced a mean $^{87}$Sr/$^{86}$Sr value of 0.70904 with a standard deviation of 0.00008, which were normalized 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 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 prior to 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 post exogenous feeding in Clear Lake Hitch is ~8µm wide. Therefore, the 40 µm beam
integrates $^{87}$Sr/$^{86}$Sr values over approximately 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**

A total of 37 water samples were analyzed for $^{87}$Sr/$^{86}$Sr to develop the isoscape that ranged across habitat values from 0.70499 to 0.70699 (Table 1). Average $^{87}$Sr/$^{86}$Sr values were used per sampling event when duplicate samples were collected and analyzed 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 (Figure 2). Aqueous $^{87}$Sr/$^{86}$Sr values differentiated Clear Lake from 8 of the 10 tributaries examined and clustered into five 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 “Discussion” for an explanation for 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 = 192, standard deviation = 58). 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.
The majority of 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 = 43, standard deviation = 34; Figs. 4 and 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 8 individuals assigned to SIG 2 were: 11, 21, 21, 24, 25, 29, 31, and 42. Ages at lake entry for the 6 individuals assigned to SIG 4 were: 11, 37, 52, 62, 102, and 152. Ages at lake entry for the 2 individuals assigned to SIG 5 were: 41 and 43.

Discussion

Assessing spatio-temporal variation of aqueous $^{87}\text{Sr}/^{86}\text{Sr}$ is fundamental for applications of provenance or migration studies of fishes (Elsdon et al. 2008; Hobson et al. 2010; Brennan et al. 2015). In this study, $^{87}\text{Sr}/^{86}\text{Sr}$ values underlying the isoscape were spatially stable within and among hydrologically-diverse years (representative flow data from Kelsey Creek are available here: http://cdec.water.ca.gov/dynamicapp/staMeta?station_id=KCK). Moreover, there was no overlap of $^{87}\text{Sr}/^{86}\text{Sr}$ values among SIGs, indicating robust SIG assignments that ultimately did not require statistical differentiation. The $^{87}\text{Sr}/^{86}\text{Sr}$ habitat signatures appear to be insensitive, at least at the level of resolution required for otolith $^{87}\text{Sr}/^{86}\text{Sr}$ application, to the dynamic seasonal hydrology of the watershed and the resulting flow variability within and among streams. This suggests that aqueous $^{87}\text{Sr}/^{86}\text{Sr}$ within the watershed is driven by the $^{87}\text{Sr}/^{86}\text{Sr}$ in the solutes derived by the underlying lithology rather than directly from precipitation, as we originally hypothesized based upon the geological variability of the Clear Lake watershed. These factors provide a strong foundation for the development of the isoscape and for the application of otolith $^{87}\text{Sr}/^{86}\text{Sr}$ 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 $^{87}\text{Sr}/^{86}\text{Sr}$ 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 $^{87}\text{Sr}/^{86}\text{Sr}$ values and SIG assignments in 2018 (0.70523; SIG 1) compared to those observed prior to the construction activity in 2017 (0.70679 and 0.70679; SIG 5). This change in aqueous $^{87}\text{Sr}/^{86}\text{Sr}$ did not influence the results of this study because fish assigned to SIGs were born and captured before the construction activity. Pre-construction $^{87}\text{Sr}/^{86}\text{Sr}$ values for Seigler Creek were therefore used as the relevant $^{87}\text{Sr}/^{86}\text{Sr}$ stream signature for adult cohorts in this study. The observation nonetheless underscores the value of monitoring baseline $^{87}\text{Sr}/^{86}\text{Sr}$ values spatially and temporally in systems undergoing significant stream-bed habitat alterations.

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 of its tributaries using $^{87}\text{Sr}/^{86}\text{Sr}$, circumstantial evidence suggest that within-lake spawning might 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 were members 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 $^{87}\text{Sr}/^{86}\text{Sr}$ signatures of SIG 4 (Rodman Slough), which they would have had to occupy in a migration from Scotts Creek to Clear Lake. 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 utilize 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 over-estimated due to 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.

