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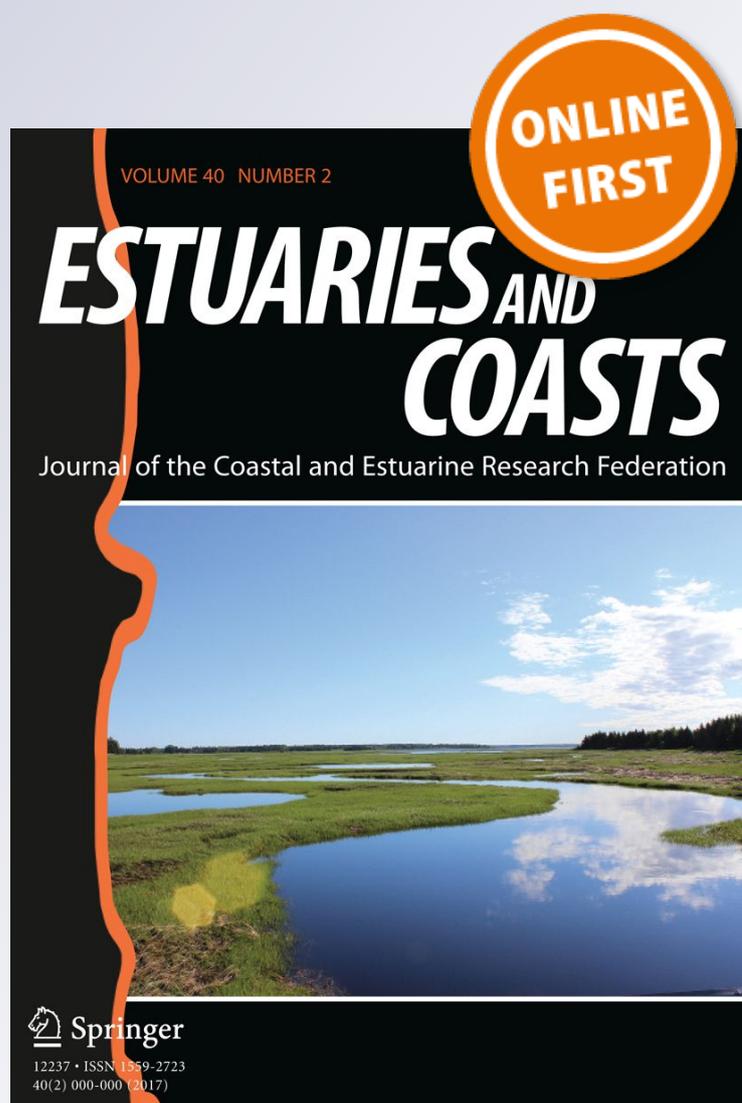
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Sampling Uncharted Waters: Examining Rearing Habitat of Larval Longfin Smelt (*Spirinchus thaleichthys*) in the Upper San Francisco Estuary

Lenny Grimaldo¹  · Fred Feyrer² · Jillian Burns¹ · Donna Maniscalco³

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Abstract The southern-most reproducing Longfin Smelt population occurs in the San Francisco Estuary, California, USA. Long-term monitoring of estuarine habitat for this species has generally only considered deep channels, with little known of the role shallow waters play in supporting their early life stage. To address the need for focused research on shallow-water habitat, a targeted study of Longfin Smelt larvae in littoral habitat was conducted to identify potential rearing habitats during 2013 and 2014. Our study objectives were to (1) determine if larval densities vary between littoral habitats (tidal slough vs. open-water shoal), (2) determine how larval densities in littoral habitats vary with physicochemical and biological attributes, (3) determine if larval densities vary between littoral habitats and long-term monitoring channel collections, and (4) determine what factors predict larval rearing distributions from the long-term monitoring channel collections. Larval densities did not vary between littoral habitats but they did vary between years. Water temperature, salinity, and chlorophyll *a* were found important in predicting larval densities in littoral habitats. Larval densities do not vary between littoral and channel surveys; however, the analysis

based on channel data suggests that Longfin Smelt are hatching and rearing in a much broader region and under higher salinities (~2–12 psu) than previously recognized. Results of this study indicate that conservation efforts should consider how freshwater flow, habitat, climate, and food webs interact as mechanisms that influence Longfin Smelt recruitment in estuarine environments.

Keywords San Francisco Estuary · Longfin Smelt · Tidal marsh · Larvae · Spawning · Restoration

Introduction

Management and conservation of estuarine species requires an understanding of the ecological processes that drive recruitment. For many estuarine fishes, early (pre-juvenile) life stages are important for determination of recruitment and year-class strength (e.g., Houde 1987; Pepin 1991; Leggett and Deblois 1994). Identification of habitats occupied by early life stages of fishes is foundational for examining and understanding processes that may drive recruitment variability. This is especially important at the geographic limits of a species' range, where environment-recruitment relationships are particularly strong (Myers 1998). The San Francisco Estuary, California, USA, is at the southern edge of the range for several imperiled fishes that are also of direct economic importance because of restrictions in water diversions to protect them (Sommer et al. 2007). The purpose of this study was to identify key rearing habitat for larvae of one of these species, Longfin Smelt *Spirinchus thaleichthys* in the San Francisco Estuary, California, USA, which represents the species' southern-most extant population.

Longfin Smelt are small (90–110 mm), schooling, pelagic fish and are found in estuarine and coastal waters along the

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Pacific Coast of North America. The Longfin Smelt population in the San Francisco Estuary is of particular management concern because it is listed as threatened under the California Endangered Species Act (ESA) and is considered warranted for listing under the federal ESA but currently precluded because of higher priority species. Yearly indices of Longfin Smelt abundance in the San Francisco Estuary have exhibited severe declines in abundance in the past decade (Sommer et al. 2007; Thomson et al. 2010), which may be attributable to changes in decreased freshwater outflow, increased water clarity, food web alterations, degraded physical habitat, shifts in habitat use, and catchability (Sommer et al. 2007; Kimmerer et al. 2009; Mac Nally et al. 2010; Thomson et al. 2010; Latour 2015). Longfin Smelt generally exhibit an anadromous life history strategy, although there are some landlocked populations (Chigbu and Sibley 1994). In the San Francisco Estuary, rearing and growth take place in coastal and estuarine habitats for 2–3 years before Longfin Smelt move landward to spawn at the end of their lifecycle (Rosenfield and Baxter 2007; Hobbs et al. 2010; Merz et al. 2013). In Lake Washington (WA), landlocked Longfin Smelt are known to spawn in shallow waters of river inlets during the spring (Moulton 1974). Specific attributes of spawning habitat remain unknown in the San Francisco Estuary.

Knowledge of habitats occupied by Longfin Smelt larvae is needed to inform water management operations, species conservation efforts, and habitat restoration projects in the San Francisco Estuary (Sommer et al. 2007; Grimaldo et al. 2009a, b; Cowin and Bonham 2013; Herbold et al. 2014). Much of the information on habitat occupied by Longfin Smelt larvae to date has come from data generated by monitoring programs that were designed for other species, or only in a small area of potential habitat they may occupy (Dege and Brown 2004; Merz et al. 2013). For example, the long-term monitoring programs do not currently target Longfin Smelt larvae in shallow waters (<2 m deep) or in tidal slough habitats, of which only very small amounts remain compared to historic conditions and which are targets for habitat restoration (Grimaldo et al. 2012; Herbold et al. 2014). In addition, the long-term monitoring stations are fixed in the upper region of the estuary (Fig. 1). Thus, while they can provide valuable information, these programs are limited in scope both geographically and with respect to potential habitat occupied by Longfin Smelt.

Previous research in the estuary has emphasized the importance of winter-spring freshwater outflow to support the Longfin Smelt population, in part, because their abundance in the fall increases by approximately 2 orders of magnitude between low and high outflows (Stevens and Miller 1983; Jassby et al. 1995; Rosenfield and Baxter 2007; Kimmerer et al. 2009; Nobriga and Rosenfield 2016). Despite this well-established relationship, mechanisms underlying why Longfin Smelt respond favorably to higher flow remain

unclear (Kimmerer et al. 2009). Recently, Hobbs et al. (2010) demonstrated with otolith microchemistry that successful recruits reared as larvae in low salinity habitat (~2–5 psu). Nevertheless, more work is needed on which habitats larvae use for hatching and rearing, and on effects of other environmental conditions that might help explain their positive response to high spring outflow.

