Modeling the Effects of Water Management Actions on Suitable Habitat and Abundance of a Critically Imperiled Estuarine Fish (Delta Smelt *Hypomesus transpacificus*)

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Abstract: The opportunity to manage estuarine inflow to benefit imperiled fishes was tested by modeling the likely effects for delta smelt (*Hypomesus transpacificus*). Endemic solely to the euryhaline portion of the San Francisco Estuary, delta smelt is a small, annual species that is on the verge of extinction. During autumn when delta smelt are nearing adulthood, the amount of suitable abiotic habitat is positively associated with estuarine inflow and has a measurable effect on recruitment of juveniles the following summer. Long-term declines in delta smelt abundance have coincided with a decline in the area of suitable abiotic habitat. Simulations based on a set of linked models for the abundance of pre-adult and subsequent juvenile delta smelt showed that management strategies allowing either (1) randomly occuring or (2) variable but persistently high estuarine inflow produced higher abundance than scenarios of (3) variable but peristantly low or (4) non-variable median inflow. Our results suggest managing estuarine inflow offers one possible tool to help assist the conservation of imperiled fish species by enhancing habitat space and other beneficial ecological processes.

Introduction

Human-caused habitat degradation represents a major threat to biota across the globe (Turner 1996; Hoekstra et al. 2005; Dobson et al. 2006). The problem is exemplified in terrestrial and aquatic ecosystems alike. A major problem for aquatic systems is that demands for water often conflict between services provided to the environment and to humans (Richter et al. 1997; Freeman et al. 2001). Effective conservation and management of aquatic resources in the face of increasing development requires understanding how development affects abiotic habitat and how abiotic habitat suitability affects populations of fish and invertebrates. Fundamental ecological theory suggests a correlation between habitat area and the number of species or individuals (MacArthur and Wilson 1967; Williamson 1981; Begon et al. 1996). Reasons that area can support more species or individuals include increased habitat diversity and resource availability, and reduced probability of extinction.

The ubiquity of species- or individuals-area relationships in ecology has focused much conservation-oriented research on defining the habitat of organisms and how habitat manipulations affect abundance. 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). As a consequence, tools to quantify the amount of area for species based on habitat suitability remain popular among many resource managers (Reiser et al. 1989; Layher and Brunson 1992; Johnson and Swift 2000). However applying such techniques in estuaries is difficult because habitat suitability is dynamic in space and time on tidal, seasonal, and annual time scales (Kimmerer 2002; Feyrer et al. 2007).

Animals with annual life cycles and limited distributions are particularly vulnerable to habitat loss or degradation. Such characteristics can lead to extreme risk of extinction from both pulse perturbations such as unusual or catastrophic events, and press perturbations such as steady long-term habitat degradation. The case of delta smelt (*Hypomesus transpacificus*), a species on the brink of extinction, exemplifies such a risk. Delta smelt is an annual fish species endemic solely to the euryhaline segment of the San Francisco Estuary (Moyle et al. 1992; Bennett 2005). Formerly one of the more abundant fishes in the estuary, a long-term decline - plus recent years with record - low indices of abundance - led federal (U.S. Fish and Wildlife Service) and state (California Department of Fish and Game, CDFG) authorities to list the species as threatened with extinction (Moyle 2002).

There are many interacting factors that affect the abundance of delta smelt, including the effects of lowered adult stock, changes in the abundance and composition of prey, predation, and water diversions (Moyle 2002; Bennett 2005; Sommer et al. 2007; Feyrer et al. 2007). Recent studies have identified habitat degradation as a key factor likely to be important in the long-term decline (Bennett 2005; Feyrer et al. 2007; Nobriga et al. 2008). In particular, abiotic habitat conditions for delta smelt have deteriorated over time in much of the estuary during both summer for juveniles (Nobriga et al. 2008) and autumn for maturing individuals (Feyrer et al. 2007), which we term "pre-adults". Summer habitat degradation has restricted juvenile delta smelt distribution (Nobriga et al. 2008), while autumn habitat degradation likely also affects the fitness of pre-adults, which may have exacerbated the effects of lowered stock since the mid-1980s (Feyrer et al. 2007).

