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Long-term Trends in Summertime Habitat Suitability for Delta Smelt (*Hypomesus transpacificus*)

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ABSTRACT

The biological productivity of river-dominated estuaries is affected strongly by variation in freshwater inflow, which affects nursery habitat quality. Previous research has shown this is generally true in the upper San Francisco Estuary, California, USA; however, one endemic species of high management importance, delta smelt (*Hypomesus transpacificus*), has shown ambiguous population responses to river inflow variation. We hypothesized that population-level associations with abiotic habitat metrics have not been apparent because the effects occur seasonally, and at spatial scales smaller than the entire upper San Francisco Estuary. We tested this hypothesis by applying regression techniques and principal components analysis (PCA) to a long-term data-set (1970–2004) of summertime fish catch, and concurrently measured water quality (specific conductance, Secchi disk depth, and water temperature). We found that all three water quality variables predicted delta smelt occurrence, and we identified three distinct geographic regions that had similar long-term trends in delta smelt capture probabilities. The primary habitat region was centered on the confluence of the Sacramento and San Joaquin rivers; delta smelt relative abundance was typically highest in the Confluence region throughout the study period. There were two marginal habitat regions—including one centered on Suisun Bay—where specific conductance was highest and delta smelt relative abundance varied with specific conductance. The second marginal habitat region was centered on the San Joaquin River and southern Sacramento-San Joaquin Delta. The San Joaquin region had the warmest water temperatures and the highest water clarity, which increased strongly in this region during 1970–2004. In the San Joaquin region, where delta smelt relative abundance was correlated with water clarity, catches declined rapidly to zero from 1970–1978 and remained consistently near zero thereafter. However, when we combined these regional results into estuary-wide means, there were no significant relationships between any of the water quality variables and delta smelt relative abundance. Our findings support the hypothesis that basic water quality parameters are predictors of delta smelt relative abundance, but only at regional spatial scales.

KEYWORDS

delta smelt, *Hypomesus transpacificus*, estuarine habitat, water quality, specific conductance, water clarity, water temperature

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INTRODUCTION

In tidal river estuaries, the size and quality of particular habitats can be functions of river inflows (Livingston et al. 1997; Peterson 2003). For instance, most tidal river estuaries have prominent frontal zones (also known as low-salinity zones and entrapment zones) where combinations of hydrodynamics and organism behavior result in conspicuous aggregations of turbidity, plankton, and young fishes. The habitat value of low-salinity zones for young fishes and other planktonic organisms may be enhanced by increased river inflows (e.g., Jassby et al. 1995). Young fishes can actively maintain position within low-salinity zones (Bennett et al. 2002), where their feeding success can be enhanced due to similar aggregations of zooplankton prey (Dodson et al. 1989; Kimmerer et al. 1998). Presumably, the enhanced feeding opportunities lead to comparatively rapid growth, and thus lower cumulative predation mortality during vulnerable early life stages (Houde 1987). The typically turbid conditions in low-salinity zones also may directly reduce predation losses to visual predators (Gregory and Levings 1998).

In the upper San Francisco Estuary (California, USA; Figure 1) (hereafter upper estuary), the linkage between river inflow and the low-salinity zone was formalized into a water quality standard using an integrative parameter called X_2, which is the distance in kilometers (km) from the mouth of San Francisco Bay at the Golden Gate Bridge to the location of the estuary where mean bottom salinity is 2 practical salinity units (psu) (Jassby et al. 1995). The abundance or survival of numerous organisms is elevated in years when mean spring and early summer X_2 locations are moved seaward (closer to the Golden Gate) by high river inflows (Jassby et al. 1995; Kimmerer 2002a). Some species' X_2 responses degraded following the introduction of the overbite clam *Corbula amurensis* in 1986 (Kimmerer 2002a; Sommer et al. 2007); however, most historically flow-responsive taxa continue to have statistically demonstrable linkages between abundance or early life stage survival and X_2 position.

The Delta Smelt

Delta smelt (*Hypomesus transpacificus*) is an annual fish endemic to the upper San Francisco Estuary low-salinity zone (Moyle et al. 1992). It is arguably the most imperiled estuarine fish species in the United States (Bennett 2005). Numerous field studies have qualitatively or semi-quantitatively described delta smelt distribution relative to salinity (e.g., Moyle et al. 1992; Bennett 2005), or its covariate, X_2 (e.g., Dege and Brown 2004). A general association with open water and, in particular, large shoal habitats in Suisun Bay and the Sacramento-San Joaquin River confluence has also been reported previously (e.g., Moyle et al. 1992; Bennett et al. 2002). Despite its distribution within the low-salinity zone, delta smelt abundance has not responded predictably to interannual river flow variation (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002a; Bennett 2005). Rather, delta smelt have undergone a long-term abundance decline characterized by an abrupt decline around 1982 (Kimmerer 2002a), and very low abundance in recent years (Sommer et al. 2007; Figure 2). The reasons for the persistently low abundance since 1982 are thought to result from multiple interacting factors including larval advection during high flows in winter–spring 1982 and 1983, a drought during 1987–1992, entrainment in water diversions, contaminant exposures, and competition from introduced species (Moyle et al. 1992; Bennett 2005).

