

RESEARCH

Forage Fish Larvae Distribution and Habitat Use During Contrasting Years of Low and High Freshwater Flow in the San Francisco Estuary

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ABSTRACT

Recruitment of estuarine organisms can vary dramatically from year to year with abiotic and biotic conditions. The San Francisco Estuary (California, USA) supports a dynamic ecosystem that receives freshwater flow from numerous tributaries that drain one of the largest watersheds in western North America. In this study, we examined distribution and habitat use of two forage fish larvae of management interest, Longfin Smelt *Spirinchus thaleichthys* and Pacific Herring *Clupea pallasii*, during a low-flow and a high-flow year to better understand how their rearing locations (region and habitat) may affect their annual recruitment variability. During the low-flow year, larval and post-larval Longfin Smelt were distributed landward, where suitable salinity overlapped with spawning habitats. During the high-flow year, larval Longfin Smelt were distributed seaward, with many collected in

smaller tributaries and shallow habitats of San Francisco Bay. Local spawning and advection from seaward habitats were speculated to be the primary mechanisms that underlie larval Longfin Smelt distribution during the high-flow year. Larval Pacific Herring were more abundant seaward in both years, but a modest number of larvae were also found landward during the low-flow year. Larval Pacific Herring abundance was lower overall in the high-flow year, suggesting advection out of the area or poor recruitment. Future monitoring and conservation efforts for Longfin Smelt and Pacific Herring should recognize that potential mechanisms underlying their recruitment can vary broadly across the San Francisco Estuary in any given year, which suggests that monitoring and research of these two species expand accordingly with hydrologic conditions that are likely to affect their spawning and larval rearing distributions.

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INTRODUCTION

Nursery habitat within estuarine ecosystems is shaped by the timing and magnitude of

freshwater flow, its influence on other dynamic habitat features (e.g., water temperature, salinity), and where it intersects with static habitat features (Peterson 2003). Variability in freshwater flow therefore influences habitat quantity and quality for many estuarine biota, especially in estuaries where freshwater flow differs substantially from year to year (Whitfield 1999; Kimmerer 2002a; Kimmerer et al. 2009; Baptista et al. 2010). Understanding where and how nursery habitat and function vary with flow can be particularly important for predicting successful recruitment of estuarine biota (Ramos et al. 2009). This is especially true for organisms that spawn and rear in shallow nursery habitats, and are sensitive to changes in salinity and water temperature (Greenwood 2007). Thus, an understanding of nursery habitats occupied by early life stages of fishes is foundational for understanding potential mechanisms that link habitat to survival, growth, and, ultimately, recruitment to later life stages.

In the San Francisco Estuary (hereafter “the estuary”), research of estuarine biota and their responses to freshwater flow has been focused in the landward region of the estuary where the predominant source of freshwater flow enters the Sacramento-San Joaquin Delta (hereafter “the Delta”) from the Central Valley watershed drainage. This landward area has a well-defined low-salinity zone that is considered important nursery habitat for many fishes and invertebrates (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer et al. 2009). This area is also important because it interacts with two large water export facilities, diverting up to 4.5 km³ of freshwater annually outside of the estuary (Brown et al. 2009). These water diversions can affect estuarine biota directly through entrainment mortality (Grimaldo et al. 2009; Kimmerer 2008) or indirectly through changes to water quality and habitat availability (Kimmerer 2002a, 2002b; Kimmerer et al. 2009).

Despite an intense management focus on how freshwater flow and water diversions affect estuarine biota in the northern region of the estuary, mechanisms underlying well-established fish-flow relationships (Kimmerer 2002a, 2002b;

Kimmerer et al. 2009) remain poorly understood because targeted studies of fishes in nursery habitats across the longitudinal span of the estuary have been limited. Additionally, the potential importance of nursery habitat and freshwater flow from smaller tributaries into the estuary has been largely overlooked in regional monitoring programs (Lewis et al. 2020). Without an estuary-wide understanding of where fish and invertebrates spawn and rear, the ability to determine mechanisms that underlie recruitment of estuarine biota as functions of flow or habitat, or both, remains limited.

The primary objective of this study was to determine how the larvae of two species of management interest, Longfin Smelt *Spirinchus thaleichthys* and Pacific Herring *Clupea pallasii*, vary in rearing location with freshwater flow during an extreme dry year (low-flow) and a wet year (high-flow). To determine this we investigated their abundance and distribution in nursery habitats along the longitudinal axis of the estuary. Regional monitoring programs indicate Longfin Smelt abundance has declined over the last 2 decades, and they are now listed under the California Endangered Species Act (CESA). Sub-adult and adult Longfin Smelt rear in the ocean or in San Francisco Bay, migrating toward low-salinity landward habitats for spawning during the early winter. This coincides with increased precipitation events and increased local freshwater runoff and river flows into the estuary (Rosenfield and Baxter 2007). Longfin Smelt age-0 abundance increases by two orders of magnitude between low and high freshwater flows in the estuary, but mechanisms that underlie this relationship remain unknown (Kimmerer et al. 2009). Longfin Smelt recruits per spawner also increase with freshwater flow (Nobriga and Rosenfield 2016), suggesting larval survival could be an important mechanism that underlies their positive age-0 abundance relationship with increased flow (Kimmerer et al. 2009). Identifying where and how Longfin Smelt larvae respond to freshwater flow is therefore the first step toward understanding potential recruitment mechanisms for juvenile life stages

(Hobbs et al. 2006; Kimmerer 2002a; Grimaldo et al. 2017; Lewis et al. 2020).

Pacific Herring are one of the most abundant forage fishes in San Francisco Bay, and support a commercial roe fishery that is largely exported outside the USA, but little is known about their early life history. In other coastal estuaries, larval herring abundance has been found to vary with prey density (Henri et al. 1985), water temperature (Alderdice and Velsen 1971), retention in shallow embayments (Hay and McCarter 1997) or fronts with strong two-layer stratification (Fortier and Gagné 1990). In the estuary, juvenile Pacific Herring survival—but not abundance—improves with freshwater flow (Kimmerer 2002a; Kimmerer et al. 2009). Like Longfin Smelt, larval Pacific Herring response to flow in the estuary may be an important factor that affects their survival in the estuary; therefore, more information on their rearing locations during low- and high-flow periods is a necessary first step for understanding potential factors that affect their survival under higher flows into the estuary.

Knowledge of habitats occupied by fish larvae can help identify potential retention and transport mechanisms (Fortier and Leggett 1983; Laprise and Dodson 1989; North and Houde 2001), spawning habitats (Grimaldo et al. 2017), and rearing habitats (Fortier and Gagné 1990). Little is known about how larval fish abundances differ between shallow and deep habitats in the estuary (Grimaldo et al. 2004, 2017; Hobbs et al. 2006). Thus, the secondary objective of this study was to examine how larval Longfin Smelt and Pacific Herring abundances differ between shallow habitats (marsh vs. open water) and between shallow and channel habitats of the estuary. Mysid shrimp were included in the second objective because they were once predominant prey for many juvenile fish species in the upper estuary. They are now relatively rare in the diets of these same fishes (Feyrer et al. 2003; Zeug et al. 2017), but little is known about their distribution between shallow and deep waters. Mysid shrimp abundance declined in the upper estuary after the introduction of the Overbite clam *Potamocorbula amurensis*, which caused a

dramatic reduction in primary producer biomass, which is a major food source of mysid shrimp (Orsi and Mecum 1996). Mysid data are included in Appendix A because only 1 year of data is available.

