Observations of the spawning ecology of the imperiled Clear Lake Hitch

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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 important migration strategy in fishes is potamodromy, which is the movement from one location to another entirely within freshwater (Morais and 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. It was originally described as a unique subspecies of *Lavinia exilicauda* (Hopkirk 1973) but has recently been proposed as a distinct population segment (Baumsteiger et al. 2019). The species lives to approximately six years of age and attains a maximum size of approximately 350 mm fork length. As juveniles and adults, it feeds primarily on macroinvertebrates, including insects and zooplankton (Geary and Moyle 1980). 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 substantially from historical levels (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 known to be 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 periods of 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 within streams have been relatively limited in scope (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 paper is to document fortuitous observations of Clear Lake Hitch spawning and holding in stream habitat to generate baseline information that is needed to manage the species. The observations facilitated addressing the following questions (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 immediate 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?

Clear Lake is in Central California, approximately 100-km north of San Francisco Bay. It is the largest natural freshwater lake completely within California (Goldman and Wetzel 1963). At full capacity, it has a surface area of approximately 17,700 ha and a total volume of approximately 1.4 billion m³. I conducted visual observations of Clear Lake Hitch in Kelsey Creek, a primary tributary to Clear Lake, during daylight hours on 01 April 2018. I observed spawning and holding behavior at sites located approximately 6.3 km and 4.6 km upstream of the confluence of Kelsey Creek and Clear Lake, respectively (Figure 1). I obtained water temperature data from a logger (ONSET HOBO Model U20L-002) deployed approximately 2.6 km upstream of the confluence of Kelsey Creek and Clear Lake. The water temperature data are available at https://doi.org/10.5066/P9L3TXNK (Feyrer 2019). I obtained flow data from a gauge operated by the California Department of Water Resources located 0.5 km upstream from the temperature logger. The flow data are available at: http:// cdec.water.ca.gov/dynamicapp/staMeta?station_id=KCK.

I observed spawning behavior in shallow, low-velocity run habitat encompassing an area of approximately 5 m in length, 3 m in width and 0.25 m in depth which encompassed approximately 50% of the width of the creek. The other approximate 50% of the channel was deeper (up to approximately 1.5 m) and accommodated most of the flow. I measured water surface velocity in the shallow and deep sections of the run using an improvised float method by recording the time it took a floating object to travel 2 m 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. I observed Clear Lake Hitch spawning in the run directly overhead from a position on the Merritt Road bridge which crossed approximately 6 m over the stream. I documented approximately 120 minutes of observation conducted in the afternoon under a bright, clear sky with photographs and video taken with a Nikon D5300 digital camera.

I observed and recorded holding behavior in pool that was approximately 6 m long, 5 m wide and 1.5 m deep that was situated at the head of a short, shallow run. I documented observations 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 facing into the current. The video camera was secured in place with rocks from the streambed; All

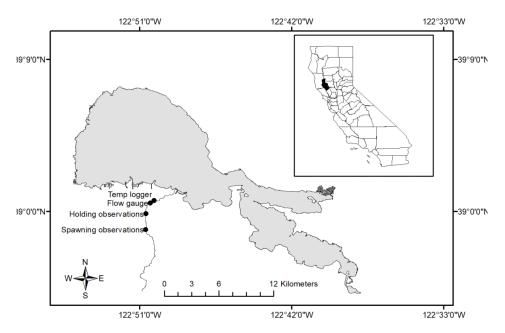


Figure 1. Map of the study area showing the location of the streamflow gauge, water temperature logger, and fish observation sites. The inset is a map of the counties of California with Lake County highlighted as the filled polygon.

observational data, in the form of representative photographs and video clips, are archived in the U.S. Geological Survey's ScienceBase catalogue and are available at https://doi. org/10.5066/P90BNFFL (Feyrer 2018).

Average daily water temperature on the date when spawning was observed was 13°C (Figure 2). Average daily flow was 3 m³/sec (Figure 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 (Figure 2).

