Title

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RESEARCH

Estuarine Recruitment of Longfin Smelt (*Spirinchus thaleichthys*) north of the San Francisco Estuary

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ABSTRACT

Longfin Smelt (*Spirinchus thaleichthys*) was an important forage fish in the San Francisco Estuary (the SFE) but was listed as threatened under the California Endangered Species Act in 2009. This has inspired research within the estuary at the southern edge of their distribution. However, populations also exist in other estuaries along the coast, which are far less described despite their potential importance in a meta-population. We surveyed Longfin Smelt populations along the northern California coast for larval recruitment. We conducted surveys in 2019 and 2020 to (1) identify estuaries north of the SFE where spawning occurs, and (2) evaluate how habitat features (e.g., salinity, temperature, dissolved oxygen, turbidity) influenced Longfin Smelt larvae abundance. We detected larvae in four of 16 estuaries we surveyed, and all were large estuaries north of Cape Mendocino. No larvae were detected in eight coastal estuaries in closer proximity to the SFE. Larvae catch probability increased with turbidity and decreased with salinity with no significant influence of temperature and dissolved oxygen. In the wet winter of 2019, we observed lower densities of larvae in Humboldt Bay and the Eel River, and detected no Longfin Smelt in the Klamath and Mad Rivers; in the dry winter of 2020, we detected larvae in two additional estuaries. Elevated freshwater outflow in 2019 possibly increased transport rates to sea, resulting in observed low larval recruitment. Our results suggest that, although populations of Longfin Smelt exist in large estuaries north of Cape Mendocino, coastal estuaries in proximity to the SFE were either under-sampled or are not permanently inhabited by Longfin Smelt. Longfin Smelt in the SFE may therefore lack resilience normally afforded by metapopulations. Increased monitoring over their coastal range under varying hydrologic conditions is needed to assess gene flow between populations.

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KEY WORDS

Longfin Smelt, osmerid, northern California, recruitment, habitat, estuary

INTRODUCTION

Understanding recruitment and dispersal is important for developing conservation and management strategies because it affects species resilience (Akçakaya et al. 2007). Not all populations are equal, with differing degrees of connectedness and productivity (Hanski 1998). Therefore, recruitment can be especially important for species at the edge of their range where conditions are more stressful, and populations must rely on immigration to sustain themselves. Furthermore, the environment can affect connectivity among populations by facilitating retention or advection and can contribute to how vulnerable a population—or set of populations—is to extinction (Tamburello et al. 2019).

Estuarine ecosystems connect freshwater and marine systems, where increased retention of food provides productive resources for fishes, birds, and marine mammals (Litvin and Weinstein 2003). Estuaries also function as critical rearing habitat for pelagic fishes that need a certain mix of salinity, temperature, oxygen, and suspended sediment loads to support early life stages (Childs et al. 2008; Froeschke and Stunz 2012; Dance and Rooker 2015). Robust populations of estuarine pelagic fishes are important because they support higher trophic levels and healthy ecosystems (Blaber and Blaber 1980; Hampel et al. 2005).

Many pelagic fish species disperse across estuaries, including Longfin Smelt, *Spirinchus thaleichthys* (Crispo and Hendry 2005). Longfin Smelt use estuaries from Alaska to central California for spawning and rearing, with potentially important population connectivity among estuaries (Moyle 2002). However, efforts to study this species have been limited to a landlocked population in Lake Washington, Washington (Chigbu 2000) and the southernmost population in the San Francisco Estuary (SFE), California (Moyle 2002). Despite the large distance between these two populations, they remain similar with a moderate degree of genetic isolation between them, suggesting potential population connectivity (Israel and May 2010). However, in 2012, the US Fish and Wildlife Service (USFWS) deemed the estuary population of Longfin Smelt as a distinct population segment from the nearest known breeding population 480 km north in Humboldt Bay and determined that southward migration to the estuary was unlikely to occur from more northern populations (Federal Register 2012; Sağlam et al. 2021).

Some adult Longfin Smelt from the estuary population exhibit anadromy, but the influence of this migratory behavior on recruitment success and population connectivity has yet to be determined (Rosenfield and Baxter 2007). Migration may support resilient populations through recruitment of larvae and via gene flow of adaptive traits. Dege and Brown (2003) proposed that one benefit of migration into the marine environment is relief from seasonably warm temperatures within the estuary. As such, the estuary population may be an important source of genetic diversity to more northern populations, which are adapted to cooler waters expected to warm with climate change (Federal Register 2012). Therefore, it is important to understand the potential for connectivity among Longfin Smelt populations along the California coast.

Fundamental to assessing potential connectivity is understanding distribution of spawning Longfin Smelt and subsequent habitat use of their progeny. Historical examination of occurrence in northern California estuaries by Garwood (2017) indicated that Longfin Smelt has been observed in estuaries between SFE and Humboldt Bay over several decades. However, its status and habitat associations in these coastal estuaries is unknown.

In the SFE, knowledge of Longfin Smelt spawning is limited to where adults spawn in December through February. Eggs are attached to rocks, aquatic vegetation, and sand (Moyle 2002; Wang

1986). Until recently, suitable salinity and habitat for spawning was thought to occur only in the upper estuary (Dege and Brown 2003; Hobbs et al. 2010; Merz et al. 2013), after which downstream flows transported early-stage, surface-oriented larvae to seaward regions of the estuary (Hieb and Baxter 1993; Moyle et al. 1995). As larvae develop (>10 mm), their distribution shifts to the center of channels and deeper in the water column, where they use vertical migration to maintain their position near the Low-Salinity Zone (LSZ) (Hieb and Baxter 1993; Bennett et al. 2002; Dege and Brown 2003). Recent discoveries of newly hatched larvae in seaward regions in years with high outflow suggest novel variation in migration distance, suitable habitat, and interactions with waterflow that deserve further examination (Grimaldo et al. 2020; Lewis et al. 2020).