While 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 instance, 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 both have meaningfully contributed to SIG 5 as they are well-known spawning locations and may benefit 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 are publicly available at:}
https://nwis.waterdata.usgs.gov/nwis/qwdata?multiple_site_no=390948122545901%2C39070712253101%2C390511122480401%2C3901181223801%2C390140122395401%2C390053122521401%2C385843122503501%2C385544122363801%2C385745122385201&group_key=NONE&sitefile_output_format=html_table&column_name=agency_cd&column_name=site_no&column_name=station_nm&inventory_output=0&rdb_inventory_output=file&TZoutput=0&pm_cd_compare=Greater%20than&radio_parm_cds=all_parm_cds&format=html_table&qw_attributes=0&qw_sample_wide=wide&rdb_qw_attributes=0&date_format=YYYY-MM-DD&rdb_compression=file&list_of_search_criteria=multiple_site_no). Clear Lake appears to have significantly lower Ba/Ca compared to Adobe Creek allowing for 100% correct classification between these two sites with the inclusion of ⁸⁷Sr/⁸⁶Sr, Sr/Ca, and Ba/Ca in the classification model. Additionally, 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. While the inclusion of additional markers show promise in providing finer-scale resolution, the lack of biological fractionation of ⁸⁷Sr/⁸⁶Sr 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 the duration of time females spend in tributaries prior to spawning. Interestingly, the pre-exogenous portion of the adult otolith, typically associated with maternal influence (< 70 µm) showed the most distinct ⁸⁷Sr/⁸⁶Sr values from Clear Lake ⁸⁷Sr/⁸⁶Sr values and best matched the aqueous isoscape (Fig. 4). The inference that can be made is that females ripen eggs while in the streams prior to spawning and that the juveniles are experiencing the same ⁸⁷Sr/⁸⁶Sr values from the natal water and maternal yolk
during otolith formation. An alternative hypothesis that can explain our data is that the otolith core 
\(^{87}\text{Sr}/^{86}\text{Sr}\) values in progeny are influenced more by water \(^{87}\text{Sr}/^{86}\text{Sr}\) in that habitat than \(^{87}\text{Sr}/^{86}\text{Sr}\) 
contribution from females [if vitellogenesis occurred in Clear Lake prior to spawning]. In either case, our 
data support the use of data from the core to 70 µm in characterizing their juvenile experience, as only 
tributary \(^{87}\text{Sr}/^{86}\text{Sr}\) values could generate the observed data.

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

Age at lake entry provides an estimate of how long individual fish reared in streams prior to 
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 are comprised of smaller ephemeral streams, and older ages at lake entry in SIG 4 
and SIG 5, which are comprised 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) prior to 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 as it is likely to generate information useful for guiding stream habitat restoration. It should be noted that our analysis is likely an over-estimate 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 relatively short-term occupation of seasonally ephemeral habitats by fishes based on otolith $^{87}\text{Sr}/^{86}\text{Sr}$. 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 imperiled 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 $^{87}\text{Sr}/^{86}\text{Sr}$. 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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Table 1. Information on site, location, date collected, $^{87}\text{Sr}/^{86}\text{Sr} \pm$ 2 standard errors (SE), and strontium isotope group (SIG) assignment for all water samples. Site superscript definitions are as follows:

