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An Investigation of Factors Affecting the Decline of Delta Smelt (*Hypomesus transpacificus*) in the Sacramento-San Joaquin Estuary

WILLIAM J. MILLER,[1] BRYAN F. J. MANLY,[2] DENNIS D. MURPHY,[3]
DAVID FULLERTON,[4] and ROB ROY RAMEY[5]

[1]San Luis & Delta-Mendota Water Authority, Point Richmond, California, USA
[2]Western Ecosystem Technology, Inc., Cheyenne, Wyoming, USA
[3]Biology Department, University of Nevada, Reno, Nevada, USA
[4]Metropolitan Water District of Southern California, Sacramento, California, USA
[5]Wildlife Science International, Nederland, Colorado, USA

The delta smelt is an annual fish that is endemic to the Sacramento-San Joaquin Estuary and is protected under federal and California Endangered Species Acts. Record low abundances have occurred since 2004. Three questions are addressed here: What is the relative importance of environmental factors with direct effects on abundance? Do factors that may have indirect effects provide an explanation of abundance changes? Are effects of environmental factors better accounted for individually or as criteria defining the volume of water with suitable abiotic attributes? Strong evidence was found of density-dependent population regulation. The density of prey was the most important environmental factor explaining variations in delta smelt abundance from 1972 to 2006 and over the recent period of decline in the abundance of the fish. Predation and water temperature showed possible effects. Entrainment of delta smelt at south Delta pumping plants showed statistically significant effects on adult-to-juvenile survival but not over the fish's life cycle. Neither the volume of water with suitable abiotic attributes nor other factors with indirect effects, including the location of the 2 ppt isohaline in the Delta in the previous fall ("fall X2"), explained delta smelt population trends beyond those accounted for by prey density.

[Supplementary materials are available for this article. Go to the publisher's online edition of *Reviews in Fisheries Science* for the following free supplemental resources: information on factor selection and specification; and estimating the volume of abiotic habitat.]

Keywords delta smelt, life-cycle model, multiple regression, effects hierarchy, pelagic organism decline

INTRODUCTION

It is a terrible juxtaposition of superlatives for the delta smelt. No other species currently protected under the federal Endangered Species Act has declined so dramatically since its listing. The index of abundance of delta smelt in the Sacramento-San Joaquin Delta has fallen almost three orders of magnitude since the fish was afforded protection in 1993 (California Department of Fish and Game [CDFG], 2010a). The need for immediate conservation responses is acute, but that need confronts another unfortunate delta smelt reality—perhaps less is known about the habitat of delta smelt, resources essential to its persistence, and the environmental stressors causing its low population numbers than is known about any other listed species. The life cycle of the tiny estuarine fish takes place in turbid, open waters, making it impossible to observe its behavior and

Address correspondence to Dr. William J. Miller, San Luis & Delta-Mendota Water Authority, 318 Arizona Avenue, Point Richmond, CA 94801, USA. E-mail: bjmiller41@gmail.com.

account for many of its vital ecological relationships. Several candidate factors have plausible mechanisms of effect on delta smelt numbers, but previous attempts to relate environmental stressors to the decline of this fish were not able to identify the factors responsible for the recent declines in the abundance index to near-extinction levels. It might be fairly argued that no other federally listed species needs more immediate conservation attention, but a lack of reliable scientific guidance has hampered focused actions in support of delta smelt recovery.

The delta smelt is predominantly an annual species, with few individuals surviving to two years (Bennett, 2005). They are endemic to the San Francisco Bay-Delta Estuary. Delta smelt rear as juveniles and sub-adults upstream and downstream of the confluence of the Sacramento and San Joaquin Rivers for about seven months of the year, from late spring until the following winter (Bennett, 2005). Moyle (2002) described delta smelt as fish that "hang out in the water column and rely on their small size and transparency to hide them from predators in turbid water" (p. 228). Some delta smelt reside upstream in low salinity and fresh waters year around (Sommer et al., 2009). In winter, adults disperse into turbid waters that are necessary for efficient feeding of larvae on zooplankton (Baskerville-Bridges et al., 2004; Mager et al., 2004), with much of the population entering the Sacramento-San Joaquin Delta (Moyle, 2002). Spawning, triggered by increasing water temperature, begins as early as late February and can continue into June (Bennett, 2005). The environmental changes that have accompanied settlement and exploitation of the Delta have forced major adjustments in resources and conditions essential to survival and persistence of delta smelt.

No field data have been derived from experiments that directly relate delta smelt population responses to variation in physical and biotic conditions; however, general agreement exists both on the environmental features that seem to determine the location of delta smelt in the estuary and on stressors that could be contributing to decline of the fish. A conceptual model that describes and relates essential resources and suspected threat factors affecting population dynamics of delta smelt and other declining pelagic organisms in the Delta was developed by a multi-agency working group (Armor et al., 2005; Baxter et al., 2008; Baxter, 2010); however, no quantitative model has been available. Several recent studies have attempted to relate delta smelt population index data to suspected environmental stressors, but those studies had deficiencies that rendered their results uninformative (Feyrer et al., 2007; Mac Nally et al., 2010; Thomson et al., 2010).

Relating delta smelt population trends to changes in environmental factors that affect survival and reproduction of the fish, both directly (for example, predation, food supply, and entrainment) and indirectly (for example, flow and phytoplankton density), risks producing uninformative or confusing results. To maximize the likelihood of identifying actual causative relationships, the analysis presented here is initiated by developing an effects hierarchy that differentiates between those environmental covariates that act directly on the survival, reproduction, or recruitment of the delta smelt and those that act indirectly through one or more factors that act directly. This article focuses primarily on environmental factors with direct effects on survival or reproduction, leaving a rigorous attempt to identify indirect factors with important effects on direct factors for subsequent analyses (see Glibert et al., 2011, for example). This approach has three advantages. First, focusing on the limited number of variables with direct effects on delta smelt reduces the confounding effects of multi-collinearity and differential measurement error. When candidate causation factors are related to or interact with one another, the factor with lower measurement error may displace factors that have greater measurement error, even when those latter factors can be demonstrated to have greater effects signals (Zidek et al., 1996). Second, it reduces the possibility that identification of important environmental factors will be uninformative to decisions about resource management. This problem can arise if a factor with indirect effects is identified as itself important, but that factor acts through other factors that have direct or indirect effects. The best management response may involve controlling, or otherwise mitigating, not the environmental factor with an indirect effect identified as important, but rather, other factors. Third, arrangement of factors according to their hierarchy of effects provides information important in choosing the analytical method. Because pathways of effects can be delineated from knowledge of the mechanisms of ecological effects, a straightforward succession of multiple regression analyses, proceeding down each vertical path of the hierarchy, is suggested as the appropriate analytical approach to identifying the factors that best predict delta smelt population dynamics.

Several analysts have previously used measures of the volume of water with suitable attributes of conductivity, Secchi depth (as a measure of turbidity), and water temperature, which have been termed "abiotic habitat," to account for changes in abundance of delta smelt (e.g., Feyrer et al., 2007). In a subsequent biological opinion on delta smelt developed by the U.S. Fish and Wildlife Service (USFWS), inferences from those analyses were used to assert that a range of suitability in the extent of those abiotic factors limits abundance of delta smelt, and that increasing that extent is important to the recovery of delta smelt (USFWS, 2008). The hypothesis was tested that the volume of water within ranges of conductivity, Secchi depth, and water temperature at which most delta smelt occur explained variations in survival and reproduction. Several measures of that volume were developed and their effects on survival and reproduction were analyzed.

