

Population Dynamics and Distribution Patterns of Longfin Smelt in the San Francisco Estuary

JONATHAN A. ROSENFELD*¹

Center for Integrated Watershed Science and Management, Academic Surge,
University of California, Davis, California 95616, USA

RANDALL D. BAXTER

California Department of Fish and Game, 4001 North Wilson Way, Stockton, California 95205-2486, USA

Abstract.—The San Francisco Estuary supports several endemic species of fish and the southernmost populations of other species. Many of these native species and populations are imperiled or have experienced recent population declines that indicate a general decline in the estuary's capacity to support pelagic fish species. We studied the distribution and abundance of one of the estuary's native species, longfin smelt *Spirinchus thaleichthys*, using data from three long-term aquatic sampling programs. Each of the sampling programs we studied revealed a substantial reduction in the abundance of longfin smelt. These trends support the idea that the estuary's capacity to support pelagic fish species has been significantly reduced over the past three decades. Longfin smelt in the estuary displayed consistent patterns in relative abundance and distribution during their life cycle. We also found significant, but weak, spatial autocorrelation among sampling stations. These patterns in distribution reveal differential habitat use and migratory behavior. Managers can use these insights into longfin smelt distribution patterns to improve interpretation of sampling program results.

The San Francisco Estuary is one of the largest estuaries in North America, covering approximately 1,235 km². The estuary drains about 40% of California's land area and receives almost 50% of the state's runoff (Lehman 2004). This ecologically significant ecosystem supports a number of endemic fish species (e.g., splittail *Pogonichthys macrolepidotus* and delta smelt *Hypomesus transpacificus*) and represents the southern limit of the breeding range for several other species (e.g., Chinook salmon *Oncorhynchus tshawytscha* and white sturgeon *Acipenser transmontanus*). This estuary is also home to several large marshes, including Napa Marsh and Suisun Marsh. The latter covers approximately 340 km² and is the largest contiguous brackish-water marsh on the Pacific coast of the United States.

This estuarine ecosystem has been and continues to be altered by a variety of human activities. Depending on the time of year, state and federal water export operations may remove as much as 65% of the freshwater flow to the estuary (Sommer et al. 2007) and these exports entrain large numbers of pelagic fish species (Brown et al. 1996). The introduction of

aquatic species is rampant in this estuary; some of the more than 200 established invaders have altered patterns of nutrient and energy flow through the ecosystem (Cohen and Carlton 1998; Feyrer et al. 2003). For example, the introduction and explosive population growth of an invasive mollusk, the Amur clam *Corbula amurensis*, has been implicated in the dramatic reduction in food resources available to juvenile pelagic fishes in this estuary (Alpine and Cloern 1992; Orsi and Mecum 1996).

Native fish species in the San Francisco Estuary have been severely affected by these and other perturbations (Moyle 2002). The delta smelt is protected under the federal Endangered Species Act (ESA) and unique populations of several other species (including two runs of Chinook salmon, steelhead *O. mykiss*, and green sturgeon *A. medirostris*) are also listed as endangered or threatened under the ESA. Following the end of the most recent drought period, populations of many native and nonnative species remained depressed despite favorable freshwater flow conditions (Moyle 2002; Sommer et al. 2007), leading to speculation that the estuary has experienced a fundamental change in its carrying capacity for pelagic fishes (Kimmerer 2000). The causes of this decline in the pelagic fish community have not been determined. One difficulty in isolating these causes is that some major changes in physical conditions (such as freshwater inflow and export volumes) and biological conditions (such as the species assemblage) have

* Corresponding author: jarosenfield@gmail.com

¹ Present address: Aquatic Restoration Consulting, 1736 Carleton Street, Berkeley, California 94703, USA.

Received June 21, 2006; accepted June 24, 2007

Published online November 5, 2007

occurred simultaneously. For example, the introduction of the Amur clam in late 1986 (Carlton et al. 1990) corresponded to the onset of a major drought that began in 1987.

The longfin smelt *Spirinchus thaleichthys* is among the native species in the San Francisco Estuary that appear to have declined significantly (Baxter 1999; Moyle 2002); despite this decline, they remain among the most abundant pelagic fish species in the estuary (Sommer et al. 2007). In some months these fish can be found throughout the estuary's brackish-water and marine habitats. Because of their relative abundance and broad distribution, the longfin smelt is believed to be an important component of the estuarine food web and a valuable indicator of ecosystem function (USFWS 1996; Moyle 2002).

Several studies have attributed the population dynamics of this longfin smelt population to changes in physical or biological conditions in the estuary. For example, a positive relationship between longfin smelt abundance and freshwater flow through the estuary has been documented (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002b). Thus, freshwater storage and export (to supply urban and agricultural demands in southern California) have been implicated as both a direct and an indirect source of mortality driving this population decline (Moyle 2002). Kimmerer (2002b) presented evidence that primary productivity sequestration by the invasive Amur clam may have negative effects on longfin smelt production. These studies were based on an index of longfin smelt abundance derived from results of the California Department of Fish and Game (CDFG) fall midwater trawl pelagic-community sampling program.

We analyzed longfin smelt population trends based on data from three long-term sampling programs in this estuary. We investigated whether the abundance of longfin smelt juveniles and prespawning adults recovered to historic levels following the end of the 1987–1994 drought. In addition, we used data from two sampling programs that operate throughout the year to investigate patterns in longfin smelt distribution throughout their life cycle. Finally, we assessed patterns of spatial and temporal autocorrelation in these data. The patterns we detected in these data can be used to improve understanding of longfin smelt population dynamics in this estuary.

Study Species

The longfin smelt is a small (~90–110 mm standard length [SL] at maturity), semelparous, pelagic fish that usually has a 2-year life cycle (Moulton 1974). Anadromous and resident populations are native to the Pacific Coast of North America. The San Francisco

Estuary population is the southernmost in the species' range and is, by far, the largest known population in California (Moyle 2002). Young juveniles feed primarily on copepods, whereas older juveniles and adults feed principally on opossum shrimp, *Acanthomysis* spp. and *Neomysis mercedis*, when available (Hobbs et al. 2006). The latter species has declined substantially in the estuary since the early 1970s (Orsi and Mecum 1996); when opossum shrimp are less available, adult longfin smelt return to feeding primarily on copepods (Feyrer et al. 2003; Hobbs et al. 2006). Substantial published research on longfin smelt ecology and behavior comes from a resident population in Lake Washington, Washington (e.g., Dryfoos 1965; Moulton 1974; Chigbu and Sibley 1994; Chigbu et al. 1998; Chigbu 2000); the behavior and ecology of this species in the San Francisco Estuary are less well understood.

Study Area

The San Francisco Estuary includes (1) "the Delta," a broad network of tidally influenced channels formed by the confluence of the Sacramento and San Joaquin rivers; (2) open water embayments downstream from this confluence and inland from the Golden Gate Bridge; and (3) large brackish marshes (Figure 1). The Sacramento River, which drains much of northern California, provides approximately 85% of the freshwater inflow to the estuary (Kimmerer 2002a). The San Joaquin River, which drains the central Sierra Nevada Mountains, contributes most of the remaining freshwater flow, followed by smaller tributaries to the estuary. Four embayments (Suisun, San Pablo, Central, and South bays) constitute the open-water regions of the estuary (Figure 1). The estuary contains several large, tidally influenced brackish marshes, including Suisun Marsh, located north of Suisun Bay.

Methods

Field Sampling

Numerous long-term sampling programs monitor the composition of the San Francisco Estuary's fish community (Honey et al. 2004). Data from these sampling programs are also used to monitor the abundance and distribution of native fish species considered at risk and important sport fishes. We compared data from three long-term sampling programs that regularly catch juvenile and adult longfin smelt to describe and analyze changes in abundance and distribution of this population over the past three decades.