Analyses such as the X_2 relationships described above (Jassby et al. 1995; Kimmerer 2002a) implicitly assume that habitat and abundance linkages are detectable at the scale of the entire upper estuary. The success of this approach suggests that it is an appropriate scale for many taxa. However, it is possible that the entire upper estuary may be too broad a spatial scale to understand the degree to which estuarine habitat conditions affect delta smelt abundance. Because of their limited distribution, we hypothesize that linkages between delta smelt abundance and abiotic habitat suitability exist at smaller spatial scales (i.e., regions of the estuary). If true, this could explain the lack of correspondence between delta smelt abundance and X_2 position in the upper estuary. An alternative hypothesis is that the abiotic components of habitat are never limiting to the delta smelt population: i.e., linkages do not exist at any spatial scale. Here, we test this hypothesis by examining long-term monitoring data collected on juvenile delta smelt and concurrently measured water-quality variables. Specifically, we addressed three study questions:

1) What is the abiotic habitat of delta smelt during summer?
2) Has summertime abiotic habitat changed?
3) Are delta smelt abundance and water quality correlated regionally and at the scale of the entire upper estuary?

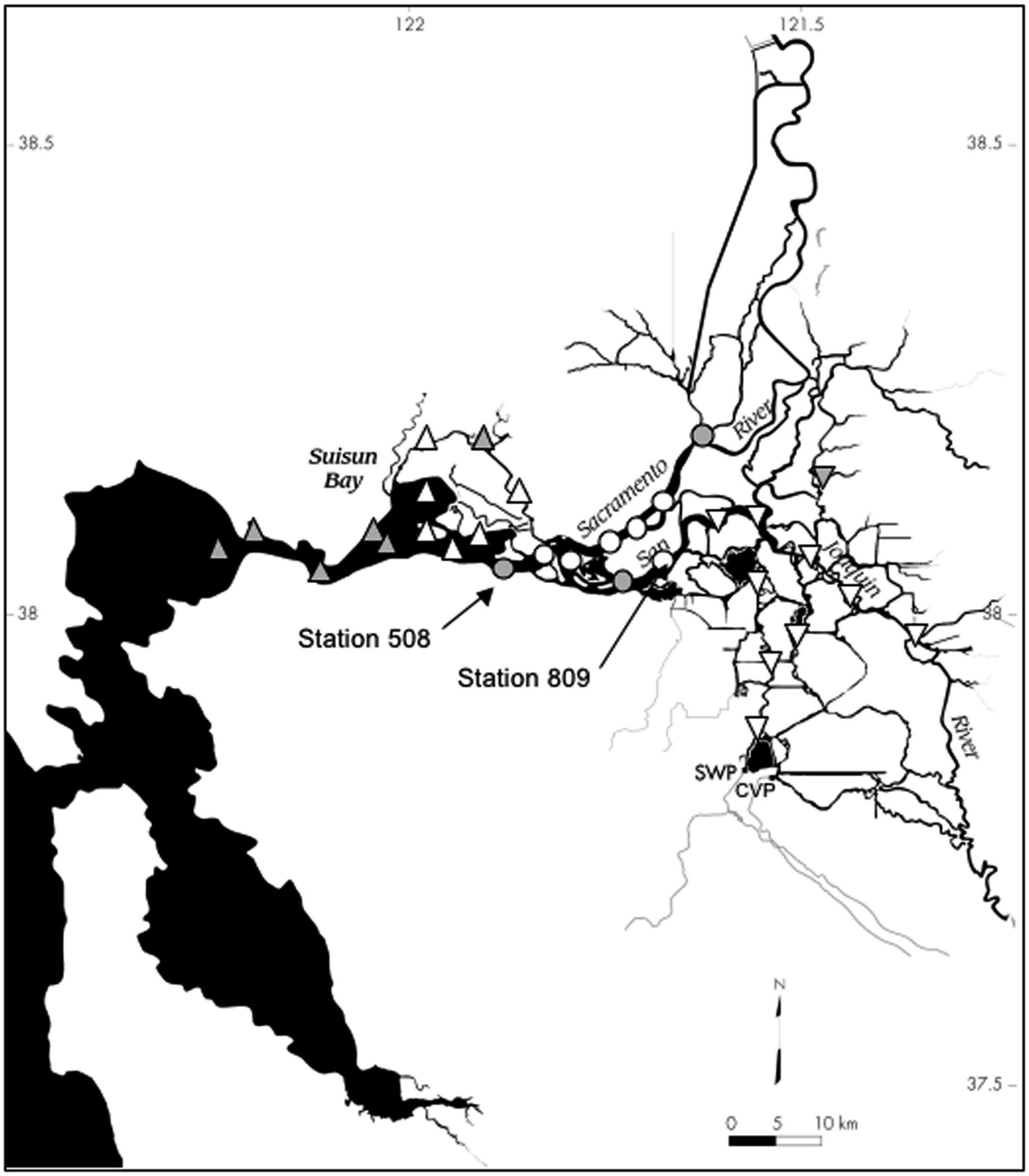

Figure 1. Map of the San Francisco Estuary showing the locations of stations sampled by the California Department of Fish and Game (CDFG) summer Tow-Net Survey (TNS; symbols). The symbols vary based on a principal components analysis (PCA) used to cluster stations showing similar time trends in delta smelt capture probabilities based on a generalized additive model: the Suisun region is depicted by upward-pointing triangles, the Confluence region by circles, and the San Joaquin region by downward-pointing triangles. Stations that were not included in the PCA due to incomplete sampling are colored gray.