Index values for relative abundance of delta smelt were derived from standard trawler-generated data, specifically, the Fall Midwater Trawl (FMWT; CDFG, 2010a) and the Summer Townet Survey (STN; CDFG, 2010b). From relative abundance estimates, annual estimates of survival from juvenile to sub-adult life stages were developed, as well as survival and reproduction (hereinafter, referred to as "survival") across generations from sub-adult to juvenile life stages. Those estimates were used as response variables. Annual values for a variety of environmental variables were then developed, each of which could plausibly affect delta smelt population size and persistence. In doing so, the resource requirements and distribution of delta smelt at different sizes and in different stages in their life cycle were considered. From those candidate factors, a limited number were selected that offer the most plausible mechanism(s) of direct effect on delta smelt survival and abundance. In so doing, well-considered direct factors were differentiated from factors that may indirectly affect the size of and trend in delta smelt numbers through their effects on direct factors. From the abiotic and biotic factors in the Delta that appear to have direct effects on delta smelt, those that may be most important were selected, based on inferences drawn from available data and analyses. Multiple regression was used with three criteria to identify environmental factors that may be most important to survival and to evaluate the relative importance of those factors: goodness of fit of equations measured by the Akaike Information Criterion (AICc), the proportion of variation accounted for, and the significance of the regression coefficients. Using this general method, analyses were conducted to address three fundamental questions with important management implications: What is the relative importance of environmental factors that have direct effects on delta smelt abundance? Do environmental factors with indirect effects further explain abundance changes once effects of factors with direct effect are accounted for? Are the effects of environmental factors best accounted for independently or as criteria by which the volume of water with suitable attributes can be measured?

Based on the availability of data, these questions were directed at three periods in the annual life cycle of delta smelt—sub-adult (fall) to juvenile (summer), juvenile (summer) to sub-adult (fall), and sub-adult (fall) to sub-adult (fall). Because delta smelt has an annual life cycle, the last period is one version of a life-cycle model. Such a model has been identified as critically important in the development of a program to encourage recovery of delta smelt and to prevent jeopardizing its existence (Wanger, 2010). Analysis of the two within-year periods was carried out to better understand the factors that affect delta smelt survival between intermediate life stages during the year.

METHODS

Period of Analysis

The period of analysis covered the years 1972 through 2006. The initial year was selected because it was the first year of comprehensive surveys for zooplankton density throughout regions of the estuary occupied by delta smelt. The year 2006 was chosen because at the time this analysis began, comprehensive environmental data were only available through that year, and the period 2000 to 2006 includes the sharp decline in abundance of delta smelt that has persisted with little change since 2006.

Abundance and Survival

Two trawler-based surveys provide time-series population data from which long-term measures of annual delta smelt abundance can be estimated—the FMWT (1967–present), which samples sub-adult delta smelt, and the STN (1959–present), which samples for juveniles. Those data were used to provide the response variables representing delta smelt population size through time. An index of relative abundance has been calculated from both surveys by the CDFG since before 1970 (http://www.dfg.ca.gov/delta/). The indices are calculated by averaging catch per unit effort (for FMWT) or catch (for STN), assuming that volumes of water passing through the net are approximately the same for all STN tows over each Delta sub-region, then weighting the resulting averages by the estimated volume of water in the respective sub-region and summing sub-region estimates of abundance over all sub-regions. The FMWT index was used as calculated by the CDFG (http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT); this index is generally assumed to be the most accurate long-term index of delta smelt abundance, because it samples larger fish at approximately the same times each year over more stations than the STN. FMWT surveys were not conducted in 1974 and 1979, so those years were eliminated from the analysis.

There were concerns about the STN index. It is based on data from the first two surveys each year, and starting dates for the first survey can vary from year to year by as much as six weeks. Furthermore, more than one tow typically is made at each station, and catch is summed over all tow samples rather than averaged. It could not be confirmed that volumes of water in each sub-region used for the STN index were as accurate as those derived by detailed analysis of NOAA navigation charts. Therefore, despite the decades-long use of the STN index by analysts in this estuary, it was concluded that its flaws were too serious to justify its use as one of the two abundance variables in the present analyses, so an alternative estimate of summer juvenile delta smelt abundance was derived to overcome these problems. This estimate is referred to as “July abundance.” It is based only on STN surveys that occur all or in part in July (the only month in which surveys occur each year), uses average rather than summed catch per tow, and uses updated volumes for each sub-region of the Bay Delta system.

Delta smelt survival is the response variable in the statistical analyses in this study. In these analyses, survival, as measured by index values, includes reproduction that occurs during the fall-to-summer period (that is, from pre-spawning adults in the fall to the next generation’s juveniles in the July) and the fall-to-fall period (that is, a complete life cycle from pre-spawning adults in the fall to the next generation’s pre-spawning adults the following fall). Three measures of delta smelt survival can be derived from the two abundance indices—fall-to-summer survival, summer-to-fall survival, and fall-to-fall survival. Environmental factors that can reasonably be surmised to affect each of these three measures of survival were analyzed. Analyses of the former two measures provided insight into more important factors affecting fall-to-fall survival.

Environmental Factors and Their Hierarchy of Effects

Drawing on agency reports, several dozen biotic and abiotic factors were specified, that is, identified and quantified, along with variations of those factors, that have plausible mechanisms of effect on the abundance of delta smelt (Armor et al., 2005; Baxter et al., 2008; USFWS, 2009; Baxter, 2010) and for which data were available. Each factor was carefully specified, with consideration of the distribution of delta smelt and ranges of factor variation at different times of the year. Data on delta smelt distribution and environmental factors were segregated into sub-regions of the estuary, shown in Figure 1. Based on their mechanisms of effects, environmental factors were segregated into those with direct effects on delta smelt abundance and those with indirect effects, that is, effects that act through other factors that have direct effects. Factors that have direct effects on survival of delta smelt were grouped into categories (for example, water temperature, prey densities, entrainment at water export pumps); the same was done for factors with indirect effects on the smelt. Descriptions of each factor are in supplemental material to this article, along with the rationale for the selection of each factor and method used for its quantification. Figure 2 illustrates the general categories of factors, arranged as an "effects hierarchy." Apparent in the diagram is that certain factors—such as turbidity, water temperature, and flows through the Delta—appear at several locations in the hierarchy and may act indirectly on delta smelt, often in combination with other indirect factors. Data were available for all direct factors except disease and contaminants; however, effects of disease and contaminants on factors with indirect effect would be manifested as changes in factors with direct effect.

A Sawtooth Pattern in Survival

A pronounced inter-year "sawtooth" pattern in the survival of delta smelt was identified, that is, a persistent pattern of alternating years with higher and lower survival. This pattern was nearly identical in fall-to-summer and fall-to-fall index sequences, as shown in Figure 3. The probability was simulated that alternating peaks and troughs for 13 years would occur, as they did for years 1987 to 2000, if survival were random from year to year. This probability was estimated as 0.025—likely an overestimate because of the actual decreasing trend in delta smelt abundance over that period. Based on this analysis, it was concluded that there was a very low probability that this pattern occurred by chance. Two possible causes of the pattern were considered, one being the effect on delta smelt numbers of an environmental factor or combination of factors that exhibit corresponding, year-to-year sawtooth variation, and the other being an inherent aspect of the physiological ecology and/or