To improve understanding of where Longfin Smelt larvae hatch and rear in the San Francisco Estuary, the specific goals of this study were twofold. First, a targeted littoral study in tidal slough and open-water shoal habitats of the upper region of the San Francisco Estuary was conducted to determine if Longfin Smelt larvae were present and rearing in these shallow habitats. The second goal of this study was to examine Longfin Smelt larvae data collected from the California Department of Fish and Wildlife (CDFW) Smelt Larval Survey to better understand how larval rearing habitats varied among a larger set of years. The CDFW survey is a long-term monitoring program designed for assessing relative densities and trends for Longfin Smelt larvae; sampling is focused in deep channels and some offshore shoal habitats in the upper San Francisco Estuary. Also, because the field study of littoral habitats and the long-term monitoring survey target different sampling depths, the two data sets provide an opportunity to examine the relative effectiveness of the long-term monitoring survey (hereafter referred to as the “channel survey”) to characterize Longfin Smelt rearing habitat in this region of the estuary.

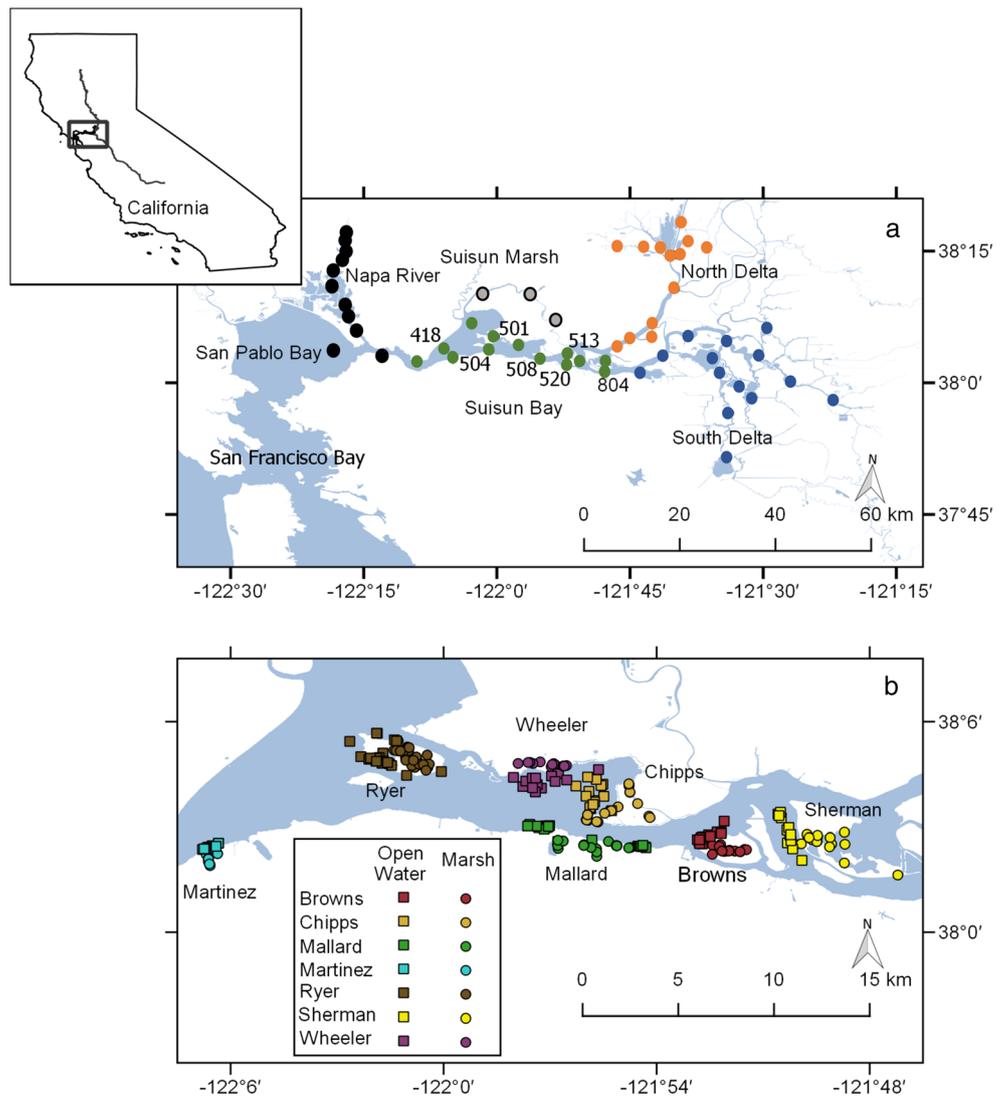
The primary questions of this study were the following: (1) Does density of Longfin Smelt larvae vary between tidal slough and adjacent open-water shoal habitat? (2) How does density of Longfin Smelt larvae in littoral habitats (tidal sloughs and open-water shoals) vary with physicochemical (e.g., water temperature and salinity) and biological (chlorophyll *a*) habitat features? (3) Does density of Longfin Smelt larvae vary between littoral habitats and channel survey collections? And (4) What factors predict annual Longfin Smelt larval hatching and rearing distributions from the channel survey?

Methods

Study Area

The San Francisco Estuary is located on the Pacific Coast of the United States in central California (Fig. 1). It has an open water surface area of approximately 1235 km² and a mean depth of 4.6 m. From its relatively narrow connection to the Pacific Ocean at the Golden Gate Bridge, the estuary opens up into several relatively large embayments that are strongly affected by seasonal and yearly variation in freshwater outflow from the watershed. The system predominantly becomes a

Fig. 1 Map of the San Francisco Estuary and study region. Longfin Smelt larvae examined for habitat evaluation included those collected during a long-term channel survey conducted by the California Department of Fish Wildlife (CDFW) and those collected during a targeted study of littoral habitats (**b**; tidal sloughs and open-water shoals) in 2013 and 2014. *Numbers* in panel **a** indicate channel stations used for comparison of Longfin Smelt larval densities with littoral collections from the same months and years (2013 and 2014). Panel **a** also includes regions of interest for the analysis and discussion (Suisun Bay = *green markers*, North Delta = *orange markers*, Suisun Marsh = *gray markers*, South Delta = *blue markers*, and Napa River = *black markers*). Panel **b** includes sites sampled during littoral collections



freshwater environment in the Sacramento-San Joaquin Delta, an expansive maze of tidal sloughs encapsulating dry and inundated tracts of land, which is formed at the confluence of the Sacramento and San Joaquin rivers, the two longest rivers in California.