Finally, the third objective of this study was to examine how larval Longfin Smelt, Pacific Herring, and mysid shrimp abundances vary with environmental factors (e.g., water temperature, salinity, turbidity) to better identify conditions when stationary habitat becomes suitable habitat for these species. Because this study was conducted during extreme high- and low-flow years, and sampling extended over a substantial area of the estuary, it provides one of the most spatially robust habitat assessments for larval Longfin Smelt and Pacific Herring to date in the estuary. Ultimately, this information could be useful for identifying management (e.g., flow) and conservation actions (e.g., restoration) to bolster management of both species.

METHODS

Study Area

The estuary is located on the Pacific Coast of the United States in central California (Figure 1). It has an open water surface area of approximately 1,235 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 into several large embayments to the north and south. The estuary comprises two major bays in the north: San Pablo Bay (volume = $0.9 \times 10^9 \text{ m}^3$; area = 260 km²) and Suisun Bay (volume = $0.3 \times 10^9 \text{ m}^3$; area = 100 km²); and two in the south: Central Bay (volume = $2.5 \times 10^9 \text{ m}^3$; area = 220 km²) and South Bay (volume = $1.9 \times 10^9 \text{ m}^3$; area = 470 km²) (Kimmerer et al. 2002b). A broad deep shipping channel (6 to 30 m deep) extends from the Golden Gate Bridge toward the northern estuary where the Delta drains the Sacramento and San Joaquin rivers (Figure 1). Semidiurnal tides roughly vary between 0.5 and 2.5 m in height across the estuary, depending on region (Kimmerer et al. 2002b). To the north, in Suisun Bay, there are several smaller marshes along the shoreline

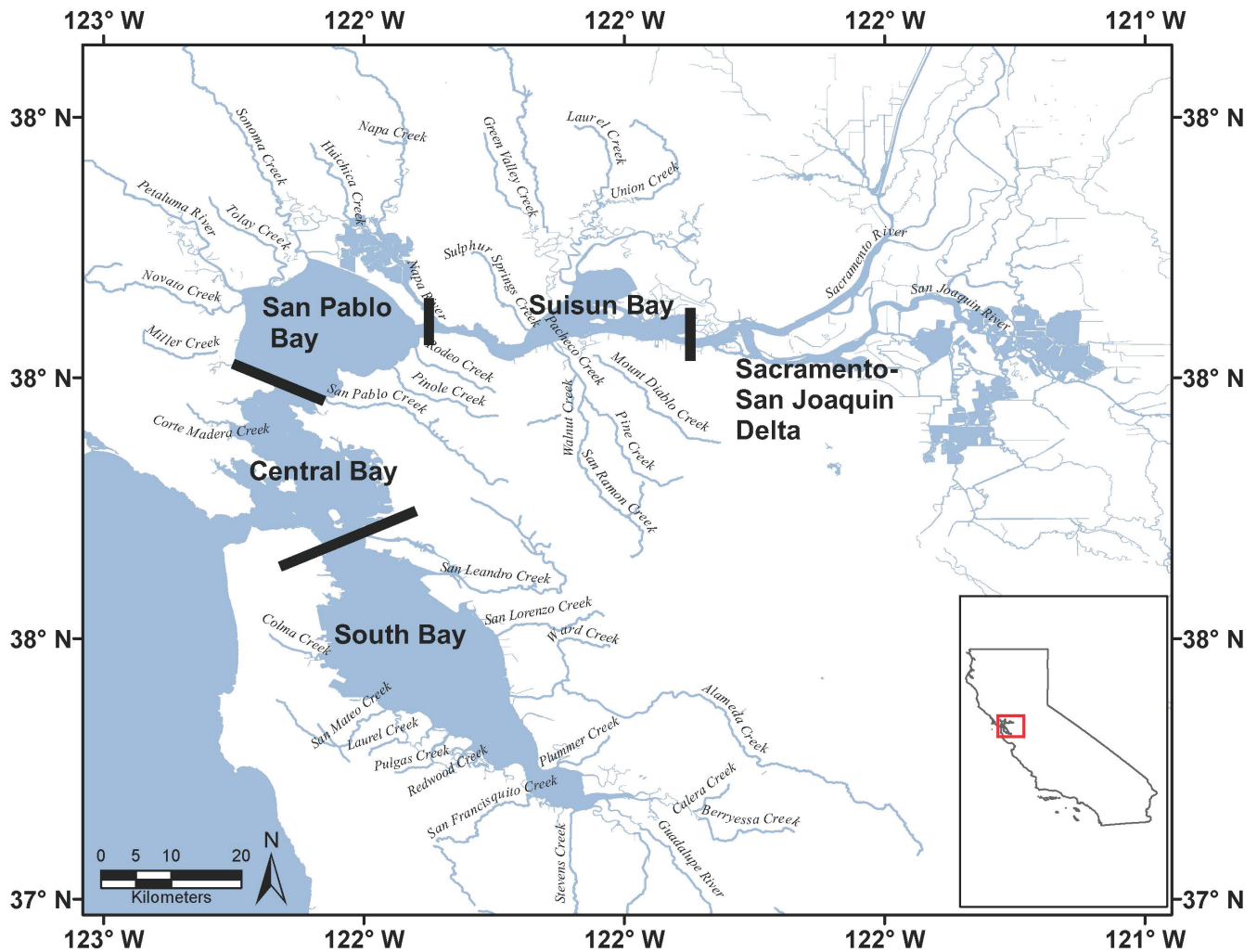


Figure 1 Map of the San Francisco Estuary with key regions identified: Sacramento–San Joaquin Delta; Suisun Bay, and San Francisco Bay, which includes San Pablo Bay, Central Bay, and South Bay.

or isolated as islands with tidal marsh sloughs (small, interior marsh channels). San Pablo Bay's shoreline is heavily urbanized or modified, with industrial buildings on the eastern shoreline and mostly diked areas to the west and north. Tidal marshes are mostly located in or near tributaries along the northern and eastern rim of San Pablo Bay; major tributaries include the Petaluma River, Napa River, and Sonoma Creek (Figure 1). South Bay is a shallow embayment that receives the majority of its flow from Coyote Creek and other small tributaries (Figure 1). South Bay is connected to several restored salt marshes that have been returned to tidal inundation in recent years (Williams and Orr 2002).

Study Design and Data Collection

To address the first study objective of how larval Longfin Smelt and Pacific Herring differ across estuary regions and by habitat, we applied a random-stratified sampling design to Suisun Bay and San Pablo Bay during 2016 and 2017 (Figure 1). Sampling occurred bimonthly between January and April of each year, except in March and April in San Pablo Bay during 2016 because salinity increased above suitable limits for Longfin Smelt larvae (> 15 psu; see Grimaldo et al. 2017). We selected sampling sites with ArcMAP GIS software (ESRI, Redlands, California, USA) based on habitat and location. In 2017, we conducted additional sampling in South

Bay during March, when adult Longfin Smelt spawning was documented in the area (Lewis et al. 2020), and because high freshwater flow from Coyote Creek created suitable low-salinity conditions to support larval Longfin Smelt rearing (up to about 12 psu; see Grimaldo et al. 2017). We also selected sample sites in South Bay using a random-stratified sampling design.

To address the second study objective about how larval Longfin Smelt, Pacific Herring, and mysid shrimp rearing locations vary with habitat, we sampled in two shallow habitats during 2016 (Longfin Smelt and Pacific Herring only) and in shallow and deep channel habitats during 2017. For shallow areas (<3 m deep), we sampled in open water (hereafter “shoals”), and in marshes and interior tidal marsh channels (hereafter “tidal marshes”). For deep channels (>6 m depth), we conducted paired fixed-depth sampling at the “channel surface” (upper 1 to 2 m) and near the “channel bottom,” which was defined as the bottom one-third of the water column from the channel surface to the channel bed. We addressed the third objective to determine how forage fish larvae and mysid shrimp vary with water quality and depth by measuring these parameters at each sample location.