The grave situation for delta smelt exemplifies the elevating worldwide problem of balancing water resources between ecosystems and growing human populations. San Francisco Estuary is highly modified and managed to supply water to over 25 million people as well as a multibillion-dollar agricultural industry (Nichols et al. 1986). Control of the estuary's hydrodynamics and water exports are closely tied to protecting delta smelt on a daily basis during substantial portions of the year, but this has not prevented long-term decline in estuarine fish including delta smelt (Sommer et al. 2007). Conflicts between the needs of humans and those of the estuarine environment for a limited amount of freshwater received international attention recently when water exports were dramatically reduced by court order to protect delta smelt (Service 2007; Sommer et al. 2007). The concern triggered by this event illustrates the pressing need to base water management decisions on sound science. At the most fundamental level this requires understanding how management activities affect estuarine biota. Hence, our primary objective herein was to evaluate whether estuarine inflow can be managed as a conservation measure to benefit delta smelt habitat and abundance. Our basic approach was to expand upon our recent descriptive modeling of delta smelt habitat (Feyrer et al. 2007) by (1) determining how suitable abiotic habitat is affected by estuarine inflow, (2) how, in turn, suitable abiotic habitat affects abundance, and (3) modeling the likely effects of several estuarine inflow scenarios on the future abundance of delta smelt. Our results will immediately enable resource managers to consider the effects of water project operations on this imperiled fish species, and therefore aid real-world decisions about allocating a limited resource between humans and the environment.

Methods

The first step in our analyses involved updating our recent descriptive modeling of delta smelt habitat (Feyrer et al. 2007) with two years of new data (2005 and 2006). We used a generalized additive model (GAM) to determine how three water quality variables measured during fish sampling – temperature (˚C), Secchi depth (m), and specific conductance ($\mu s \cdot cm^{-1}$) – affect the presence of delta smelt (Feyrer et al. 2007). The data analyzed originate from a midwater trawl survey conducted during autumn at 100 stations across the estuary by CDFG (Stevens and Miller 1983). We used a binary response (presence or absence) rather than a measure of abundance to minimize the influence of outliers (i.e., extremely anomalous abundance values) and bias associated with previously reported abundance declines through time. Recent simulations based on assumed underlying distributions suggest that 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. 2008). We evaluated models by traditional statistical significance and approximate coefficients of determination which describe how each independent variable reduces the null deviance in the model.

The second step of our analyses involved translating the GAM-generated occurrence probabilities into a measure of surface area (ha) of suitable abiotic habitat. Because the occurrence probability values range from 0.0 to 1.0, this translation required setting criteria which define suitable abiotic habitat within that range. Rather than setting a single arbitrary value, we chose an approach analogous to a model sensitivity analysis by evaluating three different values representing a range of increasingly strict criteria.

The values we selected (≥ 0.10, ≥ 0.25, and ≥ 0.40) approximately bracketed the frequency distribution of the 12,874 values for each sample generated by the GAM; values for the median and third quartile were 0.11 and 0.31, respectively. We used a subset of 62 of the 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. Total surface area of suitable abiotic habitat was the sum of the 62 individual surface areas representing each sampling station in which the criteria were met. The surface areas represented by these stations were obtained from CDFG and are shown in our previous study (Feyrer et al. 2007). Individual surface areas for each station ranged from 90 to 1,251 ha, with a total of 18,781 ha. In a few instances of missing environmental observations, the spatial autocorrelation in the data (i.e., conditions at adjacent stations were similar) permitted us to fill blanks with data from immediately adjacent stations (Feyrer et al. 2007).

The third step of our analyses was to describe the relationship between the total amount of suitable abiotic habitat and freshwater flow. We plotted these variables and used locally weighted regression scatterplot smoothing (LOWESS) to develop data-driven curves defining the relationships. We used the position of the 2‰ isohaline (termed X2) as an indicator of estuarine inflow. X2 is defined as the distance (km) from the Golden Gate to the location in the estuary where mean bottom salinity is 2‰ (Jassby et al. 1995). Because the position of X2 has ecological relevance with positive correlations to the abundance or survival of numerous estuarine biota (Jassby et al. 1995; Kimmerer 2002), it is an important regulatory tool used to manage inflows in San Francisco Estuary. Although previous analyses have not shown simple relationships between X2 and delta smelt abundance (Jassby et al. 1995; Kimmerer 2002; Bennett 2005), recent studies have identified links between estuarine salinity and recruitment of juveniles (Feyrer et al. 2007). Moreover, X2 clearly affects the spatial distribution of delta smelt in the estuary. For this analysis, we plotted X2 position averaged from September to December against the three scenarios of total surface area of suitable habitat. Consistent with our previous study (Feyrer et al. 2007), we focused on the entire four month autumn period to avoid issues surrounding the aliasing of the sampling data that occurs at shorter temporal scales because samples are taken irrespective of tidal conditions across a geographic region with large tidal excursions. Furthermore, from a management perspective, manipulating X2 at shorter temporal scales is particularly challenging.

