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ARTICLE

Population Dynamics of an Estuarine Forage Fish: Disaggregating Forces Driving Long-Term Decline of Longfin Smelt in California's San Francisco Estuary

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Abstract

Forage fish production has become a central concern of fisheries and ecosystem managers because populations of small fish are a critical energetic pathway between primary producers and predator populations. Management of forage fish often focuses on controlling exploitation rates, but it is also possible to manage productivity of these species in coastal ecosystems, particularly estuaries. Like several forage fish species that are native to the San Francisco Estuary (SFE) in California, the Longfin Smelt *Spirinchus thaleichthys* has experienced dramatic population declines over the past few decades. This population is not fished commercially or recreationally; trends in its relative abundance have been described statistically, but the mechanisms that drive population dynamics are still poorly understood. Our objective was to evaluate alternative conceptual models of Longfin Smelt population dynamics to better understand the forces that may constrain the species' productivity during different phases of its life cycle. We created contrasting variants of a generalizable population model (the Ricker model) and parameterized those variants using empirical data from a long-term sampling program in the SFE. Predictions from alternative models were compared with empirical results from a second (independent) data series of relative abundance to identify the model variants that best captured the empirical trend. The results indicated that (1) freshwater flow had a positive association with recruits per spawner and (2) both recruits per spawner and spawners per recruit appeared to be density-dependent life stage transitions. Juvenile survival may have declined to some extent, but we could not conclusively demonstrate this. By constraining the possible timing and location of mechanisms that modulate productivity at different life stages, the present results improve our understanding of production for a key native forage fish in the SFE.

Forage fishes serve as energy conduits between zooplankton and higher-trophic-level predators (Pikitch et al. 2014). The central role of forage fishes in aquatic food webs means that forage fish production is critical to sustainable fisheries management (Alder et al. 2008), desired ecosystem functions (Hall et al. 2012), and, in some cases, the maintenance of biodiversity (Trathan et al. 2015). For instance, seabirds around the world display reduced and more variable productivity

when forage fish biomass drops below one-third of the maximum levels observed in long-term studies (Cury et al. 2011). Thus, marine fisheries and ecosystem management is increasingly focused on protecting forage fishes from overexploitation. Management may also be directed toward maintaining or restoring the habitats and processes that support the production of forage fish, especially in estuarine ecosystems (Kennish 2002; Hughes et al. 2014).

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A general conceptual model of forage fish productivity in coastal ecosystems, including estuaries, is that recruitment is strongly influenced by the interplay of zooplankton production and piscivore predation on forage fishes (Walters and Juanes 1993; Essington and Hansson 2004). The matches and mismatches between forage fishes and their prey can be affected by physical conditions, such as ocean currents (Genin 2004) and upwelling (Reum et al. 2011). For species that rely on low-salinity environments to complete their life cycle, variation in freshwater flow rates can also play an important role in aligning young fish with their prey and protecting them from predators (Turner and Chadwick 1972; North and Houde 2003). Fish behavior and physiological capacities can influence the details of this conceptual model, particularly for euryhaline fishes (Kimmerer 2006; Peebles et al. 2007).

The protection of forage fish habitats in developed rivers and their receiving estuaries can be very difficult, as human economic systems' strong reliance on freshwater results in competition for limited freshwater resources (Vörösmarty et al. 2010; Cloern and Jassby 2012). Many estuarine forage fishes (and their supporting food webs) that are tolerant of or

dependent upon low-salinity and freshwater habitats are influenced by the timing, duration, and magnitude of freshwater flow and its effects on estuarine hydrodynamics (Jassby et al. 1995; North and Houde 2003; Gillson 2011). The biological productivity and accessibility of freshwater that were historically provided by river–estuary systems have attracted considerable human settlement and exploitation, which have in turn led to intensive changes that include large-scale reclamation of estuarine landscapes, water pollution, nonnative species introductions, modification of estuarine hydrodynamics, and declines in native biota (Kennish 2002; Lotze et al. 2006; Shan et al. 2013). California's San Francisco Estuary (SFE; Figure 1) is a well-known example of an estuary that has undergone tremendous physical, chemical, and biological transformation (Kimmerer 2002a; Cloern and Jassby 2012). The declines of once-productive fisheries and the potential ongoing loss of native fish biodiversity are key aquatic resource concerns for the SFE and its watershed (Moyle 2002; Sommer et al. 2007; Katz et al. 2013).

One formerly abundant forage fish that has undergone a substantial decline within the SFE is the Longfin Smelt

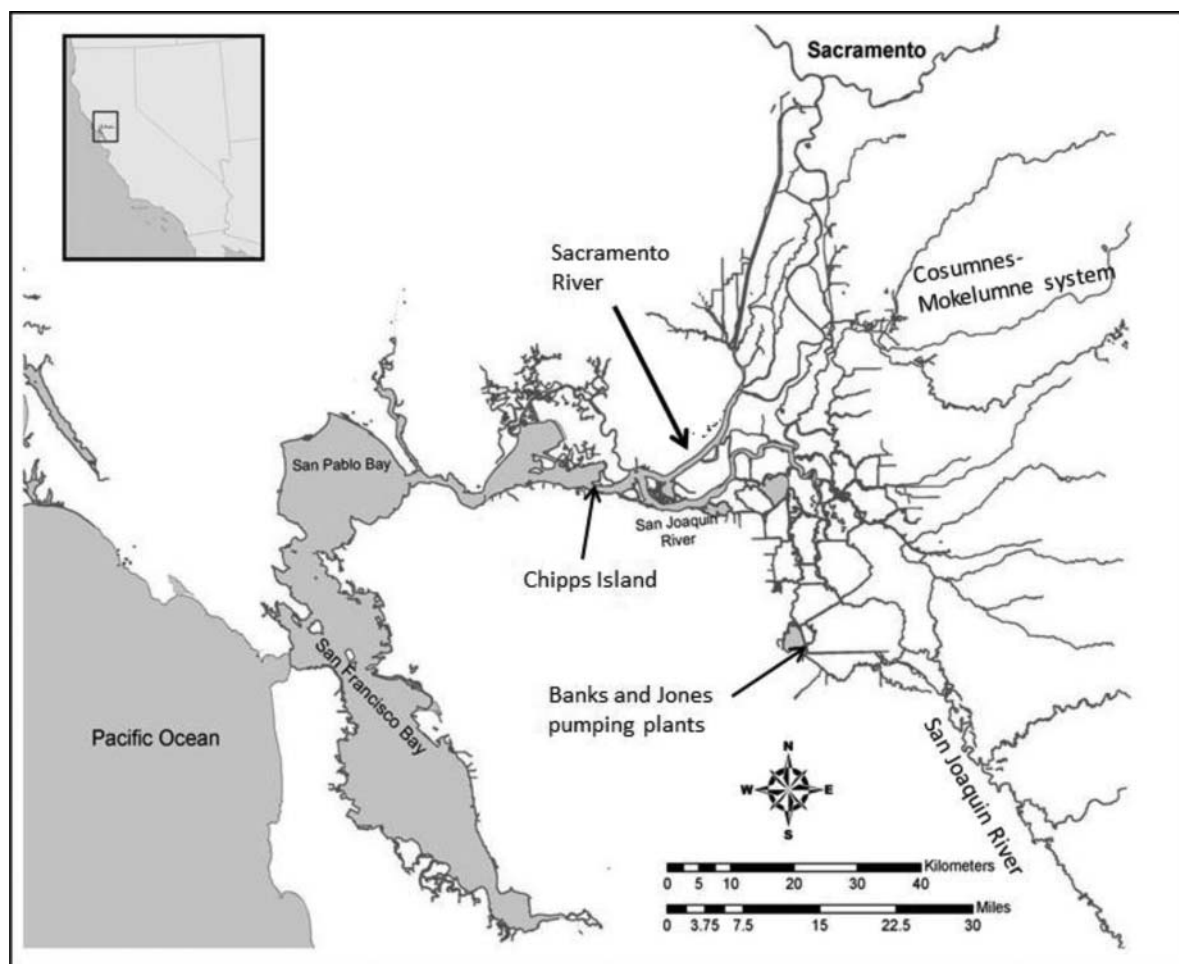


FIGURE 1. Map of the San Francisco Estuary. The Pacific Ocean enters the estuary under the Golden Gate Bridge; the Sacramento–San Joaquin Delta encompasses the waterways to the east of Chipps Island (sampling locations for California Department of Fish and Wildlife monitoring stations are available at www.wildlife.ca.gov/Regions/3).