We sampled larval fish and mysid shrimp using a 75-cm-diameter ring net (0.44 m² mouth area) mounted with 505- μ m-mesh net towed from the stern of a motorboat (about 10 to 40 m behind stern, depending on depth) for 10 minutes at approximately 1.2 rpms. We affixed a smaller ring net (0.35 m² mouth area with 150- μ m-mesh net) to the larger ring net to concurrently sample zooplankton with fish; these data are being prepared in a companion manuscript on larval Longfin Smelt diets (J. Burns, unpublished data, see “Notes”). We attached flow meters (General Oceanics model 2030R, Miami, Florida, USA) to the opening of each net to estimate the volume of water (m³) the net filtered during a sample. In 2017, we attached ball weights (2 to 4 kgs) and pressure sensors to the ring net during channel-bottom tows to keep the net in the bottom third of the water column. We typically sampled during flood tides to maximize access to shallow areas

inside marshes. We measured water temperature (°C), salinity (psu), and turbidity (NTU) just before sampling with a hand-held multi-parameter sonde (YSI Inc., Yellow Springs, Ohio, USA). We measured water depth (m) for each sample with a commercially available sonar unit affixed to the boat; we recorded starting and ending depths of each tow to calculate an average depth for each sample. We obtained flow data from the California Department of Water Resources (<https://water.ca.gov/Programs/Environmental-Services/Compliance-Monitoring-And-Assessment/Dayflow-Data>) and the United States Geological Survey (<https://waterdata.usgs.gov/ca/nwis/rt>). We preserved larval fish and mysid shrimp in formalin and sent them to the laboratory for identification. Mysid shrimp were only identified from 2017 samples. Larval fish and mysid shrimp were identified to the lowest practical taxon; Longfin Smelt and Pacific Herring larvae were measured to nearest mm total length (TL).

Data Analysis

We segregated fish into larval and post-larval stages based on swim bladder development. Longfin Smelt generally hatch between 4 and 8 mm TL and develop swim bladders around 12 to 13 mm TL (Wang 2007). Pacific Herring generally hatch between 8 and 12 mm TL, and develop swim bladders between 12 and 15 mm TL (Wang 1986). We visually inspected the swim bladders of larvae collected during this study for development stage, and qualitatively determined that most larvae had fully inflated swim bladders by 13 mm TL. Based on this information, we segregated both Longfin Smelt and Pacific Herring into larval (<13 mm TL) and post-larval life stages (>13 mm TL) for analyses. We excluded fish greater than 20 mm TL from analysis. All data analysis was performed in R programming software (Venables and Smith 2010).

We examined mean differences in water-quality variables by month (January to April), region (Suisun Bay, San Pablo Bay, and South Bay), year (2016 and 2017) and habitat (shoal and tidal marsh in 2016; shoal, tidal marsh, channel surface, and channel bottom in 2017) using analysis of variance (ANOVA). We made post-hoc comparisons

using Tukey's range test for multiple comparisons of means. To determine if water quality varied between paired channel surface and bottom samples, we applied a Wilcoxon signed-rank test to the salinity, turbidity, and water temperature data.

To answer our first and second questions (if larval and post-larval Pacific Herring and Longfin Smelt and mysid shrimp abundance varied across the longitudinal axis of the estuary during low- and high-flow years, and with habitat), we applied a zero-inflated negative binomial hurdle model for count data with excess zeroes to the data; region and habitat (tidal marsh, shoal, channel surface, and channel bottom) were included as treatment effects. We combined samples in San Pablo Bay and South Bay into a single region (San Pablo and South bays) for comparison against Suisun Bay, the latter being an area of intense monitoring and management interest because it encompasses a large low-salinity area, and supports numerous species of special concern (Kimmerer 2002a; Sommer et al. 2007; Kimmerer et al. 2009; Cowin and Bonham 2013). South and San Pablo bays represent the seaward region of the estuary where larval life stages are not currently monitored. The hurdle analysis involved a two-part truncated negative binomial regression with a log-link count model and a binomial logit model. We analyzed species, life stages, and years separately

because, as mentioned above, we sampled only shallow habitats (shoals and tidal marshes) in 2016, whereas we added deep channel habitats in 2017. After preliminary analysis, we determined that as a result of singularities in the models (those too complex to be supported by the data) some subsets needed to be modeled additively, while for other subsets we could examine interactions between habitat and region (Table 1). We did not capture enough post-larval Longfin Smelt in 2016 to run a model, so we analyzed them descriptively (Table 1). We combined mysid shrimp species for habitat and regional statistical analyses. Tow volume (m^3) was an offset for the catch data in the hurdle model, which we implemented with the 'pscl' package (Jackman et al. 2020).

We used generalized additive models (GAMs) to test how Longfin Smelt, Pacific Herring, and mysid shrimp count data varied with temperature, turbidity, salinity, and depth; we included tow volume as an offset in the model. We implemented GAMs separately for each species and life stage with the 'mgcv' package version 1.8-28 (Wood 2006). We fit GAMs with a negative binomial distribution because of over-dispersion. We allowed cubic regression spline smoothing functions and the upper limit of the effective degrees of freedom to vary with each physical attribute, controlled

Table 1 Negative binomial hurdle model regression model variables and fit indices applied to Longfin Smelt, Pacific Herring, and mysid data collected in the San Francisco Estuary during 2016 and 2017

Subset	Year	Model variables	Log-Likelihood	Degrees of freedom
Longfin Smelt larvae	2016	Count ~ Habitat	-278.7	5
	2017	Count ~ Region + Habitat + Region x Habitat	-445.9	17
Longfin Smelt post-larvae	2016	---		
	2017	Count ~ Region + Habitat	-107.6	11
Pacific Herring larvae	2016	Count ~ Region + Habitat + Region x Habitat	-685.3	9
	2017	Count ~ Region + Habitat	-763.5	11
Pacific Herring post-larvae	2016	Count ~ Region + Habitat + Region x Habitat	-272.5	9
	2017	Count ~ Region + Habitat	-536.9	11
Mysids	2016	---		
	2017	Count ~ Region + Habitat + Region x Habitat	-753.2	17

a. Detected only in shoals in Suisun Bay, not modeled.

b. Not identified from samples.

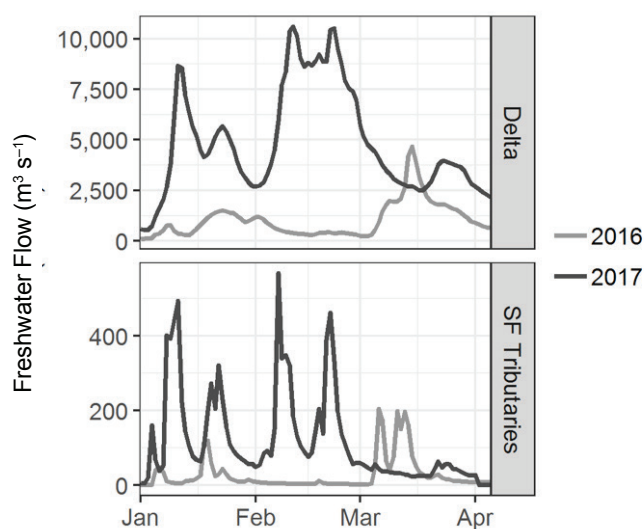


Figure 2 Freshwater flow (m^3s^{-1}) entering the San Francisco Estuary from the Sacramento-San Joaquin Delta (*top panel*) and major tributaries of San Francisco Bay (*bottom panel*) during 2016 and 2017. San Francisco Bay tributary flow data includes Napa River, Novato Creek, Corte Madera Creek, San Lorenzo Creek, Sonoma Creek, San Ramon Creek, Guadalupe River, Coyote Creek, San Mateo Creek, San Francisquito Creek, and Alameda Creek. Flow data for other tributaries in San Francisco Bay are unavailable.

by the degree of penalization associated with a Generalized Cross Validation fit. For all GAM runs, observed pairwise concurvity ranged from 4.0^{-35} to 0.44, which assumes no concurvity, allowing for all water quality variables to be included in each model. For this analysis, we combined catch data from 2016 and 2017, and we added year as a parametric covariate for all species models except mysid shrimp, which were not identified from 2016 samples. We conducted GAMs on the three most abundant mysid shrimp species, and did not combine them because the mysid shrimp species collected in this study are likely to have different responses to salinity (Orsi 1986; Orsi and Mecum 1996).

