1 **Modeling the Effects of Water Management Actions on Suitable Habitat and**

2 **Abundance of a Critically Imperiled Estuarine Fish (Delta Smelt *Hypomesus***

3 ***transpacificus*)**

4

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18

19 **Abstract:** The opportunity to manage estuarine inflow to benefit imperiled fishes was

20 tested by modeling the likely effects for delta smelt (*Hypomesus transpacificus*).

21 Endemic solely to the euryhaline portion of the San Francisco Estuary, delta smelt is a

22 small, annual species that is on the verge of extinction. During autumn when delta smelt

23 are nearing adulthood, the amount of suitable abiotic habitat is positively associated with

24 estuarine inflow and has a measurable effect on recruitment of juveniles the following

25 summer. Long-term declines in delta smelt abundance have coincided with a decline in

26 the area of suitable abiotic habitat. Simulations based on a set of linked models for the

27 abundance of pre-adult and subsequent juvenile delta smelt showed that management

28 strategies allowing either (1) randomly occuring or (2) variable but persistently high

29 estuarine inflow produced higher abundance than scenarios of (3) variable but peristantly

30 low or (4) non-variable median inflow. Our results suggest managing estuarine inflow

31 offers one possible tool to help assist the conservation of imperiled fish species by

32 enhancing habitat space and other beneficial ecological processes.

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36 **Introduction**

37 Human-caused habitat degradation represents a major threat to biota across the globe

38 (Turner 1996; Hoekstra et al. 2005; Dobson et al. 2006). The problem is exemplified in

39 terrestrial and aquatic ecosystems alike. A major problem for aquatic systems is that

40 demands for water often conflict between services provided to the environment and to

41 ~~humans (Richter et al. 1997; Freeman et al. 2001). Effective conservation and~~

42 management of aquatic resources in the face of increasing development requires

43 understanding how development affects abiotic habitat and how abiotic habitat suitability

44 affects populations of fish and invertebrates. Fundamental ecological theory suggests a

45 correlation between habitat area and the number of species or individuals (MacArthur and

46 Wilson 1967; Williamson 1981; Begon et al. 1996). Reasons that area can support more

47 species or individuals include increased habitat diversity and resource availability, and

48 reduced probability of extinction.

49 The ubiquity of species- or individuals-area relationships in ecology has focused

50 much conservation-oriented research on defining the habitat of organisms and how

51 habitat manipulations affect abundance. Reviews on this topic have confirmed that

52 habitat loss and degradation is a major factor in the loss of species worldwide (Wilcove et

53 al. 1998; Brooks et al. 2002). As a consequence, tools to quantify the amount of area for

54 species based on habitat suitability remain popular among many resource managers

55 (Reiser et al. 1989; Layher and Brunson 1992; Johnson and Swift 2000). However

56 applying such techniques in estuaries is difficult because habitat suitability is dynamic in

57 space and time on tidal, seasonal, and annual time scales (Kimmerer 2002; Feyrer et al.

58 2007).

59   Animals with annual life cycles and limited distributions are particularly

60   vulnerable to habitat loss or degradation. Such characteristics can lead to extreme risk of

61   extinction from both pulse perturbations such as unusual or catastrophic events, and press

62   perturbations such as steady long-term habitat degradation. The case of delta smelt

63   (*Hypomesus transpacificus*), a species on the brink of extinction, exemplifies such a risk.

64   Delta smelt is an annual fish species endemic solely to the euryhaline segment of the San

65   Francisco Estuary (Moyle et al. 1992; Bennett 2005). Formerly one of the more abundant

66   fishes in the estuary, a long-term decline - plus recent years with record - low indices of

67   abundance - led federal (U.S. Fish and Wildlife Service) and state (California

68   Department of Fish and Game, CDFG) authorities to list the species as threatened with

69   extinction (Moyle 2002).

70   There are many interacting factors that affect the abundance of delta smelt,

71   including the effects of lowered adult stock, changes in the abundance and composition

72   of prey, predation, and water diversions (Moyle 2002; Bennett 2005; Sommer et al. 2007;

73   Feyrer et al. 2007). Recent studies have identified habitat degradation as a key factor

74   likely to be important in the long-term decline (Bennett 2005; Feyrer et al. 2007; Nobriga

75   et al. 2008). In particular, abiotic habitat conditions for delta smelt have deteriorated

76   over time in much of the estuary during both summer for juveniles (Nobriga et al. 2008)

77   and autumn for maturing individuals (Feyrer et al. 2007), which we term "pre-adults".

78   Summer habitat degradation has restricted juvenile delta smelt distribution (Nobriga et al.

79   2008), while autumn habitat degradation likely also affects the fitness of pre-adults,

80   which may have exacerbated the effects of lowered stock since the mid-1980s (Feyrer et

81   al. 2007).

82 The grave situation for delta smelt exemplifies the elevating worldwide problem

83 of balancing water resources between ecosystems and growing human populations. San

84 Francisco Estuary is highly modified and managed to supply water to over 25 million

85 people as well as a multibillion-dollar agricultural industry (Nichols et al. 1986). Control

86 of the estuary's hydrodynamics and water exports are closely tied to protecting delta

87 smelt on a daily basis during substantial portions of the year, but this has not prevented

88 long-term decline in estuarine fish including delta smelt (Sommer et al. 2007). Conflicts

89 between the needs of humans and those of the estuarine environment for a limited amount

90 of freshwater received international attention recently when water exports were

91 dramatically reduced by court order to protect delta smelt (Service 2007; Sommer et al.