Spirinchus thaleichthys (Rosenfield and Baxter 2007). This species is a small, facultatively anadromous, pelagic fish that typically reaches adult sizes of 80–150 mm FL (Moyle 2002). Longfin Smelt inhabit lakes, coastal river estuaries, and near-shore marine environments from Alaska to central California; the SFE is the southern limit of the species' inland distribution along the Pacific coast of North America. Most Longfin Smelt live for 2 years and are semelparous. In the SFE, Longfin Smelt spawn in tidally influenced freshwater habitats, but low-salinity habitats may also provide suitable spawning areas (microhabitat requirements for Longfin Smelt spawning are unknown). Spawning typically peaks in the winter (December–February), when water temperatures range from about 7.0°C to 14.5°C (Moyle 2002). Larvae and small juveniles aggregate in low-salinity waters during the late winter through spring (Dege and Brown 2004) and then move seaward into mesohaline to marine waters of central San Francisco Bay and the coastal ocean during the summer (Rosenfield and Baxter 2007). Juveniles and adults begin to move landward again during the fall (September–December).

The Longfin Smelt was once among the most abundant and widespread fishes in the SFE (Moyle 2002; Sommer et al. 2007). The species' former abundance and broad distribution strongly suggest that it once played an important role in the SFE food web; however, given an abundance decline of approximately 99.9%, Longfin Smelt are currently too rare to serve as an important prey species for piscine, avian, or mammalian predators foraging in the estuary. The Longfin Smelt is one of several fish populations that play a central role in California water management because in 2009, it was listed as threatened under the California Endangered Species Act (CESA), and regulations that were developed as part of the CESA listing can limit diversions of freshwater from the SFE. The U.S. Fish and Wildlife Service also recently determined that protection of the SFE Longfin Smelt population under the U.S. Endangered Species Act (ESA) is warranted (USOFR 2012).

Many details of Longfin Smelt ecology in the SFE are virtually unknown, as the species has not been targeted by a sport fishery or commercial fishery for many decades (Moyle 2002). Longfin Smelt are caught as bycatch in a limited bait fishery for bay shrimp *Crangon franciscorum*; although the California Department of Fish and Wildlife (CDFW 2009) considered this a factor limiting Longfin Smelt recovery, we know of no evidence that bycatch rates have increased substantially in recent times. Furthermore, until the species' recent listing under the CESA, the status of Longfin Smelt did not factor directly into decisions about water diversions. As a result, current scientific understanding of the SFE population is largely derived from correlation-based analyses of abundance indices (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002b), evaluations of the catch data that underlie those indices (Rosenfield and Baxter 2007; Kimmerer et al. 2009; Latour, in press), and the presumption (e.g., Moyle 2002) that the SFE population is fundamentally similar to the

better-researched (but landlocked) population of Longfin Smelt in Lake Washington, Washington (Chigbu 2000).

The Longfin Smelt is also one of several SFE fishes that have shown a strong and persistent association between juvenile production and the freshwater flow variation experienced early in the life cycle (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002b; Rosenfield and Baxter 2007; Thomson et al. 2010; Maunder et al. 2015). However, little attention has been given to whether and how freshwater flow rates might affect production of Longfin Smelt beyond the first year of life. It is well established that Longfin Smelt production per unit of flow has declined (Kimmerer 2002b; Rosenfield and Baxter 2007; Thomson et al. 2010), but with only one very recent exception (Maunder et al. 2015), researchers have not attempted to evaluate the population dynamics of SFE Longfin Smelt in a classical spawner–recruit framework.

Food web alteration has been considered a primary factor contributing to the decline of Longfin Smelt in the SFE; however, the details of when and where prey production may limit Longfin Smelt recruitment have not been determined. Furthermore, predation on SFE Longfin Smelt has not been studied, so the role of predators in driving the population can only be speculated upon. The zooplankton assemblages that Longfin Smelt likely prey upon began changing dramatically after the overbite clam *Potamocorbula amurensis* invaded the SFE in 1986. Changes included abrupt declines in chlorophyll (Alpine and Cloern 1992) and several crustaceans, including mysid shrimps (Kimmerer 2002b); changes in the distribution (Kimmerer 2006; Sommer et al. 2011) and diet composition (Feyrer et al. 2003; Nobriga and Feyrer 2008) of several fishes were also observed. In addition, wastewater ammonium limits the growth rate of diatoms in the SFE (Wilkerson et al. 2006), and this may be another, more gradually changing factor that acts to suppress production of the Longfin Smelt's zooplankton prey.

We explored the population ecology of SFE Longfin Smelt in an attempt to identify when during the life cycle (and, by extension, where) productivity has changed and how temporal changes in these productivity parameters may explain the long-term decline of the population. To do this, we employed conceptually different variants of a standard population modeling framework (the Ricker model) to determine which formulations of the model best explained the empirical trends. We did not attempt to develop a model that would precisely recreate Longfin Smelt population dynamics; rather, our objective was to evaluate alternative conceptual models of the species' population dynamics to better understand the forces potentially constraining Longfin Smelt productivity during different phases of the life cycle. Specifically, we sought to identify factors that were correlated with productivity parameters for different life stages in order to disaggregate the effects of changes in productivity at those life stages. This information would allow future research and management actions to focus on (1) the Longfin Smelt life stages that have experienced

declines in productivity and (2) the environmental variables that can be manipulated to increase the production of those life stages.

STUDY AREA

The SFE is formed by the confluence of two major California river systems: the Sacramento and San Joaquin rivers (Figure 1). These rivers meet in the Sacramento–San Joaquin Delta (hereafter, Delta) and begin to mix with Pacific Ocean waters. This estuarine mixing intensifies in a westward direction in the several embayments that comprise San Francisco Bay (Figure 1; Jassby et al. 1995; Kimmerer et al. 2013). Some portion of central San Francisco Bay, nearest to the bay's outlet to the Pacific Ocean, usually approaches marine salinity (≥ 30 psu). In the northern reach of the SFE (from San Pablo Bay through the Delta), average salinity decreases from west to east due to the influence of freshwater that flows from Central Valley rivers into the Delta. The Delta comprises a network of tidal freshwater channels from which large quantities of water are exported to more arid parts of California for agricultural and municipal use. The U.S. Central Valley Project has been exporting water to the San Joaquin Valley since 1951, and the State Water Project has been exporting water to the San Joaquin Valley and southern California municipalities since 1968. The historical changes associated with the development of California's surface water supplies and the diversion of water from the Delta have been reviewed extensively (Arthur et al. 1996; Enright and Culbertson 2010; Cloern and Jassby 2012).

METHODS

Overview.—Fisheries stock assessments have long relied on spawner–recruit models (e.g., Ricker 1954). These mathematical tools link the production of new cohorts of fish (recruits) to the available spawning stock and often also attempt to explain

residual variation in recruitment by using environmental covariates (Myers 1998). Stock assessments are usually applied to harvested fishes, particularly those in marine ecosystems. Although the Longfin Smelt is not targeted for harvest in the SFE, it is nonetheless useful to construct explicit spawner–recruit relationships so as to evaluate different conceptual models of Longfin Smelt recruitment (see also Maunder et al. 2015).