Study Area

The upper San Francisco Estuary is the mixing zone for Pacific Ocean water that enters San Francisco Bay under the Golden Gate Bridge, and freshwater inputs from numerous streams, most notably the Sacramento

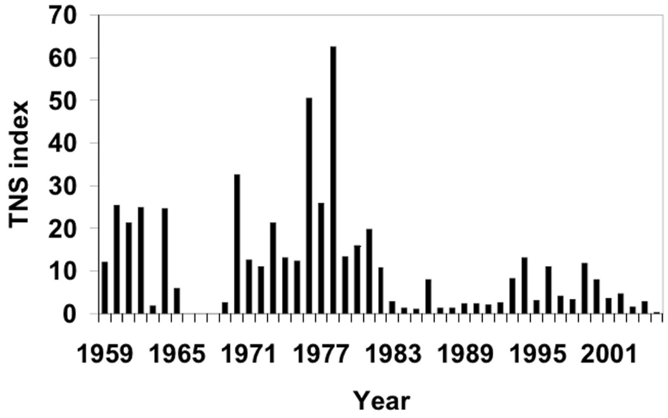

Figure 2. Time series of delta smelt relative abundance based on the CDFG Summer TNS. Data are abundance indices (solid line) developed by Moyle et al. (1992).

and San Joaquin Rivers (Figure 1). The estuary is, in all aspects, a highly altered ecosystem (Nichols et al. 1986; Kimmerer 2002b). For instance, the Sacramento and San Joaquin Rivers drain about 40% of California's surface area, and their inflows strongly affect estuarine salinity (Jassby et al. 1995), but, whenever possible, river inflows are regulated. The Sacramento-San Joaquin Delta is maintained as a permanently freshwater environment (but still under tidal influence) to support regional agriculture and the export of large quantities of freshwater out of the delta for agricultural and municipal users to the south and west (Kimmerer 2002b). The largest export diversions are located in the San Joaquin River basin (Figure 1), but most of the export is supported by reservoir releases from the Sacramento River basin, which receives considerably more precipitation. During January–June, estuarine salinity standards based on X_2 positions require significant freshwater inputs to the estuarine ecosystem (Kimmerer 2002b). Major changes in the upper estuary during the 1970–2004 study period included: increased rock reinforcement of levees, increased freshwater exports (Kimmerer 2002b), increased autumn salinity intrusion (Feyrer et al. 2007), increased species invasion rates (Cohen and Carlton 1998), decreased pelagic productivity, increased water clarity (Jassby et al. 2002), the proliferation of submerged macrophytes (Brown and Michniuk 2007), and decreased native fish abundance (Matern et al. 2002; Brown and Michniuk 2007).

METHODS

The California Department of Fish and Game Summer (CDFG) Tow-Net Survey (TNS) was developed to index age-0 striped bass (*Morone saxatilis*) relative abundance; the data have been used extensively to analyze striped bass population dynamics (Turner and Chadwick 1972; Stevens et al. 1985; Kimmerer et al. 2000). However, the TNS has also always collected delta smelt incidentally because of their similar distribution to young striped bass. Delta smelt collected by the TNS generally range from about 25–50 millimeter (mm) fork length. Delta smelt relative abundance indices based on the TNS have also been developed and used to analyze long-term population trends (Moyle et al. 1992; Kimmerer 2002a; Bennett 2005). The TNS conducts three tows at each of up to 32 stations (Figure 1) during each of its component surveys using a conical net (1.5-square meter (m^2) mouth; 2.5 mm cod-end mesh) towed obliquely through the water column from bottom to surface. A minimum of two of these surveys is conducted each year. The delta smelt relative abundance index is calculated as follows. The sum of catch from the three tows at each station is multiplied by a water-volume estimate to produce station-specific estimates of catch per volume (Chadwick 1964). Next, these volumetric density estimates are summed across all stations, and the average of the summed volumetric density estimates from the first two surveys comprises the summertime abundance index (Moyle et al. 1992).

TNS Data Sampling

The TNS fish sampling began in 1959; concurrent data collection on water temperature (°C), water clarity (Secchi disk depth; cm), and specific conductance (microSiemens per centimeter [$\mu S \cdot cm^{-1}$]) began in 1970. Note that specific conductance is a surrogate for salinity in the estuary. The Pearson correlation coefficient between the mean April–July X_2 position used by Jassby et al. (1995) and Kimmerer (2002a), and the mean estuary-wide $\log_{10}$ specific conductance used in the present study, is 0.94. Since the two measurements are closely correlated, and because X_2 is a calculated variable, we chose to use the data actually collected during the TNS. The TNS sampling has had an average survey starting date of 13 July, but surveys have been conducted as early as 4 June and as late as 28 August in some years. To standardize the survey results across years, we used the data for each year's survey that 1) occurred closest to 13 July, and 2) had at least 28 of 32 stations sampled. When at least 28 stations were sampled, the survey grid was sampled with adequate spatial coverage. Typically, when fewer than 32 stations were sampled, the most seaward stations were dropped because they were considered unlikely to yield young-of-the-year striped bass due to high salinity. Water that is too saline for young-of-the-year striped bass is generally also too saline for delta smelt.