The forth step of our analyses was to determine the effect of habitat on delta smelt abundance. In this analysis, we tested the hypothesis that the combined effects of pre-adult abundance and the amount of suitable abiotic habitat (or X2) during autumn affect recruit abundance the following summer. The abundance indices we used for these models were obtained from CDFG and are available at http://www.delta.dfg.ca.gov/. Similar to previous studies (Moyle et al. 1992; Bennett 2005; Feyrer et al. 2007), we used the fall midwater trawl abundance index as an estimate of pre-adult (spawning stock) abundance and the summer townet abundance index as an estimate of recruit abundance. The base model was a simple linear regression of pre-adult stock versus recruit abundance. We then evaluated additional models which included fall stock abundance and one of the three habitat area estimates or mean autumn X2 position. We ran the regressions for all years combined and separated the time series into two segments, 1968-

1986 and 1987-2007. Similar to our previous study (Feyrer et al. 2007), separation of the two time periods allowed us to examine the role of suitable abiotic habitat area during periods of high and low food abundance in the estuary. This time point captures an ecological change in the food web of the estuary stemming from the invasion of the overbite clam *Corbula amurensis* (Kimmerer 2002). We compared models within each series by traditional means (level of statistical significance and comparison of r-squared values), and evaluated the relative fit of each model with an information-theoretic approach based upon Akaike's information criterion (AIC). We further evaluated the fit of significant regression models by visually examining residual plots for homogeneity of variance and used the Anderson-Darling test to determine if the residuals were normally distributed.

The fifth and final step of our analyses was to model the likely effects of various management scenarios of estuarine inflow on the future abundance of delta smelt. Modeling the effects of environmental factors on population dynamics can take many forms from simple stock-recruit models (Hilborn and Walters 1992) to extremely complex state-space models (Thomas et al. 2005). Delta smelt has an annual life cycle and exhibits statistically significant relationships between both pre-adult to juvenile and juvenile to pre-adult abundance (Bennett 2005; Feyrer et al. 2007). A set of linked models for the abundance of pre-adult and juvenile delta smelt were formulated and fit to assess the effect (on abundance) of manipulating X2 during autumn. The general formulation is as follows:

$$j_t = f(pre-adult_{t-1}, X2_{t-1}, \beta, \varepsilon_t)$$

$$pre-adult_t = g(j_t, \gamma, \eta_t),$$

where j_t is the abundance of juveniles in year t, $pre-adult_t$ is the abundance of pre-adults, and $X2_t$ is the X2 value, β and γ are vectors of parameters, and ε_t and η_t are random variables. As above, summer townet survey indices and the fall midwater trawl indices are the observations for juveniles and pre-adults, respectively.

To ensure that predicted values would not be negative, lognormal distributions were assumed for both juvenile and pre-adult abundance. For juveniles, a linear relationship with previous year pre-adults and previous year X2 values was fit (see step four above and in results). We assumed density dependent effects on the survival of juveniles (Bennett 2005), so we used Ricker Ricker and Beverton-Holt type models to predict pre-adult abundance from juvenile abundance (Bennett 2005). Based on AIC, the Ricker model was slightly better than the Beverton-Holt, and both were significantly better than linear (density independent) models. The resulting models fit were:

$$j_t : Lognormal\left(\ln[\beta_0 + \beta_1 pre-adult_{t-1} + \beta_2 X2_{t-1}], \sigma_\varepsilon^2\right) \quad (1)$$

$$pre-adult_t : Lognormal\left(\ln[\gamma_0 j_t \exp(-\gamma_1 pa_t)], \sigma_\eta^2\right) \quad (2)$$

AD Model Builder (ADMB; Otter Research) was used to calculate maximum likelihood estimates and associated standard errors of the seven parameters (β_0, β_1, β_2, σ_ε, γ_0, γ_1, and σ_η). As a technical aside, there is a constraint that the median of the lognormal distribution is positive, i.e., $\beta_0 + \beta_1 pre-adult_{t-1} + \beta_2 X2_{t-1} > 0$ and $\gamma_0 j_t \exp(-\gamma_1 j_t) > 0$. This constraint must be met for all values of the covariates ($pre-adult_{t-1}$, $X2_{t-1}$, and j_t) and finding suitable initial values for the optimization algorithm was critical. To do so, the two models were fit separately first, with initial values for the β's in the juvenile model (1) coming from a normal approximation fit

(Table 2). The standard error for the X2 coefficient (β_2) in the juvenile model is large relative to the point estimate; thus while the point estimate is negative, indicating that juvenile abundance decreases as X2 increases, the degree of uncertainty about the relationship is relatively high. Thus, the expected values for the pre-adult model tended to be overestimates of the lower values and underestimates of the higher values.