Our analysis was based on alternative formulations of the Ricker (1954) model,

$$R = aSe^{-BS}. \quad (1)$$

In this general formulation, R is the number (or biomass) of fish recruiting to a population and S is the number (or biomass) of spawners. The parameters to be solved for are a and B , where a is the recruits per spawner (in essence, the slope of the spawner–recruit relationship near the origin) and B interacts with a to adjust the intensity of density dependence between generations. Using the Ricker model, we developed alternative conceptual models to identify the best strategy for modeling SFE Longfin Smelt recruitment. A long-term, age-specific data series of Longfin Smelt relative abundance in the SFE was used to parameterize the alternative Ricker models by (1) screening variables to predict a ; (2) screening variables for predicting survival from age 0 to age 2 in order to predict S ; and (3) finding values of B that constrained predictions of R , thereby creating a contrast with model variants that lacked this constraint. We then simulated a time series of Longfin Smelt relative abundance using each alternative Ricker model and compared each simulation to an empirical time series that was measured independently of the data series used to parameterize the models.

Alternative conceptual models of recruitment.—Five alternative conceptual models of Longfin Smelt recruitment were evaluated (Table 1). All models had a recruits-per-spawner

TABLE 1. Summary of five alternative Ricker models of Longfin Smelt recruitment in the San Francisco Estuary. The alphanumeric model codes are shorthand for the embedded hypotheses: the number represents whether one life stage or two life stages were explicitly modeled; “a” denotes the inclusion of a recruits-per-spawner term (i.e., applicable to all five models); “b” indicates that a model has an explicit density-dependent exponent term (e^{-BS} ; see Methods); and “c” indicates that a model employs a time-dependent change in one or more parameters.

Model	Embedded hypotheses
1abc	The trend in age-0 relative abundance is sufficient to model long-term population dynamics; the production of age-0 fish is density dependent; and survival has changed through time (e.g., due to changes in the estuary's food web).
2a	Understanding the trend in age-0 relative abundance requires explicit modeling of spawner and recruit relative abundances; the production of age-0 fish is density independent; and survival has not changed through time.
2ab	Understanding the trend in age-0 relative abundance requires explicit modeling of spawner and recruit relative abundances; the production of age-0 fish is density dependent; and survival has not changed through time.
2ac	Understanding the trend in age-0 relative abundance requires explicit modeling of spawner and recruit relative abundances; the production of age-0 fish is density independent; and survival has changed through time.
2abc	Understanding the trend in age-0 relative abundance requires explicit modeling of spawner and recruit relative abundances; the production of age-0 fish is density dependent; and survival has changed through time.

term (a ; indicated by an “a” in the alphanumeric codes that differentiate the models described in Table 1). One model (1abc) compared age-0 abundance from one generation to the next (i.e., a estimated the recruits per recruit) to evaluate whether age-0 indices were sufficient to model long-term population dynamics—a hypothesis that could be inferred from the numerous published analyses of Longfin Smelt age-0 abundance indices (e.g., Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002b; Thomson et al. 2010). If the one-life-stage model performed as well as the four models with two life stages (i.e., models with “2” in their alphanumeric codes; Table 1), this would indicate that Longfin Smelt age-2 abundance is more or less determined by age-0 production (i.e., that survival from age 0 to age 2 is relatively invariant through the data series) and that the use of a traditional, two-life-stage spawner–recruit model is not necessary for modeling Longfin Smelt population dynamics in the SFE.

The four model variants that used two life stages incorporated a term to estimate survival between age 0 and age 2, thereby estimating S from predictions of R . These models differed in (1) their combination of an explicit density-dependent term for the spawner-to-recruit life history transition (indicated by a “b” in the model alphanumeric codes) and (2) whether their parameters were allowed to change through time (indicated by a “c” in the model alphanumeric codes; Table 1). The relative importance of these terms in describing empirical patterns in Longfin Smelt population abundance has ecological and management implications, as the terms suggest different mechanisms for constraining population dynamics.

Data sources.—The CDFW conducts several trawl-based surveys of fisheries resources in the SFE (www.wildlife.ca.gov/Regions/3). Longfin Smelt have been commonly collected in most of these surveys, and CDFW has generated indices of Longfin Smelt relative abundance from some of the surveys (Stevens and Miller 1983; Rosenfield and Baxter 2007). We obtained spawner–recruit parameters by using data from the San Francisco Bay Study (SFBS), which has been conducted by CDFW since 1980. Predictions made with the SFBS data were then compared to an estimate of Longfin Smelt relative abundance based on an independent data series originating from the CDFW’s Fall Midwater Trawl Survey (FMWT). The CDFW has generated unitless indices of Longfin Smelt abundance from the FMWT data since 1967 (except in 1974 and 1979). The methodologies of the SFBS and FMWT sampling programs have been reported elsewhere (e.g., Stevens and Miller 1983; Rosenfield and Baxter 2007) and are not repeated here. The key differences that are pertinent to this study are as follows: (1) the SFBS and FMWT sampling grids overlap, but the former program samples further seaward and the latter program samples further landward; (2) SFBS sampling occurs during all months of the year, whereas FMWT sampling takes place only during September–December; (3) the number of stations sampled in a month is considerably higher for the

FMWT (~100) than for the SFBS (~35); (4) the SFBS deploys both a bottom-oriented otter trawl and a midwater trawl at each sampling station, whereas the FMWT uses only a midwater trawl; and (5) CDFW calculates age-specific indices of Longfin Smelt relative abundance from the SFBS data but calculates only one index (essentially an age-0 index) from the FMWT data (Table 2).

The CDFW uses February–May catch data to generate an index of age-2 Longfin Smelt relative abundance for each sampling gear employed by the SFBS; May–October catch data are used to generate abundance indices for age-0 Longfin Smelt. We averaged the midwater trawl and otter trawl indices generated by the SFBS to produce unitless annual indices for each age-class of Longfin Smelt (hereafter, Bay Age-0 index and Bay Age-2 index; Table 2). We combined indices from the two sampling gears because the SFBS midwater trawl was not deployed during some years (Rosenfield and Baxter 2007), so the Bay Age-0 and Bay Age-2 indices provided continuous time series of relative abundance for 1980–2013. We did not attempt to estimate missing data (missing values were replaced with a zero before taking the average) because it was possible that estimation of missing values would be no more accurate than simply treating the missing data as zeroes. These choices reflect a trade-off between long-term data availability and the timing of peak Longfin Smelt catches (Rosenfield and Baxter 2007).

Selection of environmental covariates.—We developed one freshwater flow variable and three water quality variables to use as candidate predictors of Longfin Smelt life stage transitions. Following the work of Rosenfield and Baxter (2007), we used monthly means of the net Delta outflow index (hereafter, Delta outflow; www.water.ca.gov/dayflow/) to represent the commonly reported influence of freshwater flow on Longfin Smelt. Delta outflow is the estimated net tidally filtered river flow passing Chippis Island (Figure 1); it is the freshwater flow variable that most directly influences salinity distribution in SFE river channels and embayments (Jassby et al. 1995; Kimmerer et al. 2013). These open-water habitats comprise the major larval rearing areas for Longfin Smelt (Dege and Brown 2004; Hobbs et al. 2006). We calculated the monthly mean Delta outflow for December–May because (1) these months fully overlap with the Longfin Smelt spawning and larval rearing phases in the SFE (CDFW, unpublished data); and (2) outflow during these months is typically greater and more variable than outflow in other months. As a result, December–May outflow is most likely to influence the fate of Longfin Smelt (Jassby et al. 1995; Kimmerer et al. 2013). Estuarine hydrodynamics are also influenced greatly during droughts, which affect the fate of Longfin Smelt (Rosenfield and Baxter 2007). Delta outflow data were available for the period 1956–2013, and we converted monthly means into metric units (m^3/s).