The California Department of Fish and Game San Francisco Bay Study (hereafter, Bay Study) began monthly sampling at 35 stations in January 1980 (Figure 1; Armor and Herrgesell 1985). Additional

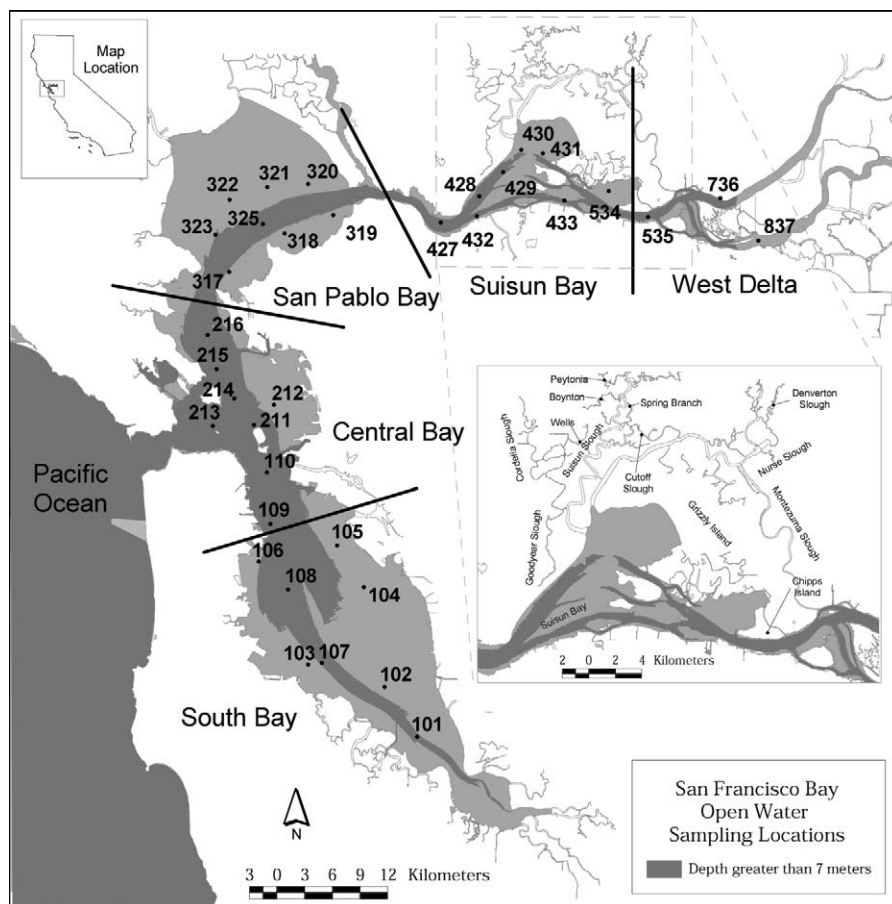


FIGURE 1.—Map of the San Francisco Estuary distinguishing depths of at least 7 m (dark shading) from depths less than 7 m (light shading). Straight lines indicate divisions of the estuary's embayments. Numbers identify Bay Study sampling stations. Sloughs sampled by the Suisun Marsh Survey and important geographic features are named in the inset. The state's Fall Midwater Trawl Survey sampled from September to December in San Pablo Bay, Suisun Bay, and the West Delta.

sampling stations were added over time, but we used data only from the original 35 stations. The Bay Study sampled fishes using both a midwater trawl (MWT) and an otter trawl (OT) at each station in every month of the year (Table 1), although, for a variety of reasons, no sampling occurred in 21 months and only one net was deployed in 14 other months (Figure 2). All fish were identified and measured to the nearest 1 mm fork length (FL). When more than 50 longfin smelt were caught in a single tow, the total number caught was counted and 50 fish were selected arbitrarily and measured; the length distribution of the 50 individuals measured was applied to the entire sample.

The University of California–Davis's Suisun Marsh Survey began monthly sampling in January 1980 (Matern et al. 2002). From the survey's inception to the present, sampling occurred in all but 11 months at

from 4 to 28 stations (Figure 2). Although more sampling stations were added through time, we include here only data from the 17 stations sampled continuously since 1980. The Suisun Marsh Survey used an otter trawl to sample fish at each sampling station (Table 1). The net was towed for 10 min in large sloughs and 5 min in smaller sloughs at approximately 4 km/h. All fish were identified to species and all those 30 mm SL and longer were measured. To compare results of the Suisun Marsh Survey with those of the Bay Study, we converted SL to FL using the following conversion: $FL = 1.07 \times SL$ (CDFG, unpublished data). Longfin smelt less than 40 mm FL were often caught by the Bay Study and Suisun Marsh Survey, but fish this small were not consistently retained in the mesh used in the Bay Study's nets. To facilitate comparison between the studies, only fish 40 mm FL

TABLE 1.—Sampling gear and methodology employed by the three long-term fish community sampling programs in the San Francisco Estuary that were analyzed in this study (max. = maximum, min. = minimum).

Sampling program	Sampling intensity	Net description
Bay Study Midwater Trawl	35 stations located in open water throughout the estuary, 1980–2001; year-round, monthly ^a	Mouth = 13.4 m ² ^b ; max. mesh size = 20.3 cm; min. mesh size = 1.3 cm
Bay Study Otter Trawl	35 stations located in open water throughout the estuary, 1980–2001; year-round, monthly ^a	Mouth = 3.4 m in width ^b ; max. mesh size = 2.5 cm; min. mesh size = 1.3 cm
Suisun Marsh Survey (otter trawl)	4–28 stations (mean = 17.9) located in the channels and sloughs of Suisun Marsh, 1980–2001; year-round, monthly ^a	Mouth = 3.3 m ² (4.4 × 0.75 m); max. mesh size = 3.5 cm; min. mesh size = 0.6 cm
Fall Midwater Trawl	57–113 stations (median = 88) located in open water throughout the estuary's three northern embayments	Mouth = 13.4 m ² ^b ; max. mesh size = 20.3 cm; min. mesh size = 1.3 cm

^a General sampling period; for actual months of sampling activity, see Figure 2.

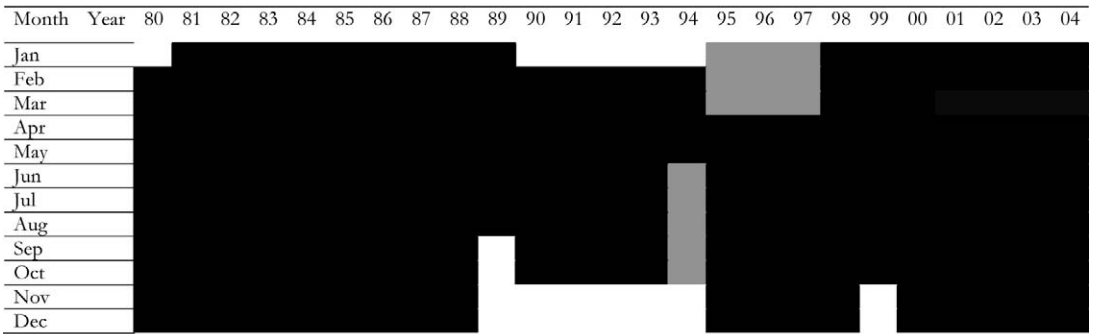
^b Estimated average when fishing under tension.

and longer were used in our analyses of Bay Study and Suisun Marsh Survey data.

The California Department of Fish and Game's Fall Midwater Trawl Survey (FMWT) began sampling at 100 stations in 1967 (Stevens 1977), but individual longfin smelt were not measured consistently (thereby precluding age-class designation) until the mid-1970s. Sampling occurred monthly between September and December of each year at from 57 to 113 (median = 88)

fixed locations in the San Pablo Bay, Suisun Bay, and the western Delta (Figure 1). Gear used by the FMWT was nearly identical to that used by the Bay Study's MWT and it was deployed in a similar manner (Table 1). Because the FMWT did not survey the longfin smelt population over the entire year or the entire geographic extent of the estuary, we could not use these data to uncover estuary-wide, year-round patterns in distribution.

(A) Bay Study Sampling Program



(B) Suisun Marsh Survey

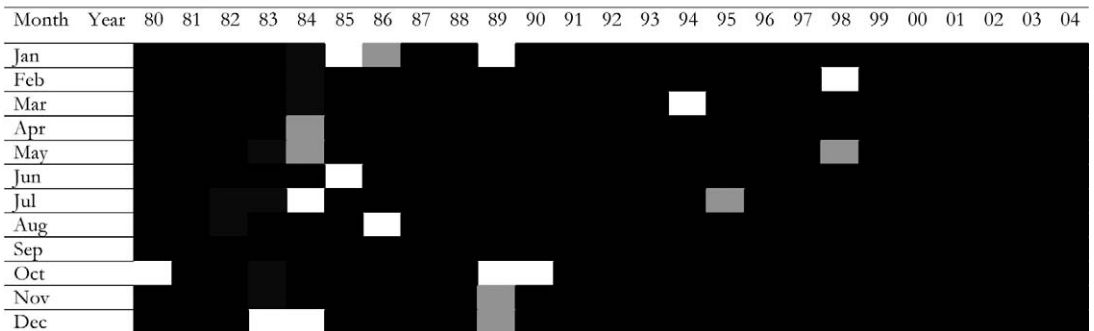


FIGURE 2.—Sampling over time in (A) the Bay Study and (B) the Suisun Marsh Survey. Black cells indicate sampling at most or all 35 Bay Study sampling stations by both otter and midwater trawls or sampling at most or all of the 17 sites sampled in Suisun Marsh. Gray cells indicate months when only the otter trawl was used in the Bay Study or months when fewer than 13 sites were sampled in Suisun Marsh. White cells indicate no sampling.

TABLE 1.—Extended.

