POPULATION DYNAMICS AND DISTRIBUTION PATTERNS OF LONGFIN SMELT IN THE SAN FRANCISCO ESTUARY

Jonathan A. Rosenfield (corresponding author)[1]
Center for Integrated Watershed Science and Management
Academic Surge,
University of California
Davis, CA 95616
jarosenfield@gmail.com

Randall D. Baxter
California Department of Fish and Game
4001 N. Wilson Way
Stockton, CA 95814-2486
rbaxter@delta.dfg.ca.gov

Running title: Longfin smelt population dynamics

Words in body of manuscript: 6687

[1] Present Address: Aquatic Restoration Consulting, 1736 Carleton St., Berkeley, CA 94703

ABSTRACT

The San Francisco Estuary supports several endemic species 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 1235 km^2, it drains ca. 40% of California's land area and receives almost 50% of the state's run-off (Lehman 2004; Kimmerer 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 ~340 km^2 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 mollusc, 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 this Estuary have been severely impacted 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, *Acipenser 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 non-native species continued to decline 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 et al. 2000; Bennett 2005). The cause(s) of this decline in the pelagic fish community have not been determined. One difficulty in isolating the cause of this decline is that some major changes in physical conditions (such as freshwater inflow and export volumes) and biological conditions (such as the species assemblage) have occurred simulataneously. 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 this 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 (USF&WS 1996; Moyle 2002).

Several studies have attributed 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 CA) 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 Mid-water trawl pelagic community sampling program.

Here, we analyze 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 pre-spawning adults recovered to historic levels following the end of the 1987-1994 drought. In addition, we use 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. 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 SL at maturity), semelparous, pelagic fish that usually has a two-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* sp. and *Neomysis mercedis*, when available (Hobbs et al. 2006). The latter species has declined substantially in the Estuary since the early 1970's (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, WA (e.g., Dryfoos 1965; Moulton 1974; Chigbu & 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 (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 of this confluence and inland of the Golden Gate; and (3) large brackish marshes (Fig. 1). The Sacramento River, which drains much of northern California, provides approximately 2/3 of the freshwater inflow to the Estuary. 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 (Fig. 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 Estuary's fish community (Honey et al. 2004). Data from these sampling programs are also used to monitor the abundance and distribution of at-risk native fish species and important sportfish. 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 (Bay Study) began monthly sampling at 35 stations in January 1980 (Fig. 1; Armor and Herrgesell 1985). Additional sampling stations were added over time, but here we used data only from the original 35 stations. The Bay Study sampled fishes using both a mid-water 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 (Fig. 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 haphazardly and measured; the length distribution of the 50 individuals that were 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 4-28 stations (Fig. 2). Although more sampling stations were added through time, we include here only data from the 17 stations that were 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 five min in smaller sloughs at approximately 4 km/hr. All fish were identified to species and all those ≥ 30 mm SL 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*SL (CDFG, unpublished data). Longfin smelt < 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 were used in our analyses of Bay Study and Suisun Marsh Survey data.

The California Department of Fish and Game's Fall Mid-water Trawl Survey (FMWT) began sampling at 100 stations in 1967 (Stevens 1977) but individual longfin smelt were not measured consistently (allowing for age-class designation) until the mid-1970's. Sampling occurred monthly between September and December of each year at 57-113 (median=88) fixed locations in the San Pablo Bay, Suisun Bay, and the western Delta (Fig. 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.

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 of longfin smelt caught by the Bay Study were distinctly bimodal (Baxter 1999). We interpreted each length-frequency mode as 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, three-month age groups (e.g, Age 4-6 months), or Age Classes. Juvenile longfin smelt were first detectable by the Bay Study in April (*see below*); 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 weight CPUE by the area sampled) from the FMWT and the Bay Study's MWT and catch-per-unit-effort data from the Suisun Marsh Survey. The traditional FWMT 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 pre-defined regions; (2) expanded those average regional densities to reflect the proportional size of the different regions; (3) and summed the regional sub-totals 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 averaged across months within each year.

We investigated whether population levels of either Age Class of longfin smelt changed during and following an extreme drought that lasted from 1987 through 1994. Bay Study sampling was incomplete during the drought period (Fig. 2) so we could only compare pre- and post-drought periods for those data. Non-parametric techniques (Kruskal-Wallace 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 (pre-drought, drought (1987-1994), and post-drought), 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 arc-sin transformed so that residuals would meet the assumptions of parametric statistics.

We assessed 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 ANCOVA's 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 arc-sin 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 from with Age Class 1 CPM as the covariate produced non-normal 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 was justified because Age Class 2 longfin smelt are believed to move into the Marsh from the pelagic waters sampled by the FMWT (Matern et al. 2002).

We also analyzed trends in longfin smelt geographic distribution by analyzing an Estuary-wide 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 1990's (Fig. 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 arc-sin transformed to produce residuals that met the expectations of parametric statistics. For all ANCOVA's, 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 presence-absence. 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 & 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, three-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 longfin smelt distribution 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 inter-annual 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 ≥ 7m deep ("channel stations") while the other half occur in habitats < 7m deep ("shoal stations"; Fig. 1). Prelinary analysis showed that the relationship between habitat depth and catch was non-linear, 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 (Fig. 1); thus, statistical comparisons between depth categories were not likely to be confounded by psuedoreplication (Hurlbert 1984). Eight, three-month age categories represented repeated measures (within-subects 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 α=0.025) to account for multiple tests of the same hypothesis.

Density and percent presence throughout the life cycle -- To describe intra-cohort 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 inter-annual 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 (Fig. 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 in every month from April (Age 4 months) through the second December of their life cycle (age 24 months). Six additional cohorts were missing $\leq$ 3 months of sampling during this period (Fig. 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 arc-sin transformed and CPUE were log-transformed prior to 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 if data from sampling stations were spatially autocorrelated. The practice of averaging CPUE results across sampling stations within pre-defined 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 inter-annual 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 to a matrix of the physical distance between sampling localities and the observed correlation between the two was compared to 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 post-drought periods (Kruskall-Wallace ANOVA, post-hoc multiple comparison: P=0.002 in both cases); no significant difference was detected between the pre-drought

and post-drought periods (P=1.0; Table 2; Fig. 3). Catches of Age Class 1 longfin smelt changed significantly across time periods in each sampling program (Table 2; Fig. 3). The percentage of stations at which Age Class 1 longfin smelt were caught did not change significantly between pre-drought and post-drought 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 non-parametric analyses (Table 3). The relationship between freshwater flow and dependent variables did not change significantly across time periods (ANCOVA, time period * freshwater flow interaction; Table 3); therefore, we employed ANCOVA models that assumed homogeneity of slopes across time periods (StatSoft 2006; Engqvist 2005). Bay Study Age Class 1 abundance index scores were significantly lower in the post-drought period than in the pre-drought period (ANCOVA, time period main effect: P=0.027). In the FMWT sampling program, Age Class 1 abundance index values during the drought period were significantly lower than those in either the pre- or post-drought periods (Tukey's HSD post-hoc multiple comparison: P<0.001 and P=0.007, respectively); abundance index values in the post-drought period were significantly lower than those observed during the pre-drought period (P=0.02). Estuary-wide percent presence of Age Class 1 longfin smelt was not significantly different between pre-drought and post-drought 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 non-normal 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; Fig. 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 pre-drought period to 11.6% in the post-drought period (Mann-Whitney U-test, P=0.001; Table 2; Fig. 4).