We also used monthly means of water temperature ($^{\circ}\text{C}$) and water transparency (Secchi depth, cm) from all available data

TABLE 2. Time series of the first principal component (PC1) from principal components analyses (PCA) of available water quantity and water quality variables, presented with time series of the Longfin Smelt relative abundance indices used in this study. The PCA on the net Delta outflow index (Delta outflow PC1; Sacramento–San Joaquin River Delta) was conducted on data for December–May; the PCAs for water temperature (water temp PC1) and water transparency were conducted on data for February–May. All abundance indices are unitless metrics of the Longfin Smelt's relative abundance in the San Francisco Estuary. The Fall Midwater Trawl Survey (FMWT) index is based on data collected during September–December. Bay indices are average results from the San Francisco Bay Study's (SFBS) two sampling gears (midwater trawl and otter trawl); the Bay Age-0 index is based on data collected during May–October, and the Bay Age-2 index is based on data collected during February–May.

Water year	Delta outflow PC1	Water temp PC1	Water transparency PC1	FMWT index	Bay Age-0 index	Bay Age-2 index
1956	2.77					
1957	−0.627					
1958	3.74					
1959	−1.14					
1960	−1.19					
1961	−1.29					
1962	−0.575					
1963	1.21					
1964	−1.5					
1965	1.3					
1966	−1.02					
1967	1.91			81,737		
1968	−1.12			3,279		
1969	2.68			59,350		
1970	0.928			6,515		
1971	0.152			15,903		
1972	−1.6			760		
1973	0.442			5,896		
1974	1.97			No data		
1975	−0.123			2,819		
1976	−1.93			658		
1977	−2.23			210		
1978	0.722			6,619		
1979	−1.05			No data		
1980	1.08	−1.22	−0.142	31,184	159,555	1,339
1981	−1.5	−0.651	−0.029	2,202	3,049	383
1982	3.04	−0.257	1.19	62,905	278,517	1,656
1983	5.91	−1.88	1.8	11,864	28,755	1,891
1984	0.492	−1.63	−1.56	7,408	36,774	4,924
1985	−1.67	0.222	−3.3	992	7,341	1,939
1986	1.71	−1.06	1.21	6,160	18,489	1,384
1987	−1.81	1.5	−0.68	1,520	2,428	1,785
1988	−1.97	0.335	−0.24	791	1,409	3,571
1989	−1.7	3.01	1.15	456	1,054	941
1990	−2.06	2.12	1.09	243	713	687
1991	−1.98	−1.43	2.33	134	188	351
1992	−1.88	2.18	−1.05	76	495	152
1993	0.006	−0.649	1.76	798	6,046	11
1994	−1.79	−0.06	0.379	545	1,424 ^a	414
1995	3.59	−1.57	0.885	8,205	354,186	252 ^a
1996	1.2	−0.451	−0.464	1,346	5,856	124 ^a
1997	1.6	0.627	1.25	690	7,638	1,432

TABLE 2. Continued.

Water year	Delta outflow PC1	Water temp PC1	Water transparency PC1	FMWT index	Bay Age-0 index	Bay Age-2 index
1998	3.11	-2.06	3.0	6,654	41,729	605
1999	0.414	0.989	0.529	5,243	58,510	748
2000	0.036	-0.511	0.322	3,437	14,202	704
2001	-1.61	0.659	-0.329	247	1,460	1,158
2002	-1.35	1.37	-0.271	707	9,652	1,752
2003	-0.468	0.81	-0.229	467	2,119	739
2004	-0.514	0.852	0.268	191	2,418	686
2005	-0.235	-0.956	0.048	129	4,538	569
2006	3.79	0.371	-0.411	1,949	12,148	188
2007	-1.73	0.799	-1.56	13	2,039	447
2008	-1.67	-0.361	0.341	139	3,681	204
2009	-1.57	0.149	-0.857	65	647	272
2010	-1.17	-0.247	-0.529	191	748	197
2011	1.21	-0.996	-3.51	477	7,833	305
2012	-1.53		0.365	61	1,284	733
2013	-1.38		-2.76	164	8,495	300

^aThe SFBS midwater trawl data were not collected in this year, but a value of zero was assumed in order to calculate the index.

collected by the SFBS. Water temperature data provided by CDFW were available for the years 1980–2011, and water transparency data were available for the period 1980–2013. We calculated monthly means of these two water quality variables for February–May (the indexing period for age-2 Longfin Smelt); during those months, age-0 Longfin Smelt are primarily in larval stages and have a center of distribution near the estuary's 2-psi isohaline (Dege and Brown 2004).

We summarized the Delta outflow, water temperature, and water transparency data separately by using principal components analysis (PCA) on the z -scored monthly means. We used PCA because sequential monthly means of flow and water quality variables can be closely correlated due to California's seasonal climate and high year-to-year variation in precipitation. This covariation makes it difficult to determine the averaging periods that best reflect the mechanistic linkages between environmental conditions and Longfin Smelt production. The first principal component (PC1) scores from each PCA (Table 2) were used as candidate predictors of Longfin Smelt recruits per spawner (a) in the regression analyses described below.

Derivation of recruits per spawner.—We represented a by using one of the following \log_e transformed ratios: (Bay Age 0 _{$t=0$})/(Bay Age 0 _{$t=2$}) for model 1abc; or (Bay Age 0 _{$t=0$})/(Bay Age 2 _{$t=0$}) for the two-life-stage models. Multiple linear regression analyses were performed to screen candidate predictors of a in an information-theoretic framework; to develop a smaller set of statistically defensible covariates, we evaluated predictors by using Akaike's information criterion corrected for small sample sizes (AIC_c). Regression analyses were conducted separately for each version of the response variable; separate regression analyses were also

conducted for tests involving water temperature variables (i.e., due to the smaller data set mentioned above). The candidate predictors and their assumed mechanistic meanings are described in Table 3.

During our analyses, we discovered that the relationship between Delta outflow and the two-life-stage version of $\log_e(a)$ was not linear. We used locally weighted scatter plot smoothing (LOESS) regression to depict the empirical shape of the relationship between these variables, and we found that the LOESS prediction was very similar to a second-order polynomial fit. We used AIC_c to confirm whether a polynomial fit was better supported than a linear fit; the polynomial regression was then used to predict a in our model variants with two life stages, as that equation was far simpler to implement than the LOESS equation.

Derivation of spawners per recruit.—In the two-life-stage models (2a, 2ab, 2ac, and 2abc), we estimated the relative abundance of age-2 Longfin Smelt to predict the relative abundance of the next generation of age-0 fish. We did this by deriving an estimator of survival from age 0 to age 2 ($S_{0 \rightarrow 2}$) and multiplying estimates of R by this survival term to estimate the next generation of spawners (i.e., S). We estimated $S_{0 \rightarrow 2}$ as the \log_e transformed ratio, (Bay Age 2 _{$t=0$})/(Bay Age 0 _{$t=2$}) (i.e., the two SFBS indices for the same cohort of fish). We then tested a set of candidate predictor variables for this ratio by following the same analytical approach used to predict a . For this analysis, we also included the birth-year FMWT index as a candidate predictor (Table 3) to evaluate whether juvenile survival might be density dependent, given similar findings for other SFE fishes (Kimmerer et al. 2000; Bennett 2005).

Derivation of the exponent term.—To evaluate whether density dependence also affected R , we imposed a carrying

TABLE 3. Variables used as candidate covariates for predicting Longfin Smelt recruits per spawner and survival from age 0 to age 2, presented with implied or explicit hypotheses associated with the use of each variable (PC1 = first principal component; Delta outflow = net Delta outflow index, Sacramento–San Joaquin River Delta; SFBS = San Francisco Bay Study, California Department of Fish and Wildlife [CDFW]; FMWT = Fall Midwater Trawl Survey, CDFW).

