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Modeling the Effects of Future Outflow on the Abiotic Habitat of an Imperiled Estuarine Fish

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Abstract Future development and climate change pose potentially serious threats to estuarine fish populations around the world. We examined how habitat suitability for delta smelt (*Hypomesus transpacificus*), a state and federally protected species, might be affected by changes in outflow in the San Francisco Estuary due to future development and climate change. Forty years of sampling data collected during fall from 1967 to 2008 were examined to define abiotic habitat suitability for delta smelt as a function of salinity and water transparency, and to describe long-term trends in habitat conditions. The annual habitat index we developed, which incorporated both quantity and quality of habitat, decreased by 78% over the study period. Future habitat index values under seven different development and climate change scenarios, representing a range of drier and wetter possibilities, were predicted using a model which related estuarine outflow to the habitat index. The results suggested that each of the scenarios would generally lead to further declines in delta smelt habitat across all water year types. Recovery targets for delta smelt will be difficult to attain if the modeled habitat conditions are realized.

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Introduction

Habitat loss or reduced suitability poses a major threat to biota across the globe (Turner 1996; Hoekstra et al. 2005; Dobson et al. 2006). In aquatic ecosystems, balancing the needs of the environment and humanity given limited water is a significant challenge to the management and conservation of fishes and other organisms (Freeman et al. 2001). At a minimum, effective conservation and management of aquatic resources requires understanding the effects of water development on abiotic habitat because biota often cannot persist where the abiotic components of their habitat are greatly altered. This is particularly important—and also challenging to accomplish—in estuaries, where there is often substantial spatial and temporal variability in abiotic habitat that is strongly affected by outflow and tides (Skreslet 1986).

Animals with annual life cycles and limited distributions are particularly vulnerable to habitat loss or reduced suitability. Such characteristics can enhance the risk of extinction from pulse perturbations such as unusual or catastrophic events and press perturbations such as steady long-term habitat deterioration. Delta

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smelt (*Hypomesus transpacificus*) is an annual fish species endemic solely to the euryhaline portion of the San Francisco Estuary, CA, USA. It is listed as a threatened species by the US Fish and Wildlife Service and as an endangered species by the State of California (Moyle 2002; Bennett 2005). This small (maximum size of about 100 mm fork length) fish species is a major focal point for conservation issues because it relies on an estuary which supplies water for 25 million people and the largest ($27 billion) agricultural industry in the USA (Service 2007; Sommer et al. 2007). Given the social and economic challenges of dividing existing water supply between delta smelt and meeting other human needs, understanding how population dynamics of delta smelt are affected by the water characteristics and hydrodynamics of the estuary is a major priority.

Delta smelt are closely associated with the low salinity zone of the upper San Francisco Estuary (Moyle et al. 1992). During late winter and early spring months (typically December–March), they migrate upstream to freshwater regions of the upper estuary for spawning. Most juveniles return to the low salinity zone in summer where they will rear through winter. There are believed to be many interacting factors that affect the abundance of delta smelt, including adult stock numbers, abundance and composition of prey, predation, and water diversions (Moyle 2002; Bennett 2005; Sommer et al. 2007; Feyrer et al. 2007). The premise for our study is that recent work has identified habitat change as a potentially important factor over the long term. In particular, abiotic habitat conditions, especially salinity and water transparency, for delta smelt have deteriorated over time in much of the estuary during both summer for juveniles (Nobriga et al. 2008) and fall for maturing individuals (Feyrer et al. 2007).

Our purpose was to examine how potential changes in estuarine outflow from future development and climate change might affect abiotic habitat conditions for delta smelt. Future development and climate change have been identified as major uncertainties for the management of the San Francisco Estuary (Kimmerer 2002). Our first step was to update our previous description of abiotic habitat (Feyrer et al. 2007) with an additional 4 years of new data. This involved using generalized additive modeling to identify habitat suitability based upon combinations of water temperature, clarity, and salinity from surveys conducted during fall (September–December) from 1967 to 2008. The next step was to develop an index that accounted for both the quantity and quality of abiotic habitat for each year of sampling and to model the index as a function of estuarine outflow. The final step was to apply the habitat index–outflow model using outflow predictions under future development and climate change scenarios.