1 unusual observation (see “Discussion” for explanation); 2 paired field duplicate; 3 paired lab duplicate; 4 paired lab duplicate; 5 paired field duplicate.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Date</th>
<th>$^{87}\text{Sr}/^{86}\text{Sr}$</th>
<th>$\pm$ 2 SE</th>
<th>SIG</th>
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<td>38°58'03.45&quot;</td>
<td>-122°49'39.25&quot;</td>
<td>04/05/17</td>
<td>0.70499</td>
<td>0.00001</td>
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<td>0.00001</td>
<td>3</td>
</tr>
<tr>
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<td>-122°43'38.25&quot;</td>
<td>05/15/17</td>
<td>0.70590</td>
<td>0.00001</td>
<td>3</td>
</tr>
<tr>
<td>Clear Lake, middle</td>
<td>39°01'17.54&quot;</td>
<td>-122°43'38.25&quot;</td>
<td>04/05/17</td>
<td>0.70591</td>
<td>0.00001</td>
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<tr>
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<td>05/02/18</td>
<td>0.70592</td>
<td>0.00001</td>
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<tr>
<td>Clear Lake, upper</td>
<td>39°05'10.99&quot;</td>
<td>-122°48'04.01&quot;</td>
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<td>0.00001</td>
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<td>Clear Lake, middle</td>
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<td>04/05/17</td>
<td>0.70592</td>
<td>0.00001</td>
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<tr>
<td>Clear Lake, upper</td>
<td>39°05'10.99&quot;</td>
<td>-122°48'04.01&quot;</td>
<td>05/11/17</td>
<td>0.70592</td>
<td>0.00001</td>
<td>3</td>
</tr>
<tr>
<td>Clear Lake, upper</td>
<td>39°05'10.99&quot;</td>
<td>-122°48'04.01&quot;</td>
<td>04/05/17</td>
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<td>0.00001</td>
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<tr>
<td>Adobe Creek, lower</td>
<td>39°00'52.69&quot;</td>
<td>-122°52'14.37&quot;</td>
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<td>0.00001</td>
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<td>03/28/18</td>
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<td>-122°53'10.58&quot;</td>
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<td>0.00001</td>
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<td>Rodman Slough</td>
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<td>-122°53'10.58&quot;</td>
<td>05/11/17</td>
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<td>-122°53'10.58&quot;</td>
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<td>Seigler Creek</td>
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<td>-122°36'38.23&quot;</td>
<td>04/05/17</td>
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<td>0.00001</td>
<td>5</td>
</tr>
<tr>
<td>Creek</td>
<td>Longitude</td>
<td>Latitude</td>
<td>Date</td>
<td>Flood Stage</td>
<td>Flow Duration</td>
<td>100 Yr</td>
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<tr>
<td>Seigler Creek</td>
<td>38°54'44.43&quot;</td>
<td>-122°36'38.23&quot;</td>
<td>05/11/17</td>
<td>0.70678</td>
<td>0.00001</td>
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<td>03/28/18</td>
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<td>0.00001</td>
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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 $^{87}\text{Sr}/^{86}\text{Sr}$ value and its standard error (SE), 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.

<table>
<thead>
<tr>
<th>Individual</th>
<th>N</th>
<th>$^{87}\text{Sr}/^{86}\text{Sr}$</th>
<th>SE</th>
<th>SIG</th>
<th>Posterior Probability (%)</th>
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<td>0.70607</td>
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</table>
Figure 1. Left panel: Map of Clear Lake and streams showing sites where water (●) and fish (+) were collected. Colors represent strontium isotope groups (SIG) based on aggregations of non-overlapping $^{87}\text{Sr}/^{86}\text{Sr}$ values shown 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 $^{87}\text{Sr}/^{86}\text{Sr}$ values corresponding to each SIG. The inset is a map of the counties of California with Lake County highlighted as the filled polygon. Right panel: 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://gispublic.co.lake.ca.us/portal/home/](http://gispublic.co.lake.ca.us/portal/home/).
Figure 2. Boxplot representation of all aqueous $^{87}\text{Sr}/^{86}\text{Sr}$ values from Table 1 aggregated into five non-overlapping strontium isotope groups (SIG). Boxes show the median and 25% and 75% quantiles. Points show the individual values with some horizontal jitter added to minimize superimposition to improve visualization. SIG colors match Figure 1.
Figure 3. Plot showing the correspondence between aqueous strontium isotope groups (SIG) and otolith SIG assignments. The vertical spreads of the horizontal bands are the ranges of $^{87}\text{Sr}/^{86}\text{Sr}$ values for each aqueous SIG based on the data in Table 1. Points are the mean (± 1 SE) otolith $^{87}\text{Sr}/^{86}\text{Sr}$ values for ablation spots < 70 µm from primordium for each individual fish examined. Point labels on the horizontal axis are the identification codes of the individuals examined. SIG colors match Figure 1. Note that numerical identification codes for each individual are the same as those in Table 2.
Figure 4. Plot showing loess smooths with standard error confidence bands fitted to otolith $^{87}\text{Sr}/^{86}\text{Sr}$ values by age for all individuals across each strontium isotope group (SIG). Note that age-0 corresponds to the first feeding check; ablation spots prior to the first feeding check cause the models to initiate before age-0. SIG colors match Figure 1.
Figure 5. Estimated age in days of individual Clear Lake Hitch at the time at which they were estimated to have entered Clear Lake for each strontium isotope group (SIG). Error bars represent a period of $\pm 7$ 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 minimize superimposition to improve visualization. SIG 3 is not shown because streams in this group cannot be differentiated from Clear Lake. SIG colors match Figure 1.
Rapid potamodromy into ephemeral streams: observations of the spawning ecology of the imperiled Clear Lake Hitch *Lavinia exilicauda chi*