We analyzed whether declines in metrics of Age Class 2 longfin smelt CPUE and percent presence were proportional to declines in Age Class 1 longfin smelt. Except where noted below, 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 post-drought periods than in the pre-drought period (Tukey's HSD multiple comparison: P=0.001 and P =0.016, respectively); no difference between the drought and the post-drought 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 effect: P=0.317, Table 3). Estuary-wide percent presence of Age Class 2 longfin smelt declined significantly between pre- and post-drought 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 * Age Class 1 index interaction: P=0.018; Table 3). The slope during the drought differed significantly from the slope in the pre-drought period (Tukey's HSD post-hoc multiple comparisons: P=0.01); however, slopes in the pre-drought and post-drought 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 post-drought periods. This analysis revealed that Age Class 2 index values declined significantly from pre-drought levels to post-drought levels (ANCOVA, time period main effect: P<0.001; Table 3). Partial correlation of residuals from the original, separate slopes model (which included all three time periods) revealed a significant negative autocorrelation at a lag of 3 years (P = 0.050; Fig. 5).

Bathymetric distribution -- For each age group, Bay Study OT CPUE was higher at channel stations that at shoal stations, but this pattern was not statistically significant (repeated-measures ANOVA, depth main effect: P=0.067; Table 4; Fig 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; Fig 6) and this effect remained consistent over the life cycle (age group * 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 between the first fall and second spring of life and between the second fall and winter of life (P<0.05; Fig. 6). Because the significance for MWT CPUE were 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 intra-cohort fluctuations in population geographic extent (Fig. 7). The Suisun Marsh Survey and Bay Study detected juvenile ($\geq$ 40mm FL) longfin smelt as early as April in seven 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.

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, adjusted numerator *df*=5.73, adjusted denominator *df*=97.401, $P<0.001$; Fig. 8). Catch-per-unit-effort was higher in the nine months from June through February than in other months of the life cycle (Tukey's HSD post-hoc multiple comparison: $p<0.05$). Inter-annual 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, $P<0.001$; Fig. 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: $P<0.05$; Fig 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 ($P<0.05$; Fig. 8).

Spatial autocorrelation among sampling stations was detected in OT and MWT data sets for both Age Classes (Fig. 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 (Fig. 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 abundance of longfin smelt juveniles (Age Class 1) and pre-spawning adults (Age Class 2). The relationship between Delta outflow and FMWT longfin smelt abundance indices is well-established in this 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 pre-drought and post-drought periods, average Age Class 1 abundance indices declined ~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 Class 1 and Age Class 2 has declined between the pre- and post-drought 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 prior to the drought. The decline in the average number of sites whereAge 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 might be attributable to declines in the availability of food items following introduction of the Amur clam (*Corbula amurensis*) 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; Orsi and Mecum 1996; 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, but it does not conflict with other potential mechanisms driving longfin smelt decline, such as exposure to toxic pesticides (Sommer et al 2007). 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 foodweb changes related to the Amur Clam invasion. For example, catches of pre-spawning adult (Age Class 2) longfin smelt in Suisun Marsh dropped consistently after the inception of the Suisun Marsh Survey (Fig. 3). The decline in this area pre-dates 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 this decade (Fig. 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 inter-annual 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 prior to the spawning season (Figs. 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 1980's detected longfin smelt in the Pacific Ocean, providing additional evidence that some part of this population migrates beyond the Golden Gate (City of San Francisco 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 post-larval longfin smelt aggregated in deep-water habitats (Fig. 6). Longfin smelt in the Lake Washington, WA population also display a depth-stratified distribution (Chigbu et al. 1998; Chigbu 2000). Longfin smelt concentration in deepwater 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 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 (Figs. 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 for 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 Estuary during the fall. The Fall Mid-water Trawl Survey 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 similar 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 mid-water trawl 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 distances between stations, a wide spread of negative and positive pairwise correlations were detected (Fig. 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 insure 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 impacted by spatial autocorrelation because, for each year in the dataset, 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 autocorellation we detected (Fortin and Gurevitch 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 three year time lag in residuals of the FMWT Age Class 2 index (Fig. 5). At this time, see no obvious explanation for this correlation. We did not account for the 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, 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 non-native members of the Estuary's pelagic fish assemblage (Sommer et al 2007). Fish populations in this

estuary are highly variable (Kimmerer 2002(a); 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.

ACKNOWLEDGEMENTS

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 post-doctoral fellowship.

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Figure Captions:

Figure 1: Map of the San Francisco Estuary distinguishing depths ≥ 7m (dark shading) from depths <7m (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 Fall Mid-water trawl survey sampled from September-December in San Pablo Bay, Suisun Bay, and the West Delta.

Figure 2: Sampling over time in (A) the Bay Study and (B) the Suisun Marsh Survey. Black cells indicate: (A) sampling at most or all 35 Bay Study sampling stations by both the otter trawl and mid-water trawl, and (B) sampling at most or all of 17 sites sampled in Suisun Marsh. Grey cells indicate: (A) months when only the otter trawl was used in the Bay Study, and (B) months when <13 sites were sampled in Suisun Marsh. White cells indicate no sampling.

Figure 3: Abundance of longfin smelt as measured by (A) the Bay Study, (B) the FMWT, and (C) the Suisun Marsh Survey compared with (D) winter-spring freshwater outflow from the San Joaquin-Sacramento Delta. Squares represent abundance indices for Age Class 1 fish, triangles represent Age Class 2 indices. In (A) and (B) ordinal scales are logarithmic. In (C), the ordinal scale to the left represents catch-per-minute of Age Class 1 longfin smelt whereas the ordinal scale to the right represents catch-per-minute of Age Class 2 longfin smelt. Values for Age Class 2 longfin smelt are plotted in the year they were spawned (one year before they were sampled) directly underneath the Age Class 1 population from which they were derived.

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) as compared to 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 post-drought periods (ANCOVA: P=0.133). 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 post-drought period (ANCOVA: P=0.012). 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 (one year before they were sampled) directly underneath the Age Class 1 population from which they were derived.

Figure 5: Partial autocorrelation in Fall Mid-water trawl 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 (P=0.050). Dashed vertical lines represent 95% confidence intervals (SE=0.2041 for each lag).

Figure 6: Depth distribution of longfin smelt throughout their life cycle as measured by the Bay Study's Otter Trawl and Mid-water trawl. The significant depth effect in Mid-water trawl CPUE (Repeated-measures ANOVA: P<0.001) indicated that catches were generally higher at deepwater stations (>7m, "Channel") than at shallow stations (<7m, "Shoal"; P<Bonferroni adjusted α=0.025). No significant interaction was detected in results from either net (Age Group * Depth Category: Greenhouse-Geisser adjusted P>0.05). Significant differences within Age Groups are marked (*, P<0.05; **, P<0.01). Vertical bars represent 95% error bands.

Figure 7: Mean percent of sites present (bars) and catch-per-unit-effort (lines) across years throughout the longfin smelt life cycle as portrayed by the (A) the Bay Study's Mid-water Trawl; (B) Bay Study's Otter Trawl; and (C) the Suisun Marsh Survey. Calendar months in the longfin smelt life cycle are represented along the abscissa. The number of years contributing to the mean varied among months as a result of changes in the sampling programs.

Figure 8: Patterns in catch-per-unit-effort (A) and percent of sites present (B) through 21 months of the longfin smelt life cycle as represented in Bay Study OT data (N=18 cohorts). Repeated-measures ANOVA detected significant patterns in both density and distribution. Horizontal bars indicate groups of adjacent months that were statistically indistinguishable

(Tukey's post-hoc comparison; $P>0.05$). Statistical similarities among non-adjacent months are not depicted here.

Figure 9: Spatial autocorrelation across sampling stations for Age Class 1 longfin smelt in the Bay Study Otter Trawl (OT, panel A) and Mid-water Trawl (MWT, B) and for Age Class 2 longfin smelt in the OT (C) and MWT (D). Relationships between physical distance and correlation in catches among sites was 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: $P<0.05$).

Table 1: Sampling gear and methodology employed by three long-term fish community sampling programs in the San Francisco Estuary that were analyzed in this paper.