Sampling program	Net deployment and tow	Tow duration	Effort units and calculation
Bay Study Midwater Trawl	Cable out: depth = 5:1; oblique tow with current	12 min	Catch/10,000 m ³ water sampled
Bay Study Otter Trawl	Cable out: depth = 5:1; horizontal along bottom against current	5 min	Catch/10,000 m ² (= net width × distance towed)
Suisun Marsh Survey (otter trawl)	Horizontal along bottom	10 min (large sloughs); 5 min (small sloughs)	Catch/min
Fall Midwater Trawl	Cable out: depth = 5:1; oblique tow with current	12 min	Catch/rawl

Age and Life Stage Classification

We determined the age of individual longfin smelt based on FL and month of capture. For every month in almost every year, the length-frequency distributions of longfin smelt caught by the Bay Study were distinctly bimodal (Baxter 1999). We interpreted each length-frequency mode as a different age-class as did Dryfoos (1965) and Moulton (1974) based on similar patterns of size-distribution in a landlocked longfin smelt population. We used visual examination to identify length limits that separated the two modes (age-classes) in each month. Based on the timing of appearance of sexually mature longfin smelt and monthly abundance of yolk sac larvae (Baxter 1999), we assigned January as the first month of life (age 1 month), although it was clear that some fraction of each cohort hatched after January. Analyses were conducted using one of three age scales: age in months, 3-month age-groups (e.g., age 4–6 months), or annual age-classes. Juvenile longfin smelt were first detectable by the Bay Study in April (see next section); therefore, fish in their first year of detectability (ages 4–15 months) were classified as age-class 1 and those in their second year of detectability (ages 16–27 months) were classified as age-class 2.

Trends in Longfin Smelt Annual Abundance and Distribution

We studied historical trends in annual longfin smelt abundance using indices (which weighted catch per unit effort [CPUE] by the area sampled) from the FMWT and the Bay Study's MWT and CPUE data from the Suisun Marsh Survey. The traditional FMWT index combines fish of all age classes into a single metric. As a result, the traditional index reflects juvenile population size because juveniles outnumber older fish by approximately an order of magnitude. For each survey program, we created separate abundance measures for age-class 1 and age-class 2 longfin smelt. Following the traditional calculation of the FMWT index, we (1) averaged longfin smelt density (as measured by catch per trawl) in each month at stations

within each of 17 predefined regions, (2) expanded those average regional densities to reflect the proportional size of the different regions, and (3) summed the regional subtotals to create a monthly index. We averaged index values across months of the survey to generate an annual abundance index. Following a procedure similar to that applied to FMWT data, we calculated age-class-specific abundance indices from Bay Study data collected during September–December of each year. Suisun Marsh survey data were converted to catch per minute (CPM) to account for differences in sampling effort between large and small sloughs, and were averaged across months within each year.

We investigated whether the population levels of either age-class of longfin smelt changed during and following an extreme drought that lasted from 1987 to 1994. Bay Study sampling was incomplete during the drought period (Figure 2) so we could only compare pre- and postdrought periods for those data. Nonparametric techniques (Kruskal–Wallace analysis of variance [ANOVA] on ranks for FMWT and Suisun Marsh data, Mann–Whitney *U*-test for Bay Study data) were employed to assess the significance of changes in abundance. To account for the documented relationship between abundance and freshwater outflow (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002b), we conducted an analysis of covariance (ANCOVA) with age-class 1 abundance indices (or CPM for the Suisun Marsh Survey) as the dependent variable, a categorical variable representing three time periods (predrought, drought [1987–1994], and postdrought), and an estimate of freshwater outflow (calculated after Jassby et al. 1995) as a covariate. Bay Study and FMWT data were log transformed and Suisun Marsh CPM data were arcsine-transformed so that residuals would meet the assumptions of parametric statistics.

We assessed the long-term changes in age-class 2 abundance metrics after accounting for the potential effect of the abundance of age-class 1 longfin smelt in the previous year. We conducted ANCOVAs with age-class 2 abundance metrics as the dependent variable, time period as the categorical variable, and the previous

year's age-class 1 abundance metric as a covariate. Bay Study and FMWT data were log transformed and Suisun Marsh CPM data were arcsine-transformed so that residuals would meet the assumptions of parametric statistics. For uninterrupted data series, residuals from the ANCOVA were analyzed using partial correlations to determine whether significant temporal autocorrelation was present.

An ANCOVA on Suisun Marsh age-class 2 data with age-class 1 CPM as the covariate produced nonnormal residuals despite several efforts to transform the data (Lillifors test: $P < 0.01$). We substituted FMWT age-class 1 index values as the covariate in this model; residuals met the assumptions of parametric statistics in the revised model. Use of FMWT age-class 1 index values as a covariate for Suisun Marsh age-class 2 data were justified because age-class 2 longfin smelt are believed to move into the marsh from the pelagic waters sampled by the FMWT (Moyle 2002).

We also analyzed the trends in longfin smelt geographic distribution by analyzing an estuarywide percent presence metric that incorporated results from the Suisun Marsh Survey and Bay Study. Because the Bay Study and the Suisun Marsh Survey sample very different habitats with different spatial intensities, it is difficult to compare catch data between these programs within years. However, a combined percent presence metric allowed us to assess changes across years in the percentage of sites where longfin smelt were detected. The Bay Study usually sampled each site twice (once each with the OT and MWT), so, for this analysis, we measured percent presence as the number of unique stations sampled within each month at which longfin smelt were caught by at least one net. This number was added to the number of stations at which longfin smelt were caught by the Suisun Marsh Survey. The total number of sites where longfin smelt were detected in each month was divided by the number of unique stations sampled by the two sampling programs in that month (median = 51 sites, mode = 52 sites). Annual average percent presence was calculated separately for each age-class as the mean of the monthly percent presence values. The Bay Study did not sample the estuary consistently during the early 1990s (Figure 2); thus, we analyzed changes in the spatial extent (percent presence) of longfin smelt by comparing years before and after the 1987–1994 drought. Age-class 1 annual percent-presence results were analyzed using ANCOVA with freshwater flow as a covariate. Age-class 2 annual percent-presence results were analyzed using ANCOVA with the previous year's age-class 1 distribution as a covariate. In each case percent-presence results were arcsine-transformed to produce residuals that met the expectations of parametric

statistics. For all ANCOVAs, type III error decomposition was employed (Engqvist 2005).

Analyses of Distribution Throughout the Life Cycle

We used data from the Bay Study and Suisun Marsh Survey, which both sample throughout the year, to describe longfin smelt distribution patterns within and across years. We used two measures to describe longfin smelt distribution throughout the estuary: density (i.e., CPUE) and percent. Bay Study data expressed CPUE as number of fish per unit volume of water filtered for the MWT and as number per unit area of bottom swept for the OT (Table 1). The Suisun Marsh Survey expressed CPUE as catch per minute trawling (CPM). We also used presence-absence measures in our study because they are less variable between sites, months, or years than mean CPUE measures, which can be unduly influenced by years, months, or individual trawls that produce extremely high catches. For species like longfin smelt that are widespread and not very abundant, geographic distribution is expected to correlate with abundance (Hayek and Buzas 1997). For the Suisun Marsh Survey and separately for each of the Bay Study's two nets, percent presence was calculated by dividing the number of trawls in which longfin smelt were present by the number of trawls conducted for that period (e.g., month, 3-month period, or year, depending on the analysis).

Bathymetric distribution.—We used univariate repeated-measures ANOVA (von Ende 2001) on Bay Study MWT and OT data to analyze the distribution of longfin smelt with regard to habitat depth throughout their life cycle. Log-transformed mean CPUE was the dependent variable. By treating cohorts as blocks, repeated-measures ANOVA eliminated the potentially confounding effects of interannual variance in total population size. Habitat depth was incorporated into the model as a between-subjects (treatment) factor. Habitat depth was represented by a binary indicator of sampling station depth because Bay Study sampling localities were originally chosen, in part, to represent channel or shoal habitats and, as a result, half of the sampling stations occur in habitats at least 7 m deep ("channel stations") while the other half occur in habitats less than 7 m deep ("shoal stations"; Figure 1). Preliminary analysis showed that the relationship between habitat depth and catch was nonlinear, making linear analysis of a continuous depth measure inappropriate. Although sites were not assigned to depth categories at random, channel and shoal sampling stations were interspersed across the length and width of the estuary (Figure 1); thus, statistical comparisons between depth categories were not likely to be confounded by pseudoreplication (Hurlbert 1984).

Eight 3-month age categories represented repeated measures (within-subjects factor) within each longfin smelt cohort. Within-subjects main effects and interactions were assessed with Greenhouse–Geisser adjusted significance values to account for deviations from the assumption of sphericity (von Ende 2001). Because the Bay Study OT and MWT sampled the same stations at the same time, we employed a Bonferroni adjustment to α (adjusted $\alpha = 0.025$) to account for multiple tests of the same hypothesis.