Frederick Feyrer

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Abstract  The Clear Lake Hitch *Lavinia exilicauda chi* is an imperiled potamodromous cyprinid that migrates from the single freshwater lake it occupies (Clear Lake, Lake County, California, USA) into seasonally-ephemeral streams for spawning. Adult migration, spawning, embryo incubation, larval development, and juvenile emigration all occur during a short temporal window during spring when dry stream beds become temporarily inundated from seasonal rains. This study documents visual observations made of behavior of individuals spawning and holding in Kelsey Creek, a key tributary of Clear Lake. Spawning was observed during daylight hours during a period of relatively steady stream flow of 3 m$^3$/sec and water temperature of 13°C. Spawning occurred in run habitat along a shallow (0.25 m), low-velocity (0.37 m/sec) margin of the stream. Substrate was comprised of a mix of irregular cobble and gravel overlaying a bed of clean pebbles and sand. Spawning behavior was observed whereby fish milling in the run would occasionally cluster tightly together in groups of 2-6 individuals and engage in conspicuous spawning bursts. The spawning bursts consisted of one or more males gathering alongside a female and rigorously quivering, rotating and burst swimming with the female in attempt to fertilize eggs broadcast by the female. The behavior occurred in very shallow water, often shallower than the body depth of the fish. Eggs were negatively buoyant and settled into crevices of the rocky substrate. Individuals not actively engaged in spawning schooled together in low velocity sections of pool habitat and appeared to actively feed on invertebrate drift.

Keywords  Potamodromous · Migration · Ephemeral · Spawning · Stream · Cyprinid · Hitch · *Lavinia* · Threatened Species
Introduction

Migrations for the purposes of reproduction are widely documented across the animal kingdom and are particularly common in fishes and other aquatic organisms (Dingle 2014). One of the least-studied migration strategies in fishes is potamodromy, which is the movement from one location to another entirely within freshwater (Morais & Daverat 2016). Thurow (2016) estimated that worldwide there are approximately 13,000 potamodromous fish species. Potamodromous migratory behavior is thought to arise from spatial, seasonal, and ontogenetic separation of optimal habitats for growth, survival, and reproduction (Northcote 1984). Potamodromous species as a group are also relatively imperiled, owing to the loss or destruction of the diversity of habitats often required for successful reproduction and recruitment (Thurow 2016).

The Clear Lake Hitch *Lavinia exilicauda chi* is an imperiled potamodromous cyprinid that is endemic to a single freshwater lake: Clear Lake, Lake County, California, USA. The species lives to approximately six years of age and attains a maximum size of approximately 350 mm. As juveniles and adults, it feeds primarily on macroinvertebrates, including insects and zooplankton. Formerly highly abundant and a staple food for the Pomo tribes of the Clear Lake region, Clear Lake Hitch abundance is believed to have declined 100-fold from historical levels (California Department of Fish and Wildlife [CDFW] 2014). Presently, Clear Lake Hitch is listed as threatened under the California Endangered Species Act and has been petitioned for listing under the U.S. Endangered Species Act.

The Clear Lake Hitch exhibits a potamodromous life cycle, whereby adults ascend Clear Lake’s ephemeral tributaries during the spring to spawn. Adult migration, spawning, embryo incubation, larval development, and juvenile emigration all occur during a short temporal
window during the spring season when dry stream beds become temporarily inundated from seasonal rains. Some spawning has been observed along the shoreline of Clear Lake (Kimsey 1960), but within-lake spawning is not presently considered a significant source of Clear Lake Hitch production and recruitment. Anthropogenic modification and loss of stream spawning habitat are thought to be important elements driving the decline of Clear Lake Hitch (CDFW 2014).