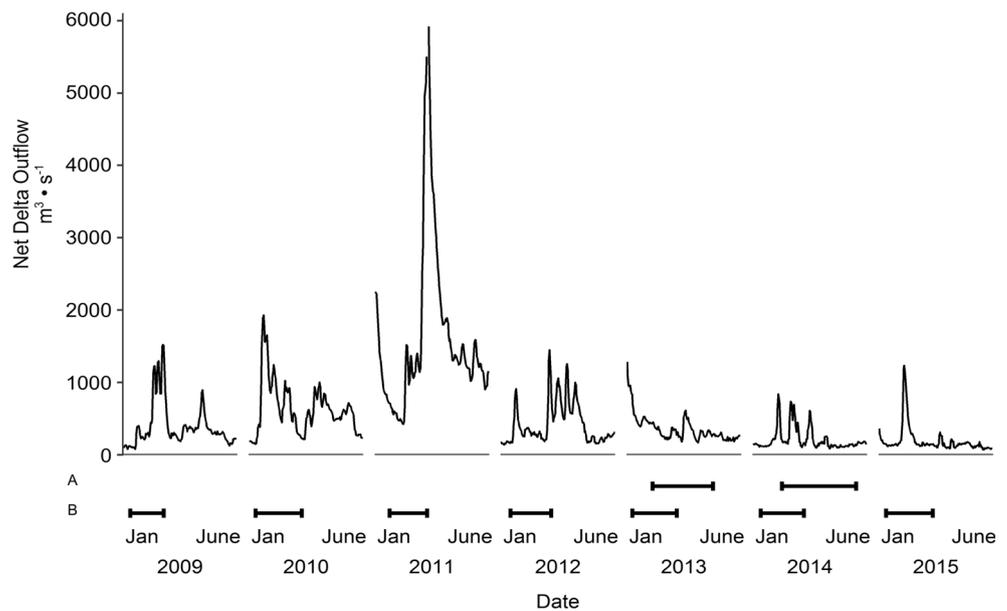
To address study questions about the value of littoral habitats to support Longfin Smelt larvae, field sampling was conducted in tidal sloughs and adjacent open-water shoals at seven locations in the upper San Francisco Estuary (Fig. 1). The shorelines of these locations were typically lined with tule *Schoenoplectus* spp. and common reed *Phragmites communis*. Substrates were a mixture of mud, peat, and sand. Sampling within marshes was done in tidal sloughs, approximately 3–10 m in width and 1–3 m in depth, which convey water and other material between the marsh and adjacent open water. Both terminal sloughs and sloughs that traversed completely through a marsh were sampled. Sampling in the open-water shoals (1–5 m depth) was conducted approximately 50–1000 m from the channel opening

to a tidal slough, depending on the location. Mixed semi-diurnal tides in this region of San Francisco Estuary range approximately 0.5–1.5 m.

Data Collection

Sampling for Longfin Smelt larvae in littoral habitats was conducted February–May in 2013 and February–June in 2014 under generally average to below average freshwater outflow for the San Francisco Estuary (Fig. 2; e.g., see Kimmerer 2002b). Sampling consisted of towing a 505- μ m-mesh net with a circular frame opening of 0.52 m² in diameter from the stern of a small motor boat during daylight. Prior to field collections, sampling sites were selected using a random stratified design for habitat and location with ArcMAP GIS software (ESRI, Redlands, CA, USA). In the field, waypoints for each site were found using GPS. Littoral areas at each of the seven locations were visited bimonthly each year.

Fig. 2 Annual freshwater flow into the San Francisco Estuary from 2009 to 2015. Periods when Longfin Smelt larvae were sampled for littoral (A) and channel (B) surveys are indicated in horizontal bars below graph



Sampling was typically conducted during flood tides to maximize access to littoral tidal sloughs. At each visit, a single tow was conducted horizontally through the water with the top of the net submerged just below the surface of the water for 10 min; because water depth was typically ≤ 3 m, oblique or bottom tows were impractical and unnecessary. A flow meter was attached to the opening of the net to estimate the volume of water (m^3) filtered by the net during a sample. In the field, sites were located using GPS. Samples were preserved in formalin. Longfin Smelt larvae present in each sample were counted and measured to the nearest millimeter total length (TL) in the laboratory. Water temperature ($^{\circ}\text{C}$), salinity (psu), turbidity (ntu), pH, dissolved oxygen concentration (DO, mg/L), and chlorophyll *a* concentration ($\mu\text{g/L}$, determined from fluorescence) were measured at the time of sampling with a handheld multiparameter sonde (YSI Inc., Yellow Springs, OH; Fig. 3). Chlorophyll *a* was considered an indicator of productivity and potential food supply. Due to probe issues, chlorophyll *a* was not measured in February and March 2014. Average water depth (m) for each sample was measured with a commercially available sonar unit affixed to the boat. Over 270 samples were collected in littoral habitat: 149 in tidal sloughs (86 in 2013 and 63 in 2014) and 123 in open-water shoals (68 in 2013 and 55 in 2014).

The channel survey uses a 505- μm -mesh net (0.37- m^2 mouth opening) mounted to a metal tube frame with skids to sample larvae at several stations throughout the upper San Francisco Estuary (Fig. 1). The net is towed for 10 min using a stepped oblique protocol (raised 1.2 m per step) so the entire water column is sampled. As with the shallow-water sampling described above, water volume sampled is based on a flow meter attached across the opening of the net. Water temperature ($^{\circ}\text{C}$), specific conductivity ($\mu\text{S/cm}$), and Secchi disk

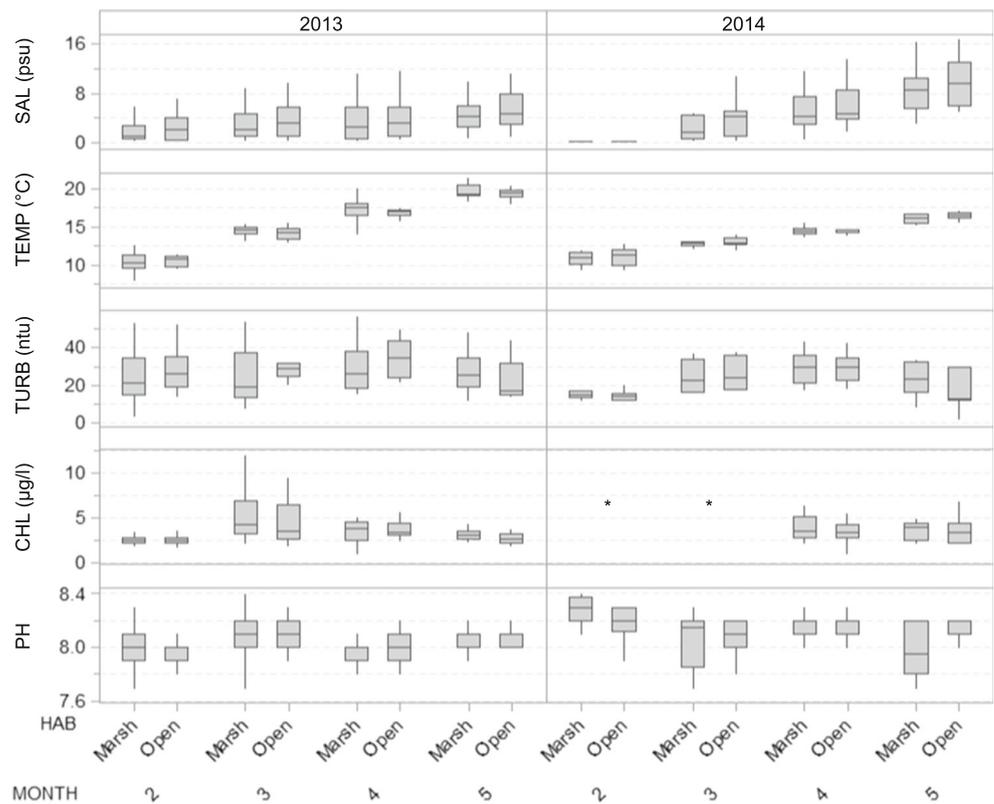
depth (cm) are measured concurrently with larval fish collections. The majority of the samples are taken in channel habitats; only 3 of the 44 stations sampled are less than 3 m deep. For data analyses, specific conductance was converted to salinity (psu) values using a regression derived from paired salinity and specific conductance data (Wagner et al. 2006). Over 1400 samples were collected during the channel survey from 2009 to 2015. Data from the channel survey were downloaded from the CDFW website, <ftp://ftp.dfg.ca.gov/Delta%20Smelt/>.

Data Analysis

To address the first question about whether Longfin Smelt larvae densities varied among littoral habitats, generalized linear modeling (GLM) appropriate for count data (O'Hara and Kotze 2010) was used to test for main and interaction effects of littoral type (tidal slough vs. open-water shoal) and year (2013 vs. 2014). The GLM was implemented with the *pscl* package (Zeileis et al. 2008; Jackman et al. 2015) in the R statistical computing environment (R Development Core Team 2014). A quasi-Poisson model was initially applied to the data but the φ value confirmed over-dispersion was present because of a high number of zeroes in the catch data, a common characteristic of count data collected in the field (Martin et al. 2005). Because of this, a negative binomial GLM was applied to the data as an appropriate statistical method to deal with the large number of zeroes.