Density and percent presence throughout the life cycle.—To describe intracohort population dynamics, we graphed mean monthly CPUE and percent presence in the Bay Study's OT and MWT and for the Suisun Marsh Survey. To analyze whether CPUE and percent presence of the longfin smelt population changed consistently throughout the life cycle, we conducted univariate repeated-measures ANOVA on CPUE and percent-presence data in each month of their life cycle. By treating cohorts as blocks, repeated-measures ANOVA eliminated the potentially confounding effects of interannual variance in total population size. For this analysis we only used data from the Bay Study's OT because that dataset contained many more cohorts that were completely sampled (i.e., sampling was conducted in every month that longfin smelt were susceptible to the net) than did the Bay Study's MWT dataset (Figure 2) and because the Suisun Marsh Survey did not catch age-class 1 or age-class 2 longfin smelt in many years. The OT data set contained 12 cohorts that were sampled every month from April (age 4 months) through the second December of their life cycle (age 24 months). Six additional cohorts were missing up to 3 months of sampling during this period (Figure 2), so we interpolated density and percent presence for the missing months using adjacent months. We were, thus, able to analyze density and percent presence over 21-month periods for 18 longfin smelt cohorts. Percent-presence data were arcsine-transformed and CPUE were log transformed before this analysis. Within-subjects main effects were assessed with Greenhouse–Geisser adjusted significance values to account for deviations from the assumption of sphericity (von Ende 2001). All of the statistical analyses described above were performed with Statistica version 6.1 (StatSoft 2002).

We analyzed Bay Study OT and MWT data to determine whether data from sampling stations were spatially autocorrelated. The practice of averaging CPUE results across sampling stations within predefined regions reflects an implicit assumption that nearby sampling localities are more likely to produce similar catches (i.e., correlated results). This assumption has not been tested and, if adjacent sites produce

correlated results, the extent of this correlation is undocumented. We used Mantel's Tests (XLSTAT 2007, version 2007.4, Addinsoft 2007) to detect significant correlations between a matrix of site-to-site correlations in CPUE and a physical distance matrix for both age-classes of longfin smelt caught in the Bay Study sampling program. Bay Study data were used because this sampling program operates over a much larger portion of the estuary than either the FMWT or Suisun Marsh Survey. We created a correlation matrix among sampling stations consisting of pairwise Kendall's correlations of total catches at each site between September and December of each year. To eliminate potentially spurious correlations caused by interannual fluctuations in total abundance of longfin smelt, sampling stations were ranked according to catches within each year (Fortin and Gurevitch 2001). This correlation matrix was then compared with a matrix of the physical distance between sampling localities and the observed correlation between the two was compared with a distribution generated from 10,000 permutations (random resampling) of the data. Spatial autocorrelation would be indicated by a significant negative correlation between these two matrices.

Results

Trends in Longfin Smelt Annual Abundance and Distribution

Freshwater outflow through the Delta was significantly lower during the 1987–1994 drought than during the pre- or postdrought periods (Kruskall–Wallace ANOVA, post hoc multiple comparison: $P = 0.002$ in both cases); no significant difference was detected between the predrought and postdrought periods ($P = 1.0$; Table 2; Figure 3). Catches of age-class 1 longfin smelt changed significantly across time periods in each sampling program (Table 2; Figure 3). The percentage of stations at which age-class 1 longfin smelt were caught did not change significantly between predrought and postdrought periods ($P = 0.132$; Table 2). Analyses of covariance that accounted for the effect of freshwater outflow on age-class 1 abundance confirmed results of the nonparametric analyses (Table 3). The relationship between freshwater flow and dependent variables did not change significantly across time periods (ANCOVA, time period \times freshwater flow interaction; Table 3); therefore, we employed ANCOVA models that assumed homogeneity of slopes across time periods (Engqvist 2005; StatSoft 2006). Bay Study age-class 1 abundance index scores were significantly lower in the postdrought period than in the predrought period (ANCOVA, time period main effect: $P = 0.027$). In the FMWT sampling program,

TABLE 2.—Summary of changes in the abundance and geographic distribution of longfin smelt and winter–spring freshwater outflow in the San Francisco Estuary across three time periods (before, after, and during the 1987–1994 drought). Kruskal–Wallace ANOVA *H*-tests are presented for the Fall Midwater Trawl (FMWT) and Suisun Marsh Survey because these sampling operations occurred in each of the three time periods. Bay Study and estuarywide percent presence metrics were measured only in the pre- and postdrought periods and were analyzed using Mann–Whitney *U*-tests.

Variable	Time periods	Test score ^a	<i>P</i>
FMWT 1 index	3	$H_{2,27} = 9.833$	0.007
FMWT 2 index	3	$H_{2,27} = 12.54$	0.002
Suisun age-class 1 catch/min	3	$H_{2,25} = 13.558$	0.001
Suisun age-class 2 catch/min	3	$H_{2,25} = 11.219$	0.004
Bay Study age-class 1 index	2	$U_{7,9} = 12$	0.042
Bay Study age-class 2 index	2	$U_{8,8} = 9$	0.015
Estuarywide age-class 1 percent presence	2	$U_{6,6} = 8$	0.132
Estuarywide age-class 2 percent presence	2	$U_{6,7} = 0$	<0.001
Delta freshwater flow (Jan–Mar)	3	$H_{2,29} = 8.575$	0.014

^a Subscripts indicate degrees of freedom.

age-class 1 abundance index values during the drought period were significantly lower than those in either the pre- or postdrought periods (Tukey’s HSD post hoc multiple comparison: $P < 0.001$ and $P = 0.007$, respectively); abundance index values in the postdrought period were significantly lower than those observed during the predrought period ($P = 0.02$). Estuary-wide percent presence of age-class 1 longfin smelt was not significantly different between predrought and postdrought periods even after accounting for changes in freshwater flow ($P = 0.078$; Table 3). Residuals from each ANCOVA model satisfied the assumptions of parametric statistical analyses. We did not determine the effect of freshwater flow on catches of age-class 1 longfin smelt in the Suisun Marsh Survey because ANCOVA on Suisun Marsh age-class 1 CPM data produced nonnormal residuals despite several transformation attempts (Lillifors test: $P < 0.001$). Partial autocorrelations of residuals from the FMWT ANCOVA revealed no significant autocorrelation at any time step.

Catches of age-class 2 longfin smelt changed significantly across time periods in each of the three sampling programs (Table 2; Figure 3). The annual average percentage of sampling stations at which age-class 2 longfin smelt were caught declined from a median of 19.4% during the predrought period to 11.6% in the postdrought period (Mann–Whitney *U*-test: $P = 0.001$; Table 2; Figure 4).

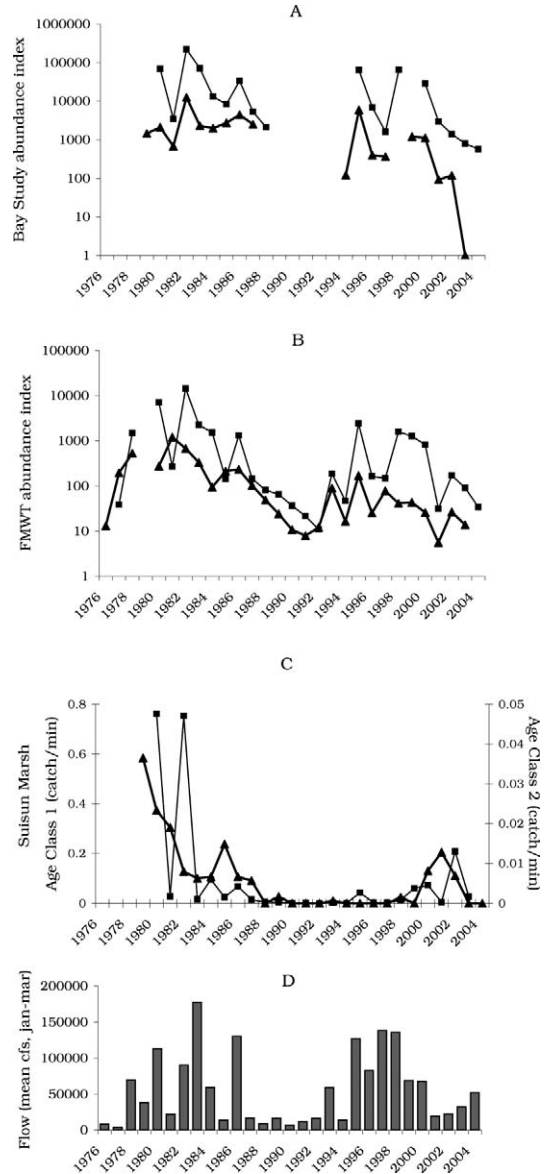


FIGURE 3.—Abundance of longfin smelt as measured by (A) the Bay Study, (B) the Fall Midwater Trawl Survey (FMWT), and (C) the Suisun Marsh Survey compared with (D) the winter–spring freshwater outflow from the San Joaquin–Sacramento Delta (1 cfs = 0.0283 m³/s). Squares represent abundance indices for age-class 1 fish, triangles those for age-class 2 fish. In (A) and (B), the scales of the y-axes are logarithmic. In (C), the scale to the left represents the catch per minute of age-class 1 longfin smelt whereas the scale to the right represents the catch per minute of age-class 2 longfin smelt. The values for age-class 2 longfin smelt are plotted in the year they were spawned (i.e., 1 year before they were sampled) directly underneath the age-class 1 population from which they were derived.