Clear Lake Hitch have been observed in streams during migration and spawning (e.g., http://lakelive.info/chicouncil/). However, aside from Kimsey’s (1960) description of spawning along the Clear Lake shoreline, descriptions of spawning behavior and habitat use have been limited to compilations of mostly anecdotal observations (Moyle 2002; Macedo 1994; Murphy 1948). For example, spawning habitat has long been characterized as clean gravel substrate at water temperatures of approximately 14-18 °C. The purpose of this study was to expand upon this limited knowledge. The objective was to observe and document fundamental aspects of the stream ecology of the Clear Lake Hitch associated with spawning to generate baseline information that is desperately needed to determine if conservation and management actions are needed to protect and rehabilitate stream spawning habitat. The specific questions addressed in this study were: (1) under what water temperature and flow conditions does spawning occur, (2) what are the major habitat features where spawning takes place, (3) what are the fundamental aspects of spawning behavior, (4) what is the fate of eggs deposited during spawning, and (5) when not engaged in spawning, what type of stream habitat is used by Clear Lake Hitch and do they actively feed?
Methods

Clear Lake is located in Central California, USA, approximately 100 km north of San Francisco Bay. It is well known for being the largest natural freshwater lake completely within California. At full capacity, it has a surface area of approximately 17,700 ha and a total volume of approximately 1.4 billion m$^3$. Visual observations of Clear Lake Hitch were made in Kelsey Creek, a key tributary to Clear Lake, during daylight hours on 01 April 2018. Observations of spawning and holding behavior were made at sites located approximately 6.3 km and 4.6 km upstream of the confluence of Kelsey Creek and Clear Lake, respectively (Fig. 1). Water temperature data were obtained from a logger (ONSET HOBO Model U20L-002) deployed for this study approximately 2.6 km upstream of the confluence of Kelsey Creek and Clear Lake. Flow data were obtained from a gauge operated by the California Department of Water Resources located 0.5 km upstream from the temperature logger (data are available at: http://cdec.water.ca.gov/dynamicapp/staMeta?station_id=KCK).

Observations of spawning behavior were made in a shallow, low-velocity run habitat. The overall area of the shallow region where spawning occurred covered approximately 50% of the width of the creek. It was not measured but was estimated to be approximately 5 m long, 3 m wide and 0.25 m in depth. The other approximate 50% of the channel was deeper (up to approximately 1.5 m) and accommodated the majority of the flow. Water surface velocity in the shallow and deep sections of the run was measured using an improvised float method. The time it took a floating object to travel 2 m was measured five separate times at three locations along the cross section of the stream, two sites in the shallow section and one site in the deep section. The behavior of Clear Lake Hitch spawning in the run was observed directly overhead from a position on the Merritt Road bridge that crossed approximately 6 m over the stream.
Approximately 120 minutes of observation was conducted in the afternoon under a bright, clear sky. Observations were documented with photographs and video taken with a Nikon D5300 digital camera.

Observations of holding behavior were made in pool habitat situated at the head of short, shallow run. The overall area of the pool was not measured but it was estimated to be approximately 6 m long, 5 m wide and 1.5 m deep. Observations were made using a video camera (SOOCOO S100Pro) positioned underwater on the stream bed at the head of the pool. The video camera was oriented to face in a downstream direction to observe 10-15 Clear Lake Hitch which were holding in the pool and oriented facing into the current. Rocks from the streambed were used to secure the video camera in place. The video camera’s small size and color appeared to blend in well with the existing substrate by human eyes and did not have any noticeable effect on fish behavior. Approximately 30 minutes of observation was recorded under the same afternoon, clear sky conditions noted above. Representative photographs and video clips are available at https://doi.org/10.5066/P90BNFFL.

Results

Study question (1): Under what water temperature and flow conditions does spawning occur?

Average daily water temperature on the date when spawning was observed was 13°C, which was just reached for the first time in the season two days prior (Fig. 2). Average daily flow was 3 m³/sec (Fig. 2). This was on a relatively steady yet descending limb of the hydrograph following a peak flow of approximately 40 m³/sec on March 22 (Fig. 2).

Study question (2): What are the major habitat features where spawning takes place?