To address the second question about how density of Longfin Smelt larvae in littoral habitat varies with key physical and biological habitat features, relationships between the density of Longfin Smelt larvae and candidate predictor variables were developed with a generalized additive model

Fig. 3 Box-whisker plot of environmental variables measured during littoral Longfin Smelt larvae collections in 2013 and 2014 (*asterisk* = not measured). The *central box* denotes 50% of the data values (with median indicated as the *horizontal line*) between the lower and upper quartiles (*whiskers*). All variables were included in the GAM analyses to determine factors that affect larval Longfin Smelt densities



(GAM). The GAM was implemented with the *mgcv* package in the R statistical computing environment (Wood 2006). GAMs are nonparametric extensions of general linear models useful for describing non-linear relationships between variables (Guisan et al. 2002). They are data-driven and do not presuppose a particular functional relationship between variables; smoothers characterize the empirical relationships between predictor and response variables (Wood 2006).

Predictor variables considered for inclusion in the GAM accounted for habitat type, environmental conditions present at sampling, and year (Table 1). Littoral habitats were tidal slough or open-water shoal. Environmental conditions summarized in Table 1 were measured at the time of sampling. The response variable in the GAM was the count of Longfin Smelt larvae. Sampling effort (volume, m³) was included as an offset.

The GAM was fit with a Poisson distribution and cubic regression spline smoothing functions, except that year and habitat were modeled as linear functions. The *k* parameter was set to 4 to prevent overfitting of the data (Wood 2006). A full model was built in a forward stepwise procedure by adding individual statistically significant predictor variables in a manner that maximized the cumulative explained deviance at each step. To compare models, Akaike Information Criteria (AIC) values were calculated, $AIC = 2 \times k - 2 \times \log(\text{Likelihood})$, where *k* = the number of parameters. AIC simultaneously

quantifies goodness of fit, as defined by the likelihood of the data, and model complexity (as measured by *k*), and models with the smallest AIC values are considered preferable. Relationships between significant predictor variables and the density of Longfin Smelt larvae are shown graphically in

Table 1 Description of predictor variables considered for inclusion in generalized additive models (GAMs) for predicting density of Longfin Smelt larvae in littoral and channel surveys. See text for details on timing of collections for continuous variables

Variable	Description
HAB	Habitat; binary variable indicating where samples were taken in littoral habitats (marsh, open-water shoal)
YEAR	Year; calendar year sample was collected
TEMP	Water temperature (°C)
SAL	Salinity (psu)
TURB	Turbidity (ntu)
DO	Dissolved oxygen concentration (mg/L)
CHL	Chlorophyll <i>a</i> florescence (µg/L)
PH	pH
DEP	Depth (m); average depth between start and end of sample
SEC	Secchi disk depth (cm)

separate plots depicting response curves of the relative influence of a predictor variable. Response curves are based on partial residuals, plotted on a log-scale, and standardized to an average value of 0 (Wood 2006).

To address the third question about whether Longfin Smelt larvae abundance varied between littoral habitats and channel survey collections, Longfin Smelt densities were analyzed from the two surveys for differences using the negative binomial GLM procedure outlined above. The effects of year and habitat, including their interaction, were tested for collections made during the same months (February and March) in 2013 and 2014. Because the primary focus of this question was to determine if densities differed between littoral habitats and channels, only collections from littoral habitats taken in depths less than or equal to 3.5 m were used for the analysis (94% of all tows). For the channel survey, only stations that were located adjacent to littoral collections and were greater than 3.5 m were used in the analysis (CDFW Stations = 418, 501, 504, 508, 513, 520, 801, 804; see Fig. 1).

To determine which factors affect variation in annual hatching and rearing distribution, densities of Longfin Smelt larvae from the channel survey (all stations during 2009 to 2015) were calculated and examined for each year for each of the major regions of the survey: (1) South Delta, (2) North Delta, (3) Suisun Bay, and (4) Suisun Marsh. In addition, the relative abundance of yolk-sac larvae from each region was calculated by extrapolating the catches to the volume of the region sampled. Napa River data were excluded from these analyses because collections in this area were initiated only in 2014 and not routinely sampled each month like the other stations. Examination of channel habitat length-frequency data indicated that most yolk-sac larvae range between 4 and 9 mm TL among years with abundance peaks at 6 and 7 mm TL (Fig. 4). This pattern of yolk-sac larvae is consistent with larval hatch sizes observed previously in the estuary (5 to 8 mm TL; Wang 2007) and consistent with sizes observed in littoral habitat (Fig. 4). Based on these data, analyses were constrained to all larvae in the survey ≤ 9 mm TL to better understand critical habitat and factors that affect their abundance within days of emergence. Because CDFW only measures a subsample (typically up to 50) of Longfin Smelt larvae collected in the channel survey (most fish in 2009 and 2010 were measured), the proportion of newly hatched larvae measured in the subsample was extrapolated to the total count in the sample. From these data, relationships between newly hatched larvae and environmental variables were also explored using a GAM with environmental variables (water temperature, salinity, water clarity) measured concurrently during the channel habitat surveys (Table 1). Similar to question 2, the GAMs for channel habitat data were fit using a Poisson distribution with cubic regression spline smoothing functions for environmental variables.

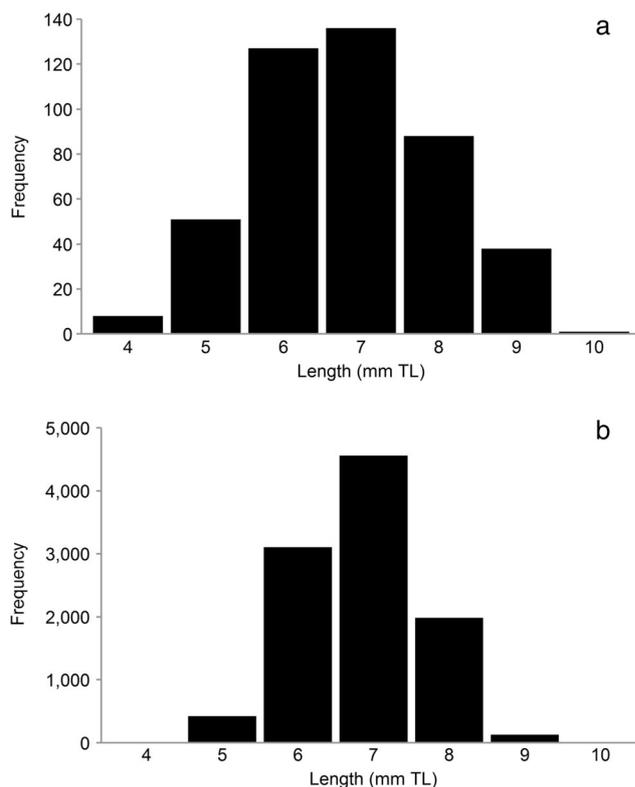


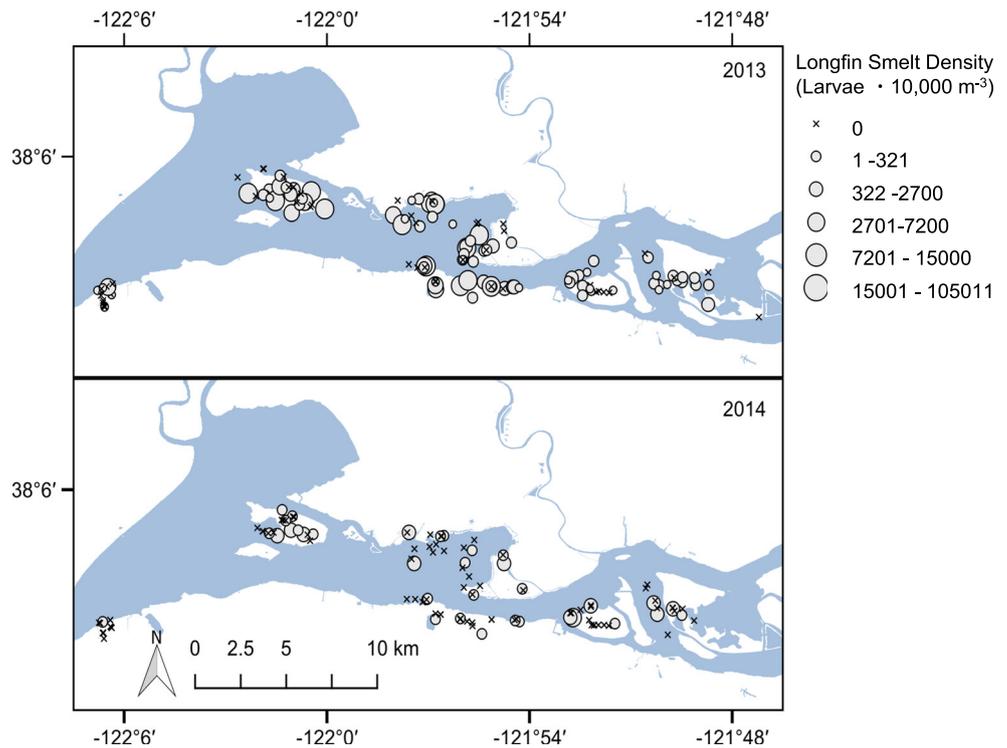
Fig. 4 Length-frequency plots of yolk-sac Longfin Smelt larvae collected during littoral (a) and channel surveys (b)