TABLE 3.—Analyses of covariance of various metrics of longfin smelt abundance in the San Francisco Estuary. Equality of slopes, indicated by nonsignificant interaction terms in the separate-slopes models, was tested prior to performing analyses of covariance on the homogenous-slopes models (Engqvist 2005). In each case the main effect is the time period; covariates are listed on the second line in each section. A significant main effect in the homogenous-slopes models indicates variation in abundance among the three time periods examined (before, after, and during the 1987–1994 drought). Abbreviations are as follows: MS = mean square; FMWT = Fall Midwater Trawl Survey.

Source	Separate slopes models				Homogenous slopes models			
	df	MS	F	P	df	MS	F	P
log_e(FMWT age-class 1 index)								
Time period	2	0.075	0.381	0.688	2	1.354	7.216	0.004
Freshwater flow	1	3.833	19.364	<0.001	1	6.421	34.218	<0.001
Interaction	2	0.08	0.403	0.673				
Residual	21	0.198			23	0.188		
log_e(FMWT age-class 2 index)								
Time period ^a	2	0.862	9.746	0.001	1	2.926	22.734	<0.001
FMWT age-class 1 index	1	1.655	18.709	<0.001	1	0.453	3.522	0.082
Interaction	2	0.444	5.018	0.018				
Residual	19	0.0885			14	0.129		
log_e(Bay Study age-class 1 index)								
Time period	1	0.1	0.301	0.593	1	1.882	6.203	0.027
Freshwater flow	1	3.638	11.2	0.006	1	3.593	11.843	0.004
Interaction	1	0.045	0.139	0.716				
Residual	12	0.325			13	0.303		
log_e(Bay Study age-class 2 index)								
Time period	1	1.206	3.925	0.076	1	0.4016	1.099	0.317
Bay Study age-class 1 index	1	4.483	14.593	0.003	1	5.516	13.906	0.003
Interaction	1	1.006	3.275	0.1				
Residual		0.307			11	0.371		
Arcsin-square root(Suisun Marsh age-class 2 catch/min)								
Time period	2	0.008	3.715	0.045	2	0.019	7.84	0.003
FMWT age-class 1 index	1	<0.001	0.061	0.808	1	0.003	1.365	0.256
Interaction	1	0.004	1.919	0.176				
Residual	18	0.002			20	0.002		
Arcsin-square root(estuarywide percent presence age-class 1)								
Time period	1	0.001	0.075	0.792	1	0.039	2.732	0.133
Freshwater flow	1	0.048	3.053	0.119	1	0.056	3.94	0.078
Interaction	1	0.003	0.16	0.7				
Residual	8	0.016			9	0.014		
Arcsin-square root(estuarywide percent presence age-class 2)								
Time period	1	<0.001	0.215	0.663	1	0.025	12.544	0.012
Age-class 1 percent presence	1	0.026	11.057	0.021	1	0.028	13.862	0.01
Interaction	1	<0.001	0.154	0.711				
Residual	5	0.002			6	0.002		

^a Heterogenous slopes were detected among the three time periods. However, the slopes in the pre- and postdrought periods were homogenous (post hoc multiple comparison; $P > 0.05$). For this reason the homogenous-slopes model compares only the pre- and postdrought periods.

We analyzed whether the declines in the metrics of age-class 2 longfin smelt CPUE and percent presence were proportional to those in age-class 1 longfin smelt. Except where noted later in Results, the relationship between covariates and dependent variables did not change across time periods (ANOVA, interaction effect; Table 3); therefore, we employed ANCOVA models that assumed homogeneity of slopes. Residuals from each ANCOVA satisfied the assumptions of parametric statistical analyses. Significant changes in Suisun Marsh age-class 2 CPM values were detected among time periods (ANCOVA, time period main

effect; $P = 0.003$; Table 3). Age-class 2 CPM values in Suisun Marsh were lower in the drought and postdrought periods than in the predrought period (Tukey's HSD multiple comparison: $P = 0.001$ and $P = 0.016$, respectively); no difference between the drought and the postdrought period was detected ($P = 0.385$). Partial correlations on residuals from this analysis showed no evidence of significant temporal autocorrelation. Bay Study age-class 2 index values were not significantly different across time periods after accounting for the effect of the age-class 1 index value from the previous year (ANCOVA, time period main

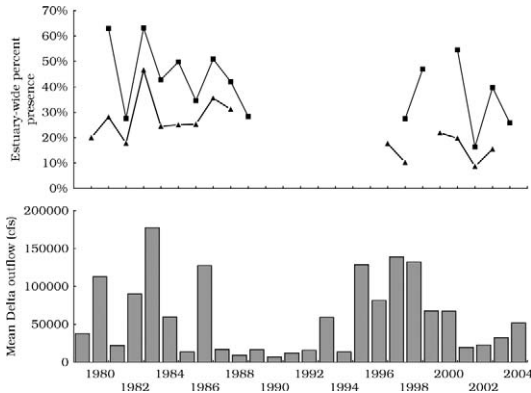


FIGURE 4.—Average percent presence of age-class 1 (boxes) and age-class 2 (triangles) longfin smelt at sites sampled by the Bay Study and the Suisun Marsh Survey (upper panel) compared with the mean winter–spring freshwater outflow from the San Joaquin–Sacramento Delta (lower panel). After accounting for the positive relationship between freshwater outflow and age-class 1 abundance, no significant change in age-class 1 percent presence was detected between pre- and postdrought periods. After accounting for the relationship between percent presence of age-class 1 longfin smelt, a significant decline in age-class 2 percent presence was detected in the postdrought period. Missing years indicate periods when sampling by the Bay Study was incomplete. Distribution values for age-class 2 fish are plotted in the year they were spawned (1 year before they were sampled) directly underneath the age-class 1 population from which they were derived.

effect: $P = 0.317$; Table 3). Estuary-wide percent presence of age-class 2 longfin smelt declined significantly between pre- and postdrought periods even after accounting for the decline in age-class 1 distribution (ANCOVA, time period main effect: $P = 0.012$; Table 3).

The slope of the relationship between the FMWT age-class 2 index and the covariate (the previous year’s FMWT age-class 1 index) differed significantly among time periods (ANCOVA, time period \times age-class 1 index interaction: $P = 0.018$; Table 3). The slope during the drought differed significantly from the slope in the predrought period (Tukey’s HSD post hoc multiple comparisons: $P = 0.01$); however, slopes in the predrought and postdrought periods were not significantly different ($P = 0.06$); therefore, we excluded results from the drought period and conducted a separate ANCOVA assuming homogenous slopes in the pre- and postdrought periods. This analysis revealed that age-class 2 index values declined significantly from predrought levels to postdrought levels (ANCOVA, time period main effect: $P < 0.001$; Table 3). Partial correlation of residuals from the original separate-slopes model (which included all

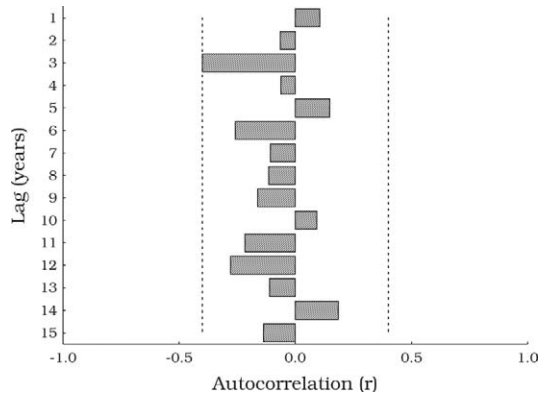


FIGURE 5.—Partial autocorrelations in the Fall Midwater Trawl Survey age-class 2 abundance index residuals after accounting for the effect of age-class 1 abundance. A negative correlation ($r = -0.40$) at the 3-year time lag was significant. The dashed vertical lines represent 95% confidence intervals ($SE = 0.2041$ for each lag).

three time periods) revealed a significant negative autocorrelation at a lag of 3 years ($P = 0.050$; Figure 5).

Bathymetric distribution.—For each age-group Bay Study OT CPUE was higher at channel stations than at shoal stations, but this pattern was not statistically significant (repeated-measures ANOVA, depth main effect: $P = 0.067$; Table 4; Figure 6). Bay Study MWT CPUE was significantly higher at sampling stations located over the channel than at shoal stations (repeated-measures ANOVA, depth main effect: $P = 0.002$; Table 4; Figure 6) and this effect remained consistent over the life cycle (age-group \times depth category interaction: Greenhouse–Geisser corrected $P < 0.376$; Table 4). Catch per unit effort was greater at channel sites than at shoal sites in each age-group and the difference was significant from the first fall through the second spring of life and between the second fall and winter of life ($P < 0.05$; Figure 6). Because the significance for MWT CPUE was less than the Bonferroni-adjusted α (0.025), the overall null hypothesis that there was no difference in CPUE between channel and shoal stations was rejected.

Density and percent presence throughout the life cycle.—Visual inspection indicates that the Bay Study’s two nets and the Suisun Marsh Survey portrayed similar patterns in the timing of intracohort fluctuations in population geographic extent (Figure 7). The Suisun Marsh Survey and Bay Study detected juvenile (≥ 40 mm FL) longfin smelt as early as April in 7 of 25 years. In most years, juvenile longfin smelt were first detected in May. Mean geographic distribution peaked during November in Suisun Marsh, December in the OT dataset, and January in the MWT dataset.