RESULTS

Physical Variables

Total freshwater flow through the Delta was approximately five times higher in 2017 than it was in 2016 (Figure 2). Freshwater flow from smaller tributaries into San Pablo and South bays was also higher in 2017 compared

to 2016 (Figure 2). Salinity differed by month ($F_{3,369} = 9.884$, $p < 0.001$), region ($F_{2,369} = 115.71$, $p < 0.001$), year ($F_{1,369} = 173.17$, $p < 0.001$), and habitat ($F_{3,369} = 7.660$, $p < 0.001$); salinity was higher in San Pablo and South bays during both years (Figure 3). Turbidity did not vary by year ($F_{1,369} = 1.329$, $p = 0.15$), region ($F_{2,369} = 2.739$, $p = 0.066$), or habitat ($F_{3,369} = 0.937$, $p = 0.4230$), but did vary by month ($F_{3,369} = 17.85$, $p < 0.001$; Figure 3). Water temperature increased each month ($F_{3,369} = 274.6$, $p < 0.05$) and year ($F_{1,369} = 301.3$, $p < 0.001$), and differed between regions ($F_{2,369} = 117.9$, $p < 0.001$) (Figure 3), but there was no discernible difference between habitats ($F_{3,369} = 0.686$, $p = 0.561$). For paired channel surface and bottom samples, we found differences for salinity (Wilcoxon signed-rank test; $n = 43$, $p < 0.001$; Figure 4) and water temperature (Wilcoxon signed-rank test; $n = 43$, $p < 0.001$; Figure 4). Turbidity did not vary between channel surface and bottom samples (Wilcoxon signed-rank test; $n = 42$, $p = 0.23$; Figure 4).

Fish and Mysid Shrimp Collections

Overall, we collected over 1,700 Longfin Smelt, 179,000 Pacific Herring, and 106,000 mysid shrimp (2017 only; Table B1, Table A1) in 421 total tows between 2016 (162 tows) and 2017 (159 tows). Longfin Smelt larvae ranged between 4 to 30 mm TL over the 2-year study, with median lengths of 8.8 and 9.2 mm TL in 2016 and 2017, respectively (Figure 5). Pacific Herring larvae ranged in size between 8.0 and 32.0 mm TL, with median sizes of 11.3 and 11.5 mm TL in 2016 and 2017, respectively (Figure 5). Over 95% of the Longfin Smelt and Pacific Herring larvae captured were less than 20 mm TL.

Comparing Abundance and Distribution Between Low and High-Flow Years

During the low-flow year, larval and post-larval Longfin Smelt were mostly distributed in Suisun Bay, whereas in the high-flow year, larval Longfin Smelt were mostly found in San Pablo and South bays (Figure 6). Larval Pacific Herring were mostly found in San Pablo and South bays during both years, but were also collected in modest abundance in Suisun Bay during the low-flow year (Figure 7). Post-larval Longfin Smelt were mostly distributed in San Pablo and South

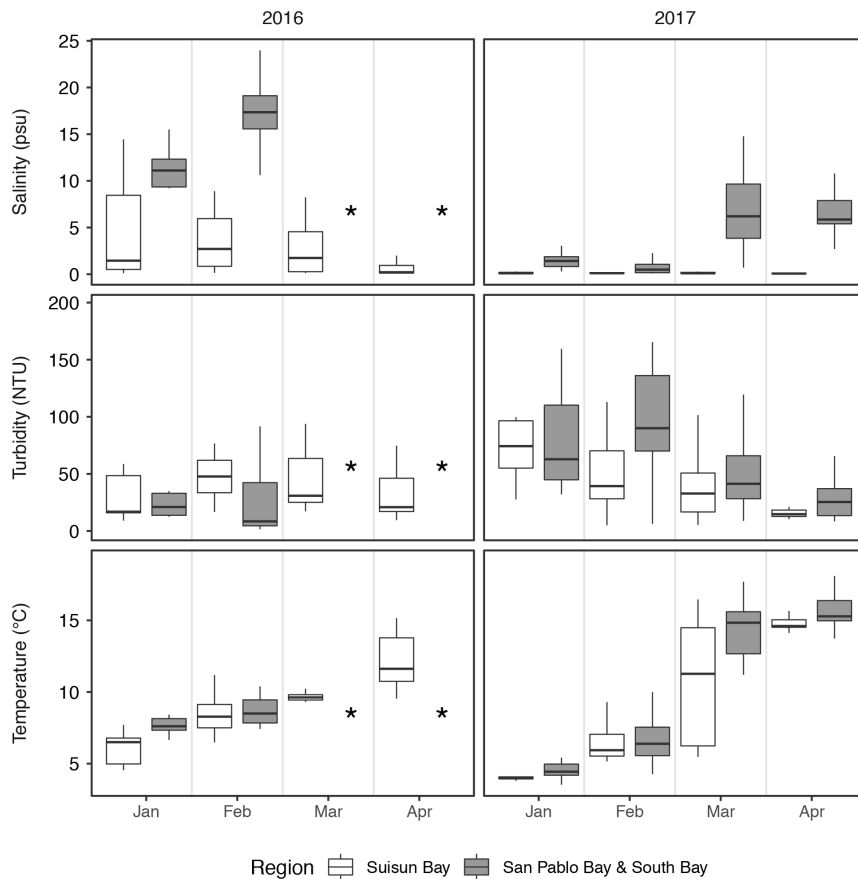


Figure 3 Box-whisker plot of environmental variables measured during low-flow (2016) and high-flow (2017) years by region and month. The central box denotes 50% of the data values (median indicated as the horizontal line) between lower and upper quartiles (*whiskers*). Asterisk (*) indicates that sampling was not conducted in San Pablo Bay during March and April of 2016 (see text for details).

bays during 2017, and none were collected in these bays during the low-flow year (Figure 6). Post-larval Pacific Herring were also mostly distributed in San Pablo and South bays during the high-flow year, with just a few individuals collected in Suisun Bay during the low-flow year (Figure 7).

Hurdle model results revealed that there was variability in both habitat and region (South and San Pablo bays versus Suisun Bay) between years for larval Longfin Smelt and Pacific Herring (Tables 2 and 3; Table B1). In contrast, post-larval Longfin Smelt and Pacific Herring abundances were consistent between regions, as well as habitat use, during 2017, and between shoals and tidal marshes in 2016 (Table B1).