The primary objective of this study was to conduct a systematic survey to document Longfin Smelt larvae presence during the spawning season in coastal estuaries extending north of the SFE to the Oregon border. We also evaluated how habitat features (e.g., salinity, temperature, dissolved oxygen, turbidity) were associated with Longfin Smelt larvae presence across 2 years.

MATERIALS AND METHODS

Study Area

The study area extended from the Oregon border south to the SFE (Figure 1). Estuaries along this coastline are characterized by river-dominated systems, bar-built lagoons, or embayments. Our surveys did not include other smaller coastal tributaries because of lack of accessibility and safety concerns with high river stage and flows where access may have been possible. Grimaldo et al. (2017) discovered high densities of newly hatched larvae in large tidal sloughs and open-water shoals in the SFE, so we focused on sampling similar habitats. Our surveys did not include other smaller coastal tributaries because of lack of accessibility and safety concerns with high river stage and flows where access may have been possible. Lake Earl is a lagoon that episodically opens to the ocean during winter. The Klamath River drains a large watershed that extends into central Oregon, and the lower estuary contains a dynamic network of islands and sloughs (Lowe et al. 2018). The Mad River has relatively low flow because of its smaller watershed. Land-use changes on the coastal plain surrounding the lower Mad River and the risk of flooding prompted the channel to be straightened and the banks armored (Stillwater Sciences 2010). Humboldt Bay is the second largest estuary in California and receives freshwater inputs from several creeks including Freshwater Creek that drains into Freshwater Slough and Eureka Slough (Watershed Professionals Network 2003), hereafter referred to collectively as Eureka Slough. The Eel River is one of the largest rivers in California and contains two sub-basins near its mouth including tidal sloughs and alluvial floodplains (CDFG 2010). South of Cape Mendocino, Pudding Creek and the Noyo, Big, Albion, Navarro, and Gualala rivers have relatively small watersheds with more seasonal flow (Downie et al. 2006). Only 96 km north of the San Francisco Estuary is the Russian River, which drains a relatively large watershed and seasonally closes off to the ocean when flows are reduced in spring, summer, and fall (Goodwin et al. 1994). Breaching of the Russian River to the ocean during winter may occur naturally through high flows, or artificially when flood conditions develop (Goodwin et al. 1994). Located just north of the SFE, Tomales Bay is a tectonic estuary that hosts a variety of habitats including intertidal habitats as well as salt marshes and is supplied freshwater by two relatively small watersheds that drain into its tributaries: Lagunitas Creek and Walker Creek (Tomales Bay Watershed Council 2007).

Study Design and Data Collection

We conducted multiple (3 to 13) sampling tows at each of 16 estuaries (Table 1) nearly every 2 weeks from January to April of 2019 (Table 2). In 2020, we followed the same sampling pattern from January to March and once in May. In some cases, it was not feasible to access every estuary, resulting in a slightly uneven sampling effort (Table 1). We timed sampling to coincide with high tides in daylight hours.