Average surface velocity was 0.36 m/sec in the run where spawning took place and 0.77 m/sec in the adjacent main channel (individual measured velocity values were as follows: run
transect 1: 0.36, 0.41, 0.42, 0.29, 0.37; run transect 2: 0.29, 0.36, 0.33, 0.41, 0.39; main channel transect: 0.95, 0.81, 0.85, 0.78, 0.77). The substrate where spawning was observed was comprised of a mix of irregular-shaped cobble and gravel overlaying a bed of fine pebbles that was clear of sediment (Fig. 3). Substrate in the rest of the channel of the immediate area was similar and also included a few larger cobbles and small boulders. Average water depth in the run was not measured but was estimated to be approximately 0.25 m. There was no riparian vegetation in the area other than a few small, isolated unidentified bushes that appeared to be of no significance to the fish or their activity.

Study question (3): What are the fundamental aspects spawning behavior?

The run in which spawning occurred was actively occupied by numerous (10-15+) individual Clear Lake Hitch milling in the area. Observed spawning activity consisted of groups of 2–6 individuals occasionally clustering tightly together and engaging in relatively short but very active and conspicuous spawning bursts (Fig. 4). The spawning bursts consisted of one or more males gathering alongside a female and rigorously quivering, rotating and burst swimming with the female in attempt to fertilize eggs broadcast by the female. The behavior occurred in very shallow water, often shallower than the body depth of the fish, such that individuals were often observed squirming over rocks with a majority of their bodies exposed to the air. Spawning bursts occurred at seemingly random times and locations within the confines of the run. Concurrently, dozens of non-spawning Clear Lake Hitch were holding in low velocity sections of an adjacent pool. Movements of individuals between the pool and the run could not be quantified with the observation methods employed.

Study question (4): What is the fate of eggs deposited during spawning?
Eggs broadcast by a female were fertilized by sperm broadcast by one or more males during the spawning bursts. The eggs were negatively buoyant and quickly settled into crevices of the rocky substrate (Fig. 3).

Study question (5): When not engaged in spawning, what type of stream habitat is used by Clear Lake Hitch and do they actively feed?

Individual fish not actively engaged in spawning held together in schools in relatively low velocity pool or margin habitat in various areas throughout the stream. Individuals in the pool habitat monitored with the video camera held in a tight school milling near the bed in the lowest velocity sections of the pool. Individual fish were occasionally observed to quickly dart up in the water column and then returned to their original position, giving the appearance of feeding on invertebrate drift.

**Discussion**

Clear Lake Hitch release eggs and sperm over unprepared substrate and can therefore be characterized as broadcast spawners, the most common and primitive form among the eight proposed functional categories of spawning modes of North American minnows; the other seven forms are crevice spawning, pit building, pit-ridge building, saucer building, mound building, egg clumping and egg clustering (Johnston 1999). Johnston (1999) noted that over 60% of North American minnows are broadcast spawners. Perhaps unique to broadcast-spawning minnows, as well as many other fishes in general, Clear Lake Hitch undergo potamodromous migrations to spawn in lentic habitats which are typically dry for much of the year.

Potamodromous migrations in fishes are thought to have evolved as a means to optimize fitness through enhanced growth and/or survival (Northcote 1984). In the case of Clear Lake Hitch, stream spawning must have provided evolutionary fitness benefits to the population,
otherwise there would be little reason for it to persist as a dominant trait. Why this trait developed and has persisted, especially given that spawning in permanently-wetted lake habitat is possible (Kimsey 1960), is not clearly understood but it is postulated as a means to improve fitness of offspring via optimal environmental conditions and/or refugia from predation. The overall fitness benefits are apparently sufficient to offset a presumed high risk of survival for eggs and larvae. Clear Lake Hitch observed in this study, and anecdotally by others, deposited eggs in extremely shallow water on the descending limb of the hydrograph. Such circumstances risk, and have sometimes been observed to result in, the desiccation of eggs before embryos can develop and hatch or the stranding of larvae or juveniles. It is possible that this risk may potentially have been exacerbated with the altered modern-day stream hydrographs.

Interestingly, potamodromy at Clear Lake is not unique to Clear Lake Hitch as Sacramento Sucker *Catostomus occidentallis* and the now extinct Clear Lake Splittail also have/had similar life history strategies, suggesting broad, generalized benefits to migrating out of Clear Lake for reproduction.