In 2016, the count portion of the hurdle model showed Longfin Smelt larvae abundance was similar between habitats (shoals versus tidal marshes), and the binomial portion of the model

agreed with similar presence between the two habitats (Table B1). In 2017, the count portion of the hurdle model showed that Longfin Smelt larvae were found in higher abundance in both shoals and in tidal marshes in San Pablo Bay and South Bay compared to Suisun Bay (Table 2), though their use of the channel surface and bottoms was similar between the two regions (Table B1). The binomial portion of the model agreed with the count portion, with larval Longfin Smelt having a higher presence in the shoals and tidal marshes of San Pablo Bay and South Bay than in Suisun Bay (Table 2). Larval Longfin Smelt presence was similar between channel surface and bottom samples in both regions (Table B1). In 2016, post-larval Longfin Smelt were found only in the shoals of Suisun Bay. The count portion and the binomial portion of the hurdle model agreed that post-larval Longfin Smelt abundance and presence were

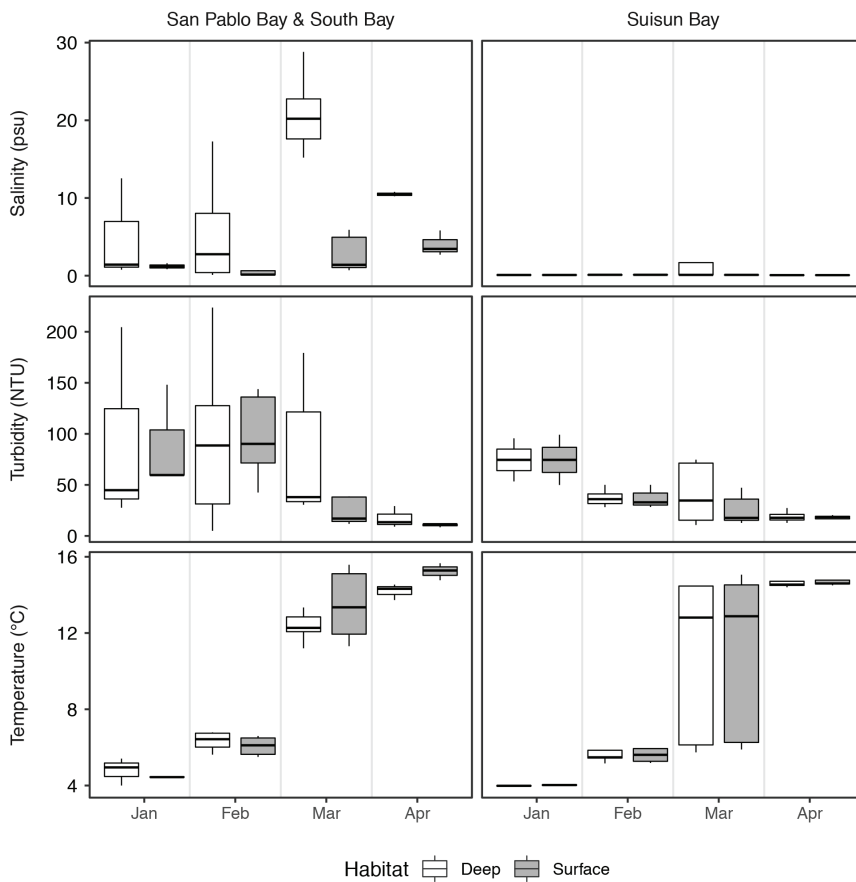


Figure 4 Box-whisker plot of salinity, turbidity, and water temperature for paired channel surface and bottom samples measured during 2017 (see text for details)

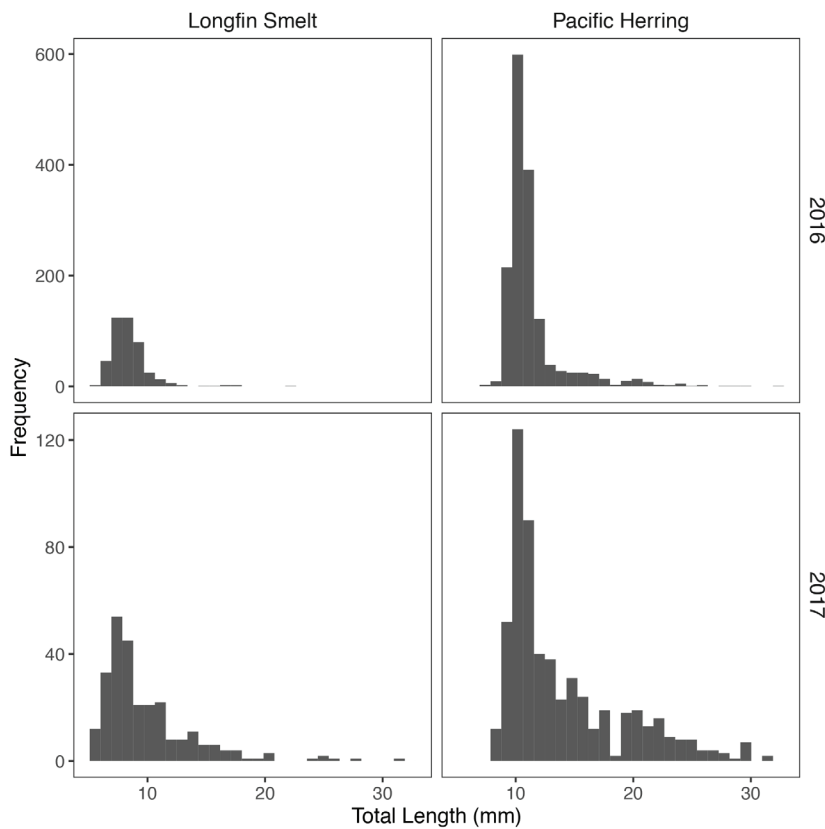
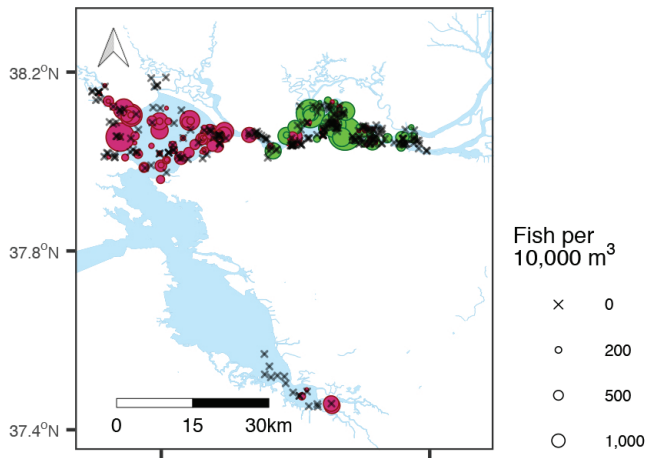
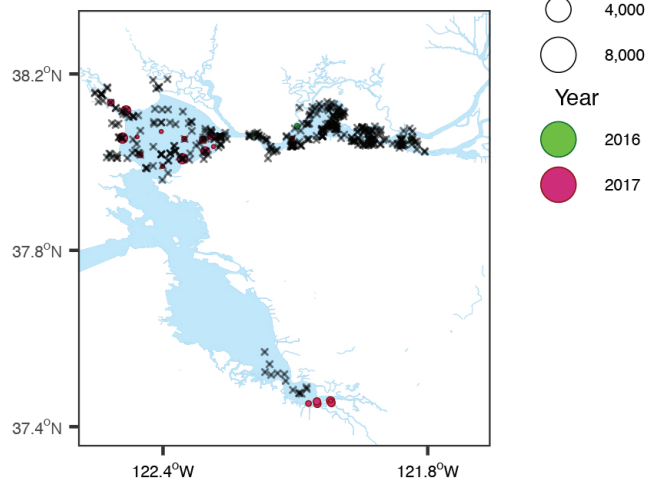


Figure 5 Length-frequency distribution of Longfin Smelt and Pacific Herring by year