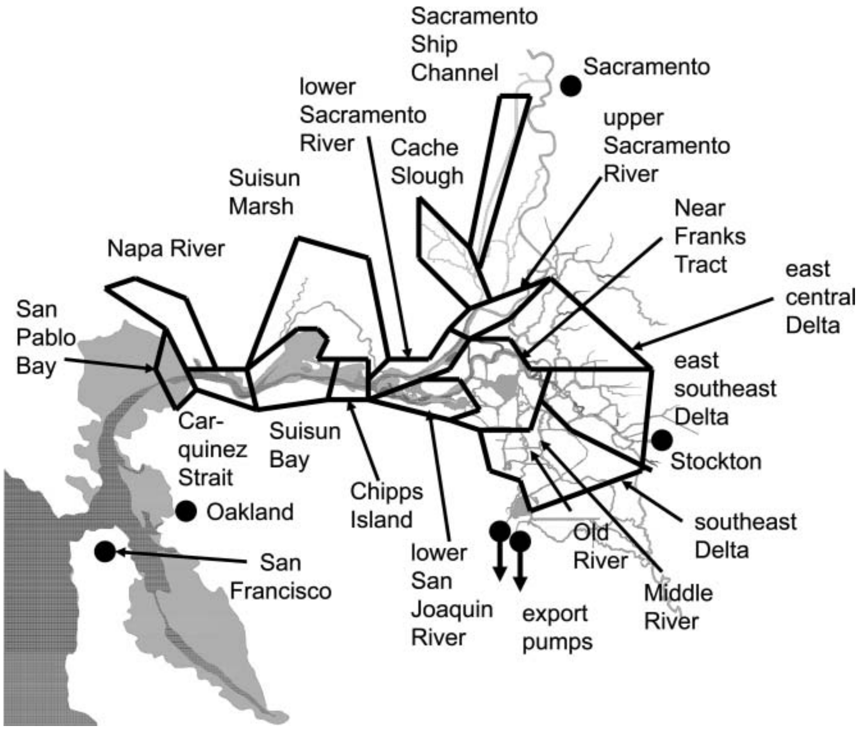
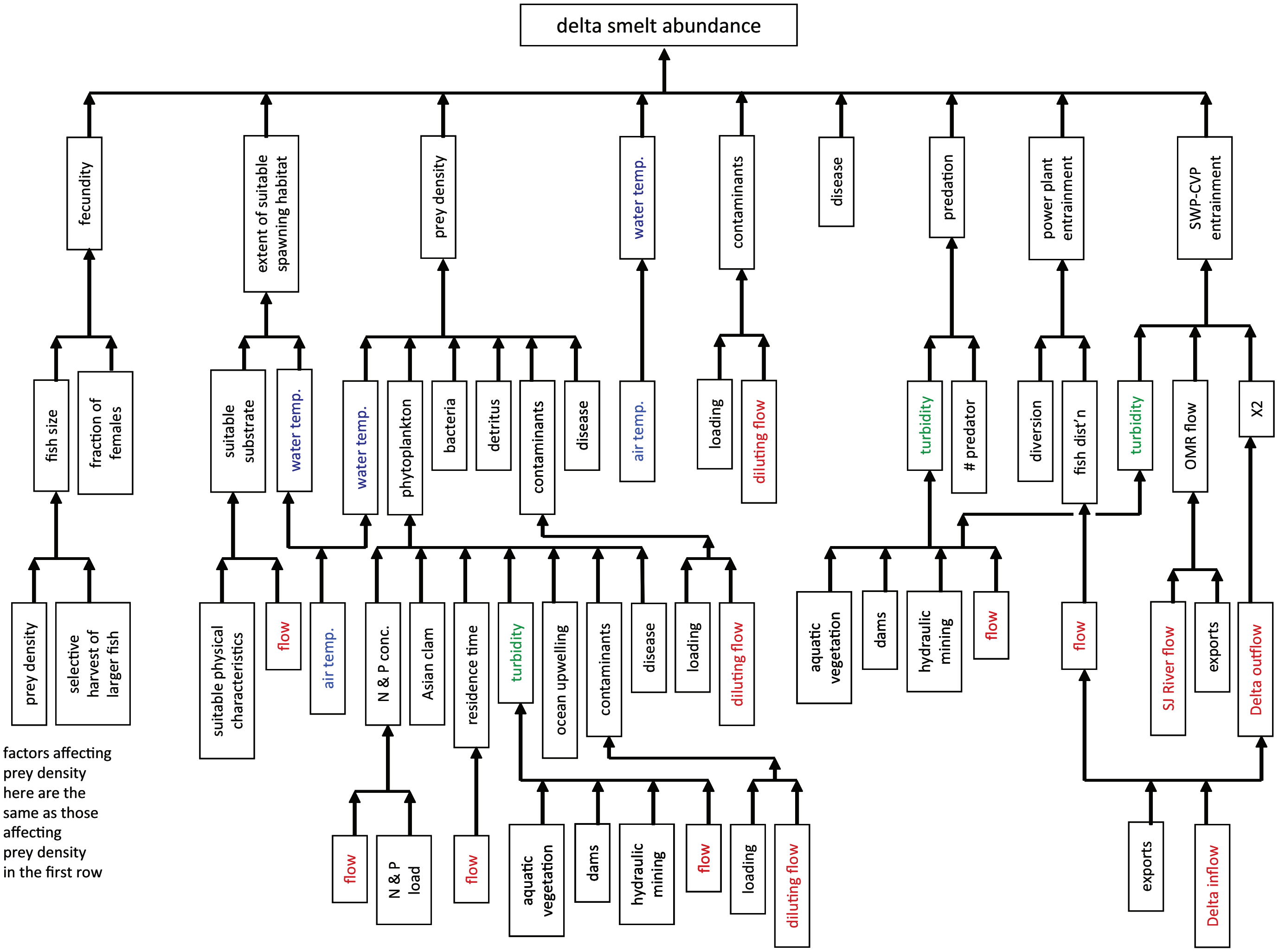


Figure 1 Sub-regions of the Bay-Delta Estuary.



factors affecting prey density here are the same as those affecting prey density in the first row

Figure 2 A simplified effects hierarchy of factors affecting delta smelt abundance. Row one, below delta smelt abundance, shows the factor categories that act directly to affect delta smelt. Row two includes factors that act indirectly on the fish. Rows three and four represent second-order and third-order indirect factors. Factors appearing in several locations are colored (color figure available online).

behavior of delta smelt. Relationships were examined between the sawtooth pattern and environmental factors with both direct and indirect effects on delta smelt. No factor or factors could be identified that explained the sawtooth pattern for more than a few sequential years, so it was concluded that an inherent cause seems more tenable. This effect was captured by including abundance from the year previous to that over which survival was estimated, a term referred to herein as "previous-previous fall abundance."

Identifying Best Regression Equations Using Factors with Direct Effect

General Approach

From each category of environmental factors with direct effects, represented as the factors in the first row in Figure 2, one or two initial factor quantifications were selected that, based on available knowledge of delta smelt biology, were likely to be most important in determining delta smelt survival. Values of those environmental factors are shown in Table 1. The reasons for their selection are presented in supplemental material. Then the effect of each of these factors was analyzed, along with previous delta smelt abundance (to capture effects of density dependence) and previous-previous fall abundance (to capture effects of the sawtooth pattern in survival). Statistical methods for this analysis are described below and are based on two key assumptions: that the FMWT and July abundance indices are approximately proportional to delta smelt abundance, and that the abundance index at one point in time is proportional to the abundance index at a previous time, apart from the effects of measured variables, sampling errors, process error variation, and density-dependent effects.

The analysis was initiated using the Ricker model (Ricker, 1958). This model assumes that the population abundance at

Table 1 Factors with direct effect on delta smelt selected as most important to fall-to-summer, summer-to-fall, and fall-to-fall survival