Sampling program	Sampling intensity	Trawl type	Net description	Net deployment and tow	Tow duration	Effort units and calculation
Bay Study mid-water trawl (MWT)	-35 stations located in open water throughout the Estuary -1980-2001 -year-round, monthly [2]	Mid-water Trawl	-Mouth = 13.4m^2 [3] -Max. mesh size = 20.3cm -Min. mesh size = 1.3cm	-Cable out:depth =5:1 -Oblique tow with current	12 min	Catch/10,000m^3 water sampled
Bay Study otter trawl (OT)	-35 stations located in open water throughout the Estuary -1980-2001 -year-round, monthly [a]	Otter Trawl	-Mouth= 3.4m wide [b] -Max. mesh size = 2.5cm -Min. mesh size = 1.3cm	-Cable out:depth = 5:1 -Horizontal along bottom against current	5 min	Catch/10,000 m^2 (=net width* distance towed)

[2] General sampling period. For actual months of sampling activity, see Fig. 2.

[3] Estimated average when fishing under tension

Suisun Marsh Survey	-4-28 stations (mean=17.9) located in the channels and sloughs of Suisun Marsh -1980-2001 -year-round monthly*	Otter Trawl	-Mouth= 3.3 m^2 (4.4x0.75m) -Max. mesh size = 3.5cm -Min. mesh size = 0.6cm	-Horizontal along bottom	-10 min (large sloughs) -5 min (small sloughs)	Catch/min
Fall mid-water trawl (FMWT)	-57-113 stations (median = 88) located in open water throughout the Estuary's three northern embayments	Mid-water Trawl	-Mouth= 13.4m^2 [b] -Max. mesh size = 20.3cm -Min. mesh size = 1.3cm	-Cable out:depth =5:1 -Oblique tow with current	12 min	Catch/trawl

Table 2: Summary of changes in abundance and geographic distribution of longfin smelt and winter-spring freshwater outflow in the San Francisco Estuary across three time periods (pre-, post-, and during the 1987-1994 drought period). Kruskall-Wallace ANOVA are presented for FMWT and Suisun Marsh Survey because they operated in each of the three time periods. Bay study and estuary-wide percent presence metrics were measured in only pre- and post-drought periods and were analyzed using Mann-Whitney U-tests.

Variable	Time periods	Test score	*P*
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 CPM	3	$H_{2,25} = 13.558$	0.001
Suisun Age Class 2 CPM	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
Estuary-wide Age Class 1 % presence	2	$U_{6,6} = 8$	0.132
Estuary-wide Age Class 2 % presence	2	$U_{6,7} = 0$	<0.001
Delta Freshwater Flow (jan-mar)	3	$H_{2,29} = 8.575$	0.014

Table 3: Analyses of covariance of metrics of longfin smelt abundance in the San Francisco Estuary. Equality of slopes (left column), indicated by a non-significant interaction term, was tested prior to conducting ANCOVA using homogenous slopes models (right column; Engqvist 2005). Significant main effects from the homogenous slopes models indicate changes in longfin smelt abundance among time periods (pre-, post-, and during the 1987-1994 drought).

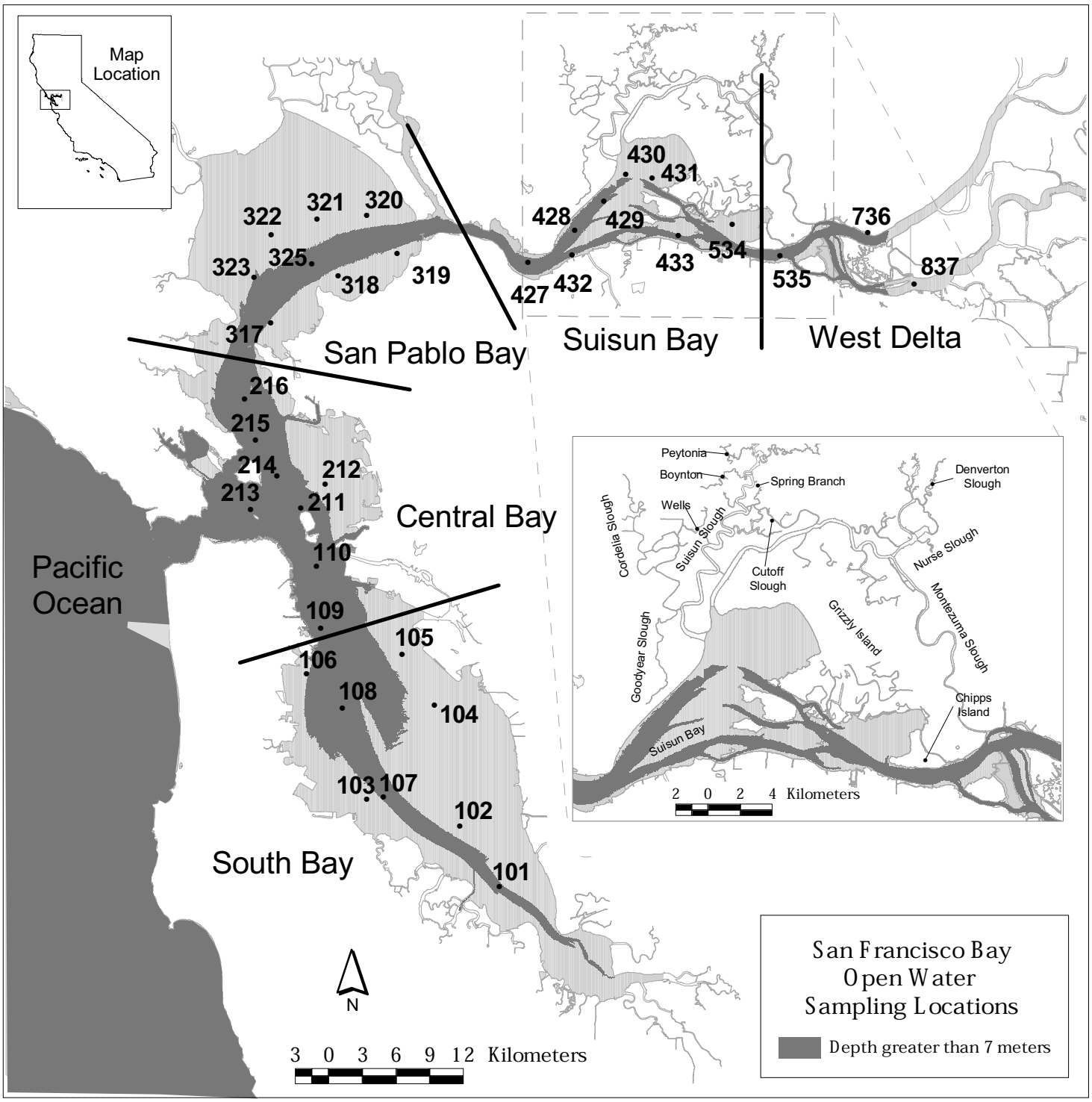
Separate Slopes Models					Homogenous Slopes Models				
Dependent variable: lg(Fall Mid-water Trawl Age Class 1 Index)									
Source	df	Mean Square	F-ratio	*P*	Source	df	Mean Square	F-ratio	*P*
Main Effect					Main Effect				
Time period	2	0.075	0.381	0.688	*Time period*	*2*	*1.354*	*7.216*	*0.004*
Covariate					Covariate				
Delta Freshwater Flow	1	3.833	19.364	<0.001	Delta Freshwater Flow	1	6.421	34.218	<0.001
Interaction (slope heterogeneity)					*Residual*	23	0.188		
*Time period * covariate*	*2*	*0.08*	*0.403*	*0.673*					
Residual	21	0.198							
Dependent variable: lg(Fall Mid-water Trawl Age Class 2 Index)[1]									
Source	df	Mean Square	F-ratio	*P*	Source	df	Mean Square	F-ratio	*P*
Main Effect					Main Effect				
Time period	2	0.862	9.746	0.001	*Time period [1]*	*1*	*2.926*	*22.734*	*<0.001*
Covariate					Covariate				
FMWT Age Class 1 index	1	1.655	18.709	<0.001	FMWT Age Class 1 index	1	0.453	3.522	0.082
Interaction (slope heterogeneity)					*Residual*	14	0.129		
*Time period * covariate*	*2*	*0.444*	*5.018*	*0.018*					
Residual	19	0.0885							
Dependent variable: lg(Bay Study Age Class 1 Index)									
Source	df	Mean Square	F-ratio	*P*	Source	df	Mean Square	F-ratio	*P*
Main Effect					Main Effect				
Time period	1	0.1	0.301	0.593	*Time period*	*1*	*1.882*	*6.203*	*0.027*
Covariate					Covariate				
Delta Freshwater Flow	1	3.638	11.2	0.006	Delta Freshwater Flow	1	3.593	11.843	0.004
Interaction (slope heterogeneity)					*Residual*	13	0.303		
*Time period * covariate*	*1*	*0.045*	*0.139*	*0.716*					
Residual	12	0.325							
Dependent variable: lg(Bay Study Age Class 2 Index)									
Source	df	Mean Square	F-ratio	*P*	Source	df	Mean Square	F-ratio	*P*
Main Effect					Main Effect				
Time period	1	1.206	3.925	0.076	*Time period*	*1*	*0.4016*	*1.099*	*0.317*
Covariate					Covariate				
BS Age Class 1 index	1	4.483	14.593	0.003	BS Age Class 1 index	1	5.516	13.906	0.003
Interaction (slope heterogeneity)					Residual	11	0.371		
*Time period * covariate*	*1*	*1.006*	*3.275*	*0.1*					
Residual		0.307							
Dependent variable: arc-sin(Suisun Marsh Age Class 2 CPM $^{1/2}$)									
Source	df	Mean Square	F-ratio	*P*	Source	df	Mean Square	F-ratio	*P*
Main Effect					Main Effect				
Time period	2	0.008	3.715	0.045	*Time period*	*2*	*0.019*	*7.84*	*0.003*
Covariate					Covariate				
FMWT Age Class 1 index	1	<0.001	0.061	0.808	lg(FMWT Age Class 1 index)	1	0.003	1.365	0.256
Interaction (slope heterogeneity)					Residual	20	0.002		
*Time period * covariate*	*1*	*0.004*	*1.919*	*0.176*					
Residual	18	0.002							
Dependent variable: arc-sin(Estuary-wide % presence Age Class 1 CPM $^{1/2}$)									
Source	df	Mean Square	F-ratio	*P*	Source	df	Mean Square	F-ratio	*P*
Main Effect					Main Effect				
Time period	1	0.001	0.075	0.792	*Time period*	*1*	*0.039*	*2.732*	*0.133*
Covariate					Covariate				
Delta Freshwater Flow	1	0.048	3.053	0.119	Delta Freshwater Flow	1	0.056	3.94	0.078
Interaction (slope heterogeneity)					Residual	9	0.014		
*Time period * covariate*	*1*	*0.003*	*0.16*	*0.7*					
Residual	8	0.016							
Dependent variable: arc-sin(Estuary-wide % presence Age Class 2 CPM $^{1/2}$)									
Source	df	Mean Square	F-ratio	*P*	Source	df	Mean Square	F-ratio	*P*
Main Effect					Main Effect				
Time period	1	<0.001	0.215	0.663	*Time period*	*1*	*0.025*	*12.544*	*0.012*
Covariate					Covariate				
Age Class 1 % presence	1	0.026	11.057	0.021	Age Class 1 % presence	1	0.028	13.862	0.01
Interaction (slope heterogeneity)					Residual	6	0.002		
*Time period * covariate*	*1*	*<0.001*	*0.154*	*0.711*					
Residual	5	0.002							