Explanatory variable	Data source	Hypothesis for relationship to recruits per spawner	Hypothesis for relationship to survival from age 0 to age 2
PC1 for Delta outflow (m ³ /s)	Dayflow ^a	Freshwater flow has a positive influence on survival of developing eggs, larvae, or early age-0 fish.	Freshwater flow has a positive influence on catchability of age-2 fish or survival from age 0 to age 2. ^b
PC1 for water transparency (Secchi depth, cm)	SFBS	Water transparency has a negative influence on survival of developing eggs, larvae, or early age-0 fish.	Water transparency has a negative influence on spatial distribution, catchability, or survival of age-2 fish.
PC1 for water temperature (°C)	SFBS	Intra-annual temperature change between winter and spring has a negative influence on survival of developing eggs, larvae, or early age-0 fish.	Intra-annual temperature change between winter and spring has a negative influence on spatial distribution, catchability, or survival of age-2 fish.
Mean water temperature (°C)	SFBS	Temperature has a negative influence on survival of developing eggs, larvae, or early age-0 fish.	Temperature has a negative influence on spatial distribution, catchability, or survival of age-2 fish.
Year		Dummy variable to indicate that an important variable with a continuous time trend had been missed (e.g., regional trends in Secchi depth; ammonium inhibition of phytoplankton growth rates)	Dummy variable to indicate that an important variable with a continuous time trend had been missed
Step-decline		Binary variable reflecting that the discontinuous time trend associated with some food web impacts (e.g., linked to the overbite clam invasion) had affected the survival of age-0 fish	Binary variable reflecting that the discontinuous time trend associated with some food web impacts had affected the survival of fish older than age 0
FMWT index	FMWT	Not applicable	The abundance of age-0 fish affects subsequent survival.

^aCalifornia Department of Water Resources (www.water.ca.gov/dayflow/).

^bThis hypothesis was tested by determining whether survival from age 0 to age 2 could be better predicted by including flows that occurred during spawning (e.g., the ratio of [Bay Age-2 index in 1982]/[Bay Age-0 index in 1980] tested for an influence of the flow during 1982). The influence of freshwater flow on the year in between birth and spawning was also tested but was not statistically significant and therefore is not reported in this paper.

capacity on the models identified with a “b” in their alphanumeric codes (Table 1). Inclusion or exclusion of the exponent term e^{-BS} allowed us to investigate whether interannual variation in environmental conditions was sufficient to produce a natural limit on the production of age-0 Longfin Smelt (models 2a and 2ac) or, conversely, whether an explicit carrying capacity provides for better-fitting models (models 1abc, 2ab, and 2abc). To do this, we found values for B that reflected empirical relative abundance maxima given our estimates of a . The maximum FMWT index for Longfin Smelt was 81,737 in 1967. The maximum a , indexed as (Bay Age 0_{*t=0*})/(Bay Age 0_{*t=2*}), was 59 in 1995. We rounded these values up slightly and found a B -value that, when multiplied by hypothetically increasing numbers of spawners, would limit the ability of

model 1abc to predict FMWT indices greater than 82,000 when a was equal to 60. Similarly, for the two-life-stage models, the maximum observed a (indexed as [Bay Age 0_{*t=0*}]/[Bay Age 2_{*t=0*}]) for the 10 years with the highest age-2 abundance was 168 in 1982. We rounded these values up slightly to calculate a B -value that would limit the ability of simulations from the two-life-stage models to predict FMWT indices greater than 82,000 when a was equal to 170.

Evaluating changes in model parameters assumed to result from changes in the San Francisco Estuary food web.—The feeding habits of juvenile Longfin Smelt in the SFE are basically undescribed, particularly for individuals foraging in mesohaline to marine waters (but see Hobbs et al. [2006] for data on larvae inhabiting the low-salinity zone). Hypothesized

changes in Longfin Smelt foraging success are either abrupt (e.g., due to the invasion of the overbite clam) or gradual and continuous (e.g., due to altered nutrient concentrations or changes in water transparency). We explored the predictive power of several temporal variables as surrogates for food web changes in the regression analyses (Table 3). Specifically, Kimmerer (2002b) used 1987 as a change point associated with invasion of the overbite clam; thus, we used a step-decline in that year as a predictor variable for a in model 1abc because fish that were spawned in 1987 would have been the first to be impacted by the high density of overbite clams detected in that year and thereafter. However, Thomson et al. (2010) found that evidence for a step-decline in Longfin Smelt relative abundance was strongest between 1989 and 1991. In our two-life-stage models, we tested step-declines in survival for 1989 and 1991; fish that were spawned in 1987 would have reached adulthood in 1989, so we would expect to see the overbite clam's first effects on $S_{0 \rightarrow 2}$ during that year. We also screened "year" as a predictor variable to test for the possibility that trends in survival were not well represented as step-declines (Table 3).

Spawner-recruit simulations.—Using each of the five alternative spawner-recruit models, we generated 58-year time series of predicted Longfin Smelt FMWT indices (1958–2013). We started each simulation by seeding 1956 and 1957 with the median observed FMWT index (798). The simulations then predicted all Longfin Smelt abundance indices from 1958 through water year 2013. The simulations were stochastic; each year of each simulation was iterated 1,000 times by using randomly drawn values of every regression parameter; the parameter estimate was assumed to be the mean, and the SE was used to scale the random variability. We restricted the simulations such that juvenile survival had to remain less than or equal to 1.0 (i.e., $\leq 100\%$). This is an extremely high upper limit on survival, but it is not greatly beyond the observed data: the index ratio we used to represent survival had a maximum empirical value of 0.98 in 2012.

Model variants were evaluated based on their ability to predict the empirical FMWT time series and based on the frequency with which they produced results that were clearly spurious. Each of the resulting 5,000 simulations was compared to the empirical FMWT indices by calculating the mean square error (MSE). Because FMWT data were available for 1967–1973, 1975–1978, and 1980–2013, those years were extracted from our simulations for use in this comparison. The central 95% of MSE estimates (i.e., 950 of the 1,000 iterations) were summarized by using box plots. We also evaluated the relative performance of model variants with the lowest MSEs by summarizing how frequently they predicted Longfin Smelt quasi-extinction, defined here as a FMWT index value less than 1 (the lowest empirical FMWT index value was 13 in 2007). Lastly, the time series predictions from the best-performing models were summarized graphically to more

explicitly illustrate their performance relative to the observed FMWT index time series.

RESULTS

The PC1s for Delta outflow, water transparency, and water temperature had eigenvalues of 3.5, 2.0, and 1.5, respectively, and explained 58, 50, and 37% of the variance in the time trends for these variables. The PC1 for Delta outflow and the PC1 for water transparency were highly concordant with multiple-month means of each year (Delta outflow: Pearson's product-moment correlation coefficient $r = 0.99$; water transparency: Pearson's $r = 0.98$). In contrast, the PC1 for water temperature was not correlated with mean water temperature (Pearson's $r = 0.17$) and instead reflected variation within years; the PC1 for temperature segregated the years with relatively large temperature changes between winter and spring (i.e., cool February–March and warm April–May) from the years with less seasonal variation. Therefore, we tested both the PC1 and the mean of water temperature as candidate predictor variables for a and $S_{0 \rightarrow 2}$.

Recruits per Spawner

The linear regression analyses that were used to screen candidate predictor variables indicated positive effects of Delta outflow PC1 and the binary step-change at 1987 as predictors of a for use in model 1abc (Table 4). The step-change variable was not significant ($P = 0.07$), and its sign was opposite our expectation (i.e., a was predicted to increase after 1987), but its inclusion was supported by the change in ACI_c . The final model selected was $\log_e(a) = [0.596 \pm 0.146(\text{Delta outflow PC1})] + [1.54 \pm 0.829(\text{step-decline in 1987})] - (1.39 \pm 0.748)$. The similar analyses for models 2a, 2ab, 2ac, and 2abc supported only the use of Delta outflow PC1 as a predictor of a ; in that case, a nonlinear fit was better supported than a linear fit (Table 4). The final model selected was $\log_e(a) = [-0.148 \pm 0.049(\text{Delta outflow PC1})^2] + [0.954 \pm 0.152(\text{Delta outflow PC1})] + [2.94 \pm 0.303]$; neither the linear fit nor the nonlinear fit showed evidence of a monotonic residual time trend (Figure 2).