92 2007). The concern triggered by this event illustrates the pressing need to base water

93 management decisions on sound science. At the most fundamental level this requires

94 understanding how management activities affect estuarine biota. Hence, our primary

95 objective herein was to evaluate whether estuarine inflow can be managed as a

96 conservation measure to benefit delta smelt habitat and abundance. Our basic approach

97 was to expand upon our recent descriptive modeling of delta smelt habitat (Feyrer et al.

98 2007) by (1) determining how suitable abiotic habitat is affected by estuarine inflow, (2)

99 how, in turn, suitable abiotic habitat affects abundance, and (3) modeling the likely

100 effects of several estuarine inflow scenarios on the future abundance of delta smelt. Our

101 results will immediately enable resource managers to consider the effects of water project

102 operations on this imperiled fish species, and therefore aid real-world decisions about

103 allocating a limited resource between humans and the environment.

104

105 **Methods**

106 The first step in our analyses involved updating our recent descriptive modeling of delta

107 smelt habitat (Feyrer et al. 2007) with two years of new data (2005 and 2006). We used a

108 generalized additive model (GAM) to determine how three water quality variables

109 measured during fish sampling – temperature (°C), Secchi depth (m), and specific

110 conductance ($\mu s \cdot cm^{-1}$) – affect the presence of delta smelt (Feyrer et al. 2007). The data

111 analyzed originate from a midwater trawl survey conducted during autumn at 100 stations

112 across the estuary by CDFG (Stevens and Miller 1983). We used a binary response

113 (presence or absence) rather than a measure of abundance to minimize the influence of

114 outliers (i.e., extremely anomalous abundance values) and bias associated with previously

115 reported abundance declines through time. Recent simulations based on assumed

116 underlying distributions suggest that habitat curves based on presence-absence are

117 conservative relative to catch per trawl because high frequencies of occurrence could be

118 associated with both high and moderate catch per trawl (Kimmerer et al. 2008). We

119 evaluated models by traditional statistical significance and approximate coefficients of

120 determination which describe how each independent variable reduces the null deviance in

121 the model.

122 The second step of our analyses involved translating the GAM-generated

123 occurrence probabilities into a measure of surface area (ha) of suitable abiotic habitat.

124 Because the occurrence probability values range from 0.0 to 1.0, this translation required

125 setting criteria which define suitable abiotic habitat within that range. Rather than setting

126 a single arbitrary value, we chose an approach analogous to a model sensitivity analysis

127 by evaluating three different values representing a range of increasingly strict criteria.

128   The values we selected ($\geq 0.10, \geq 0.25$, and ≥ 0.40) approximately bracketed the

129   frequency distribution of the 12,874 values for each sample generated by the GAM;

130   values for the median and third quartile were 0.11 and 0.31, respectively. We used a

131   subset of 62 of the 100 sampling stations for this analysis, excluding stations on the

132   periphery of the sampling grid where delta smelt were rarely encountered or where the

133   sampling record was inconsistent. Total surface area of suitable abiotic habitat was the

134   sum of the 62 individual surface areas representing each sampling station in which the

135   criteria were met. The surface areas represented by these stations were obtained from

136   CDFG and are shown in our previous study (Feyrer et al. 2007). Individual surface areas

137   for each station ranged from 90 to 1,251 ha, with a total of 18,781 ha. In a few instances

138   of missing environmental observations, the spatial autocorrelation in the data (i.e.,

139   conditions at adjacent stations were similar) permitted us to fill blanks with data from

140   immediately adjacent stations (Feyrer et al. 2007).

141   The third step of our analyses was to describe the relationship between the total

142   amount of suitable abiotic habitat and freshwater flow. We plotted these variables and

143   used locally weighted regression scatterplot smoothing (LOWESS) to develop data-

144   driven curves defining the relationships. We used the position of the 2‰ isohaline

145   (termed X2) as an indicator of estuarine inflow. X2 is defined as the distance (km) from

146   the Golden Gate to the location in the estuary where mean bottom salinity is 2‰ (Jassby

147   et al. 1995). Because the position of X2 has ecological relevance with positive

148   correlations to the abundance or survival of numerous estuarine biota (Jassby et al. 1995;

149   Kimmerer 2002), it is an important regulatory tool used to manage inflows in San

150   Francisco Estuary. Although previous analyses have not shown simple relationships

151 between X2 and delta smelt abundance (Jassby et al. 1995; Kimmerer 2002; Bennett

152 2005), recent studies have identified links between estuarine salinity and recruitment of

153 juveniles (Feyrer et al. 2007). Moreover, X2 clearly affects the spatial distribution of

154 delta smelt in the estuary. For this analysis, we plotted X2 position averaged from

155 September to December against the three scenarios of total surface area of suitable

156 habitat. Consistent with our previous study (Feyrer et al. 2007), we focused on the entire

157 four month autumn period to avoid issues surrounding the aliasing of the sampling data

158 that occurs at shorter temporal scales because samples are taken irrespective of tidal

159 conditions across a geographic region with large tidal excursions. Furthermore, from a

160 management perspective, manipulating X2 at shorter temporal scales is particularly

161 challenging.