Materials and Methods

We used a generalized additive model (GAM) to define the abiotic habitat of delta smelt as follows:

$$\pi_{y,m,s} \sim \mathrm{f}_1(\mathrm{temp}, \mathrm{Secchi}, \mathrm{cond}) + \varepsilon_{y,m,s}, \qquad (1)$$

where the probability of occurrence of delta smelt (π) for a given year (*y*), month (*m*), and sampling station (*s*) is a function of water temperature (*temp*; °C), Secchi depth (Secchi; m), and specific conductance (cond; $\mu s \times cm^{-1}$, a surrogate for salinity) (Feyrer et al. 2007). We also fit a second form of this model that included a term for abundance—the fall midwater delta smelt abundance index. GAMs are extensions of generalized linear models useful for describing non-linear relationships between variables (Guisan et al. 2002). They are data driven and do not presuppose a particular functional relationship between variables; smoothers characterize the empirical relationships between variables (Guisan et al. 2002). Link functions are used to establish relationships between the response variable and a smoothed function of the predictor variables; we used the cubic spline as our smoothing technique in the S-Plus language. The data come from a midwater trawl survey that samples approximately 100 stations across the estuary each month from September to December (Stevens and Miller 1983). This period is especially important because it is when delta smelt recruit to the adult population. The stations extend beyond the range of delta smelt and therefore index its full distribution. In fact, as described later, we used a subset of 73 of the 100 stations for our analyses. Each station was sampled once per month, each of the 4 months, from 1967 to 2008 with a single 10-min tow. The only exceptions were that sampling was not conducted in 1974 or 1979, and in 1976 was only conducted in October and November. Measurements of the water quality variables are normally taken coincident with each sample. In total, there were nearly 14,000 individual samples with complete data for analysis spanning 42 years.

For the GAM, we chose to model probability of occurrence (i.e., presence–absence data) rather than a measure of abundance (e.g., catch per trawl) to minimize the possible influence of outliers and bias associated with long-term abundance declines. This approach is also supported by recent simulations, based on assumed underlying statistical distributions of fish catch, that suggest habitat curves based on presence–absence are conservative relative to catch per trawl because high frequencies of occurrence could be associated with both high and moderate catch per trawl (Kimmerer et al. 2009). We evaluated model fits in terms of the reduction in deviance relative to the null model: $(D_{\mathrm{null}} - D_{\mathrm{residual}})/D_{\mathrm{null}}$.

We developed an annual habitat index (H_y) that accounted for both the quantity and quality of habitat as follows:

$$H_y = \sum_{S=1}^{73} \left[A_S \frac{1}{4} \sum_{m=\mathrm{Sep}}^{\mathrm{Dec}} \hat{\pi}_{y,m,s} \right], \quad (2)$$

where A_s is the surface area of station s and $\hat{\pi}_{y,m,s}$ is the GAM estimate of the probability of occurrence (Eq. 1). Station surface areas were obtained from the California Department of Fish and Game and were originally shown in Feyrer et al. (2007). Surface areas were generated by GIS and ranged from 90 to 1,251 ha for the 73 stations. We used a subset of 73 of the more than 100 sampling stations for this analysis, excluding stations on the periphery of the sampling grid where delta smelt were rarely encountered or where the sampling record was inconsistent. Note that delta smelt has a 'core distribution' in the sampling grid that was well-covered by the 73 stations. Summation of the suitability corrected surface areas provides a habitat index that accounts for both the quantity and quality of abiotic habitat for delta smelt.

We used locally weighted-regression scatterplot smoothing (LOESS regression) to develop a data-driven relationship between the habitat index and estuarine outflow:

$$H_y = \mathrm{f}_2(\mathrm{X2}_y) + \varepsilon_y, \quad (3)$$

where $X2$ is an indicator of outflow. LOESS regression is useful to derive data-driven models when no single functional form is appropriate (Trexler and Travis 1993). In the San Francisco Estuary, $X2$ is defined as the distance (km) upstream from the Golden Gate Bridge to where mean bottom salinity is 2‰ (Jassby et al. 1995). Consistent with the habitat index described above, we used the September–December average $X2$. We averaged the data over the 4-month fall period to minimize the influence of sampling error that could occur if the data were summarized over shorter temporal scales. For instance, shorter averaging periods might be less reliable because samples are taken irrespective of tidal conditions across a geographic region with large tidal excursions, and because abundance estimates, and by extension, distribution can be highly variable among months (Newman 2008). Because $X2$ is correlated with the abundance or survival of numerous organisms (Jassby et al. 1995; Kimmerer 2002; Kimmerer et al. 2009), it is one of the primary regulatory tools used to manage outflow in the San Francisco Estuary.