	July abundance	FMWT index	Previous FMWT index	Spawning period, days of water temperature 11–20°C	Average water temperature Apr–Jun (°C)	Average water temperature July (°C)	Maximum two-week average water temperature Jul–Sep (°C)	Minimum *Eurytemora* + *Pseudodiaptomus* Apr–Jun (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* July (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Jul–Aug (#/m^3)	Secchi depth Apr–Jun (cm)	Adjusted Kimmerer proportional entrainment	Previous Sep–Dec striped bass adult abundance and Secchi depth	Previous Sep–Dec abundance other predators and Secchi depth	Apr–Jun abundance of other predators and Secchi depth	Sep–Dec striped bass adult abundance and Secchi depth	Sep–Dec abundance other predators and Secchi depth	Average length of delta smelt in December (mm)
Year	*Jab*	*Fab*	*PFAb*	*SpDys*	*TpAJ*	*TpJul*	*TpJS*	*EPAJ*	*EPJul*	*EPJA*	*SecAJ*	*Entrain*	*PStBass*	*PPreds1*	*Preds2*	*StBass*	*Preds1*	*DSLth*
1972	20,005	1,265	1,303	110	17.8	21.3	21.8	1,244	4,725	4,303	30	0.229	24,855	490	354	36,498	586	65.3
1973	11,185	1,145	1,265	104	18.6	21.3	21.9	754	1,547	2,082	32	0.110	36,498	586	793	27,596	1,041	65.3
1974	12,147		1,145	85	17.7	21.0	22.5	614	4,202	3,799	30	0.091	27,596	1,041	446	32,314	850	65.3
1975	8,786	697		92	17.2	20.1	21.5	480	1,520	1,545	26	0.094	32,314	850	280	41,650	735	65.1
1976	24,000	328	697	130	17.6	21.4	21.9	666	4,125	2,895	31	0.262	41,650	735	6,118	65,427	19,410	65.3
1977	25,965	480	328	118	17.0	21.1	21.5	581	4,194	3,972	33	0.256	65,427	19,410	7,095	40,655	22,324	65.6
1978	31,758	572	480	110	17.8	21.1	22.4	1,458	2,082	1,391	30	0.077	40,655	22,324	8,423	28,399	14,726	65.3
1979	5,484		572	90	18.0	21.0	22.1	517	947	722	28	0.160	28,399	14,726	18,631	25,761	37,712	67.8
1980	7,068	1,654	137	137	16.8	20.5	22.5	428	548	647	34	0.038	25,761	37,712	15,120	20,254	20,360	70.3
1981	6,300	374	1,654	108	18.7	21.8	22.8	788	922	724	37	0.199	20,254	20,360	17,070	20,621	22,248	67.2
1982	7,242	333	374	105	17.0	20.6	21.4	19	636	670	37	0.069	20,621	22,248	23,570	21,560	30,605	66.2
1983	1,390	132	333	102	17.3	20.7	22.2	271	530	544	34	0.020	21,560	30,605	13,957	31,059	28,422	62.2
1984	779	182	132	100	18.3	22.4	22.8	251	1,560	1,545	41	0.144	31,059	28,422	20,444	35,459	29,082	69.5
1985	387	110	182	105	18.5	22.0	22.5	135	548	543	43	0.231	35,459	29,082	30,364	46,997	62,483	69.1
1986	3,057	212	110	122	18.1	21.2	21.5	649	626	534	36	0.019	46,997	62,483	22,921	22,752	30,255	68.1
1987	2,743	280	212	102	19.0	20.6	21.3	534	392	519	44	0.199	22,752	30,255	26,771	41,144	42,089	64.8
1988	764	174	280	125	17.8	22.4	23.1	119	364	360	43	0.282	41,144	42,089	26,668	30,207	36,828	69.5
1989	647	366	174	108	17.9	21.1	21.7	384	2,558	3,641	42	0.222	30,207	36,828	24,067	29,441	38,551	67.8
1990	747	364	366	100	18.4	22.0	22.7	200	3,616	3,837	43	0.274	29,441	38,551	26,671	32,336	57,128	63.9
1991	2,486	689	364	108	17.2	21.3	21.8	151	2,542	3,059	38	0.231	32,336	57,128	23,754	39,881	63,209	62.5
1992	471	156	689	99	19.2	21.3	22.5	532	2,733	2,828	44	0.201	39,881	63,209	42,138	44,102	89,736	57.9
1993	5,763	1,078	156	112	17.8	21.5	22.2	603	1,184	1,425	42	0.119	44,102	89,736	25,301	27,938	48,487	54.7
1994	4,156	102	1,078	102	17.8	21.1	21.4	1,112	965	856	56	0.139	27,938	48,487	53,729	32,635	61,942	62.9
1995	2,490	899	102	142	17.0	21.5	22.0	574	2,366	1,431	44	0.064	32,635	61,942	38,412	34,966	59,091	58.5
1996	6,162	127	899	115	18.3	21.4	22.6	381	533	731	49	0.016	34,966	59,091	52,547	44,927	72,056	55.1
1997	2,362	303	127	104	19.3	21.2	21.8	369	590	800	44	0.093	44,927	72,056	33,056	56,551	64,436	57.6
1998	2,209	420	303	117	16.3	21.3	22.6	272	1,002	842	40	0.003	56,551	64,436	21,106	32,979	25,623	59.3
1999	7,478	864	420	112	17.3	21.3	22.0	752	1,308	1,091	41	0.052	32,979	25,623	21,961	42,465	29,853	59.1
2000	4,178	756	864	118	18.9	20.8	22.2	411	825	1,007	44	0.097	42,465	29,853	50,114	60,639	74,907	59.3
2001	2,897	603	756	73	19.5	21.3	22.0	424	758	484	42	0.133	60,639	74,907	50,992	48,811	81,186	63.5
2002	1,115	139	603	108	18.6	21.8	22.2	105	641	462	45	0.206	48,811	81,186	59,540	32,632	75,565	62.2
2003	1,329	210	139	106	18.0	22.2	23.2	136	787	1,525	47	0.175	32,632	75,565	56,424	40,081	86,509	58.6
2004	649	74	210	108	19.1	21.3	22.3	154	354	1,012	44	0.187	40,081	86,509	50,151	82,253	109,036	62
2005	393	27	74	123	18.1	22.0	22.8	57	849	466	51	0.049	82,253	109,036	68,310	58,943	119,419	59.6
2006	352	41	27	95	17.8	22.6	23.7	122	1,321	884	43	0.012	58,943	119,419	53,328	41,977	116,848	58
Fall-to-summer	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨			▨
Summer-to-fall	▨	▨					▨			▨						▨	▨	
Fall-to-fall	▨		▨	▨	▨		▨	▨		▨	▨	▨			▨	▨	▨	▨

The last three rows are shaded to indicate the survival period to which each factor is relevant.

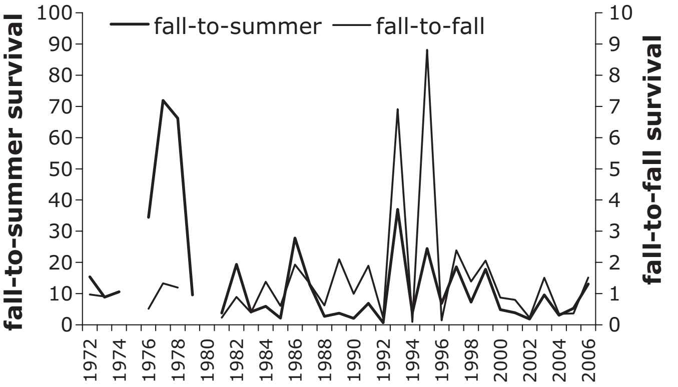


Figure 3 Delta smelt survival values from fall to summer and from fall to fall, which are derived from survey index values.

time $t + 1$ is related to the abundance at time t by an equation of the form

$$N_{t+1} = N_t \mathrm{Exp}\{r(1 - N_t/k)\}, \qquad (1)$$

where r is the intrinsic growth rate, and k is the carrying capacity for the population. Taking natural logarithms gives

$$\mathrm{Ln}(N_{t+1}/N_t) = r - (r/k)N_t$$

and a linear relationship of the form

$$\mathrm{Ln}(N_{t+1}/N_t) = A + BN_t \qquad (2)$$

relating the change ratio N_{t+1}/N_t to the density-dependent term BN_t. A generalization of this model assumes that the right-hand side of equation 1 also includes multiplicative effects of p variables $X_1, X_2, \ldots, X_p$, so that

$$N_{t+1} = N_t \mathrm{Exp}\{r(1 - N_t/k)\} \times \mathrm{Exp}(\alpha + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p), \qquad (3)$$

where α is a constant. Equation 2 then becomes

$$\mathrm{Ln}(N_{t+1}/N_t) = \beta_0 + BN_t + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p, \qquad (4)$$

where $\beta_0 = A + \alpha$ is a constant.

A further generalization of the Ricker model includes a term for delta smelt abundance two years before a given population year, allowing characterization of the sawtooth pattern in survival, so that it becomes

$$\mathrm{Ln}(N_{t+1}/N_t) = \beta_0 + BN_t + CN_{t-1} + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p, \qquad (5)$$

where C is another regression coefficient. This equation applies when the change in abundance from time t to time $t + 1$ depends to some extent on population abundance both at time t and at time $t - 1$.