Imperilment of broadcast-spawning North American minnows is broadly associated with loss or degradation of spawning habitat, especially through siltation of spawning substrates (Johnston 1999). Spawning habitats of Clear Lake Hitch are vulnerable to similar broad problems. While flushing flows from seasonal rains likely wash spawning substrate clean of debris accumulated during the dry season, human activities that extract or disturb substrate in dry stream beds can alter or impair the quantity and quality of instream habitat used for spawning and rearing.

Effective conservation of imperiled species fundamentally requires knowledge of the habitats which contribute to production. The fundamental aspects of the spawning habitat and
behavior of the Clear Lake Hitch described in this study will be useful for resource managers tasked with the conservation of this imperiled species. This study expands upon previous anecdotal descriptions of spawning by documenting specific aspects of stream habitat, substrate, temperature, velocity and flow conditions occupied by actively spawning fish. While this study represents a critical first step, further study is needed to more fully understand the stream ecology Clear Lake Hitch. For example, basic information is lacking on the conditions which trigger the migration of Clear Lake Hitch into streams, whether the species exhibits philopatry, and the full range of flow, velocity, temperature, substrate and other habitat features used for holding and spawning. Such information will help resource managers further refine strategies to conserve the Clear Lake Hitch.

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References


Figure 1. Map of the study area showing the location of the streamflow gauge, water temperature logger, and fish observation sites. The inset is a map of the counties of California with Lake County highlighted as the filled polygon.
Figure 2. Hydrograph and water temperature of Kelsey Creek, 16 February – 11 June 2018.

Flow data were from the California Department of Water Resources and temperature data were from an ONSET HOBO Model U20L-002 logger deployed for this study. The black marker denotes the date when fish observations occurred.
Figure 3. Representative photographs of negatively-buoyant Clear Lake Hitch eggs and the irregular rocky substrate into which they settled. For reference, fertilized egg diameters are approximately 1.0-2.0 mm (Swift 1965).
Figure 4. Two representative examples of Clear Lake Hitch spawning behavior. Top panel: Two smaller males positioned alongside a single larger female immediately prior to a spawning burst. Bottom panel: Typical spawning burst behavior whereby several males are attempting to fertilize eggs broadcast by a female.
Clear Lake Hitch Status

- Unique sub-species *Lavinia exilicauda chi*
- Occurs only in Clear Lake, Lake County, CA
- Abundance believed to have declined ~100-fold
- Listed as THREATENED under California ESA
- Petitioned for listing under Federal ESA
George A. Coleman, speaking of surveys done in 1925:

The “Hitch” or “Chigh” – *Lavinia exilicauda*, Baird and Girard. The most abundant fish in all these lakes, including Blue Lakes. They run up all the creeks, entering from the lakes in March, spawning in the shallow riffles. They are then so abundant that one can hardly step without stepping on several. They are excellent eating and people should be encouraged to use more of them.

Source: Coleman, G.A. 1930. A biological survey of Clear Lake, Lake County. California Fish and Game 16(3)221-227
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Threats to Clear Lake Hitch

- Loss of spawning habitat
- Loss of nursery habitat
- Predation and competition with non-native species
- *Suitability of lake habitat (wait for it...*)
Clear Lake Hitch Ecology

- Large-bodied
- Long-lived
- Opportunistic
- Potamodromous life history

Photos by Richard Macedo
Where do Clear Lake Hitch live in the lake?

Study objectives

• Abundance and distribution
• Habitat associations
Dates: June 26-29 & July 17-21, 2017
Method: Short-duration gill net sets (N=261)
   Experimental – 5 mesh panels
   Random site selection
Strata: Upper lake, Middle Lake, Lower lake
Habitat: Shoreline, Surface, Bottom
WQ: Temp, DO, Turb, Chl, SpCon, fDOM
   Spot measurements & vertical profiles

Key point: We sampled hard!
Key point: Uncommon but a meaningful component of fish the community.
Key point: Most abundant in middle and upper lake. Least abundant in bottom samples.
Key point: Small fish most abundant inshore. Large fish most abundant offshore.
Key point: Population dominated by 1- and 2-year old fish. *Pending contemporary age data.
Key point: No superficial patterns in fish condition.
Key point: No superficial patterns in fish condition.
Key point: Superficially all fish appeared healthy except for one individual.
Key point: Hypoxic dead zone encompassed large area of lake bottom.
Clear Lake Hitch
Frequency of occurrence in samples