Using climate model forecasts of outflow ($X2$), under varying development and climate change scenarios, we used f_2 (Eq. 3) to predict future habitat indices. Forecasts of outflow ($X2$) were obtained from modeling studies conducted to evaluate the sensitivity of future water project operations to potential climate change and sea level rise (Brekke 2008). The $X2$ forecasts were generated by CALSIM II, a mathematical simulation model developed for statewide water planning in California (Draper et al. 2004). CALSIM II simulates 82 years of hydrology on a monthly time step for the Central Valley region using observed river flows from 1922 to 2003. However, the water demands (including environmental requirements) imposed on this time series of Central Valley runoff can be varied. The model employs an optimization algorithm to find ways to store and move water via the Federal Central Valley and State Water Projects in order to meet assumed water demands on a monthly time step. The movement of water in the system is governed by an internal weighting structure that ensures regulatory and operational priorities are met. For the purposes of the present analysis these model runs were not intended as well-defined predictions of the future, which would be difficult given uncertainties about future climate conditions and the vulnerability of the system to catastrophic floods or earthquakes (Mount and Twiss 2005). Rather, these model runs are intended to reflect a reasonable range of possible alternatives in the absence of major structural changes to the estuary.

We examined seven development and climate scenarios (Table 1). The first scenario (A) represented present-day (year 2005) water demands, operations (reservoir releases, water diversion rates, and regulations), and climate. We included this scenario as a comparison to actual historic $X2$, allowing us to examine whether the model outputs showed substantial bias. The second scenario (B) represented projected future development and operations in the year 2030, with the same present-day climate assumptions used in A. The remaining five scenarios included the projected 2030 development given one of several alternative climate scenarios. Scenario C represented a 0.33 m increase in sea level coupled with a 10% increase in tidal range. Scenarios D through G coupled scenario C with 'bookend' climate change projections. These bookends cannot be summarized simply except in qualitative terms. Very extensive details on these outputs and the models used to derive them are provided in Brekke (2008) and only brief qualitative descriptions are provided here. The bookends represented 10th and 90th percentiles of predicted changes in precipitation and temperature for the period 2011–2040 relative to 1971–2000 conditions. Generally, climate change models suggest that the Central Valley will be warmer in the future, but are indeterminate as to whether precipitation will increase or decrease (e.g., Dettinger 2005). Thus, the climate change bookends include drier and wetter possibilities, but do not include cooler futures relative to current conditions. Thus, the temperature bookends can be called 'warmer' and 'warmer still.' Scenario D is a wetter and warmer simulation, E is a wetter and warmer still simulation, F is a drier and warmer simulation, and G is a

Table 1 Description of the seven modeled conditions of outflow in the San Francisco Estuary

Scenario	Estimated level of development	Qualitative climate change relative to the present	Climate model	Emissions pathway	Simulation run number
A	2005 (present day scenario)	–	–	–	–
B	2030	–	–	–	–
C	2030	0.33 m increase in sea level coupled with 10% increase in tidal range	–	–	–
D	2030	Wetter and warmer	mri cgcm2.3.2a	A2	5
E	2030	Wetter and warmer still	ncar ccsm3.0	A1b	3
F	2030	Drier and warmer	mri cgcm2.3.2a	A2	2
G	2030	Drier and warmer still	ukmo hadcm3	A2	1

See the text and Brekke (2008) for more extensive details

drier and warmer still simulation. Because outflow and $X2$ vary by water year type (e.g., flood vs. droughts) the analyses were organized by water year type as defined in the State Water Resources Control Board Decision 1641 (see http://www.waterrights.ca.gov/baydelta/d1641.htm).