TABLE 4.—Repeated-measures ANOVA of changes in longfin smelt depth distribution through their life cycle. Catch per unit effort was measured at “channel” stations (depth > 7 m) and “shoal” stations (depth < 7 m) in eight 3-month age categories within longfin smelt cohorts. A Bonferroni correction was employed to account for multiple tests of the same hypothesis ($\alpha = 0.025$). Longfin smelt catches in the Bay Study Midwater Trawl were significantly higher at channel stations than at shoal stations. Greenhouse–Geisser adjusted *P*-values, which correct for deviations from sphericity, are presented for within-subjects effects (von Ende 2001). The significant age-group (within-subjects) main effect reflects seasonal variation and the overall decline in CPUE through the life cycle.

Source	df	Mean square	<i>F</i>	<i>P</i>	Greenhouse–Geisser adjusted <i>P</i>
Bay Study Midwater Trawl					
Between subjects					
Depth category	1	6.930	56.398	<0.001	
Error	16	0.123			
Within subjects					
Age-group	7	1.687	10.562	<0.001	<0.001
Depth × age-group	7	0.163	1.021	0.417	0.376
Error	217	0.160			
Bay Study Otter Trawl					
Between subjects					
Depth category	1	4.063	3.563	0.067	
Error	36	1.140			
Within subjects					
Age-group	7	5.240	27.387	<0.001	<0.001
Depth × age-group	7	0.056	0.295	0.955	0.790
Error	252	0.191			

Statistical analysis revealed that across years Bay Study OT CPUE was consistently higher in certain months than it was in other months (repeated-measures ANOVA: Greenhouse–Geisser, epsilon = 0.286,

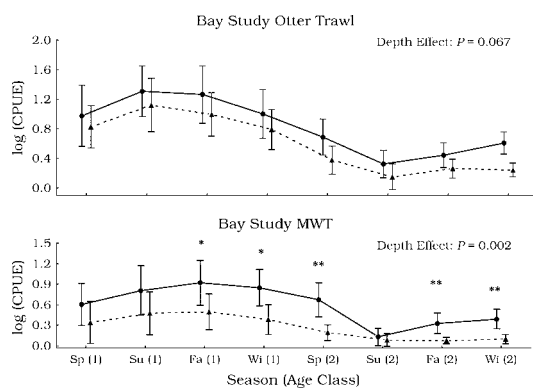


FIGURE 6.—Depth distribution of longfin smelt throughout their life cycle as measured by the Bay Study’s otter trawl (OT) and midwater trawl (MWT) surveys. Circles indicate CPUE at channel stations (≥ 7 m); triangles indicate CPUE at shoal stations (< 7 m). Eight age-groups are listed on the x-axis according to season and annual age-class (in parentheses) in which catches occurred. The significant depth effect in MWT CPUE indicated that catches were generally higher at deepwater stations than at shallow stations. No significant interaction between age-group and depth category was detected in the results from either net. Significant differences within age-groups are indicated ($P < 0.05^*$; $P < 0.01^{**}$); the vertical bars represent 95% confidence intervals.

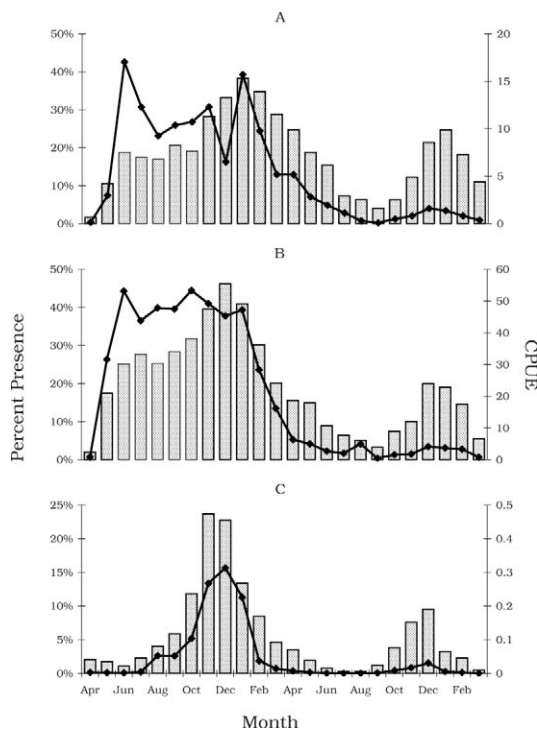


FIGURE 7.—Mean percent of sites at which longfin smelt were present (bars) and CPUE (lines) across years throughout the longfin smelt life cycle as portrayed by (A) the Bay Study’s midwater trawl survey, (B) the Bay Study’s otter trawl survey, and (C) the Suisun Marsh Survey. The number of years contributing to the mean varied among months as a result of changes in the sampling programs.

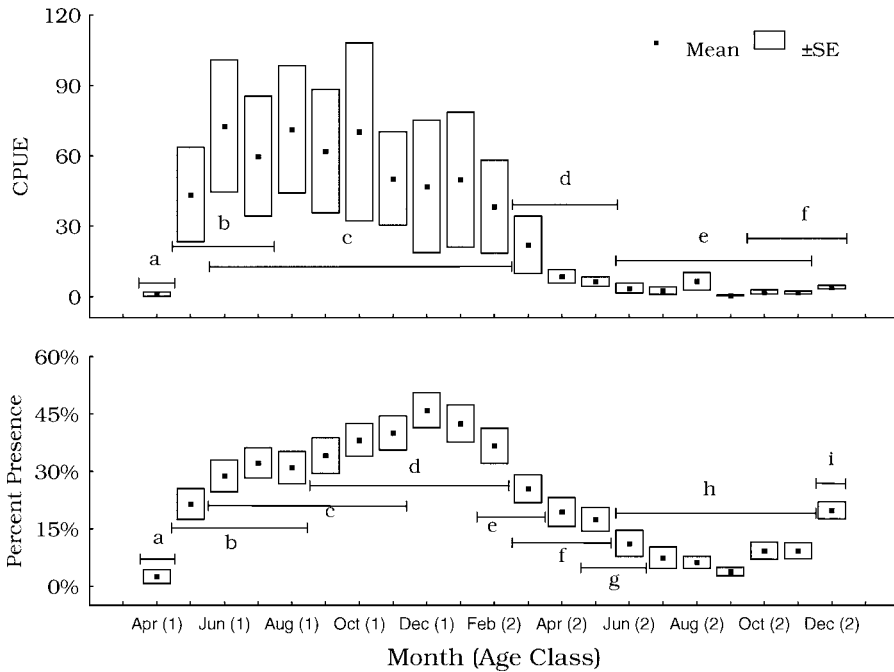


FIGURE 8.—Patterns in (A) CPUE and (B) percent of sites at which longfin smelt were present over 21 months of the longfin smelt life cycle as represented in Bay Study otter trawl data ($N = 18$ cohorts). Repeated-measures ANOVA detected significant patterns in both density and distribution. Horizontal bars and lowercase letters indicate adjacent months that were statistically indistinguishable (Tukey's post hoc comparison; $P > 0.05$). Statistical similarities among nonadjacent months are not depicted here.

adjusted numerator $df = 5.73$, adjusted denominator $df = 97.401$, $P < 0.001$; Figure 8). Catch per unit effort was higher in the 9 months from June through February than in other months of the life cycle (Tukey's HSD post hoc multiple comparison: $P < 0.05$). Interannual patterns in percent presence were also significant (repeated-measures ANOVA: Greenhouse-Geisser, $\epsilon = 0.38$, adjusted numerator $df = 7.593$, adjusted denominator $df = 121.493$, $P < 0.001$; Figure 8). Mean percent presence peaked during the first December of the longfin smelt life cycle; percent-presence scores between the first September and the second February of life were significantly higher than in other months (Tukey's HSD post hoc multiple comparison; $P < 0.05$; Figure 8). After reaching their respective peaks, CPUE and percent presence declined through the second summer of life. Aside from the first April of life (age 4 months) in which longfin smelt were rarely caught by the OT, CPUE was lowest between the second June and November of life ($P < 0.05$). Percent presence between the second June and November of life was significantly less than all other months after the first April of life ($P < 0.05$). Both percent presence and CPUE increased significantly in the second December of life ($P < 0.05$; Figure 8).

Spatial autocorrelation among sampling stations was detected in the OT and MWT data sets for both age-classes (Figure 9). In each case the relationship between pairwise correlations in sampling station CPUE and physical distance between sites was negative, indicating increasing correlation in longfin smelt catches as between-site distance decreased. Whereas these trends were statistically significant ($P < 0.05$ for each analysis) substantial variation in the relationships was evident (Figure 9). Positive and negative between-site correlations were detected across the range of physical distances between sites.