Modeling

We used binomial generalized additive modeling (GAM; smoother = cubic spline) to explore relationships between delta smelt occurrence (distribution) and water quality variables. Generalized additive modeling can depict nonlinear responses to environmental gradients (Stoner et al. 2001; Stratoudakis et al. 2003; Feyrer et al. 2007). For this analysis, we converted the raw delta smelt count data into occurrence (binomial or presence/absence) data, which provides a conservative but robust means of constraining the underlying, highly-skewed error distributions that typify raw count data based on trawl sampling. We developed GAMs for each water quality variable individually to estimate their explanatory power, and for all three variables combined. The model including all three variables lowered the null deviance (analogous to variance in parametric statistics) in the data by at least 8% more than any single variable. The *P*-values for each water quality variable were also always < 0.05 (usually much less) whether considered individually or together. However, this was due, in part, to the very high degrees of freedom in the model. Thus, in addition to *P*-values, we used findings from laboratory physiology studies (Swanson et al. 2000) and other field studies of delta smelt distribution (Dege and Brown 2004; Nobriga et al. 2005; Feyrer et al. 2007) to guide our interpretation of the relevance of GAM results (see Discussion).

In addition to being statistically robust, we expected delta smelt occurrence to be relatively resistant to declining catches through time, particularly in association with water quality combinations representing the best available habitats. We assumed the population decline would lower catches even in the best available habitats, but that delta smelt would still be present where conditions remained most suitable. Lastly, we assumed that error in the association between delta smelt occurrence and water quality attributable to tidal time-scale variation from taking point measurements of water quality was insignificant for two reasons. First, the large amount of data (> 30 years; n = 954 samples) provided a large buffer against this type of random error. Second, delta smelt move actively in conjunction with tides to maintain position within the low-salinity zone (Bennett et al. 2002), so it is likely they generally remain associated with suitable water quality combinations. The GAM was essentially a test of this assumption.

Testing Abundance Trends

We also tested for associations of water quality and delta smelt relative abundance. We tested for water quality–abundance relationships at two spatial scales, regional and estuary-wide. For the former, we first used principal components analysis (PCA) to group stations with similar time trends in delta smelt capture probabilities based on the GAM. We used this step to provide an objective spatial context to subsequently explore regional relationships between water quality and delta smelt relative abundance. The PCA result indicated that the estuary could be divided into three regions (see Results; Figure 1). Only 21 of the 32 sampling stations were sampled every year, so the PCA was restricted to these 21 stations; however, stations from all but the westernmost part of the sampling array were well represented (Figure 1).

To explore regional habitat-abundance associations, we divided the water quality and delta smelt catch data into the PCA-derived regions. Then, for each region, we calculated mean delta smelt catch per tow and means of the water quality parameters. To ensure the regions represented distinct habitats, we tested for differences in means of water quality parameters using one-way ANOVA and Tukey post-hoc multiple comparison tests. We performed a separate ANOVA for each water quality variable. We also tested for long-term regional trends in each water quality variable using linear regression. The water quality data were log$_{10}$-transformed before the ANOVAs to improve their conformance with the assumptions of parametric statistical testing. We evaluated regional time trends in log$_{10}$ + 1-transformed delta smelt relative abundance using LOWESS regression to facilitate interpretation of nonlinear trends (Trexler and Travis 1993). Lastly, we used Spearman's rank correlation to test for regional habitat–abundance associations. We used Spearman's correlation because some of the regional habitat–abundance relationships were unidirectional but curvilinear, and, in some cases, variance in the response (delta smelt relative abundance) was a function of the predictor variable; the use of ranked data was therefore appropriate. The significance level chosen for all of the regional analyses was $\alpha < 0.05$.

We used multiple linear regression to test for habitat–abundance relationships at the scale of the entire upper estuary. In this analysis, we regressed the TNS abundance indices shown in Figure 2 on the mean water temperature, water clarity, and specific conductance values shown in Figure 3. All variables were log$_{10}$-transformed prior to the analysis to bring the variance closer to the normal distribution assumed for parametric statistical tests. We used multiple linear regression in this case because scatter-plots did not indicate any obvious habitat–abundance associations, but it was not possible to tell visually whether interactions among the water quality variables were important. The overall model was considered statistically significant if the F-statistic obtained had a probability of < 0.05. Likewise, the contributions by individual water quality variables to the overall model were considered statistically significant at $\alpha < 0.05$.