We considered four different management scenarios based on X2: (1) Scenario 1 (random); X2 varies randomly according to its historical distribution of values, 1967-2007 (2) Scenario 2 (static): X2 is constant and equals the median historical value, (3) Scenario 3 (random high): X2 varies randomly according to the historical distribution of values at or above the median historical value, (4) Scenario 4 (random low): X2 varies randomly according the historical distribution of values at or below the median historical value. In all cases the historical distribution of X2 values was based upon the period 1967 through 2007.

To evaluate the effects of these four scenarios, abundances were simulated using two stages of randomization. First, uncertainty in the parameter values was simulated by generating β's and γ's from two multivariate normal distributions with mean vectors equal to the maximum likelihood estimates and covariance matrices based on the standard errors and correlation matrix (Table 2). According to large sample theory, maximum likelihood estimates are approximately multivariate normal. Second, given these simulated parameter values, a simulated sequence of 50 years of X2 values (simulated according to each scenario), and an initial adult abundance, two time series of juvenile and pre-adult abundances were simulated forward in time, 10,000 times, using the lognormal distributions (equations 1 and 2), alternating between simulation of juveniles and pre-adults.

A practical complication was the fact that values of the β's and the γ's simulated from the multivariate normal distributions do not necessarily satisfy the condition that the median values of the lognormal distributions remain positive for all combinations of covariates. Once a median value went negative, the future time series could not be projected forward; one could make an argument that the frequency of times that such an event occurred was a prediction of the probability of extinction. However, such events were also a function of uncertainty of parameter values. The percentage of times that projections led to negative abundances varied considerably between scenarios. For Scenario 1 (random), about 54% of the projections went negative, while for Scenario 2 (static) it was about 23%, for Scenario 3 (random high) it was about 52%, and for Scenario 4 (random low) it was about 33%. However, the probability of negative abundances was largely a function of uncertainty in the parameter values as increasing the initial number of adult fish in the fall, even to 1,000, did not noticeably affect the probabilities. If uncertainty in the parameter estimates is ignored, i.e., the maximum likelihood estimates are treated as constants, then the probability of negative abundances is 0% for Scenarios 1 (random) and 3 (random high) and about 12% for Scenarios 2 (static) and 4 (random low).

Results

The GAM results indicated that water temperature, Secchi depth, and specific conductance were all statistically significant predictors of the occurrence of delta smelt

(P-values < 0.05). Individually, specific conductance accounted for the most deviance (18.3%), followed by Secchi depth (13.1), and temperature (0.1%). Although temperature was a statistically significant variable, we excluded it from our final model because it accounted for negligible deviance. Our final model included specific conductance and Secchi depth and captured 25.3% of the deviance in the data set. The response predictions generated by this model exhibited a unimodal trend against specific conductance and a negative trend against Secchi depth, indicating that delta smelt was most likely to occur at intermediate salinity (~2 ppt) with low water transparency (Figure 1).

The three different criteria for suitable abiotic habitat expectedly produced different values for total surface area (medians for each time series: 0.10 = 14,109 ha; 0.25 = 8,059 ha; 0.40 = 3,532 ha) but exhibited very similar long-term trends and were were all significantly correlated with each another (Pearson correlation coefficients ≥ 0.85, $P < 0.001$) (Figure 2). Since about 2000, each time series had values consistently well below their long-term medians. This had also occurred during a period from about the mid 1980s to early 1990s, and also in 1976-1977. The first two of these instances corresponded with droughts while the most recent instance occurred during wetter hydrologic conditions.

Surface area for each of the three different criteria of suitable abiotic habitat exhibited negative relationships with X2 (Figure 2). This indicates that under each criterion the total surface area of suitable abiotic habitat for delta smelt increased when X2 was closer to the Golden Gate. The LOWESS Curves for the two most stringent abiotic habitat scenarios (0.40 and 0.25) were approximately sigmoidal, with surface area responding primarily to X2 between approximately 65 and 85 km. The curve for the least stringent abiotic habitat criterion (0.10) exhibited a more smooth logarithmic shape, with a similar asymptote but with an immediate response to X2 position.

The results of the stock-recruit modeling support the hypothesis that the amount of available habitat has affected delta smelt abundance during 1987-2007 (Table 1). None of the regression models for the entire study period, nor the 1968-1986 period, were statistically significant ($P > 0.05$). However, all 1987-2007 models were statistically significant ($P < 0.004$). Based upon r-squared and AIC values (Table 1), the models ranked from worst to best in the following order: stock, stock + 0.10, stock + 0.25, stock + 0.40, stock + X2. The highest AIC-ranked model, stock + X2, accounted for 66% of the variability in recruit abundance, with the next best model accounting for 61%. The residuals for this model were normally distributed (Anderson-Darling P-value = 0.21) and exhibited no distinct trend versus time or the predicted values, indicating a linear fit was appropriate.