Discussion

Trends in Longfin Smelt Annual Abundance and Distribution

We detected significant declines in the abundance of longfin smelt juveniles (age-class 1) and prespawning adults (age-class 2). The relationship between Delta outflow and FMWT longfin smelt abundance indices is well established in the San Francisco Estuary (Stevens and Miller 1983; Kimmerer 2002b) and we found that freshwater outflow was a significant covariate in Bay Study and Suisun Marsh data as well. Despite comparable flow conditions in the predrought and

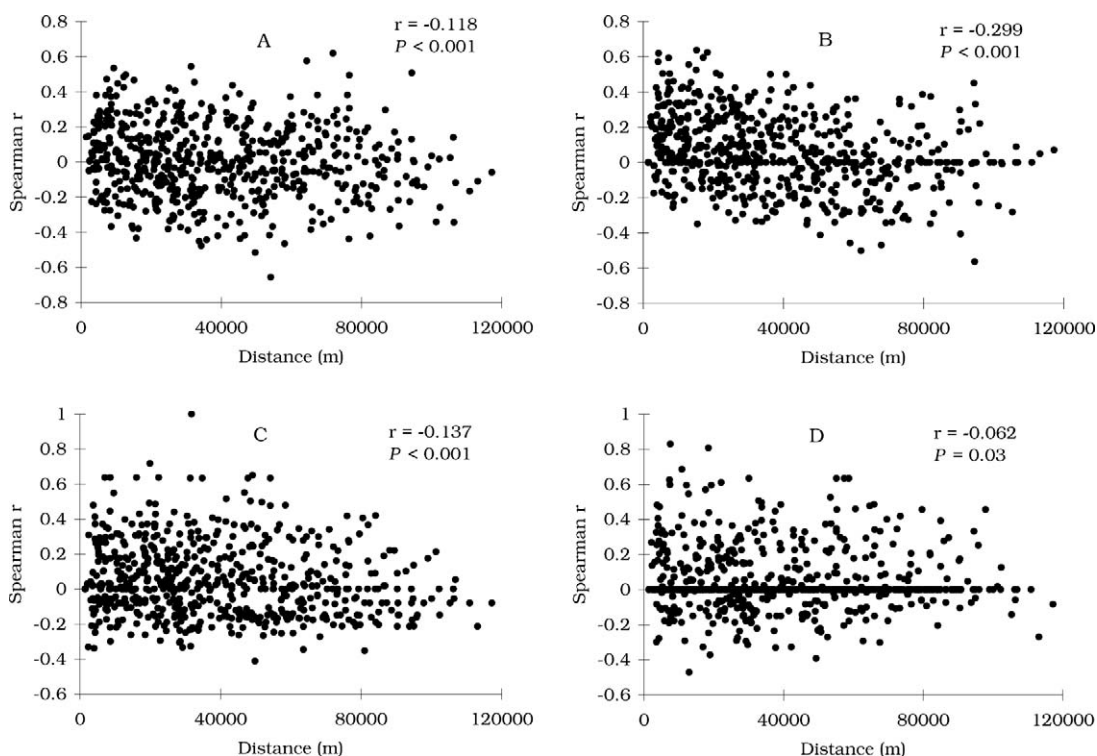


FIGURE 9.—Spatial autocorrelation across sampling stations for (A) age-class 1 longfin smelt in Bay Study otter trawl (OT) sampling, (B) age-class 1 longfin smelt in Bay Study midwater trawl (MWT) sampling, (C) age-class 2 longfin smelt in the OT sampling, and (D) age-class 2 longfin smelt in the MWT sampling. The relationships between physical distance and the correlation in catches among sites were negative for each age-class and sampling program, indicating that, in general, sites produced less similar results as the distance between them increased (Mantel test; $P < 0.05$).

postdrought periods, average age-class 1 abundance indices declined about 90%. Age-class 2 abundance declined and the decline in the FMWT and Suisun Marsh data sets was greater than would be expected based on the decline in juvenile abundance. This suggests that survival between age-classes 1 and 2 has declined between the pre- and postdrought periods. Percent presence of age-class 2 fish declined following the drought as well. We found no evidence that following the drought, longfin smelt were consistently absent from particular sites in the estuary where they had occurred before the drought. The decline in the average number of sites where age-class 2 longfin smelt were detected probably reflects a decline in population density toward a threshold of detectability.

Kimmerer (2002b) suggested that the decline in the estuary's longfin smelt population to declines in the availability of food items following introduction of the Amur clam in 1986. The explosive population growth of this filter-feeding clam (Carlton et al. 1990) has diverted energy and nutrient flow from the primary

consumers that longfin smelt eat (Alpine and Cloern 1992; Feyrer et al. 2003). Food limitation is consistent with our finding of reduced age-class 1 productivity and the disproportionate reduction in age-class 2 recruitment. Hobbs et al. (2006) documented poor growth and condition of longfin smelt in certain regions of Suisun Bay.

Some aspects of the longfin smelt decline are not explained by food web changes related to the Amur clam invasion. For example, catches of prespawning adult (age-class 2) longfin smelt in Suisun Marsh dropped consistently after the inception of the Suisun Marsh Survey (Figure 3). The decline in this area predates the onset of the 1987–1994 drought or the introduction of the Amur clam. Longfin smelt of spawning age returned to the marsh at low levels in the early part of the current decade (Figure 3). Additional study of longfin smelt habitat requirements and their use of the marsh in particular should be directed towards understanding whether recent environmental changes have diminished the Marsh's carrying capacity for this species.

Distribution throughout the Life Cycle

Longfin smelt in the San Francisco Estuary were broadly distributed both temporally and spatially during the study period, and interannual distribution patterns were relatively consistent. Seasonal patterns in density and percent presence indicate that this population of longfin smelt is, at least partially, anadromous. The decrease in density and distribution apparent in both the Bay Study and the Suisun Marsh Survey after the first winter of the longfin smelt life cycle cannot be attributed solely to mortality because both density and distribution increased during the second winter of the life cycle, just before the spawning season (Figures 7, 8); migration out of and back into the sampling zone would explain this consistent seasonal abundance pattern. Sampling by the City of San Francisco during several years in the early 1980s detected longfin smelt in the Pacific Ocean, providing additional evidence that some part of this population migrates beyond the Golden Gate Bridge (City of San Francisco and CH2M Hill 1985). Anadromous populations of longfin smelt occur elsewhere in their range, but the duration of this anadromous phase of their life cycle is unstudied as are the ecology and behavior of longfin smelt in marine environments. Detection of longfin smelt within the estuary throughout the year suggests that anadromy may be an alternative life history strategy in this population. Our lack of knowledge about the extent, duration, and benefits of marine migration in this population complicates the search for mechanisms behind the apparent decline in recruitment success from age-class 1 to age-class 2 individuals.

Sampling data also revealed a consistent pattern of bathymetric distribution for longfin smelt. Bay Study CPUE indicated that postlarval longfin smelt aggregated in deep-water habitats (Figure 6). Longfin smelt in the Lake Washington population also display a depth-stratified distribution (Chigbu et al. 1998; Chigbu 2000). Longfin smelt concentration in deep-water habitats combined with migration into marine environments during summer months suggests that longfin smelt may be relatively intolerant of warm waters that occur seasonally in this estuary.

We detected intra-annual variance overlying patterns in longfin smelt distribution. This variance may be statistical "noise" or it may reveal important ecological and behavioral responses of longfin smelt to environmental conditions in the San Francisco Estuary. For example, we found a long period of increasing age-class 1 abundance from early May through January that probably reflected a protracted period of recruitment of fish to the Bay Study's nets (Figures 7, 8). This

extended period of recruitment suggests that longfin smelt spawn over a long period of time or that rearing conditions and growth vary substantially across rearing habitats. Hobbs et al. (2005, 2007) have used otolith microchemistry to identify rearing areas in delta smelt and a similar approach with longfin smelt may allow identification of larval rearing habitats and subsequent study of differential larval growth and developmental rates.

Implications for Interpreting Sampling Data

Longfin smelt abundance and distribution peaked in the San Francisco Estuary during the fall. The FMWT samples the northern estuary intensively during this period. Longfin smelt abundance estimates calculated from FMWT data were well correlated with those calculated from Bay Study data. Thus, despite its relatively narrow geographic and seasonal focus, FMWT data probably provide a reasonable representation of longfin smelt abundance.

We also found that other aquatic community sampling programs provide valuable information to complement that produced by the FMWT. For example, the decline in longfin smelt abundance observed in data from the Bay Study Program and Suisun Marsh Survey, both of which operate throughout the year and in habitats not sampled by the FMWT, demonstrates that the apparent decline portrayed in the FMWT abundance index did not arise from shifts in temporal or spatial distribution patterns (i.e., a shift in distribution out of the sampling zone). The decline in longfin smelt abundance we observed in three independent sampling programs provides strong evidence that this population has experienced a sustained and significant decline.

In addition, the Bay Study's OT samples longfin smelt habitat differently than either midwater trawl approach we studied and it caught large numbers of longfin smelt throughout the year and throughout the estuary. Data from this net should be considered when studying the ecology and behavior of longfin smelt or when evaluating trends in their population. Comparisons of bottom-fishing gear (like the OT) with gear that samples the middle and top of the water column would contribute to our understanding of longfin smelt habitat use and interpretation of sampling results; investigations of this sort appear warranted given our finding that longfin smelt aggregate in deepwater environments.