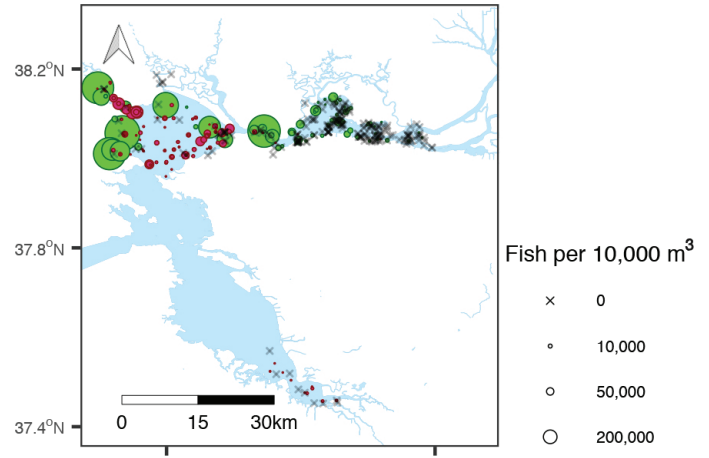
Larval Longfin Smelt (< 13 mm TL)



Post-Larval Longfin Smelt (≥ 13 mm TL)



Larval Pacific Herring (< 13 mm TL)



Post-Larval Pacific Herring (≥ 13 mm TL)

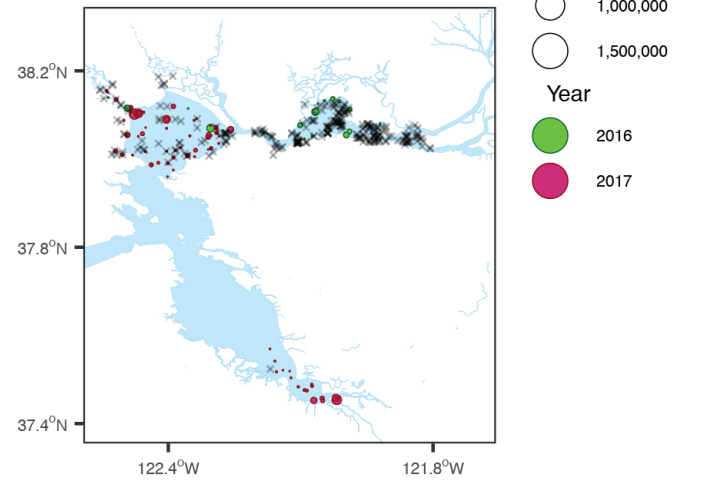


Figure 6 Longfin Smelt abundance (individuals per 10^4 m^{-3}) by life stage (larval and post-larval) during 2016 and 2017 in the San Francisco Estuary. Note: South Bay was not sampled during 2016.

Figure 7 Herring abundance (individuals per 10^4 m^{-3}) by life stage (larval and post-larval) during 2016 and 2017 in the San Francisco Estuary.

similar during 2017 between regions and across the habitats (Figure 6; Table B1).

In 2016, the count portion of the hurdle model found that there were more larval Pacific Herring in the shoals than in the tidal marshes of Suisun Bay (Table 2), though there was no difference between the two habitats in San Pablo Bay and South Bay. During 2016, differences in larval Pacific Herring presence were not detected between regions and habitats. In 2017, both the

count and binomial portion of the model found no difference between Pacific Herring larvae use of the two regions or among habitats (Figure 7; Table B1). In 2016, post-larval Pacific Herring were found in similar abundance across both bays and habitats by both the count and binomial portions of the hurdle model (Table B1). However, in 2017, the count portion of the hurdle model found that there were more post-larval Pacific Herring in South and San Pablo bays than in Suisun Bay and at similar abundance within

Table 2 Post-hoc comparison of Longfin Smelt and Pacific Herring, examining the differences in use of regions within a habitat type, and use of habitats within a region. Significant differences ($p < 0.05$) are indicated in *bold*. Only model results with $p \leq 0.10$ are shown; full model results can be found in Appendix B, Table B1.

Subset	Model	Within	Comparison	Ratio	Standard error	Degrees of freedom	T-ratio	P-value
Longfin Smelt larvae 2017	Count ^a	Shoal	Suisun Bay/San Francisco Bay	0.18	0.13	242	-2.38	0.02
		Tidal marsh	Suisun Bay/San Francisco Bay	0.01	0.01	242	-3.21	0.02
		Suisun Bay	Channel bottom/Tidal marsh	33.6	48.5	242	2.44	0.09
		Suisun Bay	Channel surface/Tidal marsh	40.3	59.1	242	2.52	0.07
	Binomial ^b	Shoal	Suisun Bay/San Francisco Bay	0.34	0.14	242	-2.55	0.01
		Tidal marsh	Suisun Bay/San Francisco Bay	0.16	0.10	242	-2.79	0.01
Longfin Smelt post-larvae 2017	Binomial ^b	No Interaction ^c	Suisun Bay/San Francisco Bay	0.19	0.11	248	-2.89	<0.01
Pacific Herring larvae 2016	Count ^a	Shoal	Suisun Bay/San Francisco Bay	0.14	0.1	153	-2.64	<0.01
		Tidal marsh	Suisun Bay/San Francisco Bay	0.02	0.02	153	-4.18	<0.01
		Suisun Bay	Shoal/Tidal marsh	3.6	1.88	153	2.45	0.02
Pacific Herring larvae 2017	Binomial ^b	No Interaction ^c	Channel bottom/Tidal marsh	4.51	2.83	248	2.4	0.10
		No Interaction ^c	Channel surface/Shoal	4.59	2.59	248	2.71	0.04
		No Interaction ^c	Channel surface/Tidal marsh	5.77	3.61	248	2.8	0.03
		No Interaction ^c	Suisun Bay/San Francisco Bay	0.02	0.01	248	-897	<0.01
Pacific Herring post-larvae 2016	Count ^a	San Francisco Bay	Shoal/Tidal marsh	60.6	1.39	153	1.79	0.08
Pacific Herring post-larvae 2017	Binomial ^b	No Interaction ^c	Suisun Bay/San Francisco Bay	0.04	0.02	248	-7.65	<0.01

- a. Count indicates the truncated positive count portion of the hurdle model.
- b. Binomial indicates the presence-absence portion of the hurdle model.
- c. No Interaction = does not contain an interaction, within variable is not applicable, see Table 1.

each habitat (Table 2). The binomial portion of the hurdle model found that there was similar presence across both regions and habitats (Table B1).

Responses to Water Quality and Depth

Larval Longfin Smelt and Pacific Herring abundances peaked between 2 and 4psu, with Pacific Herring larvae exhibiting another peak around 12psu (Figure 8). Post-larval Pacific Herring abundance also peaked around 2psu. Post-larval Longfin Smelt as well as larval and post-larval Pacific Herring abundances increased with turbidity up to approximately 80NTU and declined above 200NTU. Larval Longfin Smelt abundances were positive across the range of turbidity sampled. Relationships between water temperature and both life stages of Longfin Smelt and Pacific Herring were more variable, with

life stages of both species showing an increase in abundance above 16 °C. For depth, larval and post-larval Longfin Smelt showed similar patterns, with steady abundances observed across the range of depths sampled. Larval and post-larval Pacific Herring abundances increased slightly from 4 to 8 m depth.