The modeling simulations indicated that Scenario 4, where the X2 values vary at random but below the historical median, yielded the highest autumn abundances after projecting 50 years into the future (Figure 3). Median abundance for this scenario was an order of magnitude greater than that which has occurred during the recent years of record lows and is near the median value for 1987-2007. Scenario 1 (random X2) provided a similar range of values but with a lower median. Scenario 2 (static) and Scenario 3 (random high) had median values much lower than Scenarios 1 and 4.

Discussion

Simulation models are not expected to provide accurate and precise predictions of future population dynamics (Rose 2000). Rather, they allow, in this case, to compare the relative effects of different inflow management strategies on future abundance of delta smelt. Explicit in this approach is the assumption that the relationships developed for the ~~model hold true in the future. The degree to which this actually happens is uncertain~~ given that San Francisco Estuary is the most highly invaded and managed estuary in the world (Nichols et al. 1986; Service 2007). Future changes to climate may also have important consequences on spring-summer water temperatures and water supply, which could affect the ability to manage estuarine inflows to benefit delta smelt (King et al. 1999; Jones et al. 2006). Nonetheless, our results clearly demonstrate the importance of abiotic habitat to the persistence of delta smelt given its current population dynamics. The best way to deal with future changes in the ecosystem is to maintain an adaptive management approach, whereby the relative importance of abiotic habitat, as well as other factors, can be reevaluated as needed.

Our results suggest that managing estuarine inflow via freshwater flow or X2 during autumn can have positive effects on delta smelt habitat and abundance. These results are somewhat different than that for habitat conditions during spring, when delta smelt are spawning and in their larval stages. Freshwater habitat volume based on salinity is somewhat affected by variation in the position of X2 during spring (Kimmerer et al. 2008), but delta smelt is one of the few low-salinity zone species in the estuary that has not covaried with spring X2 (Jassby et al. 1995; Kimmerer 2002; Bennett 2005). This contrast is a consequence of the different life stages and distribution patterns of delta smelt during autumn and spring. In autumn, delta smelt are pre-adults distributed downstream in broad channels and expansive bays at the western-most portion of their range. However, during spring they are distributed upstream primarily in smaller freshwater channels at the eastern-most portion of their range where adults spawn and juveniles rear before migrating downstream in summer (Moyle et al. 1992; Dege and Brown 2004). Whereas salinity in the broad downstream channels and bays during autumn is greatly influenced by X2, the narrow relatively homogeneous upstream channels where delta smelt spawn during spring are typically well upstream of X2 where the amount of habitat may not vary substantially. Potential mechanisms for the observed effect in autumn are several fold, although none have been directly studied. First, positioning X2 seaward during autumn provides a larger habitat area which presumably lessens the likelihood of density-dependent effects (e.g., food availability) on the delta smelt population. For example, food availability during autumn for adult haddock (*Melanogrammus aeglefinus*) likely improves juvenile recruitment the following year (Friedland et al. 2008). Second, a more confined distribution may increase the probability of stochastic events that increase mortality rates of adults. For delta smelt, this includes both predation, as well as anthropogenic effects such as contaminants or water diversion loss (Sommer et al. 2007).

A key question regarding the immediate applicability of our study is whether delta smelt is currently habitat limited given its extremely low abundance. Our results strongly suggest that delta smelt are habitat limited over the long term. Comparing the first ten years of the time series to the last ten years, the amount of suitable abiotic habitat for delta smelt during autumn has decreased anywhere from 28% to 78%, based upon the least and most restrictive habitat definitions, respectively (Figure 2). Our previous studies have demonstrated that the majority of this habitat loss has occurred along the periphery, limiting the distribution of delta smelt mainly to a core region in the vicinity of the confluence of the Sacramento and San Joaquin rivers (Feyrer et al. 2007; Nobriga et al. 2008). Concurrently, delta smelt abundance as measured by the fall midwater trawl has decreased by 63%. Determining the extent to which delta smelt is habitat limited at any given point in time is dependent upon having a full understanding of all factors affecting delta smelt and their relative importance, an exceptionally difficult task.

Optimal management requires consideration of both habitat space and the ecological processes which allow populations to expand (Levin and Stunz 2005); managing the position of X2 accomplishes both of these goals. The weight of evidence suggests that abiotic habitat constriction is at least one of the primary factors affecting delta smelt. Effects of salinity on estuarine organisms was a large part of the rationale for the development of springtime X2 standards in the San Francisco estuary (Jassby et al. 1995; Kimmerer 2002). Our results indicate that managing habitat via X2 during autumn would likely provide additional benefits to the delta smelt population. Specifically, our simulations of different potential management scenarios suggest that manipulations of autumn X2 could result in substantially different population levels of delta smelt. However, because the specific mechanisms by which X2 affects delta smelt remain poorly understood, "real world" applications of these results should incorporate an adaptive management approach, allowing resource manager to adjust actions in response to new data collected on delta smelt habitat conditions and use.