Results

Question 1. Do densities of larval Longfin Smelt differ between littoral habitats: tidal sloughs versus open-water shoals? A total of 11,562 Longfin Smelt larvae were collected in littoral samples. Catches were far higher in 2013 (11,354) than in 2014 (208; Fig. 5). The negative binomial GLM data indicated a significant effect of year ($P < 0.05$) but not of habitat ($P = 0.77$) or the year \times habitat type interaction ($P = 0.77$).

Question 2. How does density of Longfin Smelt larvae in littoral habitats vary with physicochemical and biological habitat features? The full GAM developed to describe the relationships between the density of Longfin Smelt larvae and the predictor variables explained 90.4% of the deviance in the data set (Table 2). The full model included all candidate predictor variables except dissolved oxygen, which was excluded because of collinearity with other variables. Although all variables were included in the best model, there were notable differences in the relative amount of deviance explained by each variable (Table 2). Deviance plots of partial responses for the continuous predictor variables (Fig. 6) showed that the density of Longfin Smelt larvae was negatively related to water temperature and positively related to chlorophyll *a*. Relationships to other continuous predictors were more variable. For salinity, density peaked between 3 and 4 psu and

Fig. 5 Density of Longfin Smelt larvae in the San Francisco Estuary in littoral habitats sampled in 2013 (*upper panel*) and 2014 (*lower panel*)



then gradually declined; the abrupt tail-end increase at high salinity appears to be driven by a single data point in which three individual Longfin Smelt larvae were collected in a sample with a salinity of 18 psu. These results suggest relatively strong effects of water temperature, year, salinity, and chlorophyll *a*, and relatively small effects of pH, turbidity, and habitat on the density of Longfin Smelt larvae in littoral habitat.

(3) Does density of Longfin Smelt larvae vary between littoral habitats (tidal slough and open-water shoals) and channel survey collections? Mean depths used to represent shallow littoral collections in 2013 and 2014 were 2.0 m (± 0.67 SD) and 2.26 m (± 0.59 SD), respectively. Mean depths sampled at comparison channel stations in 2013 and 2014

were 10.98 m (± 3.78 SD) and 11.40 m (± 2.97 SD), respectively. Based on the negative binomial GLM, Longfin Smelt larval density was significantly greater in 2013 than 2014 ($P < 0.01$), but there was no significant difference between habitats ($P = 0.31$), with this pattern consistent in both years (year \times habitat, $P = 0.31$).

(4) What factors predict annual Longfin Smelt larval hatching and rearing distributions from the long-term monitoring channel survey? Over 71,000 Longfin Smelt larvae 9 mm TL or less were collected (based on subsample length expansions described above) during the channel survey from 2009 to 2015. Overall, larval densities in the channel survey varied by nearly 2 orders of magnitude over the time series

Table 2 Deviance explained (%), cumulative deviance (%), AIC, and Δ AIC values of GAMs predicting the density of Longfin Smelt larvae sampled in littoral habitats. Variables are defined in Table 1

Model	Deviance (%)	Cumulative deviance (%)	AIC	Δ AIC
s(TEMP)		28.4	34,178	29,664
s(TEMP) + YEAR	29.1	57.5	20,533	16,019
s(TEMP) + YEAR + s(SAL)	18.9	76.4	11,660	7146
s(TEMP) + YEAR + s(SAL) + s(CHL)	7.8	84.2	7345	2831
s(TEMP) + YEAR + s(SAL) + s(CHL) + s(PH)	4	88.2	5439	925
s(TEMP) + YEAR + s(SAL) + s(CHL) + s(PH) + s(TURB)	0.5	88.7	5224	710
s(TEMP) + YEAR + s(SAL) + s(CHL) + s(PH) + s(TURB) + s(DEP)	1.2	89.9	4708	194
s(TEMP) + YEAR + s(SAL) + s(CHL) + s(PH) + s(TURB) + s(DEP) + HAB	0.5	90.4	4514	

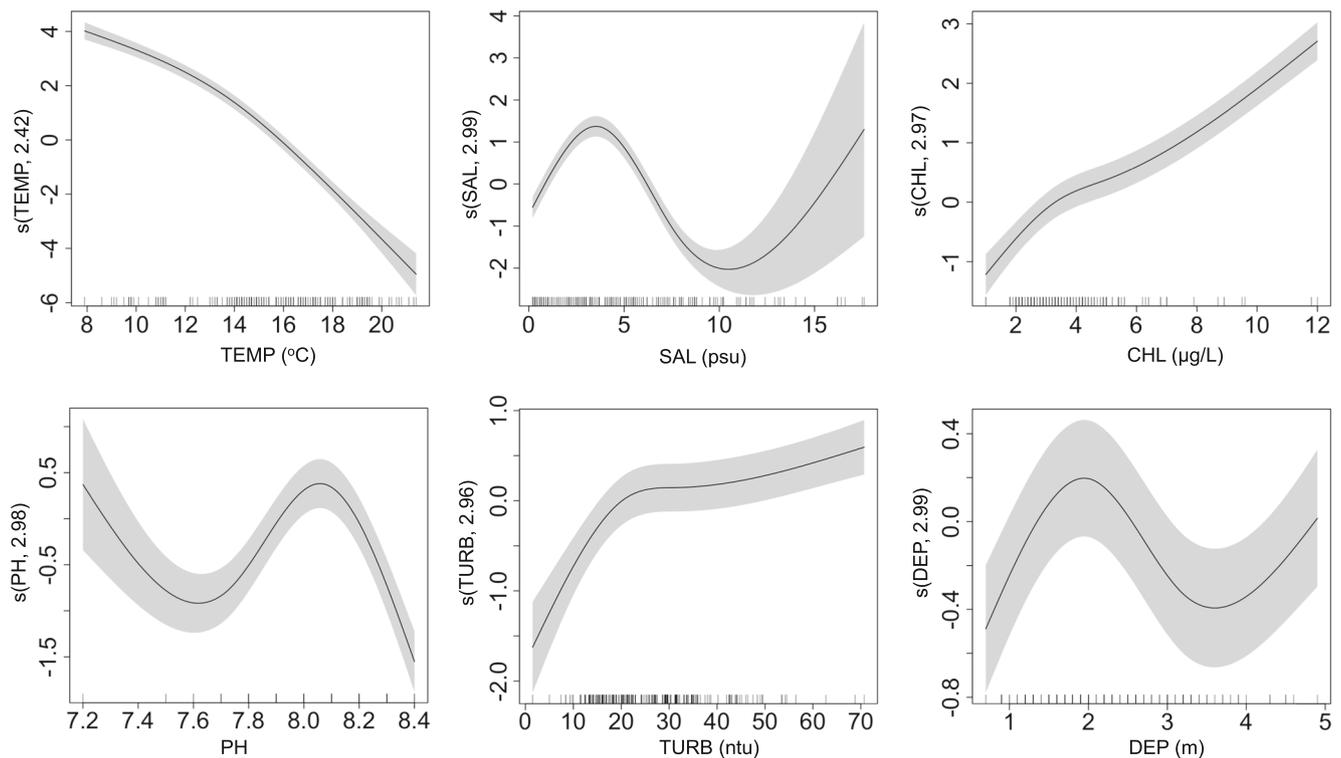


Fig. 6 Plots showing the relationships between the densities of Longfin Smelt larvae and continuous predictor variables. Plots are fitted smooths and 95% confidence intervals for partial responses from generalized

additive models. The y-axis units are centered on zero and the number in the label is the estimated degrees of freedom of the smooth. Variables are defined in Table 1

(Fig. 7); catches were highest in 2013. In all years, Suisun Bay supported the highest percentage of abundance per region. Relative abundance of larvae in the North Delta and South Delta was highest during 2009 and 2014. Annual variability in water quality conditions in channel habitat was most pronounced for salinity (Fig. 8). Water temperature increased from January to March each year and was slightly warmer during 2014 and 2015.