DISCUSSION

Differences Between Low and High Freshwater Flows

Estuarine rearing locations and habitat can vary from year to year, especially for fish larvae in estuaries with highly variable freshwater flow (Whitfield 1999; North and Houde 2001; Baptista et al. 2010). In this study, both larval Longfin Smelt and Pacific Herring presence and abundance varied between landward and seaward

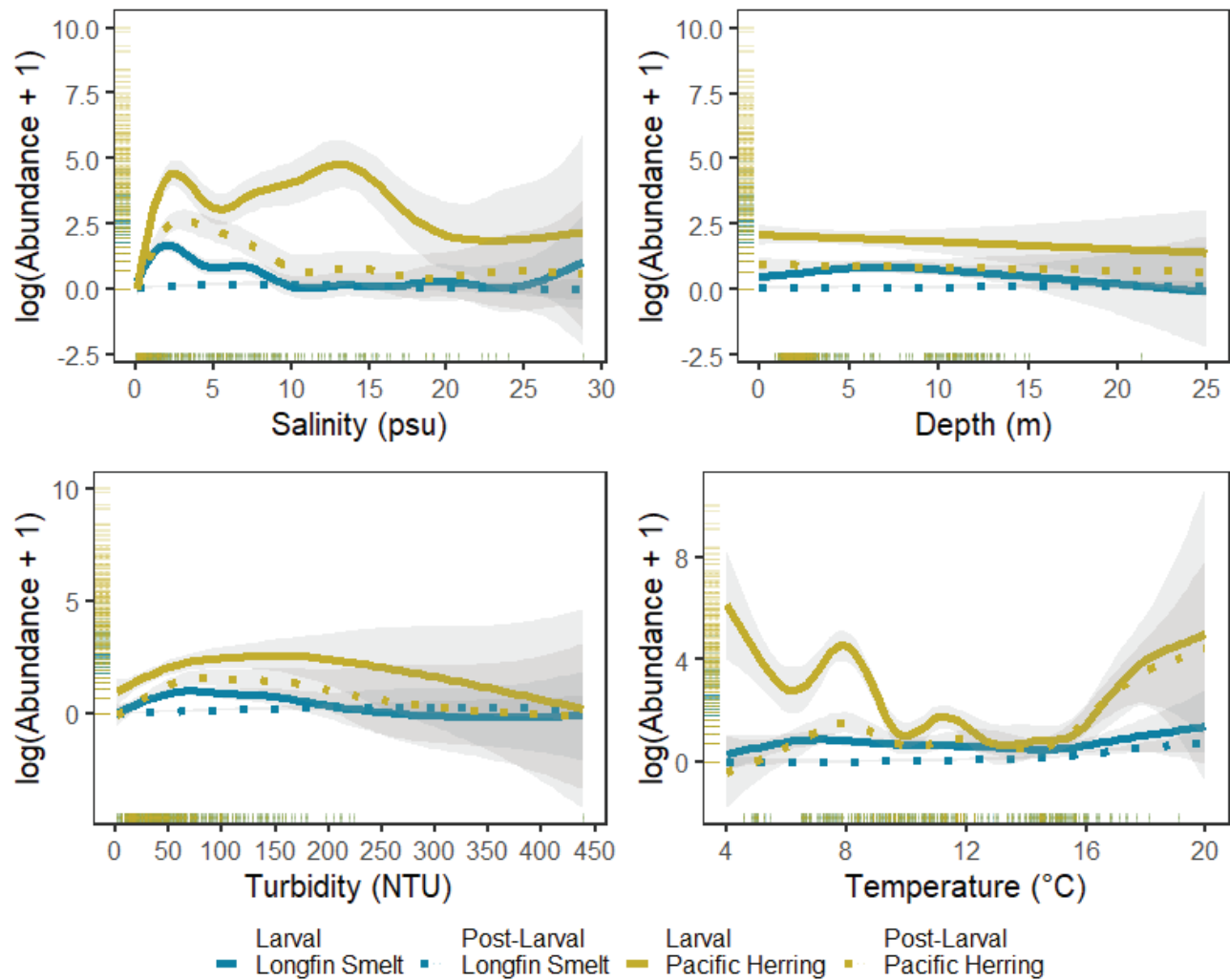


Figure 8 Plots showing the relationships between Longfin Smelt and Herring abundance and continuous predictor variables and depth by life stage. Plots show fitted smoothing splines and 95% confidence intervals for partial responses generated from GAM.

regions of the estuary between contrasting low- and high-flow years. For Longfin Smelt larvae, a couple of key mechanisms may explain the seaward shift in their distribution during the high-flow year. First, during the high-flow year, the water quality data presented here suggests that salinity was suitable for Longfin Smelt spawning (i.e., < 12 psu) throughout the estuary, but especially in San Francisco Bay. Thus, adult Longfin Smelt would not need to migrate landward into the upper estuary to find suitable salinity and habitat for spawning (Lewis et al. 2020); this primary spawning behavior has been assumed by previous researchers (Dege and

Brown 2004; Hobbs et al. 2010; Merz et al. 2013). It is important to note that many larval Longfin Smelt observed in this study were less than 8 mm TL (see Figure 5; peak length is between 6 and 8 mm TL for both years), which is within the hatching length for Longfin Smelt (5 to 8 mm TL; see Wang 2007), indicating that these larvae were recently hatched and represented some proportion of larvae that likely originated from nearby spawning habitats (Figure 6). Such speculation is supported by observations of Lewis et al. (2020), who documented Longfin Smelt spawning in marsh habitats in South Bay.

Rapid advection and dispersion from landward spawning habitats (i.e., the Delta or Suisun Bay) to seaward habitats are alternative mechanisms that may explain why larval Longfin Smelt were distributed in San Pablo and South bays during the high-flow year (Merz et al. 2013). However, this mechanism probably contributes little to the differences observed for larval Longfin Smelt collected in seaward tributaries (e.g., Petaluma River) and marshes several kilometers (about 30 to 100) seaward of the Delta and Suisun Bay. Application of a Particle Tracking Model (PTM) could be particularly useful in determining starting distribution of larvae in the estuary, and potential advection/dispersal mechanisms that promote retention in various San Francisco Bay regions (Fox and Aldridge 2000; Martins et al. 2007; Kimmerer et al. 2014).

Pacific Herring spawning is primarily monitored in South and Central bays (Watters et al. 2004). Thus, it is unknown if Pacific Herring are spawning in San Pablo Bay or Suisun Bay, or in tributaries or other marshes in these regions of the estuary. Yet, larval Pacific Herring were observed in modest abundance in Suisun Bay, in addition to San Pablo Bay, during the low-flow year. Although larval Pacific Herring are negatively buoyant at hatch (Graham 1972; Henri et al. 1985; McGurk 1989), net upstream movement from Central Bay to San Pablo Bay and Suisun Bay via two-layer gravitational circulation would have been weak during the low-flow year, suggesting that some adults potentially spawned toward landward habitats (San Pablo Bay and Suisun Bay) during the low-flow year. As with Longfin Smelt, application of a PTM could identify the supporting mechanisms (i.e., local spawning versus net upstream movement via two-layer gravitational circulation) that determine why and how larval Pacific Herring become distributed throughout San Pablo Bay and Suisun Bay.

Larval Pacific Herring are able to manipulate their position in the water column before they develop swim bladders (Clay et al. 2004), and in some cases, surface-orientated larvae get advected to the sea during extreme flood events, which can lead to high mortality and subsequently poor

recruitment in estuarine ecosystems (Stevenson 1962; McGurk 1989; Fortier and Gagné 1990). Thus, surface advection is one possible factor that contributed to the low abundance of larval Pacific Herring observed in San Francisco Bay and Suisun Bay during the high-flow year, one of the highest observed on record (see Kimmerer 2002b). The overall low abundance of larval Pacific Herring during the high-flow year may also be explained by reduced net landward movement of larval Pacific Herring into either San Pablo Bay or Suisun Bay via two-layer gravitational flow. Based on our water quality measurements, the water column was not apparently stratified by salinity during January and February of 2017 in Suisun Bay (Figure 4), which would result in very little—if any—net landward movement of larval Pacific Herring into the area. San Pablo Bay was modestly stratified during the high-flow year (Figure 4), which may explain why some larval Pacific Herring were observed in San Pablo Bay. But, overall, abundances were lower during the high-flow year compared to the low-flow year, despite slightly higher adult spawning biomass estimates observed in San Francisco Bay during the high-flow year (16,602 metric tons) compared to the low-flow year (13,517 metric tons) (CDFW 2019).