Results

Only specific conductance and Secchi depth accounted for a meaningful reduction of null deviance, 18% and 14%, respectively. Water temperature accounted for less than 1% of the deviance and therefore was omitted from the final model. The final model with specific conductance and Secchi depth accounted for 26% of the deviance. When a term for abundance was included in this model—the annual delta smelt fall midwater trawl abundance index—the amount of deviance explained increased to 30%. The response predictions for models with and without the abundance term were significantly positively correlated (Pearson correlation coefficient=0.92, $P<0.01$) and therefore exhibited essentially identical patterns. Therefore, subsequent analyses were with the model not including the abundance term. Overall, the response predictions exhibited a unimodal trend against specific conductance and a negative trend against Secchi depth, demonstrating that delta smelt most frequently occurred at intermediate salinity (~2 ppt) with low water transparency (Fig. 1). LOESS smooths for each year demonstrated that this low salinity–high turbidity association was consistent through time but that the absolute value of the response predictions varied largely depending on how many fish were caught (Fig. 1). Similar plots for GAMs that were run for each year separately showed the same pattern (not shown).

The habitat index (Eq. 2) declined by 78% from 1967 through 2008 (Fig. 2a). The habitat index exhibited a negative sigmoid relationship to $X2$ (Fig. 2b). The LOESS smooth defining this relationship had an r^2 of 0.85. The largest change in habitat suitability occurred at $X2$ values between 85 and 70 km, with less change beyond those values. Across this 15-km range of $X2$ habitat increased approximately twofold. This 15-km range in $X2$ corresponds to a geographic area that spans the confluence of the Sacramento and San Joaquin rivers, which is located at approximately 80 km. When $X2$ is located downstream of

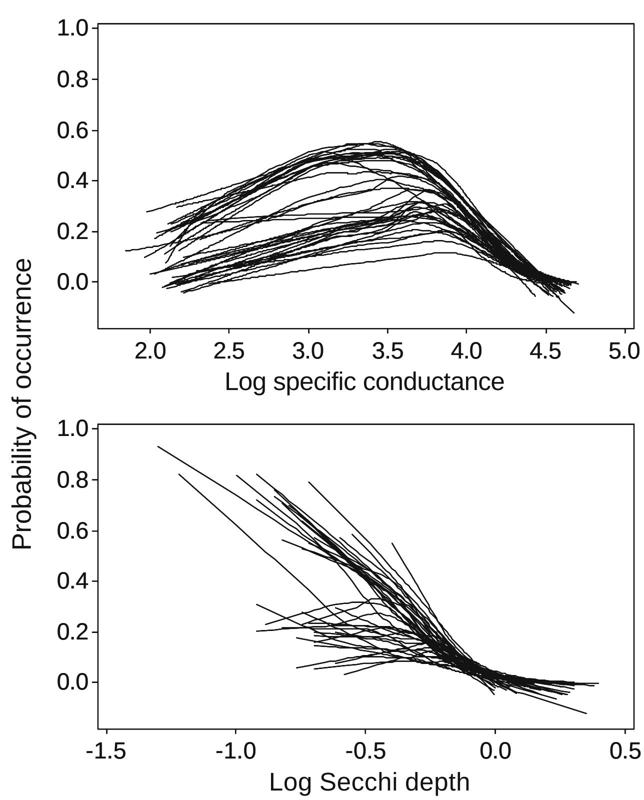

Fig. 1 Plot of the GAM response predictions (probability of occurrence) against specific conductance and Secchi depth. Individual lines are LOESS smooths drawn through the points for individual years

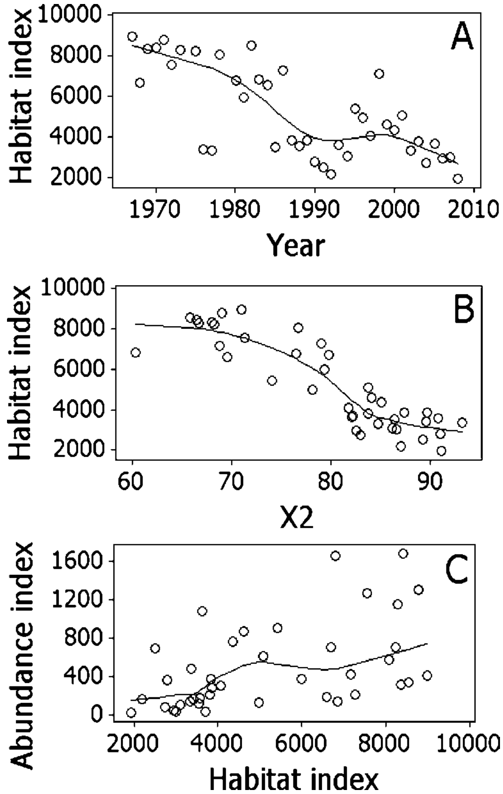

Fig. 2 Plots of the habitat index time series (**a**), relationship between $X2$ (km) and the habitat index (**b**), and relationship between the habitat index and delta smelt abundance measured as the fall midwater trawl index. Curves are LOESS smooths