162   The forth step of our analyses was to determine the effect of habitat on delta smelt

163 abundance. In this analysis, we tested the hypothesis that the combined effects of pre-

164 adult abundance and the amount of suitable abiotic habitat (or X2) during autumn affect

165 recruit abundance the following summer. The abundance indices we used for these

166 models were obtained from CDFG and are available at http://www.delta.dfg.ca.gov/.

167 Similar to previous studies (Moyle et al. 1992; Bennett 2005; Feyrer et al. 2007), we used

168 the fall midwater trawl abundance index as an estimate of pre-adult (spawning stock)

169 abundance and the summer townet abundance index as an estimate of recruit abundance.

170 The base model was a simple linear regression of pre-adult stock versus recruit

171 abundance. We then evaluated additional models which included fall stock abundance

172 and one of the three habitat area estimates or mean autumn X2 position. We ran the

173 regressions for all years combined and separated the time series into two segments, 1968-

174 1986 and 1987-2007. Similar to our previous study (Feyrer et al. 2007), separation of the

175 two time periods allowed us to examine the role of suitable abiotic habitat area during

176 periods of high and low food abundance in the estuary. This time point captures an

177 ecological change in the food web of the estuary stemming from the invasion of the

178 overbite clam *Corbula amurensis* (Kimmerer 2002). We compared models within each

179 series by traditional means (level of statistical significance and comparison of r-squared

180 values), and evaluated the relative fit of each model with an information-theoretic

181 approach based upon Akaike's information criterion (AIC). We further evaluated the fit

182 of significant regression models by visually examining residual plots for homogeneity of

183 variance and used the Anderson-Darling test to determine if the residuals were normally

184 distributed.

185 The fifth and final step of our analyses was to model the likely effects of various

186 management scenarios of estuarine inflow on the future abundance of delta smelt.

187 Modeling the effects of environmental factors on population dynamics can take many

188 forms from simple stock-recruit models (Hilborn and Walters 1992) to extremely

189 complex state-space models (Thomas et al. 2005). Delta smelt has an annual life cycle

190 and exhibits statistically significant relationships between both pre-adult to juvenile and

191 juvenile to pre-adult abundance (Bennett 2005; Feyrer et al. 2007). A set of linked

192 models for the abundance of pre-adult and juvenile delta smelt were formulated and fit to

193 assess the effect (on abundance) of manipulating X2 during autumn. The general

194 formulation is as follows:

195 $$j_t = f(pre-adult_{t-1}, X2_{t-1}, \beta, \varepsilon_t)$$

196 $$pre-adult_t = g(j_t, \gamma, \eta_t),$$

197   where j_t is the abundance of juveniles in year t, $pre-adult_t$ is the abundance of pre-

198   adults, and $X2_t$ is the X2 value, β and γ are vectors of parameters, and ε_t and η_t are

199   random variables. As above, summer townet survey indices and the fall midwater trawl

200   indices are the observations for juveniles and pre-adults, respectively.

201   To ensure that predicted values would not be negative, lognormal distributions

202   were assumed for both juvenile and pre-adult abundance. For juveniles, a linear

203   relationship with previous year pre-adults and previous year X2 values was fit (see step

204   four above and in results). We assumed density dependent effects on the survival of

205   juveniles (Bennett 2005), so we used Ricker Ricker and Beverton-Holt type models to

206   predict pre-adult abundance from juvenile abundance (Bennett 2005). Based on AIC, the

207   Ricker model was slightly better than the Beverton-Holt, and both were significantly

208   better than linear (density independent) models. The resulting models fit were:

209
$$j_t : Lognormal\left(\ln\left[\beta_0 + \beta_1 pre-adult_{t-1} + \beta_2 X2_{t-1}\right], \sigma_\varepsilon^2\right) \tag{1}$$

210
$$pre-adult_t : Lognormal\left(\ln\left[\gamma_0 j_t \exp(-\gamma_1 pa_t)\right], \sigma_\eta^2\right) \tag{2}$$

211   AD Model Builder (ADMB; Otter Research) was used to calculate maximum

212   likelihood estimates and associated standard errors of the seven parameters (β_0, β_1, β_2,

213   σ_ε, γ_0, γ_1, and σ_η). As a technical aside, there is a constraint that the median of the

214   lognormal distribution is positive, i.e., $\beta_0 + \beta_1 pre-adult_{t-1} + \beta_2 X2_{t-1} > 0$ and

215      $\gamma_0 j_t \exp(-\gamma_1 j_t) > 0$. This constraint must be met for all values of the covariates

216   ($pre-adult_{t-1}$, $X2_{t-1}$, and j_t) and finding suitable initial values for the optimization

217   algorithm was critical. To do so, the two models were fit separately first, with initial

218   values for the β's in the juvenile model (1) coming from a normal approximation fit

219   (Table 2). The standard error for the X2 coefficient (β_2) in the juvenile model is large

220   relative to the point estimate; thus while the point estimate is negative, indicating that

221   juvenile abundance decreases as X2 increases, the degree of uncertainty about the

222   relationship is relatively high. Thus, the expected values for the pre-adult model tended

223   to be overestimates of the lower values and underestimates of the higher values.