1 Heterogenous slopes were detected among the three time periods. Slopes in the pre- and post-drought period were homogenous (post-hoc multiple comparison, p>0.05). The homogenous slopes model compares only the pre- and post-drought periods.

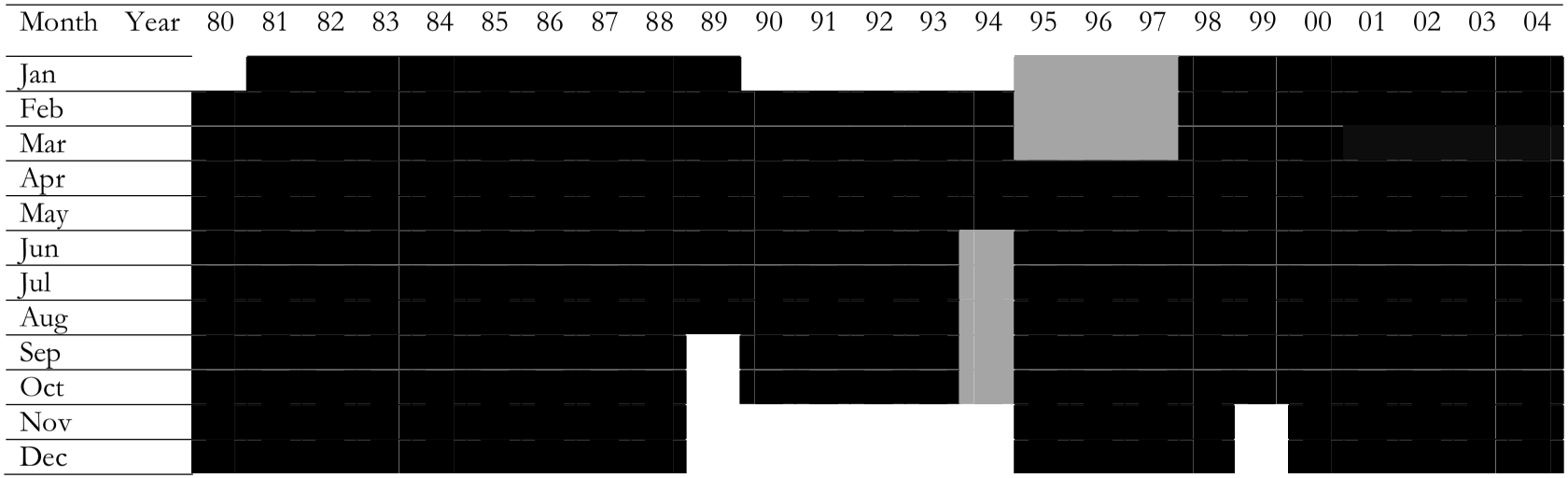
Table 4: Repeated-measures ANOVA of changes in longfin smelt depth distribution through their life cycle. Catch-per-unit-effort was measured at "channel" stations (depth >7m) and "shoal" stations (depth <7m) in eight 3-month age categories within longfin smelt cohorts. A Bonferoni correction to alpha was employed to account for multiple tests of the same hypothesis (α=0.025). Longfin smelt catches in the Bay Study MWT 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.