the confluence there is a larger area of suitable habitat because the low salinity zone encompasses the expansive Suisun and Grizzly Bays, which results in a dramatic increase in the habitat index (Fig. 3). The habitat index was significantly positively correlated with the delta smelt abundance index, albeit with increased variation in the abundance index with increasing values of the habitat index (Pearson correlation coefficient=0.51, P=0.001; Fig. 2c).

The CALSIM II modeling output did not precisely match actual historical $X2$ values for the overlapping 1967–2003 period (Fig. 4). This was probably due to several reasons, including the fact that level of development increased through the historical period while the model simulations assumed it was constant; the state and federal regulatory requirements varied over the historical period while the model simulations held them constant; and the historical and CALSIM model estimates of $X2$ were calculated using different methods. As demonstrated by fractional differences (modeled $X2$-observed $X2$)/modeled $X2$, the model tended to overestimate $X2$ during the early part of the record and underestimated it in the latter part of the record. Moreover, deviation from 1:1 was most apparent in years when the previous springs were relatively wet. This bias does not prohibit a comparison of the modeled scenarios to examine the effects of future conditions in a sensitivity analysis framework. One just needs to be cognizant of the fact that the absolute values of habitat index would likely be inaccurate, but comparisons of changes in the habitat index relative to present day conditions remain useful.

Modeled future conditions (scenarios B-G) produced smaller values of the habitat index relative to the modeled present day condition (scenario A), the only exception being in critical years when all values were similar and low (Fig. 5). In below-normal years, Scenario D, the wetter and warmer condition, produced habitat index values that were similar to the present day condition (scenario A). However, in most cases the differences were quite substantial. For example, the habitat index for the present day condition (scenario A) in below normal and dry years were similar to, and in some cases substantially greater than, the modeled future conditions (scenarios B, C, G, F) in wet and above normal years. Other than a few instances in which modeled $X2$ was just 1 km greater than that observed historically, the distribution of $X2$ values across all modeled scenarios was within the range of historic values. Thus, there was virtually no extrapolation beyond the range of historical $X2$ values in this exercise.

Discussion

All fishes depend on suitable environments to survive and reproduce. Increasing human development necessitates the identification of habitat features critical to sustaining populations of estuarine species. This is especially important for short-lived annual species, which can be particularly threatened by the loss or degradation of habitat. Because the upper San Francisco Estuary constitutes the sole habitat for delta smelt, a suitable estuarine environment is critical to the long-term health and persistence of the species. Our results suggest that delta smelt will face serious threats if water demand increases and climate change projections are realized.

The results of our study have potentially serious real-world implications for water management. Therefore, we feel it is important to address all of the possible shortcomings of the study in detail. Though relatively simplistic, our assessment of suitable abiotic habitat provides a foundation from which the effects of other stressors, both abiotic and biotic, could be examined as new data and knowledge of delta smelt become available. Our evaluation of suitable habitat could be considered limited because it ultimately included only two factors, salinity and water transparency. However, fish can only exploit resources within an area if they can occupy it in the first place. Thus, many other potential elements of delta smelt habitat suitability such as food density, entrainment risk, predation