Habitat-Use Differences

Forage fish larvae rearing habitats in estuarine ecosystems can be influenced by proximity to hatching locations (Grimaldo et al. 2017), retention via vertical migration in strong two-layer circulation areas (Fortier and Leggett 1983; Laprise and Dodson 1989; Dauvin and Dodson 1990), advection and dispersion (Henri et al. 1985; Fortier and Gagné 1990), and survival that results from suitable water quality and enhanced prey abundance (Fortier and Gagné 1990; Sirois and Dodson 2000; Hobbs et al. 2006). Here, larval Longfin Smelt abundance was not found to vary with habitat. As suggested by Grimaldo et al. (2017), the lack of habitat differences likely arises from larvae getting quickly dispersed from shallow hatching locations, especially for those that hatch along edge habitats (Chigbu 2000). It is suspected that Longfin Smelt larvae rearing within tidal marsh or shoal habitats far off the main channel have higher retention rates in these

habitats compared to channel habitats (Grimaldo et al. 2017), a question best explored with additional field studies or with a PTM (Fox and Aldridge 2000; Kimmerer et al. 2014). Increased retention in shallow habitats may result in increased survival if prey resources are abundant (Hobbs et al. 2006) or if these habitats provide increased protection from predators (Strydom 2003).

Herring typically spawn on submersed eelgrass (Yamane et al. 2019; Watters et al. 2004) and nearshore sub-tidal habitats with structure (e.g., rock pilings, Watters et al. 2004). Like Longfin Smelt larvae, larval Pacific Herring abundance was not found to vary by habitat, except in 2016, where they were found in higher abundances in shoals compared to tidal marshes in Suisun Bay. In the St. Lawrence Estuary, researchers suspect that horizontal dispersion of post yolk-sac Atlantic Herring (> 10 mm TL) into landward shallow habitats arises from enhanced transport via vertical migration (Fortier and Leggett 1983; Henri et al. 1985), which may partially explain why larval Pacific Herring were abundant in the shoals of Suisun Bay. Nonetheless, the overall lack of habitat-use differences observed here for larval Pacific Herring suggests that upon hatching, larval Pacific Herring are dispersed quickly into the water column away from nearshore or shallow spawning habitats.

Responses to Water Quality and Depth

It was once thought that Longfin Smelt spawning was centered in freshwater areas of the estuary (Dege and Brown 2004; Hobbs et al. 2010). Results presented here are consistent with previous research showing that larval Longfin Smelt peak abundance and recruitment occurs between 2 and 4 psu (Hobbs et al. 2010; Grimaldo et al. 2017). Thus, it is not surprising to observe such a large shift in Longfin Smelt larval abundance in seaward regions of the estuary, and in smaller tributaries and marshes during an extreme flow event when large areas of the estuary transform into low-salinity water. Post-larval Longfin Smelt did not show a strong response to salinity, which is also not surprising, since juvenile Longfin Smelt (about 20 to 40 mm TL) have been observed in salinities up to 30 psu (MacWilliams et al.

2016). This suggests that some Longfin Smelt can quickly manage osmoregulatory stress—although questions about their growth and survival under higher salinities remains unresolved thus warranting further investigation. In contrast, many post-larval Pacific Herring abundances decreased sharply around 10 psu, suggesting they experienced high mortality from perhaps predation or food limitation, or moved further seaward to Central Bay or the Pacific Ocean where sampling was not conducted.

Larval Pacific Herring and Longfin Smelt abundance increased with turbidity up to about 50 NTU (positive catches overall up to turbidities about 200 NTU). Gear avoidance could explain this relationship because even fish larvae with limited movements can avoid towed nets (Thayer et al. 1983; Brander and Thompson 1989; McGurk 1992). Mortality via predation can also be reduced under higher turbidity (Fiksen et al. 2002), which may explain the findings observed here. Higher turbidity enhances the feeding success of larval Pacific Herring because it is believed to provide visual contrast of prey in the water (Boehlert and Morgan 1985). A similar turbidity-feeding relationship is documented for Delta Smelt *Hypomesus transpacificus* (Hasenbein et al. 2013; Baskerville-Bridges et al. 2004). Sirois and Dodson (2000) found that Rainbow Smelt *Osmerus mordax* grew better under higher turbidity, perhaps because of lower stress related to reduced swimming activity. Thus, it is reasonable to speculate that similar mechanisms (i.e., enhanced prey detection, improved growth) are operating for larval Longfin Smelt and Pacific Herring in the estuary.

Water temperatures can affect larval Pacific Herring survival (McGurk et al. 1993), egg hatching success (Alderdice and Velsen 1971), growth (McGurk 1987), and feeding success (McGurk et al. 1993). Here, there was a general and variable pattern between increased abundance and water temperature for both larval Longfin Smelt and Pacific herring, which is consistent with previous Longfin Smelt research in the estuary (Grimaldo et al. 2017) and research for Pacific Herring in other temperate estuaries

(Alderdice and Hourston 1985). Post-larval Longfin Smelt and Pacific Herring abundances increased with water temperature, but this is expected, given the coincidence of both water temperature and fish size with season.

MANAGEMENT IMPLICATIONS

This study presents two primary management and conservation implications for the state-listed Longfin Smelt. First, this study shows that larval Longfin Smelt rearing, and likely hatching locations, are not constrained to the upper estuary as previously thought (Dege and Brown 2004; Hobbs et al. 2010). Thus, restoration of shallow habitats (marshes or open-water shoals) in San Francisco Bay and its tributaries could provide spawning and rearing habitat for Longfin Smelt during wetter hydrologic periods. Second, this study provides insights into mechanisms that underlie well established flow-abundance relationships presented for age-0 Longfin Smelt (Kimmerer et al. 2009). Specifically, this study suggests that mechanisms underlying Longfin Smelt recruitment during wetter years are largely driven by rearing conditions primarily occurring in San Francisco Bay, which may include increased spawning habitat; favorable water quality, such as salinity and turbidity that supports successful hatching and predator avoidance, respectively; or retention in favorable rearing areas (Kimmerer 2002a). These potential factors are not mutually exclusive, and likely have synergistic interactions to warrant further study to determine potential conservation and management actions (e.g., restoration, water diversion management, etc.). These recruitment mechanisms and potentially other important mechanisms, such as suitable prey availability or entrainment mortality, appear to shift landward (i.e., toward Suisun Bay and the Delta) when Longfin Smelt shift distribution upstream during low-flow years (Hobbs et al. 2006; Sommer et al. 2007; Grimaldo et al. 2009, 2017). Future monitoring and additional studies should consider the potential full range of Longfin Smelt found in the estuary and not just focus on the landward region (Lewis et al. 2020).

For Pacific Herring, larval stages were found to rear over a broad geographic area that encompasses all major bays of the estuary, demonstrating an important connectivity between landward and seaward regions and habitats. More importantly, evidence presented here suggests that spawning may be occurring further landward than currently monitored by Pacific Herring spawning surveys (i.e., South and Central bays; see Watters et al. 2004). Consideration of a wider spawning area could help improve spawning biomass estimates and improve estimates of year-class strength (O'Farrell and Larson 2005).

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NOTES

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