Juvenile Survival

The linear regression analyses that were used to screen candidate predictor variables of $S_{0 \rightarrow 2}$ strongly supported the use of the birth-year FMWT index (Table 5), suggesting that juvenile survival is density dependent. All of the temporal variables we tested had P -values ≤ 0.052 . Interestingly, the 1989 step-decline performed poorly ($AIC_c = 103$) relative to "year" ($AIC_c = 99.6$) and the 1991 step-decline ($AIC_c = 95.4$). The final model selected was $\log_e(S_{0 \rightarrow 2}) = [-0.630 \pm 0.114 \cdot \log_e(\text{FMWT index})] - [1.68 \pm 0.474(\text{step-decline in 1991})] + [3.19 \pm 1.03]$.

TABLE 4. Results of linear regression analyses exploring candidate predictors of two versions of the recruits-per-spawner parameter for Longfin Smelt in the San Francisco Estuary. In model 1abc, the response variable was the natural logarithm of (Bay Age $0_{t=0}$)/(Bay Age $0_{t=2}$). In the other models, the response variable was the natural logarithm of (Bay Age $0_{t=0}$)/(Bay Age $2_{t=0}$). The cells for each candidate predictor variable report whether the variable was tested in each model step, its *P*-value when tested, and whether it was dropped in subsequent steps due to a nonsignificant *P*-value. Akaike's information criterion corrected for small sample sizes (AIC_c) is shown; AIC_c values from steps 1 and 2 cannot be compared with those from steps 3–5 due to the increase in sample size for the latter three steps. Step 5 in the two-life-stage models tested the quadratic flow relationship against the linear version tested in step 4. See Table 3 for descriptions of the predictor variables.

Statistic or predictor variable	Step 1	Step 2	Step 3	Step 4	Step 5
One-life-stage model (1abc)					
Adjusted R^2	0.26	0.26	0.31	0.32	Not applicable
Sample size	30	30	32	32	
AIC_c	124	122	127	125	
Flow PC1	0.001	0.01	0.0005	0.0003	
Temperature PC1	Not tested	0.81	Dropped	Dropped	
Water transparency PC1	Not tested	Not tested	0.56	Dropped	
Mean temperature	0.68	Dropped	Dropped	Dropped	
Year	0.41	Dropped	Dropped	Dropped	
Step-decline in 1987	Not tested	Not tested	0.06	0.07	
Two-life-stage models (2a, 2ab, 2ac, and 2abc)					
Adjusted R^2	0.43	0.46	0.41	0.44	0.55
Sample size	32	32	34	34	34
AIC_c	123	120	130	126	119
Flow PC1	0.00003	0.0007	0.00004	0.00001	6×10^{-7}
Temperature PC1	Not tested	0.33	Dropped	Dropped	Dropped
Water transparency PC1	Not tested	Not tested	0.46	Dropped	Dropped
Mean temperature	0.66	Dropped	Dropped	Dropped	Dropped
Year	0.70	Dropped	Dropped	Dropped	Dropped
Step-decline in 1987	Not tested	Not tested	0.62	Dropped	Dropped

Model Evaluation

The MSEs of most models overlapped at least somewhat, but two of the models (2a and 2ac) had notably poorer fits to

the FMWT data and thus produced higher MSEs 63–100% of the time (Figure 3). It therefore appears that an explicit carrying capacity on R is a useful model construct. The MSEs of models 1abc, 2ab, and 2abc overlapped strongly (Figure 4), suggesting that the models provided a similar fit to the FMWT data. Compared with models 2ab and 2abc, model 1abc showed low variation in MSE among model iterations (Figure 4), but that low variability reflected model 1abc's rapid predictions of quasi-extirpation in 100% of the iterations (Figure 5). Thus, although model 1abc appeared to have a relatively good fit to the FMWT data, this model was clearly unreliable. By design, models 2ab and 2abc were equivalent until the 1991 step-decline was implemented in the latter model. Thus, FMWT predictions based on these models were nearly equivalent from 1967 to 1990 (Figure 6). Median FMWT predictions using model 2ab were closer to the empirical data from 1991 to 1994; thereafter, the median predictions from model 2ab systematically overestimated the observed FMWT time series, whereas the median predictions from model 2abc more closely matched the empirical data (Figure 6). As a result, the median predictions of model 2abc provided a better overall representation of the empirical FMWT indices (compare panels D and B in Figure 6).

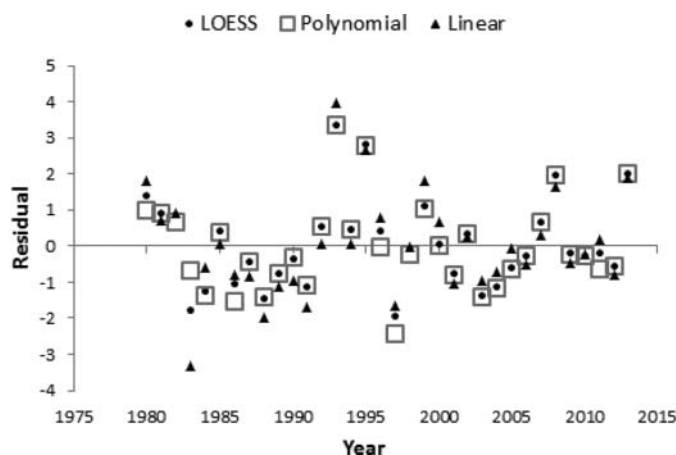


FIGURE 2. Time series of residuals from three regression analyses of the first principal component for the net Delta outflow index (December–May; Sacramento–San Joaquin Delta) in relation to the natural logarithm of Longfin Smelt recruits (age 0) per spawner (age 2) in the San Francisco Estuary (LOESS = locally weighted scatter plot smoothing).

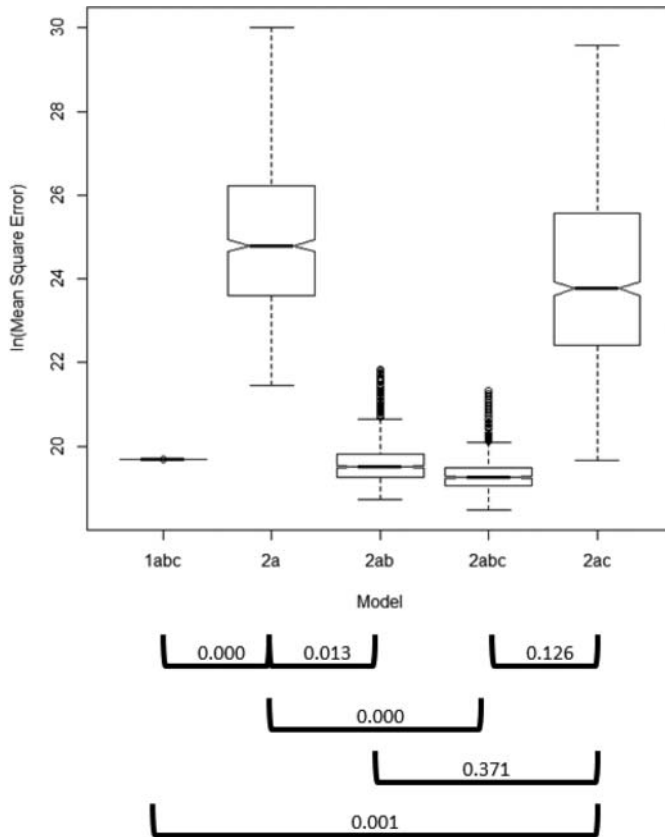


FIGURE 3. Notched box plot summarizing the mean square error (MSE; \log_e transformed) from the central 95% of predictions of the Longfin Smelt Fall Midwater Trawl Survey index using five alternative spawner-recruit models (see Table 1 for model descriptions). The ends of the box represent the first and third quartiles; the line inside the box represents the median; the ends of the whiskers represent a 95% confidence interval; outliers (open circles) are also shown. Where notches associated with MSEs from different models do not overlap, there is “strong evidence” that their medians differ (Quick R; www.statmethods.net/graphs/boxplot.html). The pairwise proportions of overlapping MSE predictions from 950 model iterations are provided below the box plot.