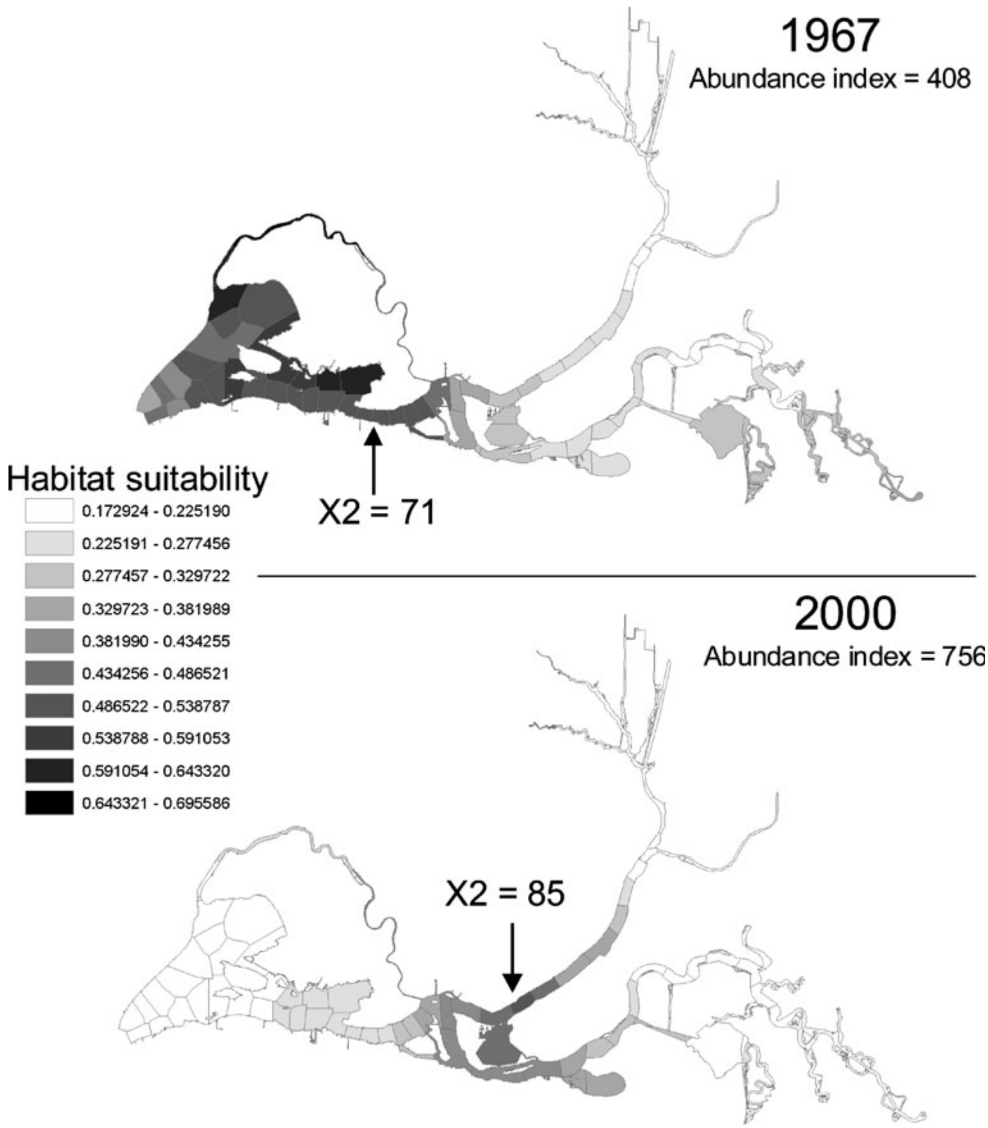

Fig. 3 Spatial distribution of habitat suitability, defined as the GAM probability of occurrence, for years in which *X*2 was either below (1967) or above (2000) the confluence of the Sacramento and San Joaquin Rivers. Abundance index is from the fall midwater trawl survey

risk, or exposure to contaminants will be influenced by the quantity, quality and spatial distribution of the water quality parameters we modeled. It is possible that other abiotic factors such as water velocity, bathymetric features, or other water quality parameters could increase the explanatory power of the model, but it should be noted that these other factors would not likely increase our estimates of suitable habitat– they could only reduce them. This is true because these microhabitat features are only usable by delta smelt when low-salinity, turbid waters overlie them. Further, data on such factors are limited and a substantial amount of interpolation in both space and time would be required in order to match them to the scale of our analysis. Biotic components can also be important as interactions between them and abiotic habitat can affect vital rates and thus density-dependent effects on population dynamics (Liermann and Hilborn 2001; Rose et al. 2001; Bennett 2005).