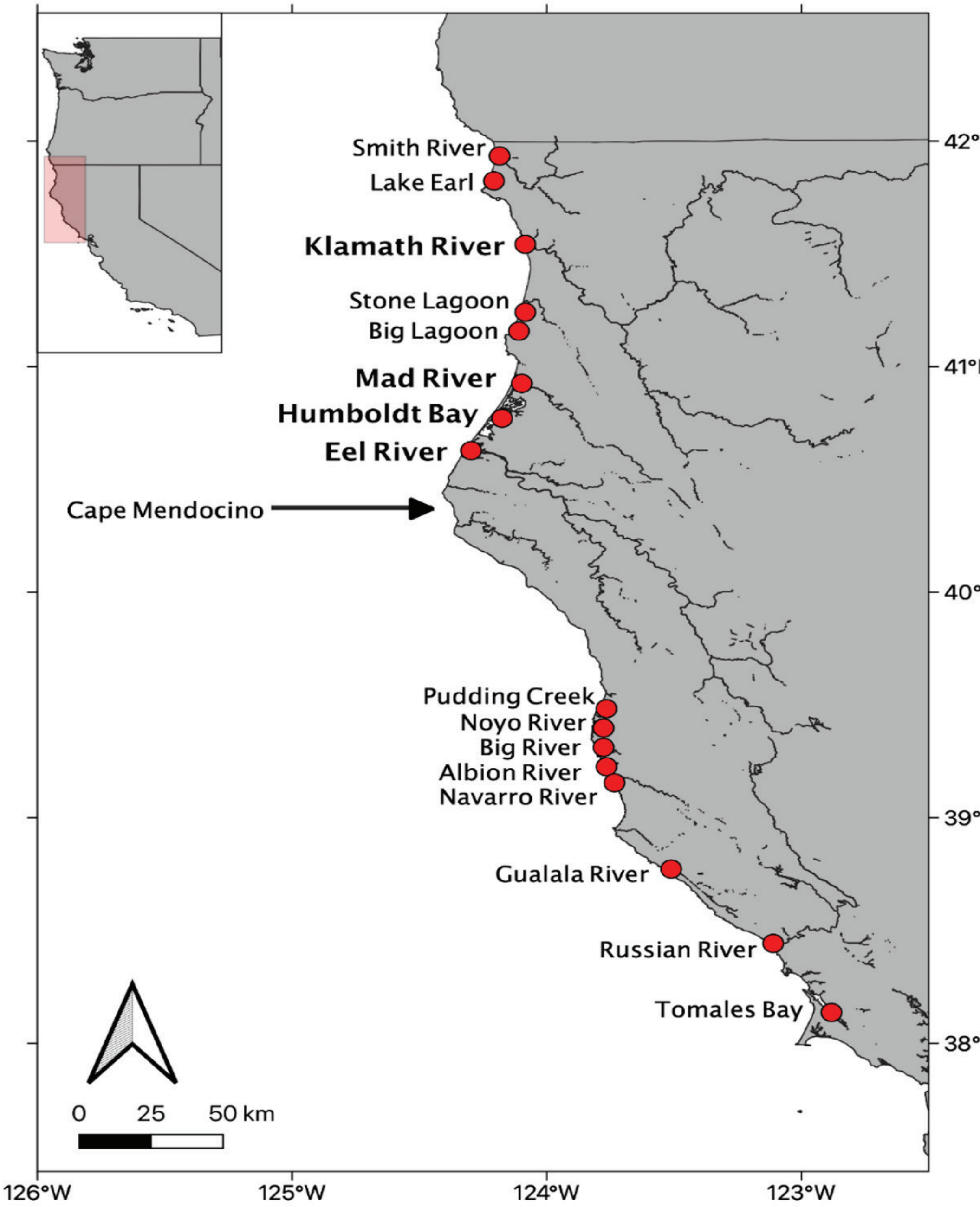

Figure 1 Map of coastal estuaries sampled in 2019 and 2020 along the northern California coast. The *red-shaded* region in the inset indicates the location of the study area along the western US coast. Cape Mendocino is indicated with the *arrow.* Names *in bold* indicate estuaries where larval Longfin Smelt were present.

Table 1 Summary of sample effort and Longfin Smelt collection in each estuary in 2019 and 2020

Year	Estuary	Number of Tows	Count of Longfin Smelt	Volume sampled (m^3)
2019	Smith River	7	0	1,166
	Lake Earl	11	0	1,653
	Klamath River	14	0	749
	Stone Lagoon	7	0	1,026
	Big Lagoon	14	0	2,736
	Mad River	7	0	804
	Eureka Slough, Humboldt Bay	18	61	3,437
	Field’s Landing, Humboldt Bay	0	0	0
	Eel River	23	2	2,708
	Mad River Slough, Humboldt Bay	33	0	5,685
	Pudding Creek	3	0	12
	Noyo River	14	0	2,685
	Big River	0	0	0
	Albion River	25	0	3,594
	Navarro River	13	0	1,837
	Gualala River	1	0	8
	Russian River	22	0	3,186
	Tomales Bay	24	0	2,915
2020	Smith River	3	0	398
	Lake Earl	3	0	429
	Klamath River	15	1	2,172
	Stone Lagoon	0	0	0
	Big Lagoon	0	0	0
	Mad River	11	1	1,079
	Eureka Slough, Humboldt Bay	34	65	6,098
	Field’s Landing, Humboldt Bay	16	0	2,235
	Eel River	55	638	8,621
	Mad River Slough, Humboldt Bay	34	0	4,857
	Pudding Creek	0	0	0
	Noyo River	11	0	1,310
	Big River	13	0	1,777
	Albion River	8	0	947
	Navarro River	4	0	583
	Gualala River	0	0	0
	Russian River	23	0	3,766
	Tomales Bay	23	0	2,343

Table 2 2019 and 2020 field survey date range

Survey	2019	2020
#1	1/21/2019–1/24/2019	1/13/2020–1/17/2020
#2	2/04/2019–2/8/2019	1/27/2020–1/30/2020
#3	2/18/2019–2/22/2019	2/10/2020–2/14/2020
#4	3/18/2019–3/22/2019	2/23/2020–3/27/2020
#5	4/07/2019–4/12/2019	3/09/2020–3/13/2020
#6		5/15/2020–5/18/2020

We sampled ichthyoplankton using a 75-cm-diameter ring net (0.44 m^2) with a mesh size of 505-µm, towed from a post mounted on the stern of a motorboat. Transects were performed in a serpentine fashion to reduce propellor turbulence into the mouth of the net. Tow duration was targeted to last for 5 minutes and depended on depth to prevent running aground or suspended sediment loads that tended to clog the net. The net was always towed at the surface, and additional sub-surface tows were conducted when depths exceeded 1.5 m by attaching a weight (1.4 kg) to the bridle of the net. A flowmeter (General Oceanics model 2030R, Miami, Florida, USA) was suspended across the center of the mouth of the net to estimate the volume of water filtered through the net. At the completion of each tow, the net was quickly raised vertically out of the water one or more times to ensure that all material was flushed into the cod end. Contents of the cod end were placed in a jar and fixed with a preservative for processing at the laboratory. Samples heavy with sediment or detritus were fixed with formaldehyde, otherwise they were fixed with ethanol. At the laboratory, larval fish were identified to the lowest taxonomic unit, assigned to a larval stage as differentiated by characteristics, measured to the nearest millimeter, and enumerated.