The full GAM developed to describe the relationships between the catch of Longfin Smelt larvae and the predictor variables explained 33.4% of the deviance in the data set and was the best model in terms of AIC (Table 3). The full model included all candidate predictor variables (water temperature, Secchi disk depth, water temperature, salinity, and year) but this was not much improvement from the full model without year. Salinity explained the highest percent of deviance (13.9%), followed by Secchi disk depth (11.1%). The contribution of depth, water temperature, and year in describing Longfin Smelt larvae densities was much smaller. Deviance plots of partial responses for the continuous predictor variables showed that larval Longfin Smelt catch was negatively related to salinity less than 2 psu and after approximately 12 psu (Fig. 9). The relationship between density and Secchi disk depth was largely negative with peak catch occurring near 50 cm. With respect to water temperature, peak

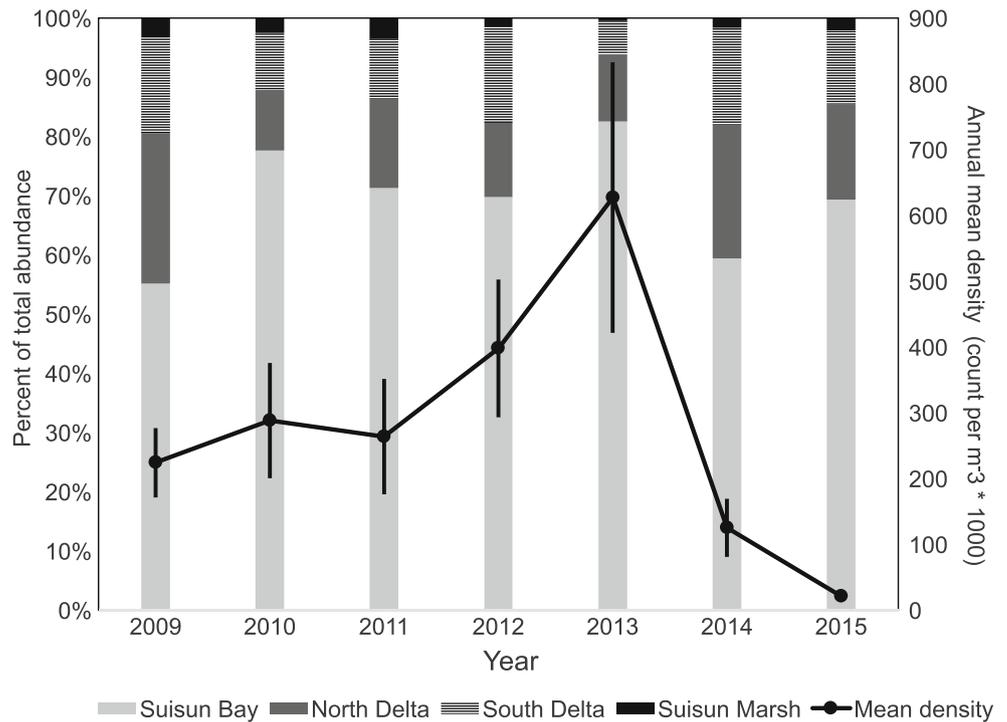
catches were observed between 8 and 12 °C. No obvious trend was detected for water depth.

Discussion

Characterizing habitat utilization and distribution shifts of estuarine organisms can provide important insights into the mechanisms that underlie growth, recruitment, and population responses to environmental conditions (Sakabe et al. 2011; Couillard et al. 2017). Until this study, Longfin Smelt spawning habitats in the San Francisco Estuary have remained unknown. High densities of newly hatched Longfin Smelt larvae observed in open-water shoals and tidal sloughs across such a broad area provide the best evidence to date that these habitats are areas where adults are spawning. This interpretation would be consistent with those of Moulton (1974) who found Longfin Smelt eggs in shallow river inlets of a landlocked population, and consistent with spawning habitats identified for other coastal osmerids (Martin and Swiderski 2001).

Another key observation of the present study was that newly hatched larvae were found in salinities up to approximately 12 psu, which is significant because it has generally been held that spawning was concentrated in upstream freshwater

Fig. 7 Percent total abundance of Longfin Smelt larvae (≤ 9 mm total length TL) by regions of management interest collected during long-term monitoring channel surveys and overall mean densities by year



regions (i.e., North Delta) of the estuary (Kimmerer et al. 2009; Hobbs et al. 2010) and that survival of small larvae (< 10 mm TL) was limited in salinities greater than 5 psu (Hobbs et al. 2010). Peak catches of Longfin Smelt larvae occurred between 2 and 4 psu in both littoral and channel survey data sets, respectively, but the channel survey data suggest a much more gradual relationship between catches and salinity up to 12 psu. Evidence for larvae surviving in salinities greater than ~ 5 psu has not been supported through otolith investigations of sub-adult and adult fish (Hobbs et al.

(2010); however, some sub-adult and adult fish had elevated salinity signatures (> 5 psu) at their otolith cores (representing the period from hatch to approximately 10 mm TL) which was attributed to maternal influences but environment influences could not be ruled out conclusively either.

Based on data from littoral collections, both physical and biological habitat features are important predictors of larval Longfin Smelt densities. The most influential variable, water temperature, characterizes the seasonality of when larvae are most abundant in the water column based upon the thermal

Fig. 8 Box-whisker plot (see Fig. 3 for details) of environmental variables measured during long-term monitoring channel surveys from 2009 to 2015 (see Fig. 1). Environmental variables are measured at each station during each month ($1 =$ January, $2 =$ February, and $3 =$ March) of the survey. Salinity (psu) values were converted from specific conductance ($\mu\text{s}/\text{cm}$); see text for details

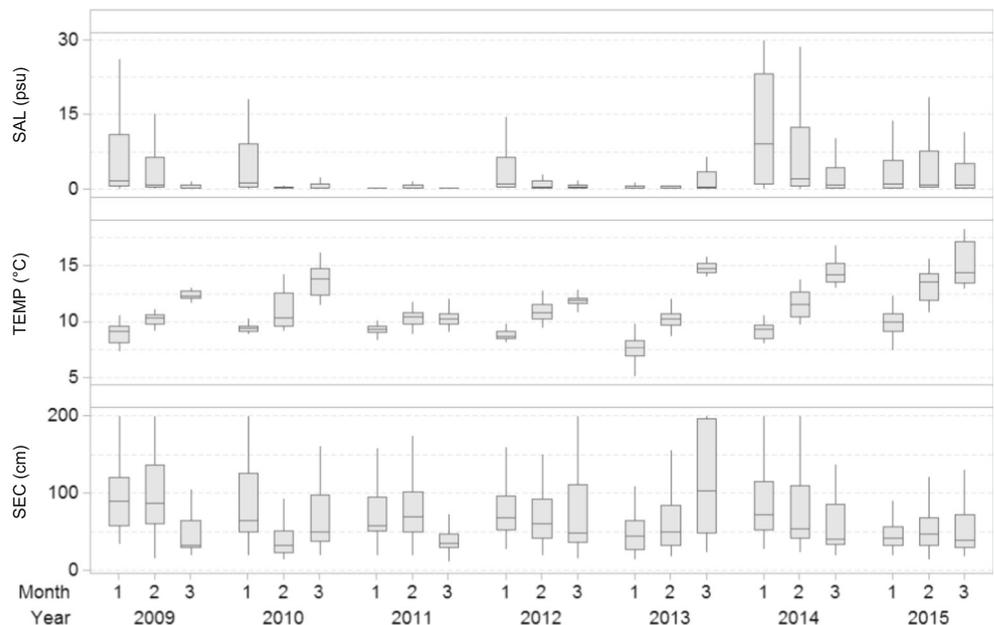


Table 3 Deviance explained (%), cumulative deviance (%), AIC, and Δ AIC values of GAMs predicting catch of newly hatched Longfin Smelt larvae (≤ 9 mm TL) in the California Department of Fish Wildlife channel surveys. Variables are defined in Table 1