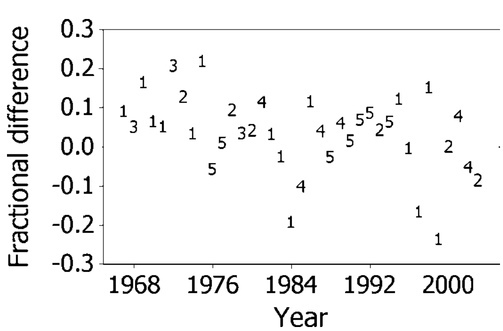

Fig. 4 Time series for the fractional difference of scenario A from empirical *X*2. Numbers represent water year types; *1* wet, *2* above normal, *3* below normal, *4* dry, *5* critical

Fall water temperatures in the estuary have rarely exceeded delta smelt thermal tolerance limits so water temperature does not explain any substantive amount of variation in delta smelt distribution during September–December. However, water temperature can constrain delta

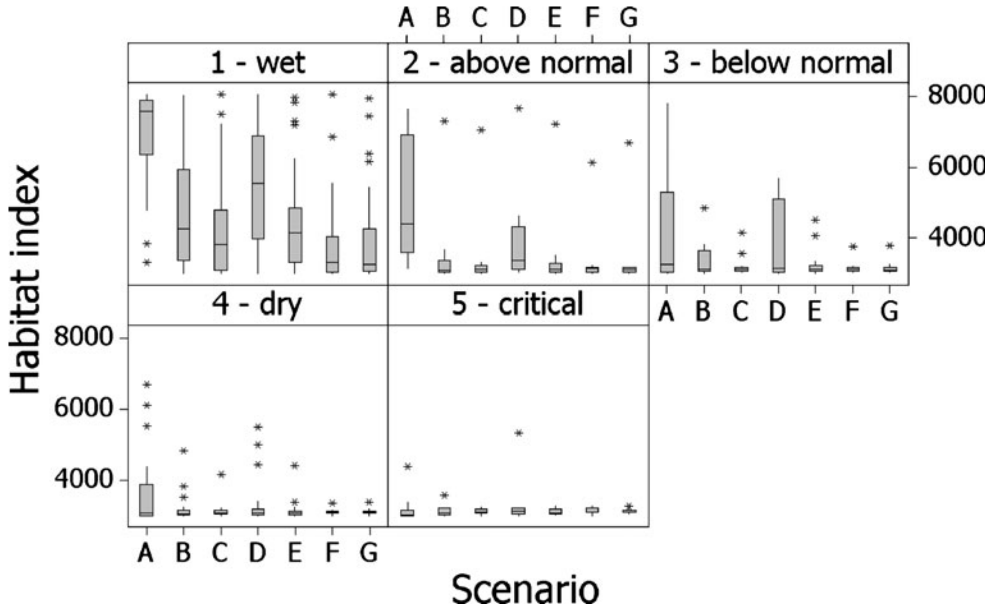

Fig. 5 Box plots of the habitat index values for each scenario across water year types. The *box plots* show medians and first and third quartiles. *Whiskers* show the highest or lowest values in the upper or lower limits, respectively. Table 1 provides details on the modeled outflow scenarios

smelt distribution during summer (Nobriga et al. 2008), when temperatures approach or exceed the species' laboratory-derived upper thermal tolerance of 25.4°C. As shown by Brekke (2008) in the climate forecasts we used in the present study, central California is expected to get warmer in the coming decades. This may increase the extent and duration of stressful water temperatures in the upper estuary causing additional reduction in habitat suitability that our model cannot predict.

One practical limitation of our study is the reliability of absence in the sample data, i.e., whether delta smelt was truly absent from a sampled volume of water or if it was just undetected, i.e., a false absence (MacKenzie 2005). Repeated surveys of the estuary (100 samples each month for four consecutive months) encompassing the full distribution of delta smelt greatly minimize such potential bias in the presence–absence data (as suggested by Fig. 1). Further, our model appears to capture a substantial amount of the variation in the outflow–habitat relationship. In general, our approach is also substantiated from evaluations by Kimmerer et al. (2009) of habitat volume simulated using the TRIM3D hydrodynamic model. They demonstrated that habitat volume was highly correlated with surface area, and that stratification of estuary water did not change the observed patterns. Kimmerer et al. (2009) also found that patterns were unaffected whether presence–absence or catch per unit effort was the GAM response variable.

There are several potential mechanisms by which habitat area can affect delta smelt. Perhaps most generally, increased habitat area provides more space for individuals to safely live and reproduce. This basic concept is clearly demonstrated by the ubiquity of species- or individuals-area relationships in ecology. Reviews on this topic have confirmed that habitat loss and degradation is a major factor in the loss of species worldwide (Wilcove et al. 1998; Brooks et al. 2002). More specifically, increased habitat area presumably lessens the likelihood of density–dependent effects on the delta smelt population (e.g., food limitation, disease, and predation). Increased habitat area also presumably lessens the probability of stochastic events that could affect mortality. This includes cropping by predators and anthropogenic effects such as contaminant events or the direct and indirect effects of water diversions (Sommer et al. 2007). A key part of the concern for delta smelt is that the lowest levels of suitable habitat coincide with the habitat being geographically located upstream in closer proximity to anthropogenic sources of mortality such as water diversions and certain contaminant sources such as agricultural runoff.