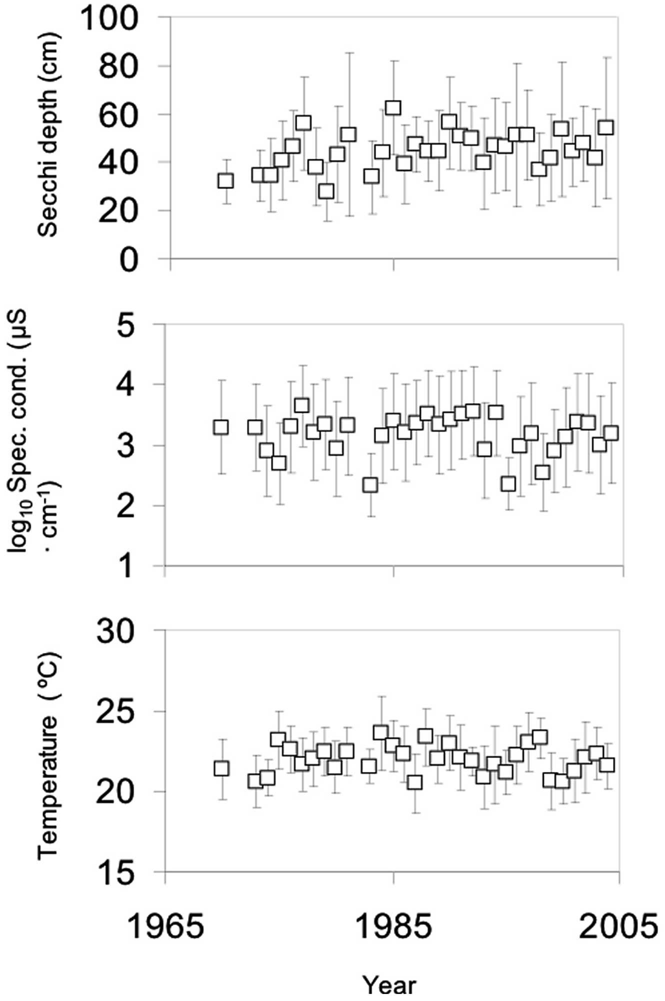

Figure 3. Time series of mean (+/- 1 SD) July water quality variables—Secchi depth (clarity), specific conductance (salinity) and temperature—based on data from the CDFG Summer TNS.

Table 1. Results of binomial generalized additive models (GAM) for delta smelt occurrence relative to water quality variables in the San Francisco Estuary. Data were available for 32 years between 1970 and 2004. The null deviance reduction was 29%. The deviance in generalized additive modeling is analogous to the variance in classical parametric statistics. All explanatory variables were log^{10}-transformed before analysis.

Water quality variable	X^2 statistic	*P*-value	Deviance reduced[a]
Specific conductance (μS · cm-1)	60.8	< 0.0000001	13%
Water clarity (cm)	27.5	0.0000038	21%
Water temperature (°C)	9.16	0.026	6.3%

[a] *This is the null deviance reduced by the variable when it was the only predictor variable used in the model. The GAM output does not discern individual deviance reduction in models with more than one explanatory variable.*

RESULTS

All three water quality variables significantly predicted delta smelt occurrence (Table 1), suggesting they all interact to influence delta smelt distribution. Delta smelt capture probabilities were highest at low specific conductance (1,000–5,000 µS · cm^{-1}; approximately 0.6–3.0 psu) and low water clarity (< 40 cm Secchi disk depth) (Figure 4). Water temperature influenced delta smelt occurrence more like a 'switch' than the other two variables; capture probabilities did not have a strong trend at temperatures lower than about 24°C, but capture probabilities decreased abruptly at higher temperatures. Note that the scatter in each panel of Figure 4 depicts the variation caused by the other two water quality variables.

