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Newly discovered spawning and recruitment of threatened Longfin Smelt in restored and underexplored tidal wetlands

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A comprehensive understanding of the life-history strategies and habitat use of species is essential for developing accurate ecological models and effective management and conservation strategies. For example, omitting critical habitats of endangered species when estimating their abundance and when designing conservation plans can severely limit our understanding of population dynamics and lead to poor management outcomes. Here we describe important new observations of the distribution and habitat use of Longfin Smelt (Spirinchus thaleichthys) in the San Francisco Estuary, California, USA. Longfin Smelt are planktivorous forage fish found in estuarine and coastal waters from San Francisco Bay, California to the Aleutian Islands, Alaska (Garwood 2017). This species was once a dominant forage fish in the estuary, even supporting a small commercial fishery prior to the 1970s (Skinner 1962, Moyle 2002); however, this genetically distinct population has collapsed to approximately 1% of its historic (pre-1980) abundance, and details regarding its life history and drivers of population dynamics remain uncertain (Nobriga and Rosenfield 2016).

Longfin Smelt are thought to live for 1-2 yrs in the coastal Pacific Ocean before returning to tidal freshwater habitats of the Sacramento-San Joaquin Delta ("upper estuary"), where they are believed to spawn (Moyle 2002, Rosenfield and Baxter 2007; Fig. 1a). Though the San Francisco Estuary is a well-studied system, long-term fishery surveys were designed for other species (e.g., striped bass); thus population models for Longfin Smelt have depended largely on data from the upper estuary and open-water bay habitats. Targeted studies are needed to assess whether existing data sets and resultant models accurately describe Longfin Smelt distributions, behaviors, and population dynamics. For example, a recent study observed high densities of Longfin Smelt larvae in previously unsampled wetland habitats in the upper estuary (Grimaldo et al. 2017). Similarly, it has been hypothesized that Longfin Smelt may also inhabit shallow tidal wetlands of the many smaller watersheds throughout San Francisco Bay and San Pablo Bay for spawning, rearing, and feeding (Fig. 1b).

From October through April, which encompasses the spawning season, and in all years from 2011 to 2019, we observed persistent and occasionally dense aggregations of adult Longfin Smelt in marshes and sloughs of the Coyote Creek watershed in the southernmost part of San Francisco Bay (Figs. 1b, 2a,b). Many of the adults were in late-stage spawning condition and expressed eggs and milt upon capture (Fig. 2c). Postlarval recruits (Fig. 2d) were also observed in April-May of 2017 and 2019, with each of these years characterized by anomalously high precipitation and freshwater outflow (and persistent low-salinity spawning and rearing habitat). Thus, the potential for spawning was apparent in all years, whereas recruitment success appeared to be limited by freshwater outflow, as has been described for Longfin Smelt in the upper estuary (Kimmerer 2002, Nobriga and Rosenfield 2016). The highest catches of recruits and adults were often within shallow recently restored tidal marshes and adjacent sloughs (Fig. 2a), suggesting that (1) previous surveys have likely omitted substantial fractions of the San Francisco Estuary Longfin Smelt population and (2) that tidal marsh restoration may benefit all life stages of this threatened species.

Surveys were conducted monthly from 2011 to 2019 at 2-3 m depth in marsh and slough habitats of the lower Coyote Creek watershed, including two restored tidal marshes and two open-water bay stations. The Coyote Creek watershed of South San Francisco Bay drains much of Silicon Valley and feeds directly into the Alviso Marsh Complex-a macrotidal Mediterranean-type estuary with a 4-m tidal range that is composed of several major tidal sloughs (Upper and Lower Coyote

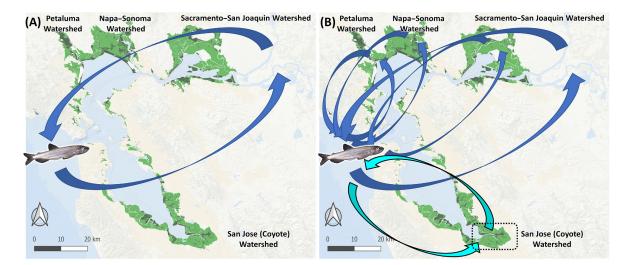


FIG. 1. Life history of the Longfin Smelt. (A) Classic life-history model showing a 2-yr semi-anadromous life history, with adults migrating upstream to spawn in the Sacramento–San Joaquin Watershed and subsequent downstream dispersal of larvae and juveniles to bay and coastal habitats. (B) Alternative life-history model indicating spawning and hatching in a variety of smaller watersheds throughout the San Francisco Estuary (SFE). Our observations in the Coyote Creek Watershed in the southern SFE (dashed box) confirm that reproductive adult Longfin Smelt visit this watershed annually and successfully spawn in years of high precipitation. This life-history strategy was likely more common and successful prior to extensive degradation of brackish wetland existing (dark) brackish wetlands (San Francisco Estuary Institute and Aquatic Science Center [SFEI ASC] 2017).

Creek, Alviso Slough, and Artesian Slough) networked throughout historically expansive salt marsh habitats. Sampling was conducted by towing an otter trawl with a 4.3×1.5 m opening and 0.6-cm cod end mesh into the current at 3 km/h for 5–10 min and counting the number of fish in each tow.