Coinciding with each sampling tow, environmental conditions of salinity (ppt), temperature (°C), dissolved oxygen (mg L^{-1}), and turbidity (NTU) were measured with a hand-held multi-parameter sonde (EXO2, YSI Inc., Yellow Springs, Ohio, USA). Depth (m) was measured at the start and end of each tow using a commercially available sonar (Garmin Ltd., Olathe, Kansas, USA) affixed to the stern of the boat. River discharge corresponding to each tow date (cubic meters per second, m^3s^{-1}) was obtained from the US Geological Survey database (USGS Surface-Water Historical Instantaneous Data for the Nation, *https://waterdata.usgs.gov/nwis/sw*) for the Smith, Klamath, Mad, Eel, Noyo, and Russian rivers.

Data Analysis

We assessed the influence of environmental variables on the presence of larval Longfin Smelt with a logit-linked binomial generalized linear model (Venables and Ripley 2002) using R statistical software (R Core Team 2021). Salinity, temperature, turbidity, and dissolved oxygen were included as continuous variables, and year was used as a categorical variable in the development of the model. A full model selection scheme evaluated each potential combination of covariates, with the most parsimonious model identified by the corrected Akaike's Information Criterion (AICc). Volume of the sample was included as an offset as a structural predictor to account for variable sampling effort. The relationships of the selected environmental factors with Longfin Smelt larvae are shown separately as plots of response curves.

RESULTS

Longfin Smelt were the fifth most abundant larval fish captured in our surveys out of 34 total taxa (Figure 2, Figure A1). Longfin Smelt larvae were detected in three of five surveys in 2019, and in five out of the six surveys in 2020 (Figure 2). We detected larval Longfin Smelt in two estuaries (Humboldt Bay and Eel River) in 2019 and 2020, and additionally in the Mad River and Klamath River in 2020. Densities of Longfin Smelt larvae were also greater in 2020 than in 2019 (Table 1). Total lengths of Longfin Smelt larvae were centered between 6 and 8 mm (Figure 3). In Humboldt Bay, the extent of larval smelt was limited to the Eureka Slough. In the Eel River, detections of Longfin Smelt larvae occurred in the mainstem and McNulty Slough and—to a limited extent—Salt River (Figure 2). Single detections at Klamath River and Mad River in 2020 were both near the mouth of the estuaries (Figure 2).

Water flow varied between sampling years: 2019 was wetter with higher river flows compared to 2020. Peak flows for the Eel River were 7.70×10^3 m^3s^{-1} and 1.32×10^3 m^3s^{-1} in 2019 and 2020, respectively (Figure 4). Klamath River had peak flows of 4.41×10^3 m^3s^{-1} in 2019 and 2.50×10^3 m^3s^{-1} in 2020. The Mad River had a