224   We considered four different management scenarios based on X2: (1) Scenario 1

225   (random); X2 varies randomly according to its historical distribution of values, 1967-

226   2007 (2) Scenario 2 (static): X2 is constant and equals the median historical value, (3)

227   Scenario 3 (random high): X2 varies randomly according to the historical distribution of

228   values at or above the median historical value, (4) Scenario 4 (random low): X2 varies

229   randomly according the historical distribution of values at or below the median historical

230   value. In all cases the historical distribution of X2 values was based upon the period

231   1967 through 2007.

232   To evaluate the effects of these four scenarios, abundances were simulated using

233   two stages of randomization. First, uncertainty in the parameter values was simulated by

234   generating β's and γ's from two multivariate normal distributions with mean vectors

235   equal to the maximum likelihood estimates and covariance matrices based on the

236   standard errors and correlation matrix (Table 2). According to large sample theory,

237   maximum likelihood estimates are approximately multivariate normal. Second, given

238   these simulated parameter values, a simulated sequence of 50 years of X2 values

239   (simulated according to each scenario), and an initial adult abundance, two time series of

240   juvenile and pre-adult abundances were simulated forward in time, 10,000 times, using

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241 the lognormal distributions (equations 1 and 2), alternating between simulation of

242 juveniles and pre-adults.

243   A practical complication was the fact that values of the β's and the γ's simulated

244 from the multivariate normal distributions do not necessarily satisfy the condition that the

245 median values of the lognormal distributions remain positive for all combinations of

246 covariates. Once a median value went negative, the future time series could not be

247 projected forward; one could make an argument that the frequency of times that such an

248 event occurred was a prediction of the probability of extinction. However, such events

249 were also a function of uncertainty of parameter values. The percentage of times that

250 projections led to negative abundances varied considerably between scenarios. For

251 Scenario 1 (random), about 54% of the projections went negative, while for Scenario 2

252 (static) it was about 23%, for Scenario 3 (random high) it was about 52%, and for

253 Scenario 4 (random low) it was about 33%. However, the probability of negative

254 abundances was largely a function of uncertainty in the parameter values as increasing

255 the initial number of adult fish in the fall, even to 1,000, did not noticeably affect the

256 probabilities. If uncertainty in the parameter estimates is ignored, i.e., the maximum

257 likelihood estimates are treated as constants, then the probability of negative abundances

258 is 0% for Scenarios 1 (random) and 3 (random high) and about 12% for Scenarios 2

259 (static) and 4 (random low).

260

261 **Results**

262 The GAM results indicated that water temperature, Secchi depth, and specific

263 conductance were all statistically significant predictors of the occurrence of delta smelt

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264 (*P*-values < 0.05). Individually, specific conductance accounted for the most deviance

265 (18.3%), followed by Secchi depth (13.1), and temperature (0.1%). Although

266 temperature was a statistically significant variable, we excluded it from our final model

267 because it accounted for negligible deviance. Our final model included specific

268 conductance and Secchi depth and captured 25.3% of the deviance in the data set. The

269 response predictions generated by this model exhibited a unimodal trend against specific

270 conductance and a negative trend against Secchi depth, indicating that delta smelt was

271 most likely to occur at intermediate salinity (~2 ppt) with low water transparency (Figure

272 1).

273   The three different criteria for suitable abiotic habitat expectedly produced

274 different values for total surface area (medians for each time series: 0.10 = 14,109 ha;

275 0.25 = 8,059 ha; 0.40 = 3,532 ha) but exhibited very similar long-term trends and were

276 were all significantly correlated with each another (Pearson correlation coefficients $\geq$

277 0.85, *P* < 0.001) (Figure 2). Since about 2000, each time series had values consistently

278 well below their long-term medians. This had also occurred during a period from about

279 the mid 1980s to early 1990s, and also in 1976-1977. The first two of these instances

280 corresponded with droughts while the most recent instance occurred during wetter

281 hydrologic conditions.

282   Surface area for each of the three different criteria of suitable abiotic habitat

283 exhibited negative relationships with X2 (Figure 2). This indicates that under each

284 criterion the total surface area of suitable abiotic habitat for delta smelt increased when

285 X2 was closer to the Golden Gate. The LOWESS Curves for the two most stringent

286 abiotic habitat scenarios (0.40 and 0.25) were approximately sigmoidal, with surface area

287 responding primarily to X2 between approximately 65 and 85 km. The curve for the least

288 stringent abiotic habitat criterion (0.10) exhibited a more smooth logarithmic shape, with

289 a similar asymptote but with an immediate response to X2 position.

290   The results of the stock-recruit modeling support the hypothesis that the amount

291 of available habitat has affected delta smelt abundance during 1987-2007 (Table 1).