- Normoxic (red) 36%
- Hypoxic (blue) 18%

Key point: Clear Lake Hitch were infrequently encountered in the hypoxic dead zone.
Key point: Clear Lake Hitch were infrequently encountered in the hypoxic dead zone.
Key point: Hypoxic dead zone constricts habitat and may contribute to fish kills.
“Dead fish islands the size of football fields”

Key point: Hypoxic dead zone constricts habitat and may contribute to fish kills.
“Famous” Dead Zones

Chesapeake Bay

Gulf of Mexico

Key point: Hypoxic dead zones are well studied and treatable. There is hope.
Conclusions

- Loss of spawning habitat?

  Typical California seasonal hydrograph but highly variable. No temporal trend in any month.

  No trend through time. To date, WY2018 is 9th lowest in 71-year time.

- No evidence of change in stream flow.
- Physical stream habitat should be evaluated.
Conclusions

- Loss of nursery habitat?

Juvenile fish use streams and nearshore lake habitat.

- Documented loss of wetlands.
- Juvenile fish habitat should be evaluated.
Conclusions

• Predation and competition from non-native species?

• Unknown effects.
• Ecological interactions should be evaluated.
Conclusions

• Suitability of lake habitat?

• Dead zone constricts lake habitat and may contribute to fish kills.
• Dead zone dynamics should be evaluated.
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Tracking natal habitat use in a freshwater migratory fish, Clear Lake hitch, with otolith strontium isotopes

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Abstract

Clear Lake Hitch (Leuciscus californicus californicus) is a threatened species by the State of California and under consideration for listing by the U.S. Fish and Wildlife Service. Adults reside within Clear Lake for much of their lives, but during the wet season migrate into the surrounding tributaries to spawn. Juveniles return to the lake in streams for varying lengths of time (1 day to 6 months) prior to migrating to the lake (Table 1). Historical spawning runs were estimated to be in the millions of individuals, but because of alteration and degradation of critical spawning areas, current runs have been reduced to 2.3 orders of magnitude. While in the past all of the tributaries were likely heavily utilized, it is unclear which tributaries presently play a vital role in supporting the persistence of the species.

Results

Water and otolith $^{87}$Sr/$^{86}$Sr values in streams and the lake during the spawning season uncovered seven discernible Strontium Isotope Groups (SIGs). Randomly sampled fish (Figures 1 and 2) collected in the lake had established natal signatures demonstrating that they were likely born in 5 of the 7 SIGs. As the lake is encompassed by Lake County, juvenile salmonids accounted for approximately half (48.3%) of total recruitment followed by Redbud Park (18.8%). Juveniles spent a significant amount of time residing in Redbud Park. SIG 5 does not have residence information because it was indistinguishable from the lake itself.

Table 1

<table>
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<tr>
<th>SIG</th>
<th>SIG ID Range</th>
<th>Water Sampling Sites</th>
<th>% of Total Recruitment</th>
<th>Nontidal Residence Range (days)</th>
<th>Average Nontidal Residence (days)</th>
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<tr>
<td>1</td>
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<td>Cole Creek, Sanger Camp</td>
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<td>n/a</td>
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<td>2</td>
<td>0.7055 - 0.7056</td>
<td>Redbud Park, Sanger</td>
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<td>3</td>
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<td>Adobe Creek, Redbud Park</td>
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<tr>
<td>5</td>
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<td>Redbud Park, Sanger</td>
<td>16.8 (6)</td>
<td>0 - 165</td>
<td>43</td>
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<tr>
<td>6</td>
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<td>Middle Creek, Sanger</td>
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</table>

Discussion

Otolith $^{87}$Sr/$^{86}$Sr provides a valuable tool to reconstruct the natal origins of Clear Lake Hitch. Previously, it had been inferred that Adobe and Kelsey Creeks likely supported the largest amount of spawning. This study demonstrates that other tributaries, including Middle Creek and Redbud Park, may be important for natal habitat use in Adobe Creek and Redbud Park, and it appears to be important for the Clear Lake Hitch population.

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