Abundance Changes from Fall to Summer

For changes in abundance from fall to summer, the equivalent to equation 5 is

$$\mathrm{Ln}(JAb_{t+1}/FAb_t) = \beta_0 + BFAb_t + CFAb_{t-1} + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p, \quad (6)$$

where JAb_{t+1} is the July abundance in year $t + 1$, and FAb_t is the fall abundance in year t.

In practice, equation 6 will have a process error; the value of the dependent variable will be the value predicted by the right-hand side of the equation plus an error e_t. Also, observed values of $\mathrm{Ln}(JAb_{t+1})$ and $\mathrm{Ln}(PFAb_t)$ and FAb_t and FAb_{t-1} will have sampling errors. This raises the possibility of biases in the estimated values of coefficients on the right-hand side of the equation, if these are estimated by ordinary multiple linear regression.

For this reason, the Solow (1998) method for fitting population models with sampling errors in abundance estimates was initially considered for the estimation of equation 6 and the models below for summer-to-fall and fall-to-fall changes in delta smelt abundance. Essentially, this method uses the principle of simulation and extrapolation (SIMEX) to first simulate an increase in the level of sampling errors in abundance estimates, then it extrapolates to estimate outputs with no sampling errors in the abundance estimates. Use of the Solow method indicated that any biases in the estimated coefficients of X variables are quite small due to sampling errors in the delta smelt abundance indices. Therefore, it was concluded that ordinary multiple regression is appropriate for estimating equation 6 and the equations for summer-to-fall and fall-to-fall changes in the abundance of delta smelt.

Nevertheless, the extent of possible biases was investigated further by simulating data based on fitted versions of equation 6. First, the value of $\mathrm{Ln}(JAb_{t+1}/FAb_t)$ was set equal to the right-hand side of the estimated equation 6 plus a normally distributed process error with a mean of zero. Normally distributed sampling errors were then added to the values of Ln(JAb) and Ln(FAb) with means of zero and standard deviations obtained by bootstrap resampling of the FMWT and STN data as described by Manly (2010a, 2010b). The simulated data with process errors and sampling errors were then used to obtain multiple regression estimates of the parameters β_0, B, C, and β_1 to β_p of equation 6. The generation of simulated data was repeated 10,000 times. Mean values of the estimated parameters were compared with the values used to generate the data to establish whether sampling errors in abundance indices introduce important biases in the estimates. Standard deviations in the simulated parameter estimates were also compared with the standard errors obtained from the original regression to estimate equation 6 using the observed data to see if any biases are introduced by sampling errors in the abundance indices. This simulation confirmed that the estimates and standard errors obtained by ordinary regression have negligible biases due to sampling errors in the abundance indices, as was expected from the Solow (1998) analysis.

Abundance Changes from Summer to Fall

For summer-to-fall abundance changes, the equivalent to equation 5 becomes

$$\mathrm{Ln}(FAb_t/JAb_t) = \beta_0 + BJAb_t + CJAb_{t-1} + \beta_1X_1 + \beta_2X_2 + \cdots + \beta_pX_p.$$

In this case, it is not clear why the abundance of delta smelt in the fall of a given year should depend on the abundance in July in the previous year. There was no evidence of a sawtooth pattern in survival from summer to fall, the effect of which might be captured by this abundance measure, and initial analyses gave no evidence for this type of effect. Therefore, the equation was modified to

$$\mathrm{Ln}(FAb_t/JAb_t) = \beta_0 + BJAb_t + \beta_1X_1 + \beta_2X_2 + \cdots + \beta_pX_p. \quad (7)$$

As for abundance changes from fall to summer, there will be process errors in the results from equation 7 and sampling errors in the abundance indices; simulation was used to ensure that these errors do not introduce large biases in the estimated parameters for the equation when they are estimated by ordinary multiple regression. The simulations were carried out in a similar fashion to the simulations used with equation 6. As for the fall-to-summer analysis, this showed negligible bias in estimates and standard errors obtained using ordinary regression due to sampling errors in abundance indices.

Abundance Changes from Fall to Fall

For the fall-to-fall changes in the FMWT abundance index, the equivalent to equation 5 becomes

$$\mathrm{Ln}(FAb_{t+1}/FAb_t) = \beta_0 + BFAb_t + CFAb_{t-1} + \beta_1X_1 + \beta_2X_2 + \cdots + \beta_pX_p, \quad (8)$$

where the terms $B\ FAb_t$ and $C\ FAb_{t-1}$ imply that the change in delta smelt abundance from one fall to the next depends on the initial abundance and also the abundance in the fall of the previous year.

As for fall-to-summer and summer-to-fall changes, the use of equation 8 will be affected by process errors and sampling errors in the estimated abundance indices. However, the sampling errors in abundances are particularly likely to introduce biases in estimated parameters for equation 8 when using ordinary multiple regression because of the estimated value of FAb_t residing on both sides of the equation. Simulation was again used to ensure that these biases are relatively small using similar methods to those used with equations 6 and 7. This simulation showed negligible biases in the estimated constant term and in the coefficients of the X variables in equation 8 and negligible biases in the estimated standard errors of these parameters. The simulation indicated that the coefficient of FAb_t has a negligible bias, but the coefficient of FAb_{t-1} has a negative bias of about 10%; at the same time, the standard errors of these estimated density-dependent effects tend to be slightly higher than the estimates from ordinary regression. Using regression to estimate the effects of factors on delta smelt abundance seems to work well, but it should be noted that there may be small bias in estimated density-dependent effects.

This initial analysis used the factors in Table 1 and was carried out as follows. Multiple regression was used to estimate the corrected AICc, to account for the proportion of variation, and to estimate the significance and sign of the regression coefficients for all possible equations using all or some of the initial-analyses factors. From among those equations selected as exhibiting explanatory importance, equations with the lowest AICc and equations with AICc values that were within two units of the lowest AICc were selected (following Burnham and Anderson, 1998). In all cases, equations were restricted to those for which each environmental factor had a level of significance less than 0.10 and coefficients with signs consistent with their hypothesized effect. This analysis identified the abundance and environmental factors that produced the best regression equations for the initial analyses.

Adding Other Factors with Direct Effect to the Best Equations from the Initial Analysis

Using the methods described above, further analyses were carried out to see if the addition of other factors with presumed direct effect, or other ways of quantifying factors from among those not selected for initial analyses, showed important effects. These factors are shown in Table 2. Factors were added sequentially to the best regression equations to assess what portion of the variation in Ln(*Survival*) was explained by each factor. If any of these "secondary" direct factors proved to be important according to the above criteria, it reflected imperfect *a priori* understanding of the relationship between delta smelt and the specific environmental variables. In subsequent analyses, regression equations were used that contained factors with direct effect that can be identified as important from the combined results of these two analyses; these are herein referred to as the best regression equations based on factors that have direct effect.

It should be noted that this method—adding factors to regression equations—cannot completely eliminate problems arising from collinearity among factors; however, because the analysis is restricted to factors that have direct effects on delta smelt, the effects of collinearity are diminished relative to those that would have occurred had all factors that may have indirect effects on delta smelt been included.