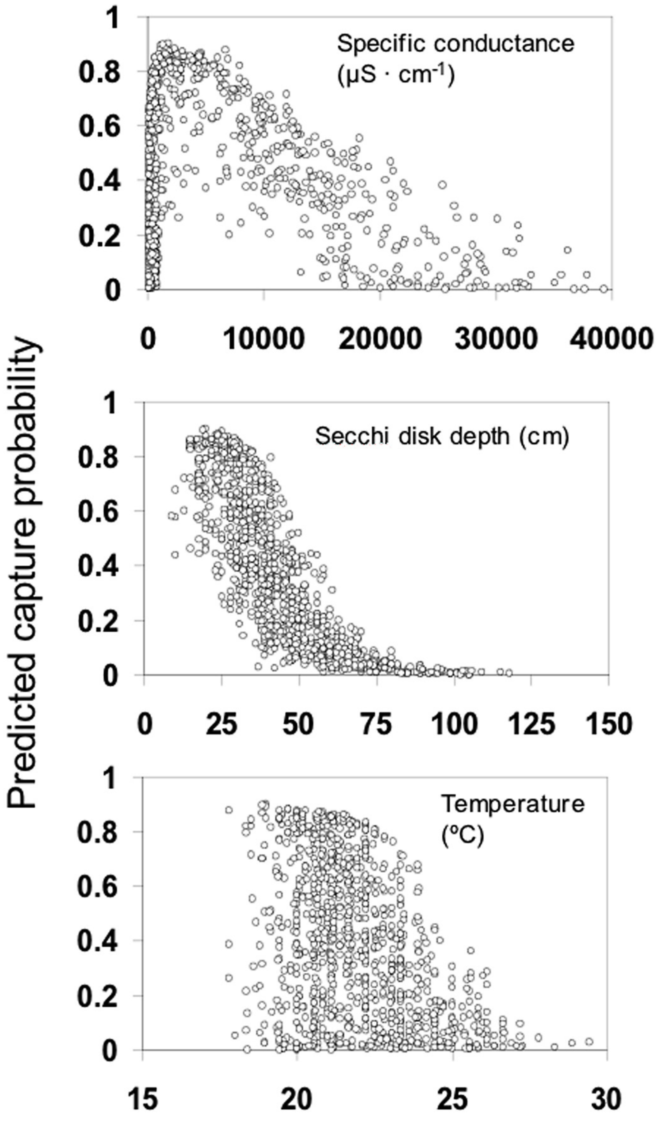

Figure 4. Predicted capture probabilities for juvenile delta smelt (*Hypomesus transpacificus*) relative to water-quality variables in the upper San Francisco Estuary. The capture probabilities were based on a binomial generalized additive model including all three water-quality variables as explanatory variables; the scatter in each panel is due to the interactive influence of the other two variables.

The PCA produced three principal components with eigenvalues > 1.0 that cumulatively explained 80% of the variance in station-specific trends in delta smelt capture probabilities (PC1, eigenvalue = 7.85, variance explained = 37%; PC2, eigenvalue = 5.86, variance explained = 28%; PC3, eigenvalue = 3.02, variance explained = 14%). All stations loaded negatively on PC1, which reflected a long-term trend of declining capture probability at every station. However, scatter-plots (not shown) indicated that the stronger the negative PC1 loading, the more strongly capture probabilities declined at that station through time. Stations numbered in the 800–900s generally had the most strongly negative trends in capture probabilities (Figure 5). We defined the San Joaquin region (Figure 1; Figure 5) based on a combination of PC1 and PC3 loadings. San Joaquin region stations had strongly negative capture probability trends

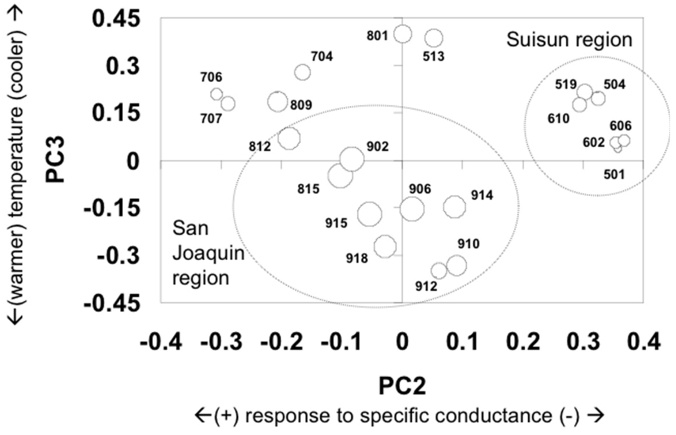

Figure 5. Scatter-plot of Summer TNS sampling station scores for axis 2 versus axis 3 from a PCA of delta smelt capture probabilities. The symbol size is scaled to scores for axis 1; the larger the symbol, the stronger the negative time trend in capture probability.

or chronically low capture probabilities likely due to high water temperature (Stations 910–912).

The stations included in the Suisun region (Figure 1; Figure 5) had the most strongly positive PC2 loadings, representing negative correlations between specific conductance and capture probability. Stations seaward of those included in the PCA were also grouped into the Suisun region.

The Confluence region (Figure 1) comprised the stations that were not included in either of the previous two regions. The boundaries of the Confluence region are somewhat subjective because station 508 was not included in the PCA (Figure 1) and because there was not a clear separation of PC1 or PC3 loadings along the San Joaquin River (Figure 5). We included Station 508 in the Confluence region because the Pearson correlation coefficient between its capture probabilities and those of the next Confluence region station (513) was 0.74, which was higher than the correlation coefficient between Station 508 and the adjacent Suisun region station (504; r = 0.64). We also included Station 809 in the Confluence region because the correlation coefficient for year versus Station 809 capture probabilities was only 0.42, suggesting a weakly declining trend. The next San Joaquin River station (812) had r = 0.55, suggesting a better-defined declining trend.

The regions were distinct in terms of their mean water quality conditions (Table 2). The Suisun region had the highest mean specific conductance, and the San Joaquin region had higher mean water temperatures and water clarity than the other two regions. The midsummer water clarity of the upper estuary increased weakly during 1970–2004, driven by a strong increase in the San Joaquin region (Table 3). Water clarity was the only water quality

Table 2. Comparisons of mean July water quality conditions for 1970–2004 among three regions of the upper San Francisco Estuary. Statistically significant regional differences (one way ANOVA with Tukey post-hoc comparisons) are separated by lines within each column.

Region	Specific conductance ($\mu S \cdot cm^{-1}$)	Secchi disk depth (cm)	Temperature (°C)
Suisun	9080	34	21
	------		------
Confluence	780	39	22
	------	------	------
San Joaquin	295	53	24

Table 3. Results of linear regression analyses of year (1970–2004) versus means of three water quality- variables based on the CDFG Summer Tow-Net Survey (TNS). The water quality variables were $\log_{10}$-transformed before analysis. The analyses were done at two spatial scales: (1) the entire upper estuary, and (2) regions that are spatially defined in Figure 1. Statistically significant results (alpha < 0.05) are denoted with an asterisk (*).