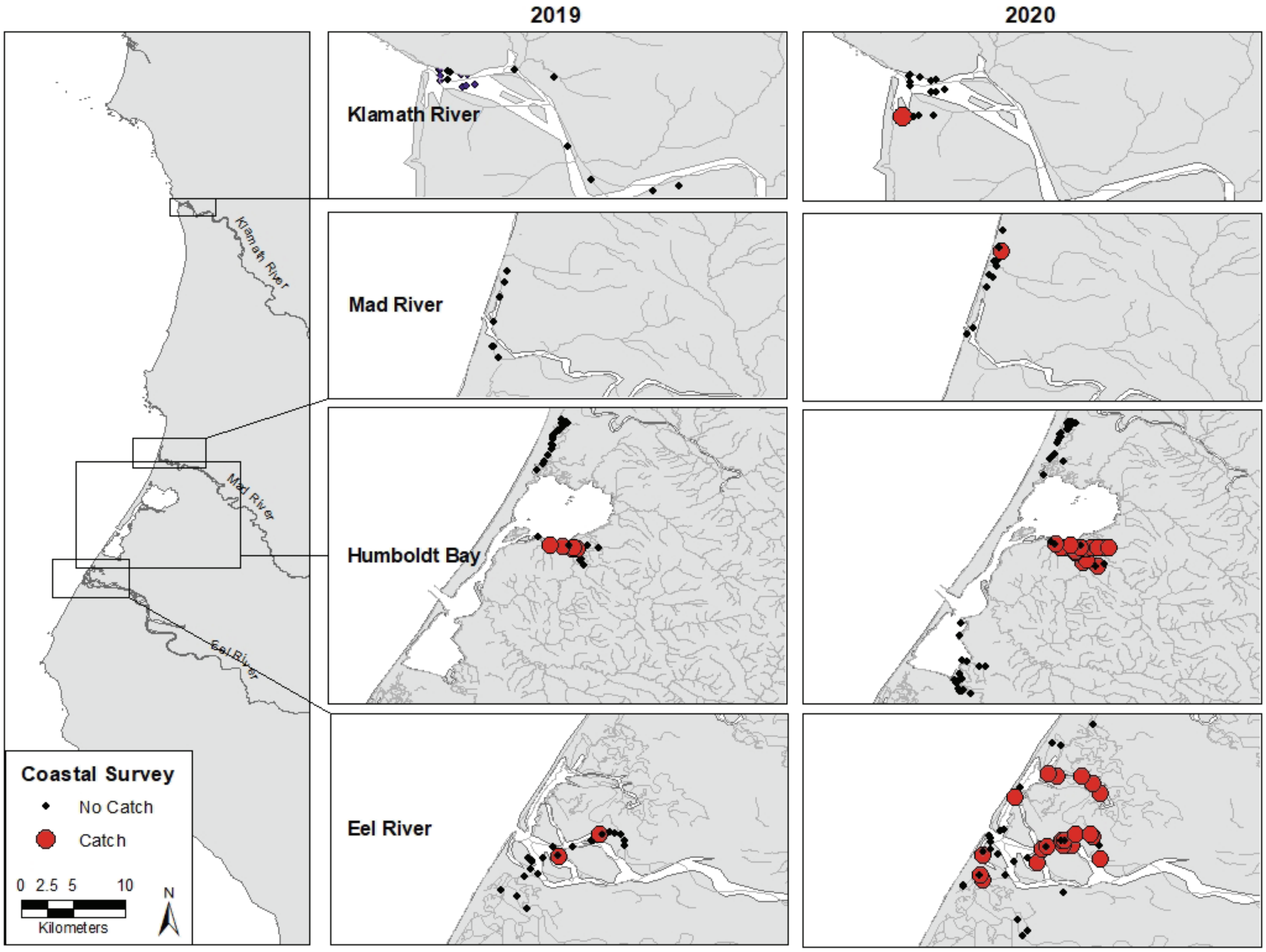

Figure 2 Positive detections of Longfin Smelt larvae were only detected in 4 of 16 estuaries sampled north of the San Francisco Estuary. The *left panel* is a reference map with *boxes* and *leader lines* corresponding to maps on the right for surveys conducted in 2019 and 2020, shown in the second and third columns, respectively. *Small black circles* denote sampling locations with no detections, and *large red circles* denote sampling locations with one or more positive detections. *Gray lines* represent tributaries to the estuaries.

peak flow in 2019 three times greater than in 2020, whereas the Noyo and Russian rivers had an-order-of-magnitude-greater peak flows in 2019.

The best fit model explaining Longfin Smelt larvae presence included salinity, turbidity, and year and explained 37% of the null deviance (Table 4; AICc = 194.7, df = 3). Turbidity had the largest impact on larvae catch probability with more larvae caught with increased turbidity ($z = 6.41$, $p < 0.05$, Table 5, Figures 5 and 6), while larvae catch probabilities decreased with salinity ($z = -2.76$, $p < 0.05$). Longfin Smelt catch was more likely in the 2020 sampling season than in 2019 ($z = 6.07$, $p < 0.05$). There was a 15% chance of catching Longfin Smelt in 2020 compared to 2% in 2019.

DISCUSSION

In this study, we examined distribution and habitat associations of larval Longfin Smelt in 16 estuaries along the Pacific coast that historically contained them, but we detected larvae only in estuaries north of Cape Mendocino, where shallow tidal wetlands and sloughs likely promote larvae retention. Within these estuaries, salinity and turbidity most strongly influenced

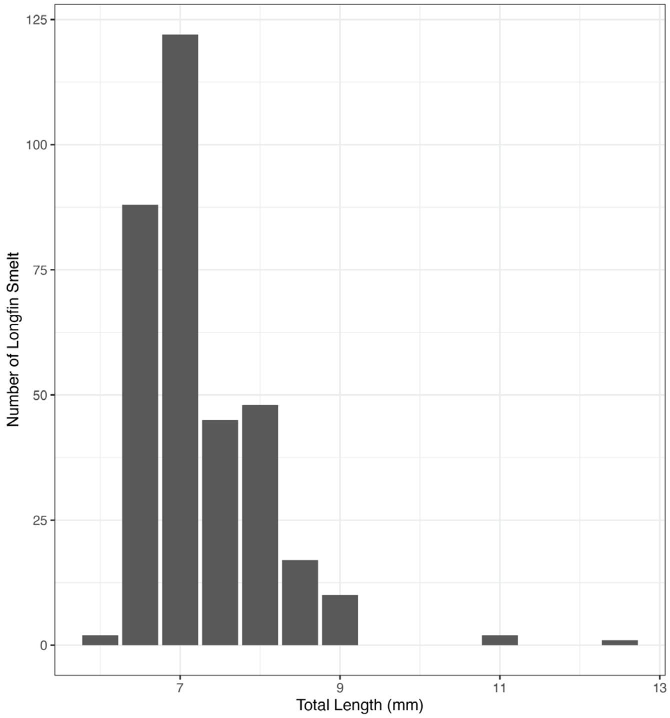

Figure 3 Histogram of total length (mm) of larval Longfin Smelt captured during both sampling seasons

the likelihood of larval presence, increasing with turbidity and decreasing with salinity—conditions that are typical of higher freshwater outflow. Larvae appear to need low-salinity water to rear. Laboratory studies observed elevated stress associated with higher salinities (Hasenbein et al. 2013). This is also consistent with field observations from the SFE (Grimaldo et al. 2017, 2020; Lewis et al. 2020). Those studies also observed newly hatched larvae in seaward regions, suggesting that either rearing can occur in salinities up to 12 or that spawning occurred in local tributaries. However, in the SFE, brackish water (salinities 0.5 to 5.0) also extends 50 to 90 km inland, providing larvae with a buffer from the marine environment (Kimmerer et al. 2014). In contrast, the smaller coastal estuaries we surveyed have narrower brackish transition zones closer to the river mouths.