Bay Study Mid-Water Trawl					
Source	df	Mean Square	F-ratio	*P*	
Between-subjects					
Depth Category	1	6.930	56.398	< 0.001	
Error	16	0.123			
Within-Subjects					Greenhouse-Geisser adjusted *P*
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			

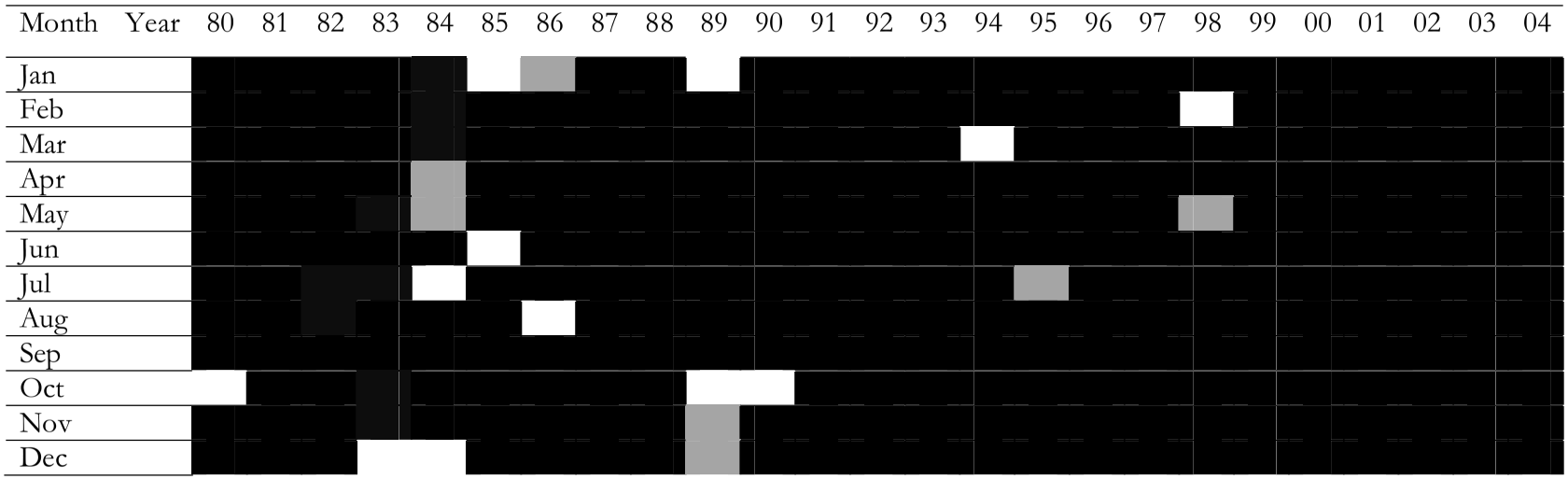
Bay Study Otter Trawl					
Source	df	Mean Square	F-ratio	*P*	
Between-subjects					
Depth Category	1	4.063	3.563	0.067	
Error	36	1.140			
Within-Subjects					Greenhouse-Geisser adjusted *P*
Age Group	7	5.240	27.387	< 0.001	< 0.001
Depth * Age Group	7	0.056	0.295	0.955	0.790
Error	252	0.191			

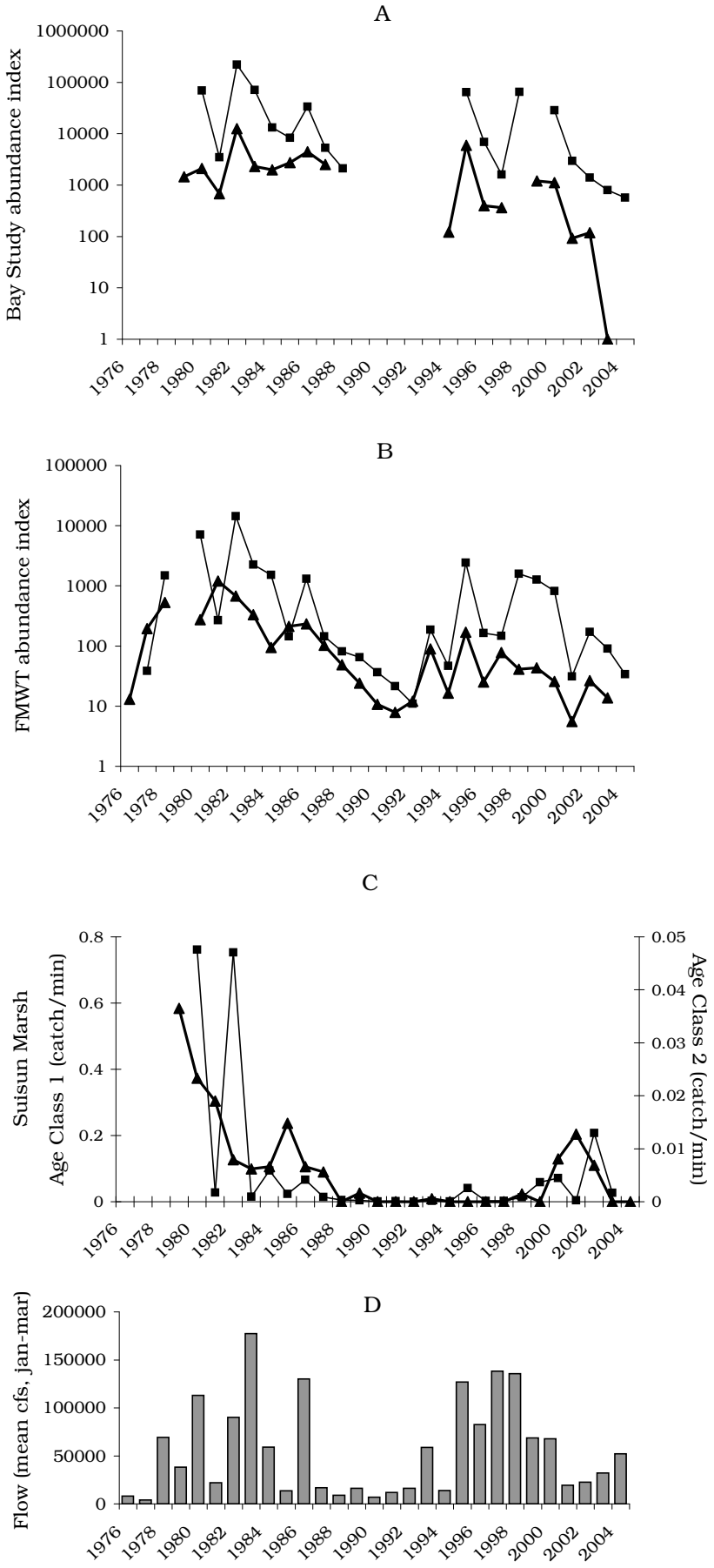

Map Location
San Pablo Bay
Suisun Bay
West Delta
Central Bay
South Bay
Pacific Ocean
322
321
320
323
325
318
319
317
216
215
214
212
213
211
110
109
105
106
108
104
103
107
102
101
430
431
428
429
433
534
535
736
837
427
432
Peytonia
Boynton
Spring Branch
Denverton Slough
Wells
Suisun Slough
Cordelia Slough
Cutoff Slough
Nurse Slough
Montezuma Slough
Grizzly Island
Goodyear Slough
Chipps Island
Suisun Bay
2 0 2 4 Kilometers
N
3 0 3 6 9 12 Kilometers
San Francisco Bay
Open Water
Sampling Locations
Depth greater than 7 meters