Region and Water Quality Variable	Slope	r^2	Probability
Entire Upper Estuary			
specific conductance	-0.0027	0.0065	0.66
Secchi disk depth	0.0034	0.18	0.016*
Temperature	-5.00×10^{-5}	7.91×10^{-4}	0.88
Suisun Region			
specific conductance	-0.0030	0.0048	0.71
Secchi disk depth	-0.0022	0.027	0.37
Temperature	-1.58×10^{-5}	7.38×10^{-5}	0.96
Confluence Region			
specific conductance	-0.0052	0.013	0.54
Secchi disk depth	0.0030	0.11	0.058
Temperature	-1.57×10^{-4}	0.0056	0.68
San Joaquin Region			
specific conductance	-0.0034	0.031	0.34
Secchi disk depth	0.0089	0.54	1.6×10^{-6}*
Temperature	7.87×10^{-5}	0.0016	0.83

variable that changed significantly at either spatial scale.

Delta smelt relative abundance was typically highest in the Confluence region throughout the study period, though the 1982 step–change (Kimmerer 2002a) is a prominent feature of the Confluence trend (Figure 6). Another prominent trend was that in the San Joaquin region, delta smelt catches declined rapidly to zero from 1970–1978 and have remained consistently near zero ever since. In the Suisun region, there were two periods of increasing and decreasing relative abundance. Relative abundance was correlated with water clarity in each region (Suisun, Spearman $\rho = -0.59$; $n = 32$; $P = 0.0004$; Confluence, Spearman $\rho = -0.51$; $n = 32$; $P = 0.003$; San Joaquin, Spearman $\rho = -0.65$; $n = 32$; $P = 0.00005$). Relative abundance also varied in the Suisun region in association with specific conductance (Spearman $\rho = -0.65$; $n = 32$; $P = 0.00005$), but specific conductance was not correlated with abundance in the other regions (Confluence Spearman $\rho = 0.26$; $n = 32$; $P = 0.15$ and San Joaquin Spearman $\rho = 0.094$; $n = 32$; $P = 0.61$). At the scale of the entire upper estuary, the water quality variables were not correlated with juvenile delta smelt relative abundance indices calculated from the TNS ($F = 2.19$; $P = 0.11$; multiple $R^2 = 0.10$; $n = 32$; P-values for individual parameters of > 0.05).

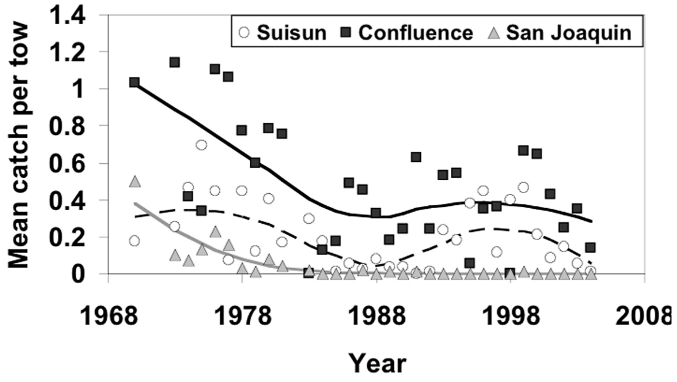

Figure 6. Time series of mean delta smelt catch · tow^{-1} ($\log_{10} + 1$ transformed) in three regions defined by principal components analysis (see Figure 1). The splines are loess regression line.

DISCUSSION

We found that the three water quality variables—specific conductance (salinity), Secchi depth (clarity), and temperature—measured concurrently with fish catches in the CDFG TNS all interact to influence delta smelt occurrence (distribution) in the upper San Francisco Estuary. Thus, they are all indicators of abiotic habitat suitability. Long-term associations of water quality variation and relative abundance were discernable at regional spatial scales, most notably on the perimeter of the species' distribution outside of the Confluence region. Delta smelt relative abundance in the Suisun region varied in association with specific conductance, which is a function of river inflow variation. This is consistent with previous findings for larvae during spring–early summer (Dege et al. 2004) and juveniles and pre-spawning adults during fall (Feyrer et al. 2007). Note that Kimmerer (2002a) reported there was no long-term trend in mean January–June X_2 position. This reflects river inflow conditions during the six months preceding the data used in our study. Thus, it is not surprising that we found no long-term trend in July specific conductance. At the landward edge of the estuary, delta smelt have essentially disappeared during midsummer.

Of the three water quality variables, only water clarity had a long-term trend. Jassby et al. (2002) had reported previously that water clarity in the Sacramento-San Joaquin Delta had increased due to significant long-term reductions in total suspended solids during most months between March and November. Thus, we propose that increased San Joaquin region water clarity has constricted delta smelt habitat, and is a major reason for its regional absence during summer. The possibility of habitat constriction was proposed by Bennett (2005) who suggested it as a possible mechanism for apparent 'density–dependence' between the summer and fall based on stock-recruitment analyses of long-term monitoring data-sets.