In summary, estuarine fish populations and their habitats are under increasing pressure from human population growth and associated development. In the San Francisco Estuary, the ability to manipulate freshwater inflows and diversions provides a real opportunity to manipulate abiotic habitat for the benefit of an imperiled species. With such actions, it is also important to consider the costs to other ecosystem services expected by humans. One such example is that the benefits to delta smelt may have to be balanced against costs to upstream habitats for salmonids, which may be affected by reservoir releases needed to manipulate X2. The relative success of this approach depends on our ability to learn from evaluations of different management actions, and to address major data gaps in our understanding of the basic biology of rare fishes such as delta smelt.

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Table 1. Regression statistics for stock-recruit models for the 1987-2006 time period. The models were based on delta smelt catch in the fall midwater trawl (FMT), three different levels of GAM habitat suitability criteria (>0.10, >0.25, >0.40), and X2 position

Constant	FMT	≥0.10	≥0.25	≥0.40	X2	*P*	r^2	AIC
28.4	0.0077				-0.323	<0.001	0.66	34.2
-0.29	0.0066			0.0008		<0.001	0.61	39.2
-1.32	0.0071		0.0004			0.001	0.56	41.3
-1.18	0.0076	0.0002				0.004	0.48	44.8
1.15	0.0082					0.001	0.46	45.6

Table 2. Maximum likelihood estimates, standard errors, and correlation matrix for the juvenile and pre-adult models. Estimates are separable and are shown as such.

			Correlation matrix			
	$\hat{\theta}$	SE	β_0	β_1	β_2	σ_ε
β_0	3.0170	5.4024	1.0000	0.0878	-0.9983	0.0000
β_1	0.0094	0.0023	0.0878	1.0000	-0.1297	0.0000
β_2	-0.0338	0.0647	-0.9983	-0.1297	1.0000	0.0000
σ_ε	0.6997	0.1080	0.0000	0.0000	0.0000	1.0000

			Correlation matrix		
	$\hat{\theta}$	SE	γ_0	γ_1	σ_η
γ_0	161.0800	39.6670	1.0000	0.7418	0.0000
γ_1	0.1502	0.0435	0.7418	1.0000	0.0000
σ_η	0.7568	0.1168	0.0000	0.0000	1.0000

Figure captions

Figure 1. Surface plot summarizing the effects of Secchi depth and specific conductance on the probability of occurrence of delta smelt generated by a generalized additive model.

Figure 2. Top panel: Time series for three scenarios of total surface area (ha) of suitable abiotic habitat for delta smelt from 1967 to 2006. Bottom panel: Three scenarios of total surface area (ha) of suitable abiotic habitat for delta smelt plotted against the geographic position of the 2‰ salinity isohaline, X2. The three scenarios are: a = 0.10, b = 0.25, and c = 0.40. See the text for full descriptions of the scenarios. Lines are LOWESS smoothers.

Figure 3. Boxplots showing the median (based on 10,000 simulations) predicted autumn abundances of delta smelt following 50 years of projections, along with the 5th and 95th percentiles, for each of four X2 management scenarios.

Figure 1.