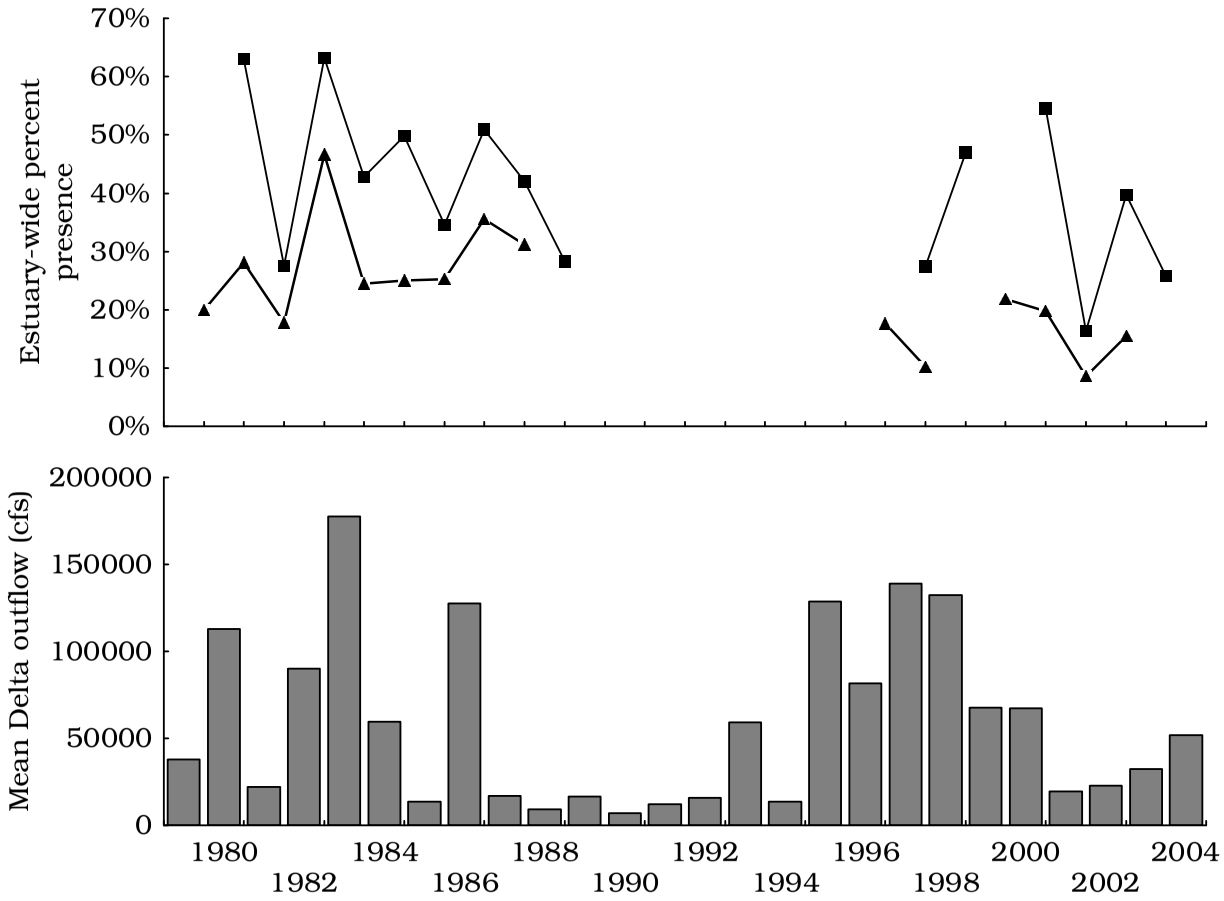
(A) Bay Study Sampling Program

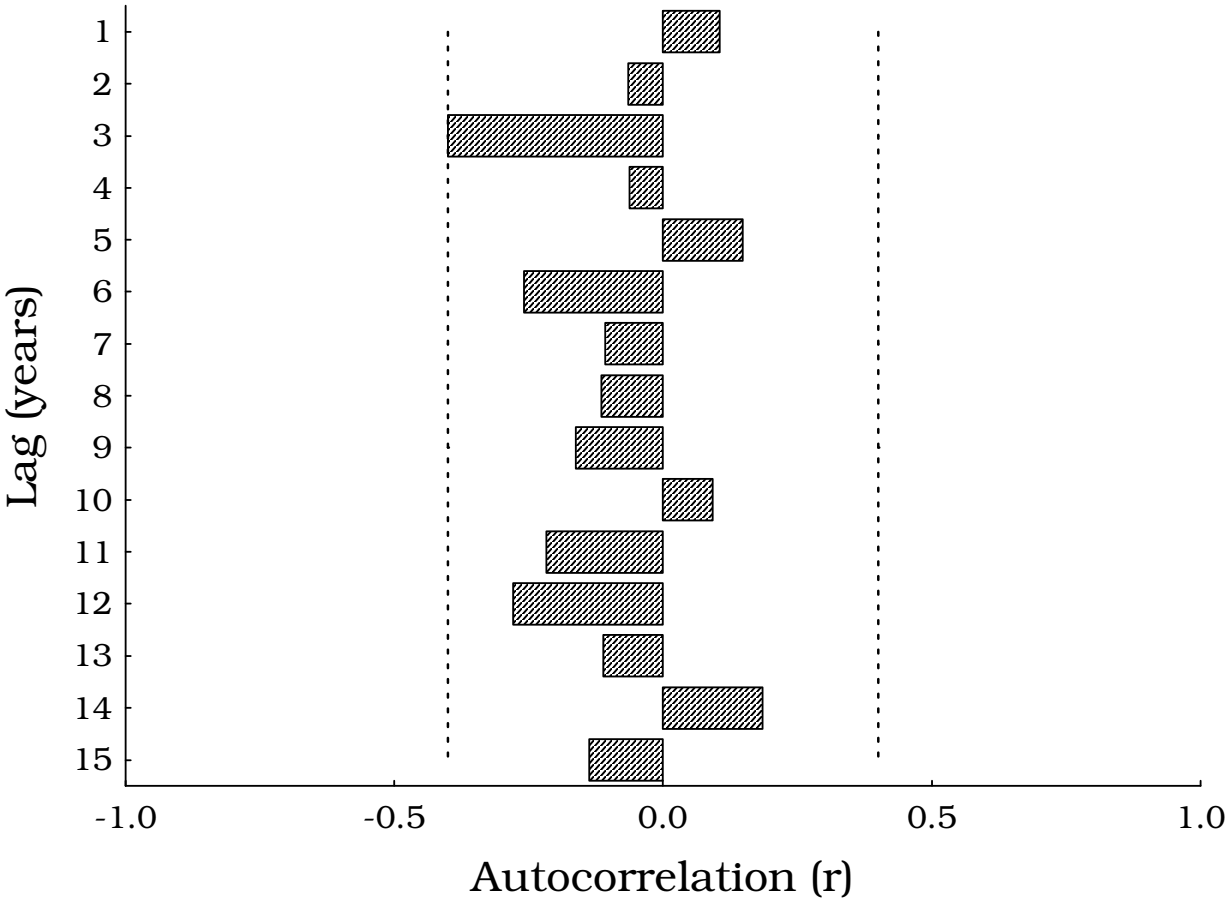


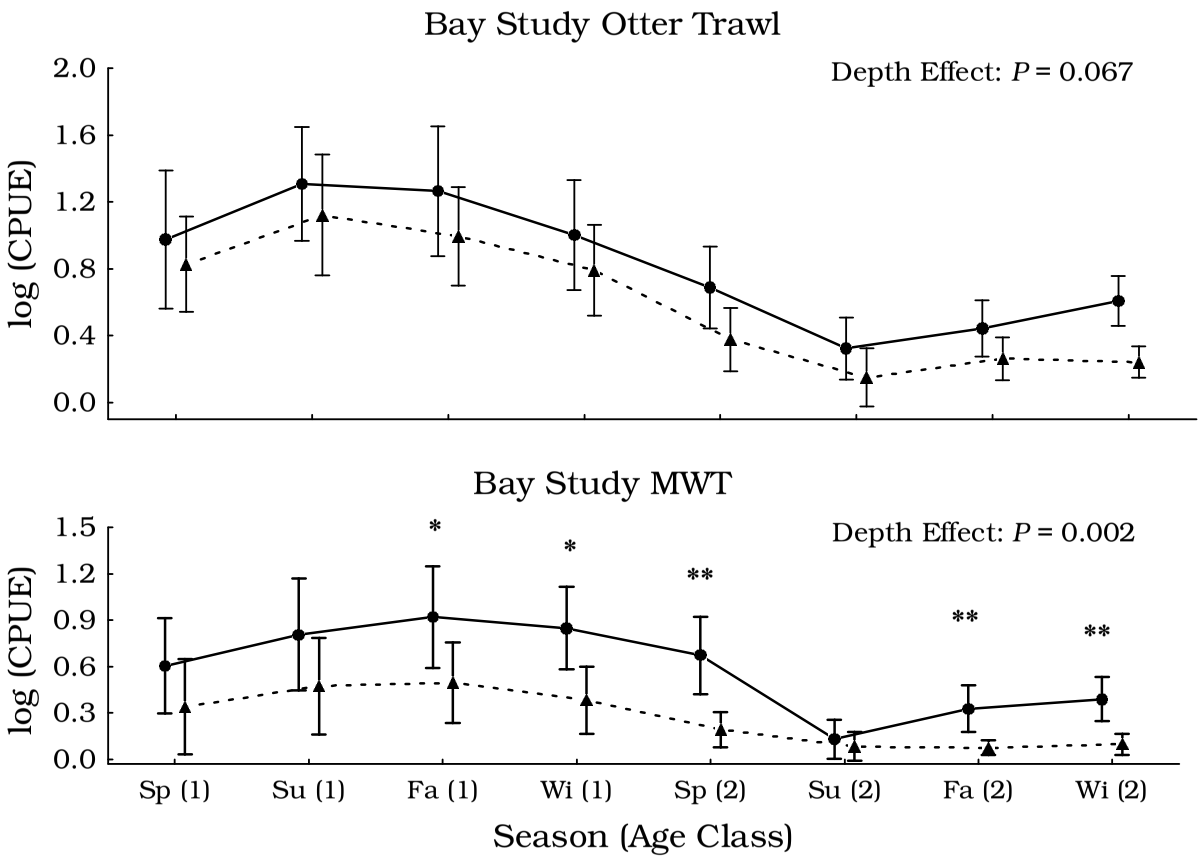
(B) Suisun Marsh Survey

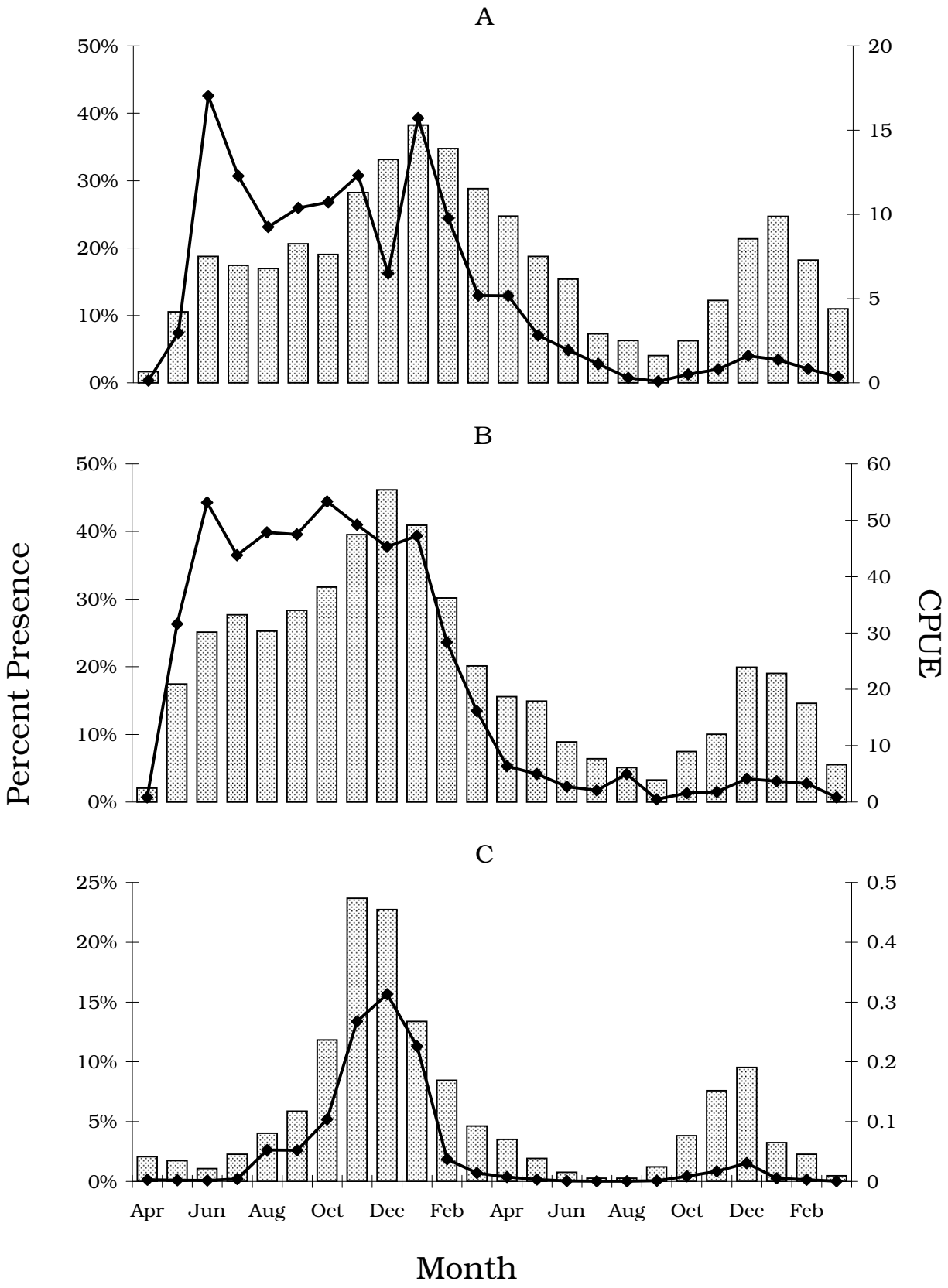


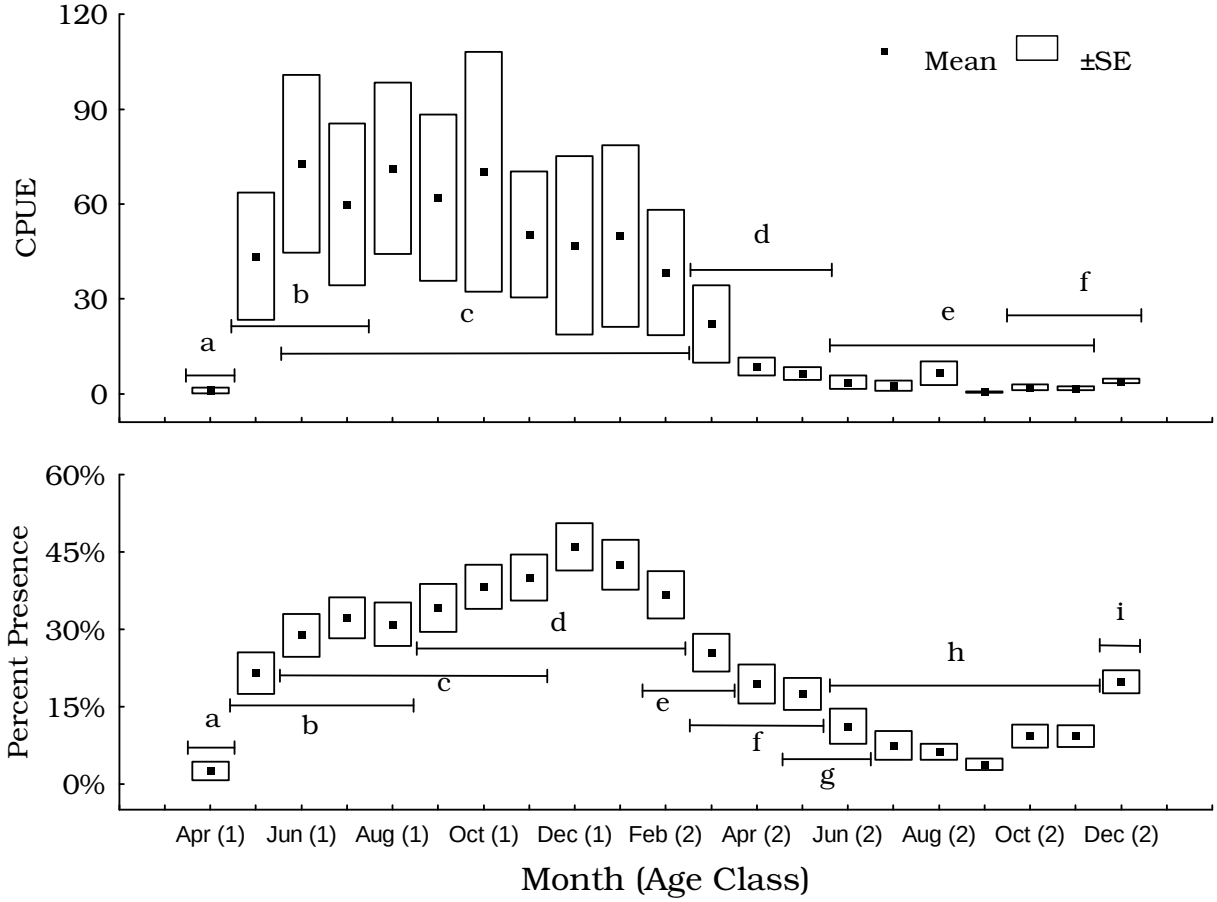

A
Bay Study abundance index
1000000
100000
10000
1000
100
10
1
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
B
FMWT abundance index
100000
10000
1000
100
10
1
C
Suisun Marsh
Age Class 1 (catch/min)
Age Class 2 (catch/min)
0.8
0.6
0.4
0.2
0
0.05
0.04
0.03
0.02
0.01
D
Flow (mean cfs, jan-mar)