292 None of the regression models for the entire study period, nor the 1968-1986 period, were

293 statistically significant ($P > 0.05$). However, all 1987-2007 models were statistically

294 significant ($P < 0.004$). Based upon r-squared and AIC values (Table 1), the models

295 ranked from worst to best in the following order: stock, stock + 0.10, stock + 0.25, stock

296 + 0.40, stock + X2. The highest AIC-ranked model, stock + X2, accounted for 66% of

297 the variability in recruit abundance, with the next best model accounting for 61%. The

298 residuals for this model were normally distributed (Anderson-Darling P-value = 0.21) and

299 exhibited no distinct trend versus time or the predicted values, indicating a linear fit was

300 appropriate.

301   The modeling simulations indicated that Scenario 4, where the X2 values vary at

302 random but below the historical median, yielded the highest autumn abundances after

303 projecting 50 years into the future (Figure 3). Median abundance for this scenario was an

304 order of magnitude greater than that which has occurred during the recent years of record

305 lows and is near the median value for 1987-2007. Scenario 1 (random X2) provided a

306 similar range of values but with a lower median. Scenario 2 (static) and Scenario 3

307 (random high) had median values much lower than Scenarios 1 and 4.

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309

310 **Discussion**

311 Simulation models are not expected to provide accurate and precise predictions of future

312 population dynamics (Rose 2000). Rather, they allow, in this case, to compare the

313 relative effects of different inflow management strategies on future abundance of delta

314 smelt. Explicit in this approach is the assumption that the relationships developed for the

315 model hold true in the future. The degree to which this actually happens is uncertain

316 given that San Francisco Estuary is the most highly invaded and managed estuary in the

317 world (Nichols et al. 1986; Service 2007). Future changes to climate may also have

318 important consequences on spring-summer water temperatures and water supply, which

319 could affect the ability to manage estuarine inflows to benefit delta smelt (King et al.

320 1999; Jones et al. 2006). Nonetheless, our results clearly demonstrate the importance of

321 abiotic habitat to the persistence of delta smelt given its current population dynamics.

322 The best way to deal with future changes in the ecosystem is to maintain an adaptive

323 management approach, whereby the relative importance of abiotic habitat, as well as

324 other factors, can be reevaluated as needed.

325   Our results suggest that managing estuarine inflow via freshwater flow or X2

326 during autumn can have positive effects on delta smelt habitat and abundance. These

327 results are somewhat different than that for habitat conditions during spring, when delta

328 smelt are spawning and in their larval stages. Freshwater habitat volume based on

329 salinity is somewhat affected by variation in the position of X2 during spring (Kimmerer

330 et al. 2008), but delta smelt is one of the few low-salinity zone species in the estuary that

331 has not covaried with spring X2 (Jassby et al. 1995; Kimmerer 2002; Bennett 2005).

332 This contrast is a consequence of the different life stages and distribution patterns of delta

333 smelt during autumn and spring. In autumn, delta smelt are pre-adults distributed

334 downstream in broad channels and expansive bays at the western-most portion of their

335 range. However, during spring they are distributed upstream primarily in smaller

336 freshwater channels at the eastern-most portion of their range where adults spawn and

337 juveniles rear before migrating downstream in summer (Moyle et al. 1992; Dege and

338 Brown 2004). Whereas salinity in the broad downstream channels and bays during

339 autumn is greatly influenced by X2, the narrow relatively homogeneous upstream

340 channels where delta smelt spawn during spring are typically well upstream of X2 where

341 the amount of habitat may not vary substantially. Potential mechanisms for the observed

342 effect in autumn are several fold, although none have been directly studied. First,

343 positioning X2 seaward during autumn provides a larger habitat area which presumably

344 lessens the likelihood of density-dependent effects (e.g., food availability) on the delta

345 smelt population. For example, food availability during autumn for adult haddock

346 (*Melanogrammus aeglefinus*) likely improves juvenile recruitment the following year

347 (Friedland et al. 2008). Second, a more confined distribution may increase the

348 probability of stochastic events that increase mortality rates of adults. For delta smelt,

349 this includes both predation, as well as anthropogenic effects such as contaminants or

350 water diversion loss (Sommer et al. 2007).

351   A key question regarding the immediate applicability of our study is whether delta

352 smelt is currently habitat limited given its extremely low abundance. Our results strongly

353 suggest that delta smelt are habitat limited over the long term. Comparing the first ten

354 years of the time series to the last ten years, the amount of suitable abiotic habitat for

355 delta smelt during autumn has decreased anywhere from 28% to 78%, based upon the

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356 least and most restrictive habitat definitions, respectively (Figure 2). Our previous

357 studies have demonstrated that the majority of this habitat loss has occurred along the

358 periphery, limiting the distribution of delta smelt mainly to a core region in the vicinity of

359 the confluence of the Sacramento and San Joaquin rivers (Feyrer et al. 2007; Nobriga et

360 al. 2008). Concurrently, delta smelt abundance as measured by the fall midwater trawl

361 has decreased by 63%. Determining the extent to which delta smelt is habitat limited at

362 any given point in time is dependent upon having a full understanding of all factors

363 affecting delta smelt and their relative importance, an exceptionally difficult task.

364 Optimal management requires consideration of both habitat space and the

365 ecological processes which allow populations to expand (Levin and Stunz 2005);

366 managing the position of X2 accomplishes both of these goals. The weight of evidence

367 suggests that abiotic habitat constriction is at least one of the primary factors affecting

368 delta smelt. Effects of salinity on estuarine organisms was a large part of the rationale for

369 the development of springtime X2 standards in the San Francisco estuary (Jassby et al.