There are two possible explanations for the increased association of larval presence with turbidity. The first is that foraging opportunities and predator avoidance improves in more turbid water (Hasenbein et al. 2013). Turbid water can increase visual contrast and facilitate prey capture (Utne–Palm 2002). Turbidity can also

Table 3 Summary statistics of environmental covariates from 2019 and 2020

Year	Parameter	Units	Minimum	Maximum	Mean	SD
2019	Water temperature	° C	5.99	15.96	10.43	2.39
	Conductivity	μS cm^{-1}	8.7	318310	13772	24740
	Turbidity	NTU	0.00	190.76	25.81	29.39
	pH	pH	6.89	9.04	7.70	0.36
	Salinity	ppt	0.04	40.23	7.56	9.29
	Dissolved oxygen	mg L^{-1}	7.27	13.86	10.51	1.50
	Chlorophyll *a*	μg L^{-1}	0.00	27.53	2.48	4.64
	Secchi depth	m^3	9	150	53	36
2020	Water temperature	° C	6.63	20.61	11.44	3.18
	Conductivity	μS cm^{-1}	72.8	46646	21947	17031
	Turbidity	NTU	0.00	72.55	9.76	17.54
	pH	pH	6.82	9.00	7.88	0.36
	Salinity	ppt	0.03	30.13	13.79	10.91
	Dissolved oxygen	mg L^{-1}	5.22	27.43	9.99	1.96
	Chlorophyll *a*	μg L^{-1}	0.00	15.98	0.90	2.12
	Secchi depth	m^3	15	300	82	69

Table 4 Model selection for predicting the likelihood of Longfin Smelt presence. The top four models all included the parameters in the most parsimonious model (lowest AICc).

Covariates	AICc	df	Chi Square	Proportion of deviance explained
Salinity + Turbidity + Year	194.70	3	110.87	0.373
Salinity + Turbidity + Water_Temp + Year	195.73	4	111.89	0.376
DO + Salinity + Turbidity + Year	196.73	4	110.89	0.373
DO + Salinity + Turbidity + Water_Temp + Year [a]	197.24	5	112.43	0.378
Turbidity + Water_Temp + Year	199.57	3	106.00	0.356

a. Indicates the full model.

Table 5 Model results predicting likelihood of Longfin Smelt presence by year and by environmental variables. Salinity, turbidity, and year all predicted capture probability ($p < 0.05$)

Parameter	Estimate	Standard error	z value	P value
(Intercept)	−10.2	0.686	−14.9	< 2e−16
Salinity	−0.0655	0.0238	−2.76	0.00582
Turbidity	0.0462	0.00721	6.41	1.47E−10
Year 2020	3.63	0.598	6.07	1.25E-09

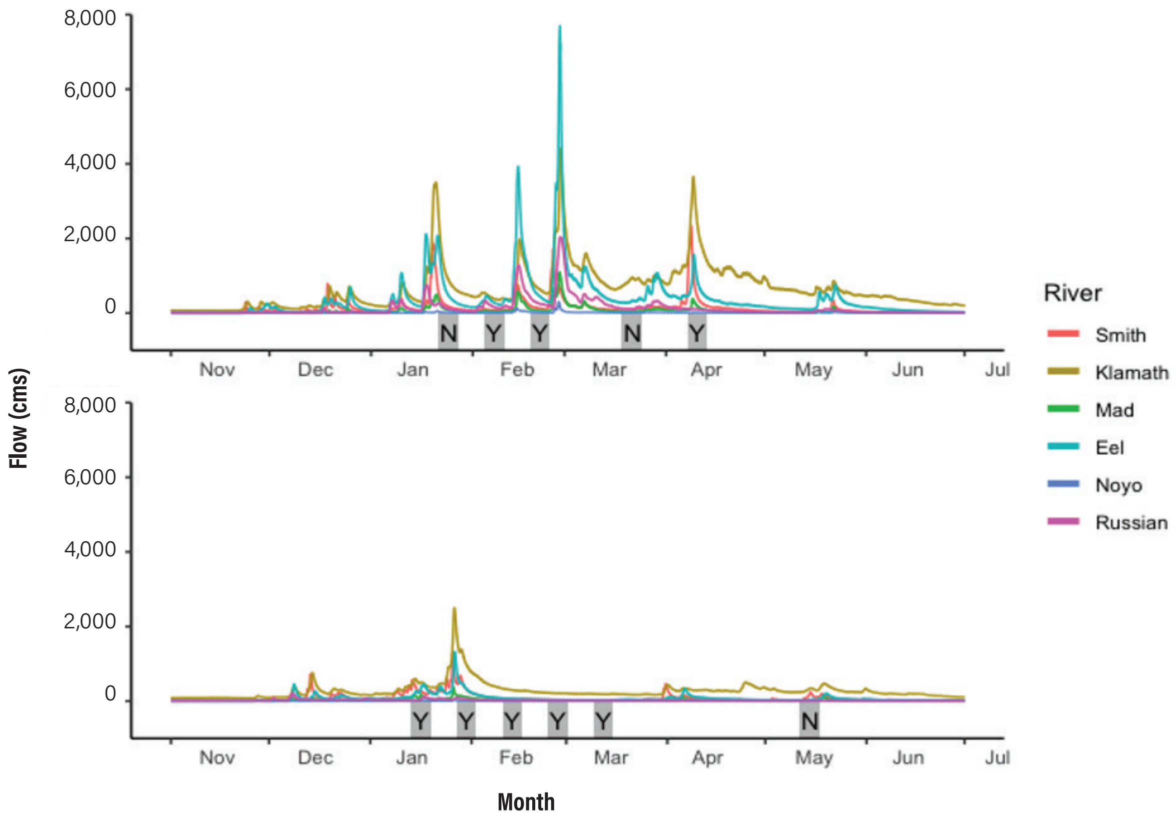

Figure 4 Flow rates ($m^3 s^{-1}$) of major rivers surveyed in 2019 (*top*) and 2020 (*bottom*). The *shaded regions* indicate the weeks when sampling was conducted. Presence or absence of larval Longfin Smelt for each sampling event are indicated by "Y" and "N," respectively.