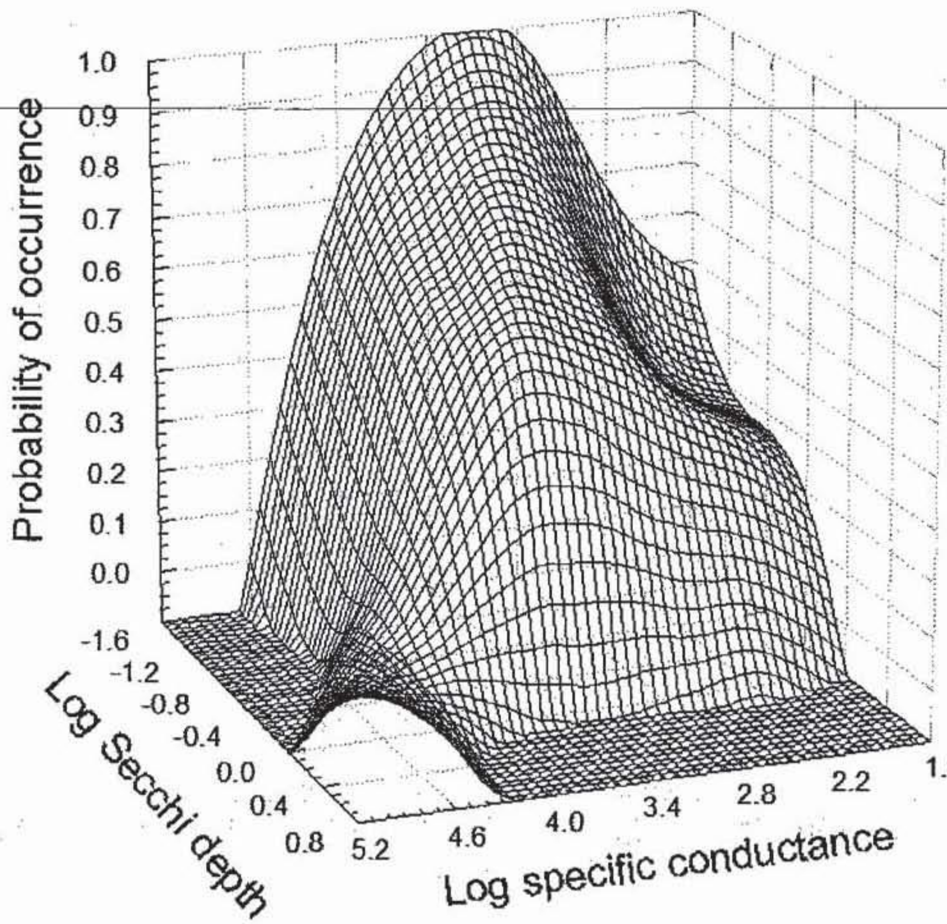

Probability of occurrence
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-1.6
-1.2
-0.8
-0.4
0.0
0.4
0.8
Log Secchi depth
5.2
4.6
4.0
3.4
2.8
2.2
1.6
Log specific conductance

Figure 2.