Model	Deviance (%)	Cumulative deviance (%)	AIC	Δ AIC
s(SAL)		13.9	178,432	41,325
s(SAL) + s(SEC)	11.1	25.0	158,186	21,079
s(SAL) + s(SEC) + s(TEMP)	7.9	32.9	139,586	2479
s(SAL) + s(SEC) + s(TEMP) + s(DEP)	0.5	33.4	138,275	1168
s(SAL) + s(SEC) + s(TEMP) + s(DEP) + YEAR	0	33.4	137,107	

spawning window of adult Longfin Smelt ($\sim 8\text{--}14$ °C; Wang 2007). Interestingly, water temperatures in littoral samples during April and May of 2013 were at or greater than 16 °C, which is about the water temperature where catches show a negative response in the GAM (Fig. 6). In contrast, water temperatures during 2014 were mostly suitable from February to May yet larval Longfin Smelt densities were much lower in 2014 compared to 2013 (Fig. 5). This suggests that water temperature is an important variable that influenced the timing of larval Longfin Smelt emergence but perhaps had a lower influence on affecting fish densities between the 2 years. This does not mean that water temperature did not have an effect on differential survival rates and growth of larvae or is unimportant overall in affecting annual abundance of larvae in other years. In Middle St. Lawrence Estuary (Canada), annual variability in abundance of larval Atlantic Herring and Rainbow Smelt was directly linked to water temperatures and freshwater flow events that were thought to

provide optimal rearing conditions necessary to support metabolic demands of larvae (Couillard et al. 2017).

The timing of freshwater flow and salinity conditions can also influence spawning success of estuarine fishes (Sakabe et al. 2011; Couillard et al. 2017). For example, Sakabe et al. (2011) found that spawning success of estuarine Black Bream was directly related to the timing of freshwater flows that provided suitable salinity conditions for spawning; salinity was thought to serve as a cue for spawning activity and had direct effects to egg survival. The importance of salinity found in the GAMs of littoral and channel data sets may have implications for the availability of suitable rearing conditions and the timing of spawning in the San Francisco Estuary as well. For example, in 2013 and 2014, salinities measured in littoral samples during the February to May sampling period were mostly within the suitable range of Longfin Smelt larvae as identified by the GAM analysis (<12 psu; Fig. 3). However, freshwater flow and salinity from the channel surveys during January of 2013 and 2014 differed markedly between the years (Figs. 2, 8). In January of 2013, freshwater flow was higher and salinity was lower than was observed in January of 2014. During January of 2014, the median salinity was 9 psu (all stations combined; upper quartile = 23 psu), indicating the upper estuary had limited suitable rearing habitat during the onset of the Longfin Smelt spawning season, which typically begins in January in the estuary (Wang 2007). Reduced salinity suitability could adversely affect egg and larval survival or potentially reduce attraction of spawning adults into the upper estuary altogether. Laboratory experiments examining egg and larval survival responses to salinity and water temperature could prove useful for understanding how year-to-year recruitment variability in the Longfin Smelt population is affected by environmental conditions (Lankford and Targett 1994).

The minor effect of turbidity on Longfin Smelt larval catch in littoral habitats is likely due to the small amount of variability observed in turbidity between tidal sloughs and open-water shoals and between years (Fig. 3). In contrast, water clarity (as indexed by Secchi disk depth) varied much more substantially in channel surveys within and among years (Fig. 8) and had a more significant effect on larval Longfin Smelt catches in the channel surveys (Table 3). The relationship between higher catches of Longfin Smelt larvae and lower Secchi disk depths

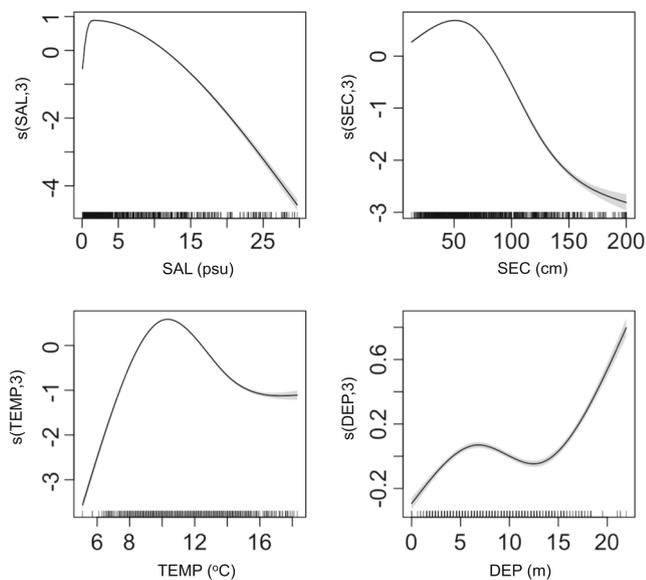


Fig. 9 Plots showing the relationships between newly hatched Longfin Smelt larvae and continuous predictor variables. Plots are fitted smooths and 95% confidence intervals for partial responses from GAMs. The y-axis units are centered on zero and the number in the label is the estimated degrees of freedom of the smooth. Variables are defined in Table 1

in the channel surveys is consistent with what has been observed for larval and juvenile Delta Smelt in the estuary (Nobriga et al. 2008; Sommer and Mejia 2013). Increased turbidity could help reduce predation risk, though this is difficult to examine for larval fishes in the wild (Leggett and DeBlois 1994). The relationship between increased larval abundance and lower water clarity could also be related to how larvae detect their prey in turbid environments (Boehlert and Morgan 1985; Utne-Palm 2002). Feeding experiments conducted on fish larvae with contrasting turbidity levels indicates turbidity enhances visual contrast with prey, which helps the larvae visualize and capture their prey (Boehlert and Morgan 1985; Utne-Palm 2002).

Food availability has been found to be an important driver of larval and juvenile fish growth and recruitment in many coastal habitats and estuaries dominated by freshwater inflow (Fortier and Gagné 1990; Grimes and Finucane 1991; Couillard et al. 2017). In the San Francisco Estuary, food availability is speculated to be an important factor in recruitment of age-0 Longfin Smelt (Kimmerer 2002a; Kimmerer et al. 2009; Nobriga and Rosenfield 2016). To date, only a handful of studies have examined this question directly for Longfin Smelt (Bennett et al. 2002; Hobbs et al. 2006). For example, Hobbs et al. (2006) found larval Longfin Smelt feeding success improved when they were collected in shallow, low velocity, productive habitats with elevated food supply compared to deeper environments with low residence time. The positive relationship between the density of Longfin Smelt larvae and chlorophyll *a* in the present study, albeit modest in deviance explained, indirectly suggests that productive habitats with greater food supply support higher densities of Longfin Smelt larvae.

Vertical migration behavior is employed by larval fish and zooplankton to maintain retention in an estuarine ecosystem (Dodson et al. 1989; Laprise and Dodson 1989; Bennett et al. 2002; Bradbury et al. 2006; Hobbs et al. 2006; Kimmerer et al. 2014). Longfin Smelt develop air bladders at approximately 12 mm TL (Wang 2007) at which point they can manipulate their vertical distribution in the water column to retain position near favorable prey fields (Bennett et al. 2002; Hobbs et al. 2006). Information about lateral transport of fish larvae between littoral and channel habitats in estuarine ecosystems is less clear but may represent an important retention process for fish larvae in estuarine environments (Fortier and Leggett 1982). The conceptual model presented here is that larvae are hatching, rearing, and are locally exchanged with adjacent channels (and vice versa) via horizontal tidal dispersion (Fortier and Leggett 1982). Exchange of larvae between shallow and channel areas can happen within hours of emergence (Fortier and Leggett 1982). This may be the reason why densities of Longfin Smelt larvae were not found to vary between littoral and channel surveys in overlapping areas.