Our conclusion that there has been a long-term habitat constriction for delta smelt is also consistent with Feyrer et al. (2007), who analyzed fall abundance data. Feyrer et al. (2007) were able to identify changes both regionally and at the scale of the entire upper estuary. They also found simple statistical associations between fall stock size, fall water quality, and abundance the following summer. We suggest that estuary-wide habitat changes are more apparent in fall than in summer because delta smelt habitat suitability progressively deteriorates over the course of the year. Adult and juvenile delta smelt use the San Joaquin region during winter through early summer, sometimes causing conflicts between water export schedules and Endangered Species Act–mandated take levels (Bennett 2005). Presumably, cooler water temperatures and lower water clarity during winter–spring flow pulses allow delta smelt to occupy the San Joaquin region early in the year. By July, the San Joaquin region is no longer suitable delta smelt habitat, and by fall, habitat suitability declines further due to a separate long-term trend toward elevated salinity in the Suisun region (Feyrer et al. 2007).

We acknowledge that the three water quality variables we analyzed cannot fully define abiotic habitat for delta smelt. For instance, estuarine fish distributions can be influenced by dissolved oxygen (Eby and Crowder 2002). Young delta smelt are also exposed to contaminants (Kuivila and Moon 2004), and some individuals show evidence of sublethal toxic exposure (Bennett 2005); the population-level consequences of contaminant exposures are unknown. However, each of the water quality variables we used has well-known effects on fish ecology. Water clarity strongly affects large river (Quist et al. 2004) and estuarine fish assemblages (Blaber and Blaber 1980). In the cited studies, water clarity was thought to mediate predator–prey interactions; there is experimental evidence for the role of turbidity as a factor influencing piscivore success (Abrahams and Kattenfeld 1997; Gregory and Levins 1998). We suggest that predation on delta smelt may be higher in relatively clear water, or that delta smelt may avoid clear water because it increases their predation risk.

The increased water transparency in the upper estuary appears to be due to the combined effects of decreasing sediment inputs (Wright and Schoellhamer 2004), sediment wash-out from very high inflows during the 1982–1983 El Nino (Jassby et al. 2005), and the proliferation of large beds of submerged freshwater macrophytes, particularly in the San Joaquin region (Nobriga et al. 2005; Brown and Michniuk 2007).These macrophyte beds may act as ‘biological filters’ for sediment. The invasion of aquatic macrophytes has already substantially changed near-shore fish assemblages. The results of the present study and of Feyrer et al. (2007) suggest the macrophyte proliferation may also have restricted pelagic fish distributions.

Specific conductance is a surrogate for salinity, which strongly affects estuarine fish distributions (Bulgar et al. 1993). The influence of salinity on the geographic distribution of young delta smelt has been noted previously (Moyle et al. 1992; Dege and Brown 2004). Swanson et al. (2000) found the upper salinity tolerance of delta smelt was about 19 psu. This corresponds well with the field data in this study; predicted capture probabilities were virtually zero at a specific conductance of 35,000 µS . cm^{-1}, which roughly corresponds to 20 psu (Figure 4). Similarly, Feyrer et al. (2007) found that delta smelt capture probabilities during fall were essentially zero at specific conductances higher than 25,000 µS · cm^{-1} (about 15 psu). The results of the present study, and of Feyrer et al. (2007), provide idealized salinity response curves that bridge previous findings and show the interactive influence of other water quality variables on delta smelt distribution along the estuarine salinity gradient.

Water temperature is an important determinant of fish metabolic and growth rates, so it affects estuarine habitat suitability through a variety of mechanisms (Lankford and Targett 1994; Marine and Cech 2004). Water temperature was the poorest predictor of delta smelt distribution in the present study, accounting for only about 6% of the null deviance in delta smelt occurrence (Table 1). Water temperature also had no significant regional or estuary-wide effects on delta smelt relative abundance. We think the low predictive power of water temperature was due more to the shape of its response curve than to low ecological importance. Essentially, delta smelt occurrence and relative abundance responded to water temperature only when it neared or exceeded the 25°C lethal limit reported by Swanson et al. (2000). Currently, the upper San Francisco Estuary averages more than 20°C during mid-summer, and the San Joaquin region already approaches the 25°C upper lethal limit (Table 2). Moreover, the shape of the predicted response curve to water temperature suggests the difference between tolerable and not tolerable can be quite abrupt (Figure 4).

Future Trends

Our results, and those of Feyrer et al. (2007), have demonstrated that delta smelt habitat suitability is sensitive to system changes. Our results also suggest that X_2 position variation and other factors need to be considered when evaluating delta smelt habitat suitability and trends. However, there is high uncertainty about future trends in factors that are likely to influence delta smelt habitat suitability that make it impossible to forecast future habitat conditions. For instance, northern California's climate is likely to get warmer by 2100, which would increase water temperatures, but future precipitation trends, which could influence salinity distributions in the estuary, are very uncertain (Dettinger 2005). Long-term salinity trends are further complicated by the potential for catastrophic natural events that could change the upper estuary landscape. Mount and Twiss (2005) estimated there is a 67% chance that flooding or earthquakes will change the landscape of the Sacramento-San Joaquin Delta by 2050. Debate about future policy direction for the Delta adds another level of uncertainty to future habitat conditions for delta smelt (Lund et al. 2007).

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