370 1995; Kimmerer 2002). Our results indicate that managing habitat via X2 during autumn

371 would likely provide additional benefits to the delta smelt population. Specifically, our

372 simulations of different potential management scenarios suggest that manipulations of

373 autumn X2 could result in substantially different population levels of delta smelt.

374 However, because the specific mechanisms by which X2 affects delta smelt remain

375 poorly understood, "real world" applications of these results should incorporate an

376 adaptive management approach, allowing resource manager to adjust actions in response

377 to new data collected on delta smelt habitat conditions and use.

378   In summary, estuarine fish populations and their habitats are under increasing

379   pressure from human population growth and associated development. In the San

380   Francisco Estuary, the ability to manipulate freshwater inflows and diversions provides a

381   real opportunity to manipulate abiotic habitat for the benefit of an imperiled species.

382   With such actions, it is also important to consider the costs to other ecosystem services

383   expected by humans. One such example is that the benefits to delta smelt may have to be

384   balanced against costs to upstream habitats for salmonids, which may be affected by

385   reservoir releases needed to manipulate X2. The relative success of this approach

386   depends on our ability to learn from evaluations of different management actions, and to

387   address major data gaps in our understanding of the basic biology of rare fishes such as

388   delta smelt.

389

390   **Acknowledgements**

396 **Literature Cited**

397 Begon, M., J.L Harper, and C.R. Townsend. 1996. Ecology, individuals, populations

398 and communities. Blackwell Science, England.

399 Bennett, W. A. 2005. Critical assessment of the delta smelt population in the San

400 Francisco Estuary, California [online]. San Francisco Estuary and Watershed

401 Science. Online serial: http://repositories.cdlib.org/jmie/sfews/vol3/iss2/art1.

402 Brooks, T.M., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, A.B. Rylands,

403 W.R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, C. Hilton-Taylor.

404 2002. Habitat Loss and Extinction in the Hotspots of Biodiversity

405 Conservation Biology 16:909–923.

406 Dege, M., and L.R. Brown. 2004. Effect of outflow on spring and summer distribution

407 and abundance of larval and juvenile fishes in the upper San Francisco Estuary.

408 Pages 49-65 *in* F. Feyrer, L.R. Brown, R.L. Brown, and J.J. Orsi, editors. Early

409 Life History of Fishes in the San Francisco Estuary and Watershed. American

410 Fisheries Society, Symposium 39, Bethesda, Maryland.

411 Dobson, A., D. Lodge, J. Alder, G.S. Cumming, J. Keymer, J. McGlade, H. Mooney, J.

412 Rusak, O. Salva, V. Woltors, D. Wall, R. Winfree, and M.A. Xenopoulos. 2006.

413 Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology

414 87:1915-1924.

415 Feyrer, F., M. Nobriga, and T. Sommer. 2007. Multi-decadal trends for three declining

416 fish species: habitat patterns and mechanisms in the San Francisco Estuary,

417 California, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 64:723-

418 734.

419   Freeman, M.C., Z.H. Bowen, K.D. Bovee, and E.R. Irwin. 2001. Flow and Habitat

420   Effects on Juvenile Fish Abundance in Natural and Altered Flow Regimes.

421   Ecological Applications 11:179-190.

422   Friedland, K.D., J.A. Hare, G.B. Wood, L.A. Col, L.J. Buckley, D.G. Mountain, J. Kane,

423   J. Brodziak, R.G. Lough, and C.H. Pilskaln. 2008. Does the fall phytoplankton

424   bloom control recruitment of Georges Bank haddock, *Melanogrammus*

425   *aeglefinus*, through parental condition? Canadian Journal of Fisheries and Aquatic

426   Sciences 65:1076–1086.

427   Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice,

428   dynamics, and uncertainty. Chapman and Hall, New York.

429   Hoekstra, J.M., T.M. Boucher, T.H. Ricketts, and C. Roberts. 2005. Confronting a biome

430   crisis: global disparities of habitat loss and protection

431   Ecology Letters 8:23–29.

432   Jassby A. D., W. J. Kimmerer, S. G. Monismith, C. Armor, J. E. Cloern, T. M. Powell, J.

433   R. Schubel, T. J. Vendlinski. 1995. Isohaline position as a habitat indicator for

434   estuarine populations. Ecological Applications 5:272-289

435   Johnson, T.L. and D.M. Swift. 2000. A test of a Habitat Evaluation Procedure for Rocky

436   Mountain bighorn sheep. Restoration Ecology 8:47–56.

437   Jones, M.A., B.J. Shuter, Y. Zhao, and J. D. Stockwell. 2006. Forecasting effects of

438   climate change on Great Lakes fisheries: models that link habitat supply to

439   population dynamics can help. Canadian Journal of Fisheries and Aquatic

440   Sciences 63:457–468.

441 King J.R., B.J. Shuter, A.P. Zimmerman. 1999. Empirical links between thermal habitat,

442   fish growth, and climate change. Transactions of the American Fisheries Society

443   128:656–665.