Kimmerer et al. (2009) recently evaluated the extent of habitat volume as a mechanism underlying the positive response of nekton to outflow in San Francisco Estuary during spring. They found that habitat volume could explain abundance patterns for two of the eight species they examined. This did not include delta smelt because the species does not exhibit a relationship between spring outflow and summer or fall abundance. However, similar to our findings for the fall, Kimmerer et al. (2009) did find that habitat volume in spring for delta smelt increased as $X2$ moved seaward.

Climate change has been demonstrated to have potential negative effects on many aquatic populations by affecting their distribution or abundance (e.g., Wood and McDonald 1997; Perry et al. 2005). For species such as delta smelt that live in environments which are major water sources for humans and cannot move to other estuaries by themselves because they cannot survive in seawater, the problems associated with climate change are exacerbated by water demand from increasing human development. Similar accounts of multiple stressors have been demonstrated for anadromous Pacific salmon (*Oncorhynchus tshawytscha*) with models that account for future climate and habitat conditions (Battin et al. 2007). In riverine systems, climate-associated reductions in flow and increased water withdrawal pose a serious extinction risk to fishes worldwide (Xenopoulos et al. 2005). Thus, climate change impacts need to be assessed in the context of other stressors, including indirect anthropogenic effects (Meyer et al. 1999; Schindler 2001; Jones et al. 2006).

Implicit in our study is the assumption that conditions underlying the applied models hold true in the future. Although the data we examined captured a reasonable range of future outflow conditions, the model runs do not account for the potential for a radically different configuration of the Delta. Specifically, Mount and Twiss (2005) showed that there is a high probability of a catastrophic change to the Delta within the near future because of the vulnerability of weak levees surrounding subsided islands to collapse from either earthquakes or floods. Widespread flooding of these islands would be expected to completely change the landscape of the Delta, and presumably its hydraulics and aquatic habitats. Similarly, the simulations do not account for potential future changes in water facilities, water conservation initiatives, new regulations or other management actions, higher water temperatures resulting from climate change, kinds and concentrations of contaminants, or new invasive species. Using threatened Pacific salmon as a model, Good et al. (2008) demonstrated that incorporating such catastrophic risk assessments could aide recovery planning and the future viability of species.

The uncertainty about future conditions does not, however, reduce concern about the status of delta smelt. The fact that all of the model outputs suggested a deterioration of habitat represents a major issue for delta smelt because of its vulnerability to extinction. In a population viability analysis, Bennett (2005) found that it took only 1.2–1.5 years to when extinction probabilities fell below the lowest calculated level of abundance. Since the Bennett (2005) analysis, which included data through 2003, delta smelt abundance has rapidly decreased and remained at less than half of its measured level in 2003, including successive record low levels in 2004, 2005, 2008 and 2009. Considered together, Bennett's (2005) population viability analysis, the anticipated changes in water temperatures and our habitat evaluation suggest a particularly grave future for delta smelt.

Given the limited resources available to regulators and natural resource managers, it is important to consider habitat conservation and restoration targets in the context of the entire life cycle (Levin and Stunz 2005; Battin et al. 2007). This includes determining whether the costs of potential habitat actions will provide true benefits to the population. For delta smelt, protecting the core estuarine habitat for maturing adults seems a critical target. However, due to the social and economic implications of water management in California (Service 2007; Sommer et al. 2007), even basic assumptions require justification. One question that often arises is whether delta smelt is habitat limited given its current record-low level of abundance. Optimal management requires consideration of both habitat space and the ecological processes which allow populations to expand (Levin and Stunz 2005). Given that the habitat index has declined by 78% over the course of monitoring (Fig. 3), and that this has been coincident with the long-term decline in abundance, it seems plausible that those habitat parameters may have been among the important factors over the long-term for delta smelt. Conserving delta smelt likely requires grappling with the problems of climate change and increasing demand for water in California.

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