However, the propagated prediction error was high even for models 2ab and 2abc (Figure 6A, C), making it impossible to conclude that one outperformed the other. In addition, both model 2ab and model 2abc considerably underpredicted and were nonlinearly related to the FMWT indices (Figure 6B, D), suggesting that our e^{-BS} term was too strongly density dependent.

DISCUSSION

Relying on a few well-supported assumptions about Longfin Smelt life history and ecology in the SFE, our two best-supported Ricker models each incorporated two life stages in which productivity was density dependent during each life stage transition. In both models, recruits per spawner were related to freshwater flow rates. Apparently, despite differences in geographic extent, timing, and sampling gears, the SFBS and FMWT sampling programs detected the same general patterns in Longfin Smelt population dynamics, and our Ricker-model-based analyses indicated that there are at least two important—but temporally distinct—population dynamic effects: (1) an influence of freshwater flow on the production of age-0 fish; and (2) density-dependent and possibly declining juvenile survival.

Implications of Spawner-Recruit Dynamics

The influence of freshwater flow on the production of age-0 Longfin Smelt has been recognized for several decades (Stevens and Miller 1983; Jassby et al. 1995; Rosenfield and Baxter 2007), although we found evidence for nonlinearities that had not been identified before (Table 4; Figure 2). Depending on its timing and magnitude, freshwater flow was observed to have both positive and negative effects on the recruitment of age-0 Longfin Smelt in Lake Washington (Chigbu 2000). There was no evidence that the ratio we used to depict recruits per spawner

TABLE 5. Results of linear regression analyses exploring candidate predictors of survival from age 0 to age 2 for Longfin Smelt in the San Francisco Estuary. The response variable was the natural logarithm of (Bay Age $2_{t=0}$)/(Bay Age 0_{t-2}). The cells for each candidate predictor variable report whether the variable was tested in each model step, its P -value when tested, and whether it was dropped in subsequent steps due to a nonsignificant P -value. Akaike's information criterion corrected for small sample sizes (AIC_c) is shown; the AIC_c values from steps 1 and 2 cannot be compared with those from steps 3–6 due to the increase in sample size for the latter four steps. See Table 3 for descriptions of the predictor variables.

Statistic or predictor variable	Step 1	Step 2	Step 3	Step 4	Step 5	Step 6
Adjusted R^2	0.44	0.46	0.39	0.41	0.35	0.48
Sample size	30	30	32	32	32	32
AIC_c	94.1	91.5	102	99.6	103	95.4
\log_e (birth-year FMWT index)	0.00009	0.00003	0.00005	0.00004	0.0002	0.00006
Flow PC1	0.38	Dropped	Dropped	Dropped	Dropped	Dropped
Temperature PC1	Not tested	0.44	Dropped	Dropped	Dropped	Dropped
Water transparency PC1	Not tested	Not tested	0.78	Dropped	Dropped	Dropped
Mean temperature	0.99	Dropped	Dropped	Dropped	Dropped	Dropped
Year	0.005	0.004	0.01	0.01	Not tested	Not tested
Step-decline in 1989	Not tested	Not tested	Not tested	Not tested	0.052	Not tested
Step-decline in 1991	Not tested	Not tested	Not tested	Not tested	Not tested	0.001

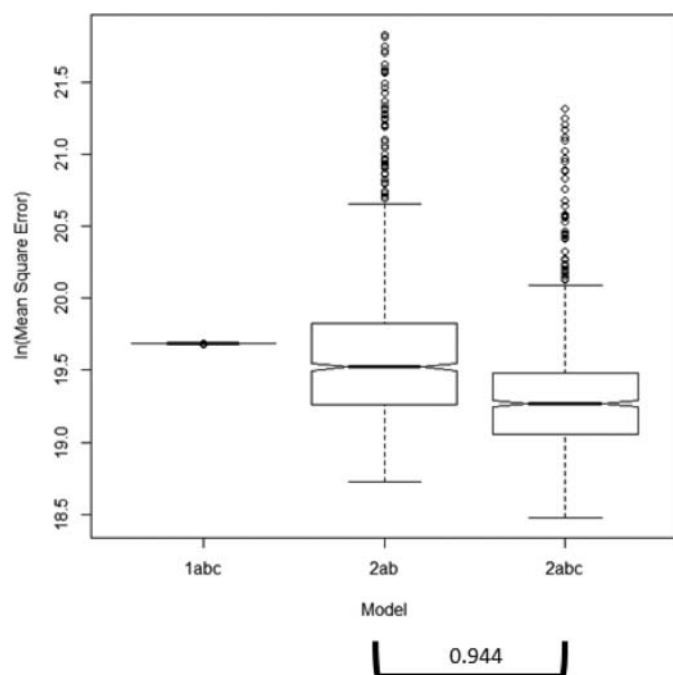


FIGURE 4. Notched box plot summarizing the mean square error (MSE; \log_e transformed) from the central 95% of predictions of the Longfin Smelt Fall Midwater Trawl Survey index based on the two best-supported spawner-recruit models as well as model 1abc (see Table 1 for model descriptions). The ends of the box represent the first and third quartiles; the line inside the box represents the median; the ends of the whiskers represent a 95% confidence interval; outliers (open circles) are also shown. Where notches associated with MSEs from different models do not overlap, there is “strong evidence” that their medians differ (Quick R; www.statmethods.net/graphs/boxplot.html). The pairwise proportion of overlapping MSE predictions from 950 iterations of models 2ab and 2abc is provided below the box plot.

has declined over time; thus, food web changes apparently have not impacted this life stage transition. However, there is some suggestion of a cyclical pattern among the residuals (Figure 2), which implies a potential ocean influence on Longfin Smelt recruitment in the SFE (*sensu* Feyrer et al. 2015). This possibility warrants further research. Improvements in the scientific understanding of when freshwater flow modulates Longfin Smelt production may help to reveal the flow-related mechanisms at work and the area where those mechanisms function. Focusing on the time and place where freshwater flow is likely to affect recruitment may assist Central Valley water project managers in optimizing freshwater flow rates so as to benefit Longfin Smelt production.