444 Kimmerer, W. J. 2002. Effects of freshwater flow on abundance of estuarine organisms:

445   physical effects or trophic linkages? Marine Ecology Progress Series 243:39-55.

446 Kimmerer, W.J, E.S. Gross, and M.L. MacWilliams. 2008. Variation of physical habitat

447   for estuarine nekton with freshwater flow in the San Francisco Estuary. Estuaries

448   and Coasts (in review).

449 Layher, W.G, and K.L. Brunson. 1992. A modification of the Habitat Evaluation

450   Procedure for determining instream flow requirements in warmwater streams.

451   North American Journal of Fisheries Management 12:47–54.

452 Levin, P.S., and Stunz, G.W. 2005. Habitat triage for exploited fishes: can we identify

453   essential "essential fish habitat?" Estuarine, Coastal & Shelf Science 64:70-78.

454 MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton

455   University Press, Princeton, New Jersey, USA.

456 Moyle, P.B. 2002. Inland fishes of California. Revised and expanded. University of

457   California Press, Berkeley, California.

458 Moyle, P. B., Herbold, B., Stevens, D.E., and Miller, L.W. 1992. Life history and status

459   of delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of

460   the American Fisheries Society 121:67-77.

461 Nichols, F.H., Cloern, J.E., Luoma, S.N., and Peterson, D.H. 1986. The modification of

462   an estuary. Science 231:567-573.

463   Nobriga, M., T. Sommer, F. Feyrer, and K. Fleming. 2008. Long-term trends in

464   summertime habitat suitability for delta smelt, *Hypomesus transpacificus*. San

465   Francisco Estuary and Watershed Science. Online serial:

466   http://repositories.cdlib.org/jmie/sfews/vol6/iss1/art1/

467   Richter, B.D., D.P. Braun, M.A. Mendelson, and L.L. Master. 1997. Threats to Imperiled.

468   Conservation Biology 11:1081-1093.

469   Rose, K. A. 2000. Why are quantitative relationships between environmental quality and

470   fish populations so elusive? Ecological Applications 10:367-385.

471   Service, R.F. 2007. Delta blues, California style. Science 317:442-445.

472   Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F.

473   Feyrer, M. Gingras, B. Herbold, W. Kimmerer, A. Mueller-Solger, M. Nobriga,

474   and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco

475   Estuary. Fisheries 32:270-277.

476   Stevens, D.E., and Miller, L.W. 1983. Effects of river flow on abundance of young

477   chinook salmon, American shad, longfin smelt, and delta smelt in the

478   Sacramento-San Joaquin River system. Transactions of the American Fisheries

479   Society 3:425-437.

480   Thomas, L., S.T. Buckland, K.B. Newman, and J. Harwood. 2005 A unified framework

481   for modelling wildlife population dynamics. Australian and New Zealand Journal

482   of Statistics 47:19-34.

483   Turner, I.M. Species loss in fragments of tropical rain forest: A review of the evidence.

484   Journal of Applied Ecology 33:200-209.

485   Wilcove, D.S., D. Rothstein, J. Dubow, A. Phiiiips, and E. Losos. 1998. Quantifying

486   threats to imperiled species in the United States. BioScience 48:607-615.

487   Williamson, M.H. 1981. Island populations. Oxford University Press, Oxford.

488

489 Table 1. Regression statistics for stock-recruit models for the 1987-2006 time period.

490 The models were based on delta smelt catch in the fall midwater trawl (FMT), three

491 different levels of GAM habitat suitability criteria (>0.10, >0.25, >0.40), and X2 position

492

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

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501 Table 2. Maximum likelihood estimates, standard errors, and correlation matrix for the

502 juvenile and pre-adult models. Estimates are separable and are shown as such.

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	$\hat{\theta}$	SE	Correlation matrix			
			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

	$\hat{\theta}$	SE	Correlation matrix		
			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