This study cannot rule out the possibility that some larvae observed in the littoral samples, especially those observed in open-water shoals, did not hatch where they were collected but rather were transported downstream (e.g., Suisun Bay) from upstream riverine habitats (e.g., Delta region). Undoubtedly, spawning is also occurring in the tidal fresh waters of the Delta (Fig. 7) and these larvae are probably quickly dispersed downstream during periods of increased freshwater flow. However, during periods of lower freshwater flow, like the period examined here (Fig. 2; except for 2011), the mechanism for riverine transport is probably reduced (Laprise and Dodson 1989). Perhaps a more fundamental question for Longfin Smelt is determining how hatching distribution relates to their tidal dispersal and riverine transport into channels and subsequent retention in the estuary. Retention mechanisms are particularly important to fish and invertebrates in estuarine ecosystems where residual circulation and salinity stratification are prominent (Fortier and Leggett 1982; Dodson et al. 1989; Laprise and Dodson 1989; Fortier and Gagné 1990; Bennett et al. 2002; Bradbury et al. 2006; Kimmerer et al. 2014). Particle tracking models could be applied to distributions of newly hatched larvae of Longfin Smelt to help resolve possible retention and dispersal mechanisms under different freshwater flows (Kimmerer et al. 2014).

Questions about where Longfin Smelt are laying their eggs and where larvae are hatching are important but it is also important to recognize that the observed rearing distribution of newly hatched larvae was centered in Suisun Bay between 2009 and 2015 in the channel surveys (Fig. 7). This may be related to the amount of shallow habitat (open-water shoals and sloughs) available for rearing relative to upstream Delta regions where shallow habitats are generally lined with rip-rap and colonized by invasive submerged aquatic vegetation (SAV; Grimaldo et al. 2012; Hestir et al. 2016). One limitation of the channel survey is that it has a compressed sampling area for Longfin Smelt larvae in the seaward direction (e.g., San Pablo Bay, see Fig. 1). Relationships presented here between Longfin Smelt larvae catches and salinity suggest the rearing distribution can extend much further downstream than currently sampled, especially under average and higher freshwater outflow when low salinity habitat extends into San Pablo Bay (Kimmerer et al. 2009). In the 1980s, CDFW conducted larval fish monitoring surveys in San Pablo Bay and San Francisco Bay (i.e., seaward of its present channel survey). These surveys routinely captured yolk-sac Longfin Smelt larvae, especially during years of increased freshwater outflow (Merz et al. 2013). Surveys of larger larvae (>12 mm TL) from channel habitats also suggests that Napa River, a tributary to San Pablo Bay, is a key spawning location for Longfin Smelt in some years (Merz et al. 2013). Outstanding questions are whether tributaries and shallow habitats downstream of the long-term channel survey are currently supporting Longfin

Smelt larvae and whether these fish are important in driving annual recruitment patterns. The application of otolith microchemistry could prove useful in identifying which of these regional cohorts survive to later life stages (Hobbs et al. 2010).

Finally, it is worth noting that annual variability in Longfin Smelt larval abundance is related to the number of age-2 adult Longfin Smelt that move back into the upper estuary for spawning (Nobriga and Rosenfield 2016). For landlocked Longfin Smelt in Lake Washington, alternating age-2 year classes show variable reproductive investment in egg production, which can translate into improved production, growth, and survival of young larvae (Moulton 1974; Chigbu and Sibley 1994). In the San Francisco Estuary, Nobriga and Rosenfield (2016) found that freshwater outflow was important for determining juvenile Longfin Smelt production, which was subsequently tempered by density-dependent survival between juvenile and adult life stages. Except for 2011, freshwater flow during the periods examined here (2009–2015) was generally below average compared to the longer-term series (Fig. 2, see Kimmerer 2002b, 2004). Yet, mean Longfin Smelt densities varied by 1–2 orders of magnitude between some years in the long-term monitoring survey (e.g., 2013 vs. 2015, 2013 vs. 2014). This suggests that mechanisms underlying variability in Longfin Smelt larval densities and abundance could be related to the number of adult spawners but also to finer-scale variability in dynamic habitat related to salinity (Sakabe et al. 2011; Couillard et al. 2017), water temperature (Secor and Houde 1995; Couillard et al. 2017), turbidity (Utne-Palm 2002), and food production (Dodson et al. 1989; Fortier and Gagné 1990; Grimes and Finucane 1991). Understanding how these dynamic variables vary as a function of freshwater outflow and overlap with available stationary habitat features (e.g., tidal sloughs, open-water shoals) remains unknown but deserves further attention (Peterson 2003; Kimmerer 2004).

Management Implications

A greater understanding of the feeding ecology, trophic linkages, and survival of fish larvae relative to flow, climate, and habitat should be prioritized for conservation plans that are currently considering freshwater flow objectives for age-0 Longfin Smelt in the estuary (Cowin and Bonham 2013). Relationships identified from this study between larval Longfin Smelt densities and salinity and water clarity (channel survey) suggest a mechanistic underpinning related to freshwater flow (e.g., salinity; Jassby et al. 1995, Kimmerer 2002b, 2004). However, water temperature, which is more influenced by regional climate patterns (see Kimmerer 2002b, 2004), could also be important. Climate can also affect wind, which can affect resuspension of sediments and local turbidity conditions. Though support was weak in this paper, food

production may also be important for the early life stages of Longfin Smelt. Unlike other estuaries where increased freshwater flow is shown to enhance food web production to secondary consumers (Hoffman et al. 2008; Hitchcock et al. 2016), there is little evidence that increased freshwater flow directly improves food web productivity to secondary consumers in the San Francisco Estuary (Kimmerer 2002a). In short, a number of drivers and factors should be considered for augmenting Longfin Smelt production in the estuary.

Tidal marsh restoration is an additional conservation measure that should be considered to improve spawning and rearing habitat for Longfin Smelt. Longfin Smelt restoration could improve localized food web pathways (Sobczak et al. 2002; Grimaldo et al. 2009a, b; Howe and Simenstad 2011), especially for larvae rearing in littoral habitats. In addition, the importance of rearing habitats seaward of current investigations should not be underestimated. Studies in San Pablo Bay and adjacent tributaries (e.g., Napa River) could be critical for understanding mechanisms that explain why Longfin Smelt have enhanced recruitment in the fall under periods of higher spring freshwater outflow (Rosenfield and Baxter 2007; Kimmerer et al. 2009). Such studies could also illuminate potential restoration projects that have yet to be considered (Cowin and Bonham 2013).

More broadly, the results presented here provide resource managers with useful information for anticipating long-term challenges to the management of Longfin Smelt populations in the face of global climate change and other ecological processes. Projections with down-scaled global climate models indicate that biota in the San Francisco Estuary are likely to be subjected to increased water temperature, elevated salinity and sea level, and decreased precipitation and freshwater outflow (Cloern et al. 2011; Feyrer et al. 2011; Brown et al. 2013). The results of the present study suggest that a future condition exhibiting elevated salinity and elevated water temperature is likely to impair the habitat of the early life stages of Longfin Smelt. Jeffries et al. (2016) recently found that Longfin Smelt can suffer cellular stress at 20 °C, which is often exceeded in the upper regions of the estuary. This problem is particularly concerning given that the San Francisco Estuary Longfin Smelt population is already at its thermal limits as the southern-most reproducing population, and that environment-recruitment relationships appear to be particularly strong at the geographic limit of a species' distribution (Myers 1998). Moving forward, a more comprehensive understanding of the mechanisms driving Longfin Smelt population dynamics is needed to develop effective conservation and management actions for the San Francisco Estuary.

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