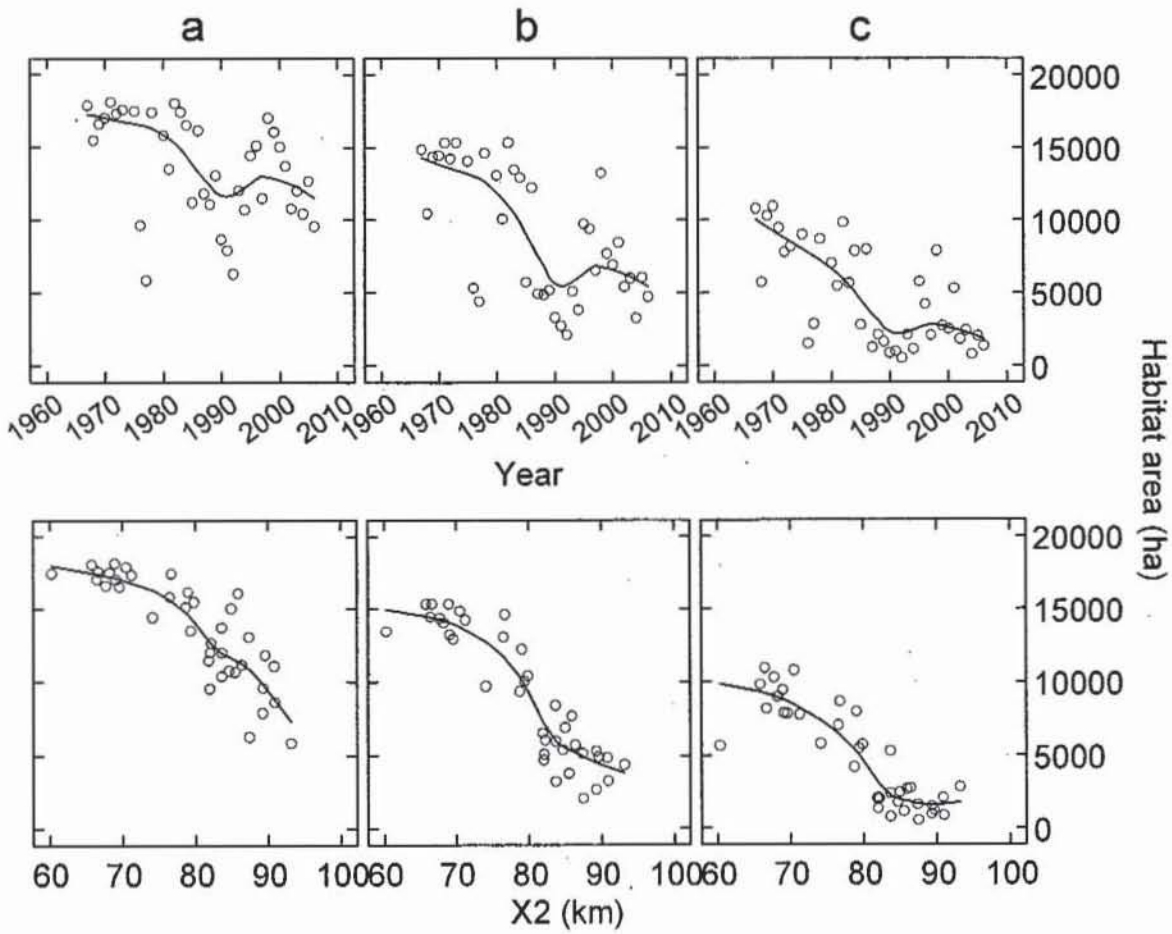
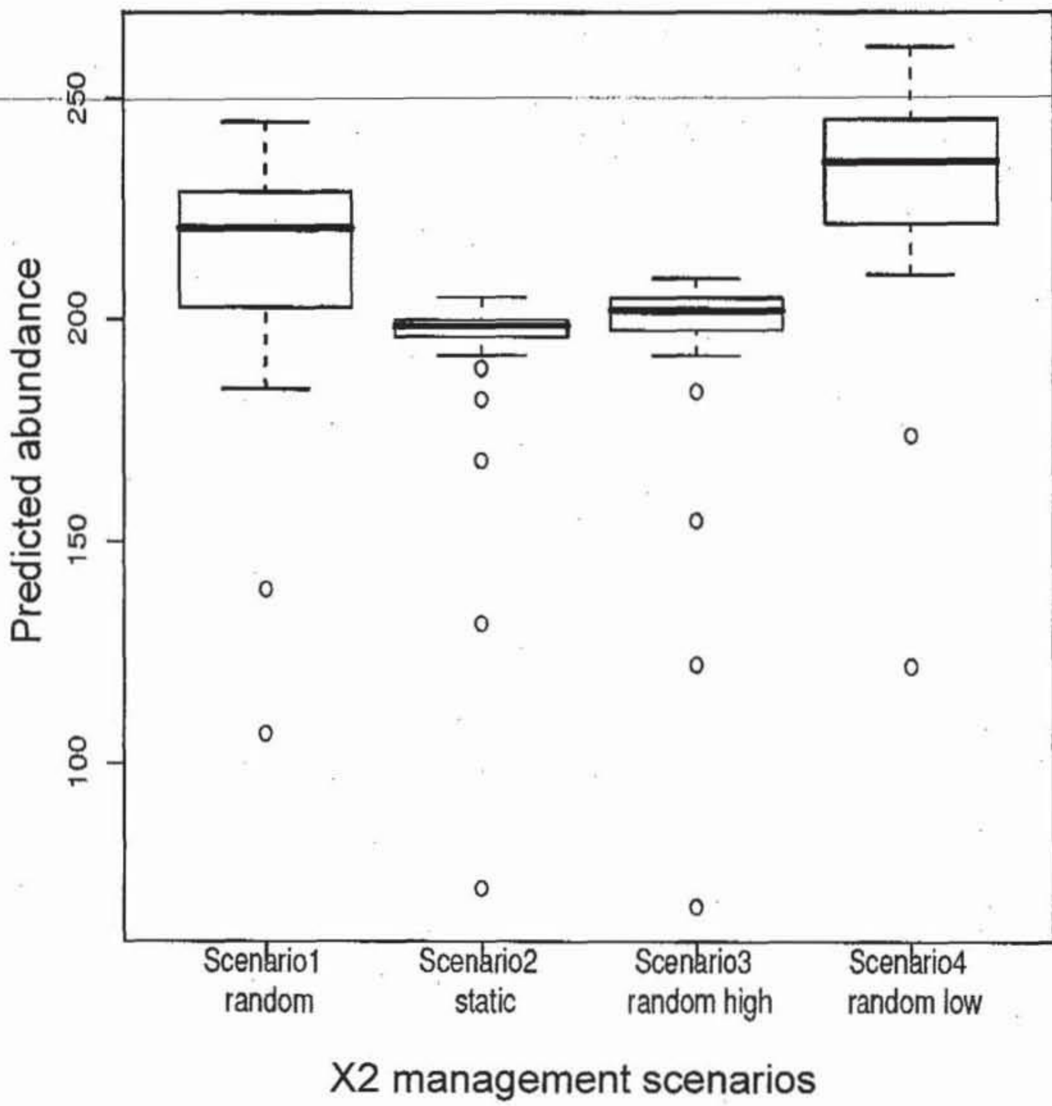

a
b
c
20000
15000
10000
5000
0
1960
1970
1980
1990
2000
2010
Year
Habitat area (ha)
60
70
80
90
100
X2 (km)

Figure 3.


Predicted abundance
250
200
150
100
Scenario1
random
Scenario2
static
Scenario3
random high
Scenario4
random low
X2 management scenarios