Implications for Juvenile Survival

We found no indication that freshwater flow moderated the survival of Longfin Smelt between age 0 and age 2, but we did detect evidence that survival during this life stage transition is density dependent (Table 5). In contrast to the production of age-0 fish, there was evidence for continuous declines or step-

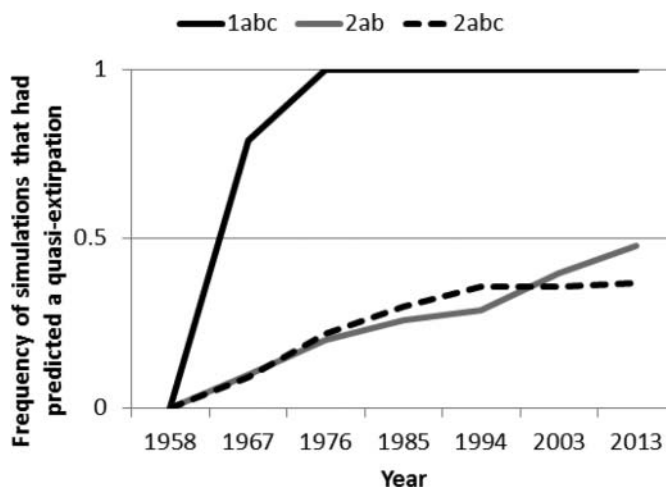


FIGURE 5. Time series showing the proportion of stochastic simulations of Longfin Smelt recruitment that predicted quasi-extirpation (defined as a predicted Fall Midwater Trawl Survey index < 1.0) from three alternative spawner-recruit models (see Table 1 for model descriptions).

declines (Table 5) in the survival of juvenile Longfin Smelt, which may reflect food-web-related impacts on this older life stage. Several other studies have detected one or more step-declines in the FMWT time series for Longfin Smelt (Kimmerer 2002b; Thomson et al. 2010). Rosenfield and Baxter (2007) noted an age-specific decline in production between age 0 and the age of spawning in Longfin Smelt; this decline may have occurred sometime during the severe drought of 1987–1994. Due to the propagation of variance, our spawner-recruit simulations were unable to robustly distinguish between the model that allowed survival rates to change (model 2abc) and the model in which survival did not change directionally (model 2ab; Figures 4, 6).

Constraining the timing and location of the density dependence and declining survival of Longfin Smelt may help to identify mechanisms that control these vital rates. The forces creating density-dependent survival and possible declines in that survival are most likely to operate during the period between (1) sampling that produces the age-0 abundance index (May–October in year 0) and (2) sampling that produces the age-2 abundance index (February–May). For most of the SFE Longfin Smelt, this part of the life cycle is primarily spent in mesohaline or marine waters (Rosenfield and Baxter 2007); therefore, the mechanisms affecting juvenile survival are more likely to operate in mesohaline or marine environments than in freshwater or low-salinity-zone waters.

Implications for Forage Fish Management in the San Francisco Estuary

Our results support some emerging generalizations about fish recruitment in the SFE. The results suggest that the general life cycle model for Longfin Smelt is very similar to

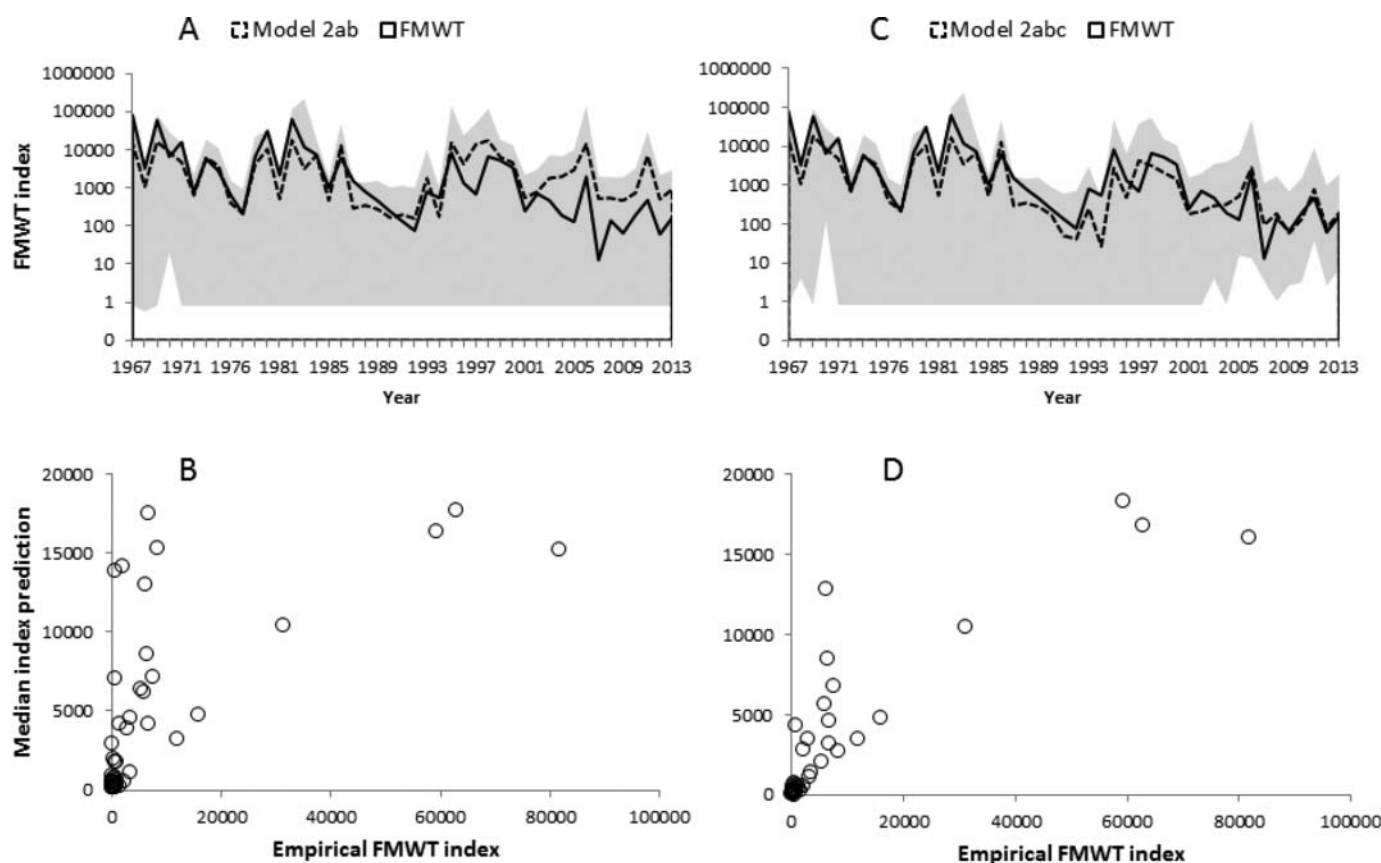


FIGURE 6. The Fall Midwater Trawl Survey (FMWT) index for Longfin Smelt, presented relative to predictions from the two best-supported spawner–recruit models: (A) the time series for the FMWT index (solid line), the median prediction (dashed line) from model 2ab (950 model iterations/year), and the range of the central 95% of predictions (gray shading); (B) scatter plot of the median FMWT index prediction from model 2ab in relation to the empirical FMWT index; (C) the time series for the FMWT index, the median prediction from model 2abc (950 model iterations/year), and the range of the central 95% of predictions; and (D) scatter plot of the median FMWT index prediction from model 2abc in relation to the empirical FMWT index.

Striped Bass *Morone saxatilis* (Kimmerer et al. 2000). For each of these species, freshwater flow variation has been linked to productivity early in the life cycle—an effect that is subsequently tempered by density-dependent survival during the juvenile life stage. Density-dependent survival may seem paradoxical in a declining fish species like the Longfin Smelt, but fisheries recruitment theory has demonstrated how a spawner–recruit relationship that appears to reflect density dependence can arise from food-web-related mechanisms that are unrelated to a population’s limitation of its own resource base (Walters and Juanes 1993).

The SFE population of Longfin Smelt is in the queue for potential listing under the ESA (USOFR 2012). By disaggregating the life-stage-specific constraints on population dynamics, our results can help to inform a future ESA listing decision for Longfin Smelt and can assist in development of the accompanying recovery plan if the population is listed. Perhaps more importantly, the present study helps to identify the portion of the Longfin Smelt’s life cycle during which productivity is limited and may be changing over

time, thus potentially informing efforts to research and monitor recruitment limitation in this species. The persistence of Longfin Smelt and several other native forage fish species in the SFE (and potentially the predators that historically relied on these populations; e.g., Striped Bass and California Halibut *Paralichthys californicus*) depends on taking steps to improve the productivity of these fishes.

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