Table 2 Factors with direct effect not selected as most important in initial analyses of fall-to-summer, summer-to-fall, and fall-to-fall survival

	July abundance	FMWT index	Previous FMWT index	Deviation of water temperature from 16°C Mar–May degree-days	Deviation of water temperature from 17°C Apr–July degree-days	Average *Eury-temora* April 30 (#/m^3)	Average *Eurytemora* + *Pseudodiapto-mus* Apr–June (#/m^3)	Minimum total calanoid copepod biomass Apr–June (mg C/m^3)	Average *Limnoithona* April–June (#/m^3)	Average *Limnoithona* July (#/m^3)	Average *Limnoithona* July–August (#/m^3)	Average *Eurytemora* + *Pseudodi-aptomus* Sep–Dec (#/m^3)	Average *Limnoithona* Sep–Dec (#/m^3)	Average *Eurytemora* + *Pseudodi-aptomus* Jan–Mar (#/m^3)	Average *Limnoithona* Jan–Mar (#/m^3)
Year	*Jab*	*Fab*	*PFAb*	*TpMM*	*TpAJ*	*EuApr*	*EPAJ1*	*CCAJ*	*LimAJ*	*LimJuly*	*LimJA*	*EPSD*	*LimSD*	*EPJM*	*LimJM*
1972	20,005	1,265	1,303	121	323	2,552	2,298	2,681	0	0	0	2,826	0	346	0
1973	11,185	1,145	1,265	232	354	2,914	1,997	2,220	0	0	0	2,042	0	767	0
1974	12,147		1,145	191	329	1,522	2,606	446	0	0	0	1,659	0	1,586	0
1975	8,786	697		274	376	734	998	711	0	0	0	666	0	184	0
1976	24,000	328	697	238	356	1,144	1,021	876	0	0	0	718	0	570	0
1977	25,965	480	328	201	300	1,071	1,022	872	0	0	0	680	0	1,193	0
1978	31,758	572	480	156	328	1,765	3,341	1,445	0	0	0	1,250	0	465	0
1979	5,484		572	207	369	893	1,140	1,494	0	0	0	907	0	513	0
1980	7,068	1,654		161	218	305	713	4,632	0	0	0	760	353	573	0
1981	6,300	374	1,654	233	415	845	1,006	2,610	5	15	824	588	1,084	516	5
1982	7,242	333	374	266	324	307	1,065	266	5	207	495	246	1,211	530	20
1983	1,390	132	333	232	377	11	594	138	0	184	757	20	2,037	25	0
1984	779	182	132	158	379	248	581	1,823	19	62	636	446	1,762	116	0
1985	387	110	182	192	337	175	327	3,496	106	1,271	2,008	494	1,490	193	0
1986	3,057	212	110	110	315	1,134	1,511	2,404	3	81	157	512	241	0	0
1987	2,743	280	212	264	326	2,015	1,184	2,466	114	633	1,056	228	998	449	0
1988	764	174	280	132	320	2,261	1,068	947	53	266	398	1,045	276	24	0
1989	647	366	174	151	266	632	2,909	1,621	48	192	134	2,255	128	117	0
1990	747	364	366	191	311	574	3,645	1,188	61	17	68	2,019	107	234	0
1991	2,486	689	364	205	315	470	1,513	162	6	27	44	1,480	91	47	0
1992	471	156	689	185	363	1,343	6,219	3,237	5	14	39	1,312	30	63	0
1993	5,763	1,078	156	153	320	776	4,074	1,783	0	218	751	1,047	5,466	125	28
1994	4,156	102	1,078	128	286	5,716	2,888	3,277	913	21,679	25,613	458	11,179	28	202
1995	2,490	899	102	168	309	560	2,046	985	894	9,070	14,901	648	4,344	52	54
1996	6,162	127	899	185	340	470	1,684	1,197	343	10,455	13,451	365	5,331	62	561
1997	2,362	303	127	192	359	650	1,924	1,494	1,917	20,440	21,622	466	17,468	66	185
1998	2,209	420	303	191	301	160	3,971	402	6,788	7,749	9,663	1,155	4,873	82	617
1999	7,478	864	420	246	323	1,740	1,710	987	1,378	17,586	18,700	540	30,340	101	1,231
2000	4,178	756	864	166	311	540	2,842	834	2,850	19,624	12,580	817	24,404	76	2,530
2001	2,897	603	756	240	433	520	1,838	1,045	4,165	37,284	33,272	222	19,672	46	1,765
2002	1,115	139	603	143	326	340	578	845	3,676	37,266	32,897	398	23,642	86	3,617
2003	1,329	210	139	167	404	80	1,411	1,996	2,137	43,190	21,778	363	18,635	94	4,197
2004	649	74	210	162	328	100	824	1,482	4,396	27,296	26,731	266	18,747	59	600
2005	393	27	74	151	361	220	726	1,233	815	19,423	26,595	295	14,849	49	395
2006	352	41	27	292	437	161	3,264	200	1,703	32,331	36,409	356	14,789	153	1,249
Fall-to-summer	▨		▨	▨	▨	▨	▨	▨	▨	▨				▨	▨
Summer-to-fall	▨	▨									▨	▨	▨		
Fall-to-fall	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

The last three rows are shaded to indicate the survival period to which each factor is relevant.

Comparing the Relative Contribution of Each Factor to the Explained Variation in Ln (Survival)

Using the best equations for fall-to-summer, summer-to-fall, and fall-to-fall survival, based on factors with direct effect, the relative contribution of each factor to the percentage of variation in Ln(*Survival*) was assessed.

Testing of Selected Factors with Potential Indirect Effect on Survival

Although the present approach to identifying the dominant environmental stressors acting on delta smelt is based on the effects hierarchy displayed in Figure 2, the analysis was extended to see if addition of selected indirect factors to equations that are based on factors with direct effects on delta smelt might further contribute to explaining variation in survival. This was done by focusing on the fall-to-fall model, both because that period of analysis represents a complete life cycle and because it limits the number of correlations that can be attempted and, therefore, limits the possibility of spurious correlations arising by chance. The selection criteria, described above for analysis of direct factors were used to test the importance of six indirect factors when added to the best fall-to-fall equation based on the direct factors. The number of indirect factors was restricted to avoid producing uninformative, multiple-factor equations by chance. Six indirect factors were selected from those identified as important to survival in other studies of pelagic fishes in the Delta (Kimmerer, 2002; Feyrer et al., 2007; Grimaldo et al., 2009; Mac Nally et al., 2010; Thomson et al., 2010). The selected factors are presence/absence of the Asian clam (*Corbula amurensis*), the value of X2 (the distance along the main channel from the Golden Gate Bridge to the 2 ppt isohaline, a measure of estuary salinity) averaged over the previous fall (“fall X2”), average Secchi depth in January–March, average ammonium concentration in the Chipps Island and Suisun Bay sub-regions (see Figure 2) in April–June, and Old and Middle Rivers (OMR) flow (that is, flows steered to the south Delta water export pumps) averaged over December–March and April–June. Values of these six indirect factors are shown in Table 3.

Testing Effects of Measures of Abiotic Habitat Volume on the Best Fall-to-Fall Regression Equation

The importance of a combination of conductivity, Secchi depth, and water temperature—deemed abiotic habitat in a previous study (Feyrer et al., 2007)—were analyzed both alone and weighted by prey density. Estimates were made of the volume of water with levels of conductivity, Secchi depth, and water temperature at which virtually all delta smelt occur. These ranges of suitable values were compared with actual values of conductivity, Secchi depth, and water temperature for each month and sub-region (see Figure 1) for the period 1972–2006. Based on estimated volumes of water in each sub-region, the volume of water with suitable abiotic (physical) characteristics available to delta smelt in each month was estimated. These estimated volumes alone were used, and they were weighted with the sum of densities of the prey species *Eurytemora* and *Pseudodiaptomus*. Seasonal average and minimum monthly values of these volumes and prey-weighted volumes were used in the best regression equations based on factors having direct effect on delta smelt abundance to establish whether volume or prey-weighted volume measures met criteria for inclusion in the best regression equation for fall-to-fall survival, either as an addition to or, in the case of prey density, replacement for factors with direct effect.

RESULTS

Statistical Analysis to Identify the Best Regression Equations Using Factors with Direct Effect

Initial analyses were carried out using the factors in Table 1—those environmental factors with direct effect on delta smelt—that were selected as most likely to be important in determining delta smelt abundances based on biological considerations. From among those factors, the most important affecting survival from fall to summer, summer to fall, and fall to fall were identified based on the above-described criteria. Results are shown in Table 4.