200000
150000
100000
50000

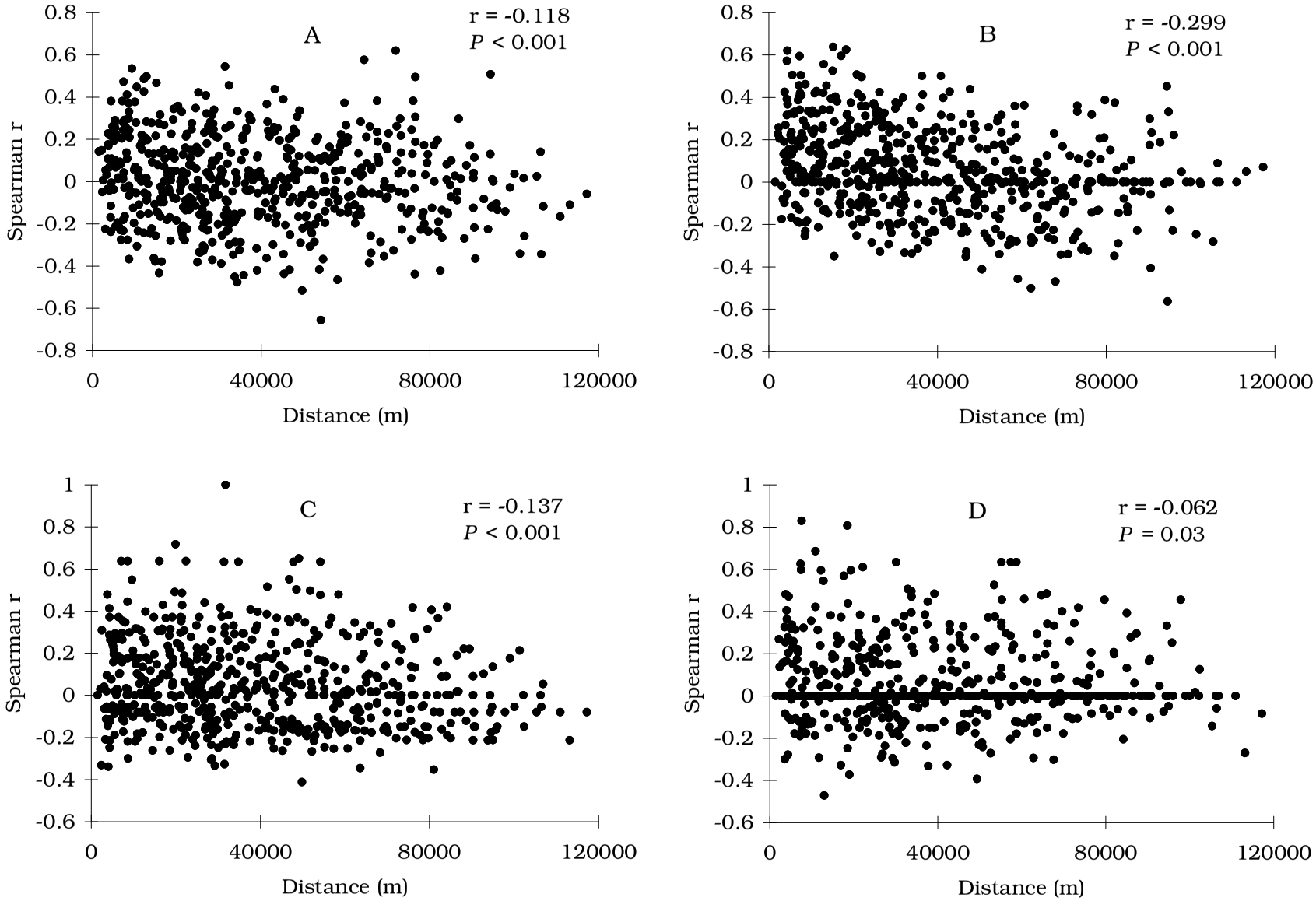

Estuary-wide percent presence
70%
60%
50%
40%
30%
20%
10%
0%
Mean Delta outflow (cfs)
200000
150000
100000
50000
0
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004


Lag (years)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
-1.0
-0.5
0.0
0.5
1.0
Autocorrelation (r)


Bay Study Otter Trawl
Depth Effect: P = 0.067
log (CPUE)
2.0
1.6
1.2
0.8
0.4
0.0
Bay Study MWT
Depth Effect: P = 0.002
log (CPUE)
1.5
1.2
0.9
0.6
0.3
0.0
*
*
**
**
**
Sp (1)
Su (1)
Fa (1)
Wi (1)
Sp (2)
Su (2)
Fa (2)
Wi (2)
Season (Age Class)


A
B
C
Percent Presence
CPUE
Month
50%
40%
30%
20%
10%
0%
25%
15%
5%
20
15
10
5
0
60
50
40
30
0.5
0.4
0.3
0.2
0.1
Apr
Jun
Aug
Oct
Dec
Feb


120
90
60
30
0
CPUE
Mean
±SE
a
b
c
d
e
f
60%
45%
30%
15%
0%
Percent Presence
a
b
c
d
e
f
g
h
i
Apr (1)
Jun (1)
Aug (1)
Oct (1)
Dec (1)
Feb (2)
Apr (2)
Jun (2)
Aug (2)
Oct (2)
Dec (2)
Month (Age Class)


A
r = -0.118
P < 0.001
B
r = -0.299
P < 0.001
C
r = -0.137
P < 0.001
D
r = -0.062
P = 0.03
Spearman r
Distance (m)
0
40000
80000
120000
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
1