We detected spatial autocorrelation among Bay Study sampling stations. The relationship was weak such that, across the range of distances between stations, a wide spread of negative and positive pairwise correlations were detected (Figure 9). The

decline in correlation between sites with increasing distance supports the current practice of averaging catch results of adjacent sites and the implicit assumption that adjacent sites may not provide completely independent results (Hurlbert 1984). This practice could be refined by careful study of the pattern of pairwise correlations to ensure that results from correlated station pairs are combined into the same regional estimate of mean longfin smelt CPUE. Spatial autocorrelation between sampling stations does not alter our analyses of long-term trends in abundance index scores because within sampling programs, each year was represented by only one index value. Similarly, our analysis of patterns in monthly CPUE and percent presence could not be affected by spatial autocorrelation because for each year in the data set, each month in the life cycle was represented by only one value (an average across all sampling stations). Comparisons between stations, embayments, or other "regions" in the estuary may need to account for the spatial autocorrelation we detected (Fortin and Gurvitch 2001).

We did not detect temporal autocorrelation among annual age-class 1 index estimates after accounting for covariates. We did detect a marginally significant negative autocorrelation with a 3-year time lag in residuals of the FMWT age-class 2 index (Figure 5). At this time, we see no obvious explanation for this correlation. We did not account for this temporal autocorrelation in our analysis of FMWT age-class 2 annual index values because, given the magnitude of the decline we documented, there was little chance that this tenuous autocorrelation would alter the outcome of the overall analysis. If this pattern of temporal autocorrelation persists in the FMWT data set in the future, an investigation of its underlying mechanisms may be warranted.

The precipitous decline of longfin smelt, among the most abundant native fish species in the San Francisco Estuary, is cause for concern. This is particularly true because the decline occurred in the context of significant declines in many other native and nonnative members of the estuary's pelagic fish assemblage (Sommer et al. 2007). Fish populations in this estuary are highly variable (Kimmerer 2002a; Matern et al. 2002), but unlike other periods of low abundance, the most recent declines in fish populations cannot be attributed to a sustained drought. A number of forces may contribute to this widespread decline including biological, hydrological, climatological, and chemical factors, only some of which are under human control (Sommer et al. 2007). Improved understanding of fish abundance and distribution patterns, and the ecological and behavioral forces that underlie those patterns, may

aid our ability to identify mechanisms driving this widespread decline in pelagic fish populations.

Acknowledgments

We thank P. B. Moyle, R. Schroeter, P. Crain, K. Small, T. Sommer, M. Nobriga, K. Fleming, Daniel Hayes, and three anonymous reviewers for comments that improved this manuscript. J.A.R.'s contribution was funded by an IEP postdoctoral fellowship.

References

- Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37:946–955.
- Armor, C., and P. L. Herrgesell. 1985. Distribution and abundance of fishes in the San Francisco Bay estuary between 1980 and 1982. *Hydrobiologia* 129:211–227.
- Baxter, R. 1999. Osmeridae. Pages 179–216 in J. Orsi, editor. Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. California Department of Fish and Game, Technical Report 63, Stockton. Available: www.estuaryarchive.org/archive/orsi_1999/. (September 2002).
- Brown, R., S. Greene, P. Coulston, and S. Barrow. 1996. An evaluation of the effectiveness of fish salvage operations at the intake to the California aqueduct, 1979–1993. Pages 497–518 in J. T. Hollibaugh, editor. San Francisco Bay: the ecosystem. American Association for the Advancement of Science, San Francisco.
- Carlton, J. T., J. K. Thompson, L. E. Schemel, and F. H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. *Marine Ecology Progress Series* 66:81–94.
- Chigbu, P. 2000. Population biology of longfin smelt and aspects of the ecology of other major planktivorous fishes in Lake Washington. *Journal of Freshwater Ecology* 15:543–557.
- Chigbu, P., and T. H. Sibley. 1994. Relationship between abundance, growth, egg size, and fecundity in a landlocked population of longfin smelt, *Spirinchus thaleichthys*. *Journal of Fish Biology* 1:1–15.
- Chigbu, P., T. H. Sibley, and D. A. Beauchamp. 1998. Abundance and distribution of *Neomysis mercedis* and a major predator, longfin smelt (*Spirinchus thaleichthys*) in Lake Washington. *Hydrobiologia* 386:167–182.
- City of San Francisco and CH2M Hill. 1985. Ocean outfall monitoring program: 1983–1984 annual report. Bureau of Water Pollution Control, San Francisco.
- Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558.
- Dryfoos, R. L. 1965. The life history and ecology of the longfin smelt in Lake Washington. Doctoral dissertation. University of Washington, Seattle.
- Engqvist, L. 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour* 70:967–971.
- Feyrer, F., B. Herbold, S. A. Matern, and P. B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: consequenc-

- es of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67:277–288.
- Fortin, M., and J. Gurevitch. 2001. Mantel tests: spatial structure in field experiments. Pages 308–326 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Oxford University Press, Oxford, UK.
- Hayek, L. C., and M. A. Buzas. 1997. *Surveying natural populations*. Columbia University Press, New York.
- Hobbs, J. A., W. A. Bennett, and J. E. Burton. 2006. Assessing nursery habitat quality for native smelts (Osmeridae) in the low-salinity zone of the San Francisco Estuary. *Journal of Fish Biology* 69:907–922.
- Hobbs, J. A., W. A. Bennett, J. E. Burton, and M. Gras. 2007. Classification of larval and adult delta smelt to nursery areas by use of trace elemental fingerprinting. *Transactions of the American Fisheries Society* 136:518–527.
- Hobbs, J. A., Q. Yin, J. E. Burton, and W. A. Bennett. 2005. Retrospective determination of natal habitats for an estuarine fish with otolith strontium isotope ratios. *Marine and Freshwater Research* 56:655–660.
- Honey, K., R. Baxter, Z. Hymanson, T. Sommer, M. Gingras, and P. Cadrett. 2004. IEP long-term fish monitoring program element review. Interagency Ecological Program for the San Francisco Bay/Delta Estuary, Sacramento, California.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Jassby, A. D., W. J. Kimmerer, S. G. Monismith, C. Armor, J. E. Cloern, T. M. Powell, J. R. Schubel, and T. J. Vendlinski. 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* 5:272–289.
- Kimmerer, W. J., J. H. Cowan, Jr., L. W. Miller, and K. A. Rose. 2000. Analysis of an estuarine striped bass (*Morone saxatilis*) population: influence of density-dependent mortality between metamorphosis and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 57:478–486.
- Kimmerer, W. J. 2002a. Physical, biological, and management responses to variable freshwater flow in the San Francisco Estuary. *Estuaries* 25:1275–1290.
- Kimmerer, W. J. 2002b. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Marine Ecology Progress Series* 243:39–55.
- Lehman, P. W. 2004. The influence of climate on mechanistic pathways that affect lower food web production in northern San Francisco Bay Estuary. *Estuaries* 27:311–324.
- Matern, S. A., P. B. Moyle, and L. C. Pierce. 2002. Native and alien fishes in a California estuarine marsh: twenty-one years of changing assemblages. *Transactions of the American Fisheries Society* 131:797–816.
- Moulton, L. L. 1974. Abundance, growth, and spawning of the longfin smelt in Lake Washington. *Transactions of the American Fisheries Society* 103:46–52.
- Moyle, P. B. 2002. *Inland fishes of California*. University of California Press, Berkeley.
- Orsi, J. J., and W. L. Mecum. 1996. Food limitation as the probable cause of long-term decline in the abundance of *Neomysis mercedis*, the opossum shrimp, in the Sacramento–San Joaquin Estuary. Pages 375–402 in J. T. Hollibaugh, editor. *San Francisco Bay: the ecosystem*. American Association for the Advancement of Science, San Francisco.
- Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F. Freyer, M. Gingras, B. Herbold, W. Kimmerer, A. Mueller-Solger, M. Nobriga, and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* 32:270–277.
- StatSoft. 2002. STATISTICA: data analysis software system, version 6. StatSoft. Available: www.statsoft.com. (October 2002).
- StatSoft. 2006. *Electronic statistics textbook*. StatSoft, Oklahoma. Available: www.statsoft.com/textbook/stathome.html. (May 2007).
- Stevens, D. E. 1977. Striped bass (*Morone saxatilis*) monitoring techniques in the Sacramento–San Joaquin Estuary. Pages 91–109 in W. Van Winkle, editor. *Assessing the effects of power-plant-induced mortality on fish populations*. Pergamon, Gatlinburg, Tennessee.
- Stevens, D. E., and L. W. Miller. 1983. Effects of river flow on abundance of young Chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento–San Joaquin River system. *North American Journal of Fisheries Management* 3:425–437.
- USFWS (U.S. Fish and Wildlife Service). 1996. *Sacramento–San Joaquin Delta native fishes recovery plan*. USFWS, Portland, Oregon.
- von Ende, C. N. 2001. Repeated-measures analysis. Pages 134–157 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Oxford University Press, Oxford, UK.