From the factors considered in these initial analyses, the most important to fall-to-summer survival (by virtue of their appearance in the best regression equation) are previous-previous fall abundance, previous fall abundance, minimum *Eurytemora* + *Pseudodiaptomus* in April–June, and proportional entrainment of adult and larval-juvenile delta smelt, with some indication that average water temperature in April–June is also important. For survival from summer to fall, the most important factors are July abundance and average *Eurytemora* + *Pseudodiaptomus* density in July–August. For survival from fall to fall, the most important factors are previous-previous fall abundance, previous fall abundance, and minimum *Eurytemora* + *Pseudodiaptomus* in April–June, with some indication that predation in April–June by predators other than striped bass (inland silverside, largemouth bass, crappie, and sunfish) is also important.

Among the factors with direct effects selected for the initial analysis, the number of days of spawning, July water temperature, *Eurytemora* + *Pseudodiaptomus* in July, Secchi depth (turbidity) in April–June, predation by striped bass, and delta smelt fecundity did not appear in the best regression equations for fall-to-summer survival. Maximum two-week average water temperature in July–September and predation did not appear in the best regression equations for summer-to-fall survival. The number of days of spawning, average water temperature in April–June, maximum two-week average water temperature in July-September, average *Eurytemora* + *Pseudodiaptomus* availability in July–August, Secchi depth (turbidity) in April–June, entrainment, predation by striped bass, and delta smelt fecundity did not appear in the best regression equations for fall-to-fall survival.

Table 3 Factors with indirect effect on delta smelt abundance, selected for analysis based on results of other studies

Year	Presence (1) or absence (0) of Asian clam	Previous Oct–Dec avg X2, km of 2 ppt line from Golden Gate	Previous Sept–Dec Secchi depth in sub-regions occupied by delta smelt habitat (cm)	Secchi depth Jan-Mar (cm)	Average ammonium in Chipps Island and Suisun Bay sub-regions, Apr–June (mg/L)	Average December–March flow in Old and Middle Rivers (cfs)	Average April–June flow in Old and Middle Rivers (cfs)
	AsClam	*PODX2*	*PFSec*	*JMSec*	*AJAm1*	*DMOMR*	*AJOMR*
1972	0	71	35	41	0.046	−2,260	−6,606
1973	0	71	38	26	0.034	953	−4,790
1974	0	66	37	35	0.024	−940	−4,955
1975	0	68	41	36	0.045	−2,093	−3,736
1976	0	70	42	51	0.047	−6,033	−5,491
1977	0	89	56	48	0.059	−4,054	−3,037
1978	0	92	58	17	0.027	−4,231	3,827
1979	0	77	40	34	0.027	−686	−5,487
1980	0	79	40	27	0.040	3,887	−1,142
1981	0	79	39	33	0.037	−4,678	−5,342
1982	0	75	42	31	0.035	−3,736	2,769
1983	0	63	42	25	0.040	9,124	14,610
1984	0	58	49	53	0.038	6,026	−5,623
1985	0	70	49	66	0.065	−5,023	−6,424
1986	0	88	61	45	0.039	−732	413
1987	1	78	41	50	0.047	−4,474	−5,471
1988	1	88	55	41	0.073	−8,006	−6,765
1989	1	90	51	44	0.058	−7,645	−7,198
1990	1	88	54	47	0.080	−9,086	−5,858
1991	1	89	62	58	0.083	−5,356	−4,752
1992	1	88	62	60	0.065	−5,561	−3,073
1993	1	87	64	29	0.034	−5,765	−2,304
1994	1	82	58	58	0.093	−4,742	−1,613
1995	1	86	60	31	0.033	−3,145	4,721
1996	1	75	55	37	0.036	−1,281	−2,848
1997	1	78	57	29	0.087	10,376	−3,972
1998	1	81	61	29	0.043	2,103	6,536
1999	1	69	45	51	0.060	−760	−2,155
2000	1	83	47	48	0.065	−5,282	−4,338
2001	1	85	53	45	0.089	−5,681	−2,919
2002	1	82	53	36	0.070	−7,731	−3,857
2003	1	84	50	36	0.055	−8,185	−5,374
2004	1	83	58	34	0.080	−8,080	−4,851
2005	1	82	65	48	0.055	−5,525	−1,055
2006	1	82	68	39	0.040	−3,214	10,026

Additional analyses were carried out using factors with direct effects that were not selected for the initial analyses. These were added to the best equations from the initial analyses to see whether they made a significant improvement. Results of this analysis, shown in Table 5, indicate that average *Eurytemora* + *Pseudodiaptomus* density in January–March should be added as an important factor that explains survival from fall to summer. Average *Eurytemora* + *Pseudodiaptomus* density in September–December should replace average *Eurytemora* + *Pseudodiaptomus* density in July–August as an important factor explaining survival from summer to fall and should be added to the regression equation for fall-to-fall survival.

Of the factors with direct effect on delta smelt population dynamics that was used for the additional analyses, the number of degree-days of deviation of water temperature from optimum in March–May or April–July; average *Eurytemora* density in late April; average *Eurytemora* + *Pseudodiaptomus* density in April–June; and average *Limnoithona* density in April–June, July, or January–March did not appear in the best regression equations for fall-to-summer survival. Average *Limnoithona* density in July–August and September–December did not appear in the best regression equation for summer-to-fall. None of these factors appeared in the best regression equations for fall-to-fall. There was some evidence that minimum calanoid copepod biomass in April–June was important for fall-to-summer survival but not survival from fall-to-fall.

The best regression equations based on factors with direct effects on delta smelt abundance were derived from the best regression equations from the initial analyses, as adjusted by results from the additional analyses using factors with direct effect that were not selected for the initial analyses.

Table 4 Summary of results of initial analyses of factors with direct effect that were selected as important based on the most reliable knowledge of delta smelt biology

			Initial analyses factors with direct effect on delta smelt survival																	
			Previous previous fall abundance	Previous fall abundance	July abundance	Spawning period, days of water temperature 11–20°C	Average water temperature Apr–Jun (°C)	Average water temperature July (°C)	Maximum two-week average water temperature Jul–Sep (°C)	Minimum *Eurytemora* + *Pseudodiaptomus* Apr–Jun (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* July (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Jul–Aug (#/m^3)	Secchi depth Apr–Jun (cm)	Adjusted Kimmerer proportional entrainment	Previous Sep–Dec striped bass adult abundance and Secchi depth	Previous Sep–Dec abundance other predators and Secchi depth	Apr–Jun abundance of other predators and Secchi depth	Sep–Dec striped bass adult abundance and Secchi depth	Sep–Dec abundance other predators and Secchi depth	Average length of delta smelt in December (mm)
Period	AICc value	Adjusted R^2	*PFAb* 1	*PFAb*	*Jab*	*SpDys*	*TpAJ*	*TpJul*	*TpJS*	*EPAJ*	*EPJul*	*EPJA*	*SecAJ*	*Entrain*	*PStBass*	*PPreds1*	*Preds2*	*StBass*	*Preds1*	*DSLth*
Fall-to-summer	**36.4**	**59%**	**0.001**	**0.000**	Not relevant to this period	–	–	–	Not relevant to this period	**0.000**	–	Not relevant to this period	–	**0.035**	–	–	–	Not relevant to this period		–
	36.9	**58%**	**0.004**	**0.000**		–	**0.048**	–		**0.000**	–		–	–	–	–	–			–
	37.0	62%	0.002	0.000		–	0.104	–		0.000	–		–	0.077	–	–	–			–
	37.4	61%	0.011	0.000		–	–	–		0.000	–		0.136	0.028	–	–	–			–
	37.7	60%	0.007	0.000		–	–	–		0.001	–		–	0.020	–	–	0.172			–
	38.1	**53%**	**0.002**	**0.000**		–	–	–		**0.000**	–		–	–	–	–	–			–
	38.1	60%	0.002	0.001		–	0.035	–		0.000	–		–	–	0.162	–	–			–
	38.5	59%	Not estimated			–	–	–		0.000	–		–	0.023	–	0.315	–			–
	38.8	58%				–	–	–		0.000	–		–	0.056	0.413	–	–			–
	39.1	54%				–	–	–		0.000	–		0.189	–	–	–	–			–
Summer-to-fall	**38.1**	**60%**	Not relevant to this period		**0.000**	Not relevant to this period			–	Not relevant to this period		**0.002**	Not relevant to this period					–	–	Not relevant to this period
	38.6	61%			0.000				–			0.003						–	0.153	
	39.2	63%			0.000				0.147			0.002						–	0.066	
	39.3	60%			0.000				–			0.002						0.239	–	
	40.0	60%			0.000				0.397			0.002						–	–	
	41.2	60%			Not estimated				0.371			0.002						0.229	–	
	41.2	60%							–			0.003						0.707	0.378	
	42.2	62%							0.169			0.002						0.969	0.172	
	46.9	49%							–			–						–	0.174	
	48.2	49%							0.322			–						–	0.109	
Fall-to-fall	30.8	59%	0.016	0.000	Not relevant to this period	–	–	Not relevant to this period	–	–	Not relevant to this period	–	–	–	Not relevant to this period		0.002	–	–	0.034
	30.9	**53%**	**0.001**	**0.000**		–	–		–	**0.009**		–	–	–			–	–	–	–
	31.7	**52%**	**0.014**	**0.000**		–	–		–	–		–	–	–			**0.015**	–	–	–
	31.8	56%	0.017	0.000		–	–		–	–		–	–	–			–	–	0.003	0.036
	31.9	56%	0.006	0.000		–	–		–	0.073		–	–	–			0.125	–	–	–
	32.1	56%	0.002	0.000		–	–		–	0.016		0.149	–	–			–	–	–	–
	32.3	61%	0.008	0.000		–	–		–	0.133		–	–	–			0.022	–	–	0.061
	32.6	54%	0.005	0.000		–	–		–	0.065		–	–	–			–	–	0.229	–
	32.8	**49%**	**0.014**	**0.000**		–	–		–	–		–	–	–			–	–	**0.029**	–
	32.9	54%	Not estimated			–	–		–	0.034		–	–	–			–	–	–	–