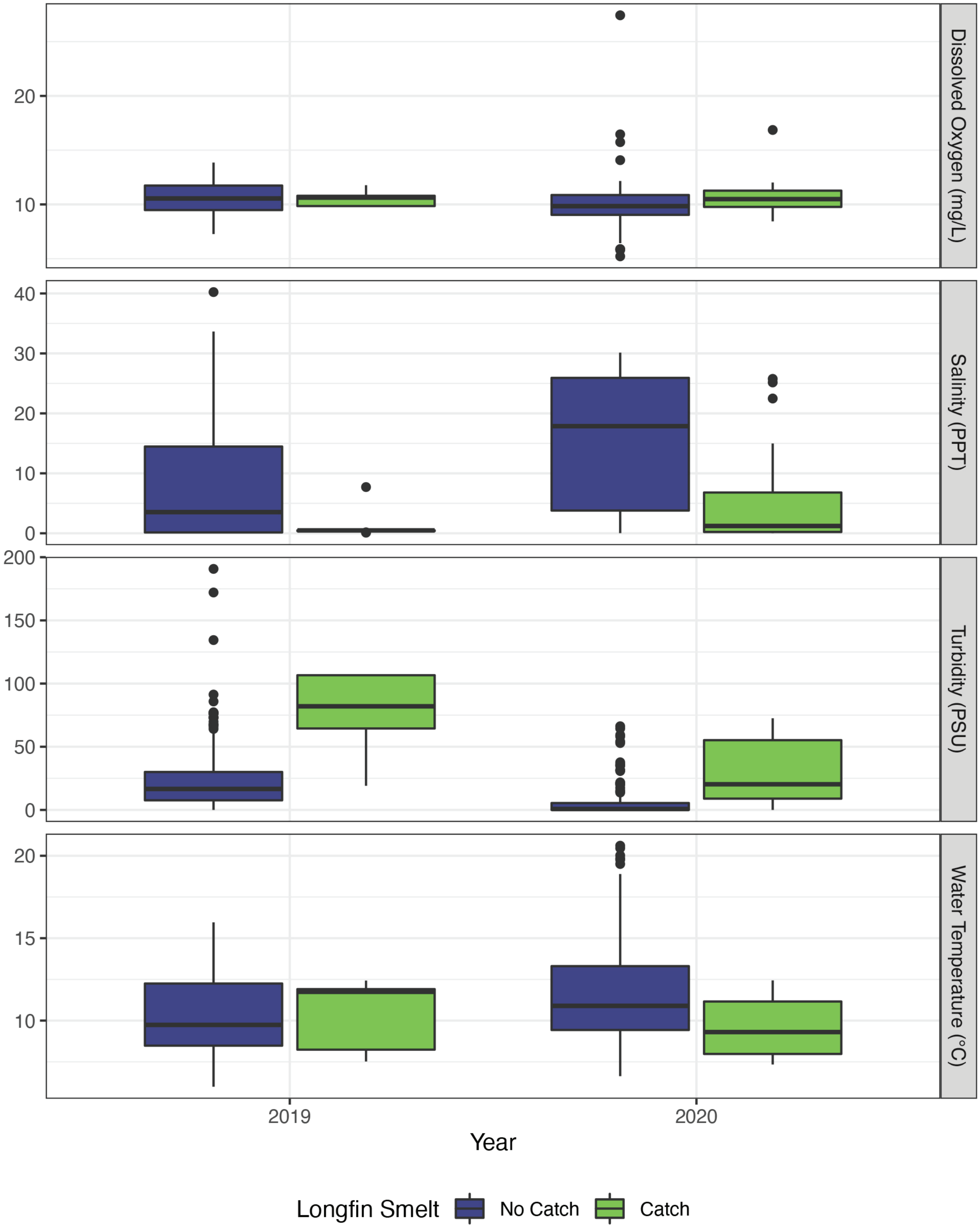

Figure 5 Box plots of presence of Longfin Smelt larvae associated with water quality variables from top to bottom: dissolved oxygen, salinity, turbidity, and water temperature