High abundances of Longfin Smelt were unexpected in these habitats, let alone evidence for successful spawning and recruitment. Most of the historic wetland habitats in the region were dredged, diked, and converted to solar evaporation ponds for salt production in the mid-1900s (Nichols et al. 1986) and little freshwater runoff reaches the estuary because of numerous upstream dams and diversions that capture and redirect most instream flows for human use (Grossinger et al. 2007). Alviso Marsh also receives over 100 million gallons per day of low-salinity, warm, and nutrient-rich wastewater effluent directly into its sloughs (San Jose-Santa Clara Regional Wastewater Facility [SJSCRWF] 2018). Historically, there has been little interest in studying ecological communities in this highly degraded ecosystem. However, recent commitments to restore 15,000 acres of wetland habitat in the region (Valoppi 2018) have provided the motivation to establish baselines and document changes in aquatic communities in response to restoration efforts over the past decade. Surprisingly, our observations suggest that Longfin Smelt are relatively abundant and can successfully spawn and rear in wetlands of South San Francisco Bay, and that restoration of marsh habitats and increases in freshwater outflow to these smaller watersheds could benefit this threatened species.

How important are brackish wetland habitats to Longfin Smelt? To answer this, future studies should build upon these observations, expanding the geographic scope of sampling to encompass other brackish marshes and sloughs, and assessing the relative importance of these habitats to the adult population. Estuary-wide sampling of brackish wetland habitats should be conducted during spawning and recruitment periods and in years with different precipitation, temperature, and other climate parameters. Multiple gear types should be deployed to quantify both larval and adult abundances, and methods should match or be calibrated against long-term monitoring programs so that relative contributions can be directly compared among habitat types and regions. Future modeling efforts could assess sensitivity and elasticity of population dynamics to production and survival of young-of-the-year age classes in different regions and habitats of the estuary.

Can tidal marsh and watershed restoration benefit Longfin Smelt? To address this, it is important to quantify the conservation value of tidal marsh habitats to Longfin Smelt. Comparative studies of abundance, feeding rates, growth rates, diets, and mortality rates of Longfin Smelt in marshes versus open-water habitats would be valuable. Trace-element chemistry of otoliths (fish ear bones) could be used to quantify the relative contributions of different regions and habitat types to

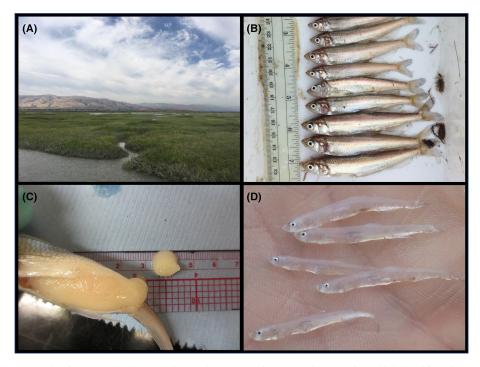


FIG. 2. (A) Example of a restored salt marsh in South San Francisco Bay where relatively high densities of (B) adult Longfin Smelt were often observed during the spawning season. Many of the adults captured were expressing (C) milt or eggs (shown), indicative of spawning. In 2017 and 2019, (D) postlarval Longfin Smelt recruits were also observed in restored marshes and adjacent sloughs, indicating successful spawning and rearing in Lower South San Francisco Bay during years of high precipitation and freshwater outflow.

adult Longfin Smelt populations (Hobbs et al. 2007). Isotopes of Sr and O in otoliths can be used to reconstruct time-resolved histories of salinity, providing key information about habitat requirements and ontogenetic movement patterns and behaviors (Hobbs et al. 2010). Additional chemical tools (e.g., δ^{34} S and Mn) could prove useful for reconstructing the use of wetland versus open-water habitats by Longfin Smelt.

Longfin Smelt are at record low abundance and likely no longer serve their historic ecological function in the San Francisco Estuary. The population was listed as "threatened" in 2009 under the California Endangered Species Act (CESA) and designated as "warranted but precluded" for listing in 2012 under the federal Endangered Species Act (ESA). For 7 years, the species has remained precluded from ESA protections despite rapid and continuous declines in abundance. In the face of numerous ecological impacts, a warming climate (Cloern et al. 2011, Jeffries et al. 2016), and precluded protection, the future of longfin smelt remains bleak in the estuary (Hobbs et al. 2017).

For nine consecutive years, however, we have observed previously undescribed aggregations of Longfin Smelt that were attempting to spawn in restored and underexplored tidal wetlands of South San Francisco Bay. Furthermore, we observed successful recruitment in years of high freshwater outflow. These observations may help explain the positive recruitment-freshwater outflow relationship and long-term decline of Longfin Smelt (Kimmerer 2002, Kimmerer et al. 2009, Nobriga and Rosenfield 2016). For example, expansion of shallow lowsalinity spawning and rearing habitats throughout the entire estuary in wet years may explain in part the positive relationship between interannual variation in freshwater outflow and Longfin Smelt recruitment. Similarly, the historic degradation of lesser watersheds and brackish wetlands throughout the San Francisco Estuary may have contributed to the long-term decline of this species. Thus, the observations reported herein could transform our fundamental understanding of the habitat needs of Longfin Smelt and the interventions needed to conserve and restore this distinct and imperiled population.

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