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507

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.
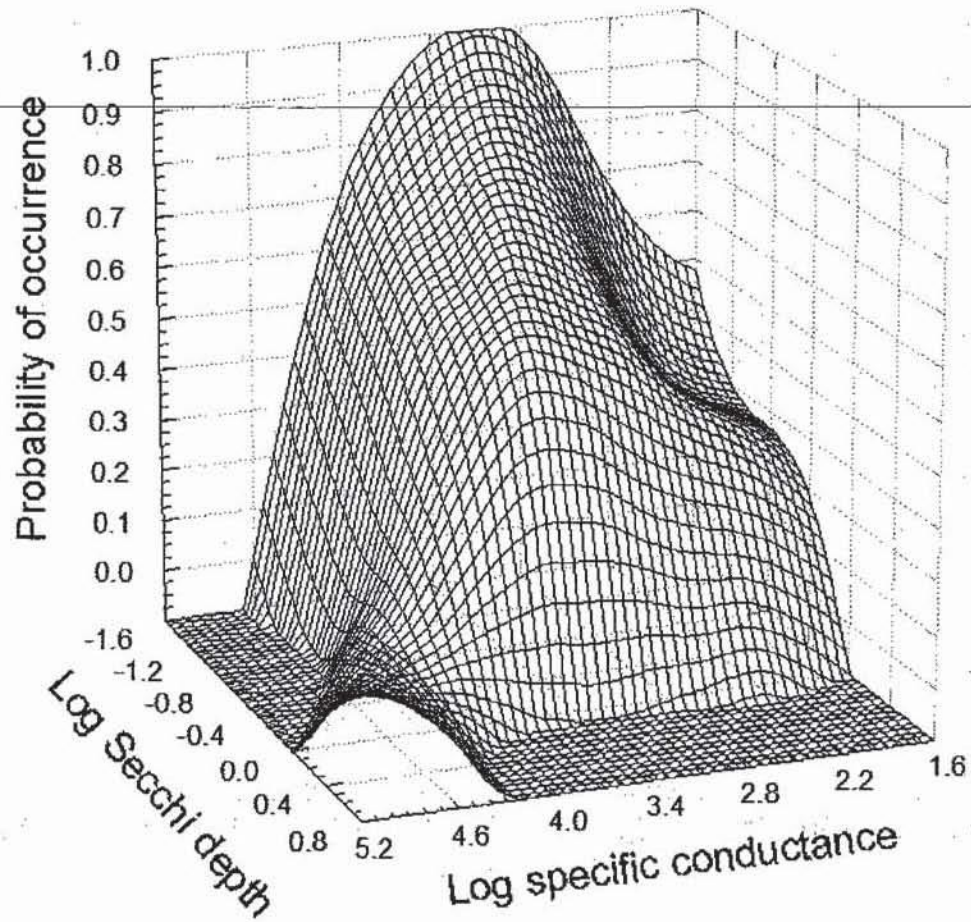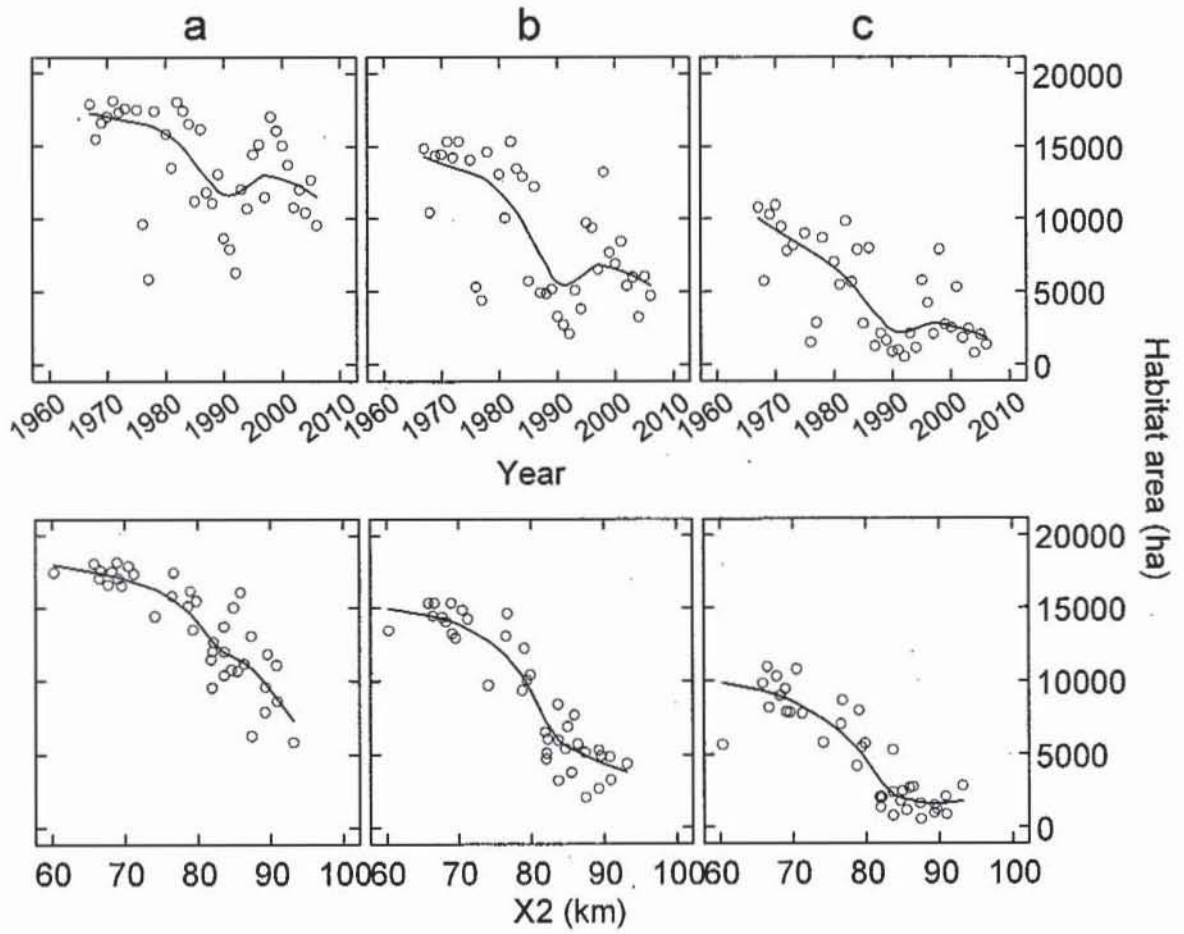
Figure 1.

Figure 2.

Figure 3.

X2 management scenarios