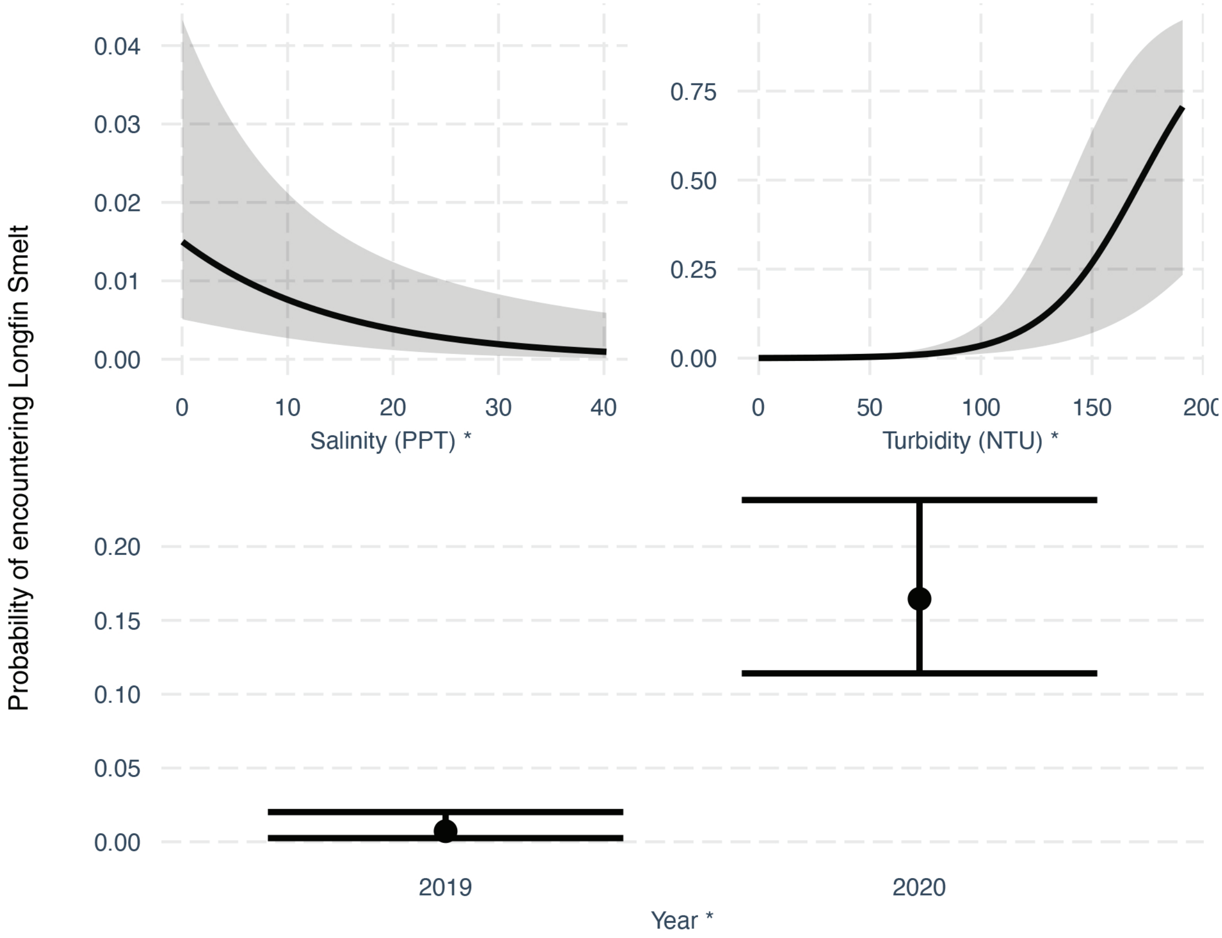

Figure 6 Relationships of covariates to the probability of encountering Longfin Smelt from the highest-ranked generalized linear model (Table 4), which included salinity, turbidity, and year as significant predictors (Table 5, $p < 0.05$). Longfin Smelt were more likely to be caught in 2020 than in 2019 (*bottom)*. Encounter probabilities decreased with salinity and increased with turbidity (*top left* and *right*, respectively).

provide visual cover from other piscivorous predators, thereby decreasing predation mortality (De Robertis et al. 2003). The second possibility is that fish are less able to detect and avoid the net, but net avoidance is more likely to be a factor with less planktonic, larger-size classes than it is with larvae observed in this study (Jůza et al. 2013; Thayer et al. 1983).

High flows may have moved the preferred water-quality range further downstream out of the sampling range of this study, or transported larvae out of coastal estuaries, thereby reducing detectability (Strydom et al. 2002; Tolan 2008; Teodósio and Garel 2015). While high flows can shift the distribution of pelagic larvae seaward, increased freshwater outflow also supports successful spawning and recruitment correlating with year class strength (Dege and Brown 2003; Kimmerer et al. 2009; Nobriga and Rosenfield 2016; Grimaldo et al. 2020). Increased sampling across years with hydrologic variation warrants further support, particularly in smaller estuaries where high flows are more likely to contribute to missed larvae detections. For example, in the Russian River, which is the nearest system to the SFE with recent observations of Longfin Smelt (Garwood 2017), we failed to detect larvae in either 2019 or 2020. Turbid water can increase visual contrast and facilitate prey capture (Utne–Palm 2002).

The management implications from this study are three-fold. First, the distinct SFE Longfin Smelt population, which is threatened under the California Endangered Species Act, appears geographically far from other spawning populations that could serve as a meta-population source. Instead, most gene flow appears to be unidirectional and northward from the SFE (Sağlam et al. 2021). Second, Longfin Smelt populations in other estuaries along the California coast appear to have reduced abundance and distribution compared to historical surveys, which supports consideration of federal listing under the Endangered Species Act (Garwood 2017). Third, habitat associations for Longfin Smelt appear to be consistent with observations in the more heavily studied SFE. Shallow, tidal wetlands in large estuaries were important for rearing habitat, and characteristics associated with increased freshwater outflows (low salinity, high turbidity) were positively associated with probability of larvae presence.

CONCLUSIONS

In conclusion, occurrence of Longfin Smelt larvae in Humboldt Bay and the Eel River—and to a lesser extent in the Klamath and Mad rivers—suggests that the SFE population has limited connectivity with northern populations and supports a distinct population segment designation by the USFWS (2012). Without access to adequate nursery habitat to facilitate retention and feeding, Longfin Smelt adults may no longer spawn in small estuaries. However, historical observations dating back to 1889 included occasional detections of Longfin Smelt in more estuaries than we observed in this study (Garwood 2017). Either the recent population declines observed in the SFE (Hobbs et al. 2017) also occurred in other coastal estuaries, suggesting a geographic change in their demographics, or more effort is needed to improve detection efficiency. Climate projections of increased saltwater intrusion could compromise rearing habitat for Longfin Smelt (Cloern et al. 2011), particularly in smaller estuaries without much spatial buffering from freshwater tributaries. Tidal wetland restoration designed to provide nursery habitat that can retain larvae under climate change conditions will be important to recover this imperiled pelagic fish.

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