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 (Figure 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.

The run in which fish were spawning was actively occupied by numerous (10-15+) individual adult Clear Lake Hitch milling in the area. 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 (Figure 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

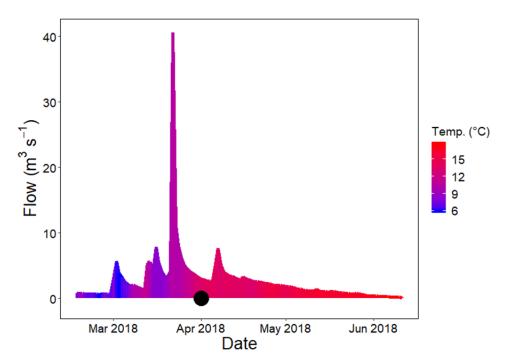


Figure 2. Hydrograph and water temperature of Kelsey Creek, 16 February -11 June 2018. Flow data were from the California Department of Water Resources, and temperature data were from an ONSET HOBO Model U20L-002 logger deployed for this study. The black marker denotes the date when fish observations occurred.

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. I could not assess the movements of individuals between the pool and the run. One or more males fertilized eggs broadcast by a female during the spawning bursts. The negatively buoyant eggs quickly settled into crevices of the rocky substrate (Figure 3).

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. Individual fish were occasionally observed to quickly dart up in the water column and then return to their original position, giving the appearance of feeding on invertebrate drift.

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 being 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. Somewhat unique to extant broadcast-spawning minnows, as well as many other fishes in general, Clear Lake



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 were approximately 1.0–2.0 mm (Swift 1965).

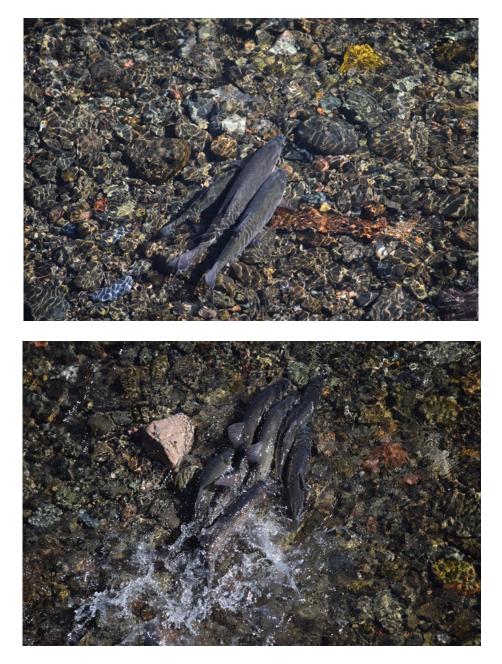


Figure 4. Two representative examples of Clear Lake Hitch spawning behavior. Top panel: Two smaller males positioned alongside a single larger female immediately prior to a spawning burst. Bottom panel: Typical spawning burst behavior whereby several males are attempting to fertilize eggs broadcast by a female. Additional photographs and video documenting behavior are available at https://doi.org/10.5066/P90BNFFL

Hitch undergo potamodromous migrations from lakes to spawn in lotic 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, either desiccation of eggs before embryos can develop and hatch or stranding of larvae or juveniles. Interestingly, potamodromy at Clear Lake is not unique to Clear Lake Hitch as Sacramento Sucker Catostomus occidentallis and the extinct Clear Lake Splittail Pogonichthys ciscoides also have/had similar life history strategies, suggesting broad, generalized benefits to migrating out of Clear Lake for reproduction (Moyle 2002).

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 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 (e.g., mining or off-road vehicle recreation) in dry stream beds can alter or impair the quantity and quality of instream habitat used for holding, 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 limited descriptions of spawning by documenting specific aspects of stream habitat, substrate, temperature, velocity and flow conditions occupied by actively spawning individuals. However, the results are based on relatively few observations. Further study is needed to more fully understand the stream ecology of 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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