Entries in the last 18 columns are significance levels for regression coefficients from two-sided tests. Gray shading shows instances of AICc greater than two units above the best equation, a level of significance above 0.10, or, in the case of delta smelt length (a measure of fecundity), a negative coefficient in the regression equation, which is contrary to the hypothesized effect. Boldface indicates factors in equations meeting all selection criteria. Tick marks indicate that the factor was not among those used in the equation that was tested.

Table 5 Results of analyses of factors with direct effect, not selected for the initial analyses, added to the best regression equations for each period, from the initial analyses

			Direct factors not selected for initial analyses											
			Deviation of water temperature from 16° C Mar–May (degree-days)	Deviation of water temperature from 17° C Apr–July (degree-days)	Average *Eurytemora* April 30 (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Apr–June (#/m^3)	Minimum total calanoid copepod biomass Apr–June (mg C/m^3)	Average *Limnoithona* April–June (#/m^3)	Average *Limnoithona* July (#/m^3)	Average *Limnoithona* July–August (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Sep–Dec (#/m^3)	Average *Limnoithona* Sep–Dec (#/m^3)	Average *Eurytemora* + *Pseudodiaptomus* Jan–Mar (#/m^3)	Average *Limnoithona* Jan–Mar (#/m^3)
Period	AICc value	Adjusted R^2	*TpMM*	*TpAJ*	*EuApr*	*EPAJ1*	*CCAJ*	*LimAJ*	*LimJuly*	*LimJA*	*EPSD*	*LimSD*	*EPJM*	*LimJM*
Fall-to-summer	**38.9**	**70%**	–	–	–	–	–	–	–	Not relevant to this period			**0.003**	–
	39.5	**73%**	–	–	–	–	0.080	–	–				**0.010**	–
	40.1	72%	–	–	–	0.127	–	–	–				0.004	–
	40.8	75%	–	–	–	0.101	0.066	–	–				0.012	–
	41.4	70%	–	–	–	–	–	–	–				0.002	0.331
	42.0	69%	–	–	–	–	–	–	0.578				0.003	–
	42.1	69%	–	0.611	–	–	–	–	–				0.004	–
	42.3	69%	0.835	–	–	–	–	–	–				0.007	–
	42.3	69%	–	–	–	–	–	0.907	–				0.004	–
	42.3	69%	–	–	0.929	–	–	–	–				0.004	–
Summer-to-fall	**39.50**	**67%**	Not relevant to this period							–	**0.012**	–	Not relevant to this period	
	41.55	66%								0.406	0.026	–		
	42.23	66%								–	0.013	0.805		
	42.23	68%								0.095	0.023	0.139		
	44.58	61%								0.169	–	–		
	45.02	62%								0.056	–	0.167		
	46.89	59%								–	–	0.783		
Fall-to-fall	**32.2**	**62%**	–	–	–	–	–	–	Not relevant to this period	–	**0.020**	–	–	–
	33.4	64%	0.120	–	–	–	–	–		–	0.010	–	–	–
	33.8	63%	–	–	–	–	0.160	–		–	0.020	–	–	–
	34.0	63%	–	–	–	–	–	–		–	0.010	0.190	–	–
	34.5	62%	–	–	–	–	–	–		–	0.010	–	–	0.300
	34.6	62%	–	–	–	–	–	0.310		–	0.010	–	–	–
	34.8	61%	–	–	0.370	–	–	–		–	0.020	–	–	–
	35.2	60%	–	–	–	0.580	–	–		–	0.060	–	–	–
	35.3	66%	0.090	–	–	–	–	–		–	0.000	0.150	–	–
	35.3	56%	–	–	–	0.160	–	–		–	---	–	–	–

Entries in the last 12 columns are significance levels for regression coefficients from two-sided tests. Gray shading shows instances of AICc greater than two units above best equation or a level of significance above 0.10. Boldface indicates factors in equations meeting both selection criteria. Tick marks indicate that the factor was not among those used in the equation that was tested.

The best regression equation for the fall-to-summer survival of delta smelt is

$$\begin{aligned}\mathrm{Ln}(\mathit{Survival}) = 2.003 - 2.197{*}\mathit{PFAb} + 0.781{*}\mathit{PFAb1}\\ + 1.988{*}\mathit{EPAJ} - 3.826{*}\mathit{Entrain}\\ + 1.143{*}\mathit{EPJM},\end{aligned} \tag{9}$$

where survival is the ratio of July abundance, a measure of juvenile abundance in July, to the previous year's FMWT index, a measure of sub-adult abundance; *PFAb* is the FMWT index of the previous year divided by 1,000; *PFAb*1 is the FMWT index of the previous-previous year divided by 1,000; *EPAJ* is the minimum *Eurytemora* + *Pseudodiaptomus* density in April–June divided by 1,000; *Entrain* is the proportional entrainment of delta smelt, as a fraction; and *EPJM* is the average *Eurytemora* + *Pseudodiaptomus* density in January–March divided by 1,000.

The best regression equation found for summer-to-fall survival of delta smelt is

$$\mathrm{Ln}(\mathit{Survival}) = -2.176 - 1.003{*}\mathit{JAb} + 0.698{*}\mathit{EPSD}, \tag{10}$$

where *Survival* is the ratio of the FMWT index, a measure of sub-adult abundance, to July abundance, a measure of juvenile abundance in July, in the same year; *JAb* is July abundance, a measure of juvenile abundance in summer divided by 10,000; *PFAb*1 is the FMWT index of the previous-previous year divided by 1,000; and *EPSD* is the average *Eurytemora* + *Pseudodiaptomus* density in September–December divided by 1,000. Note that *EPSD*, the average *Eurytemora* + *Pseudodiaptomus* in September–December, replaced *EPJA*, the average *Eurytemora* + *Pseudodiaptomus* in July–August in the best regression equation from the initial analysis because *EPJA* was no longer significant in the equation for summer-to-fall survival when other factors with direct effects were considered.

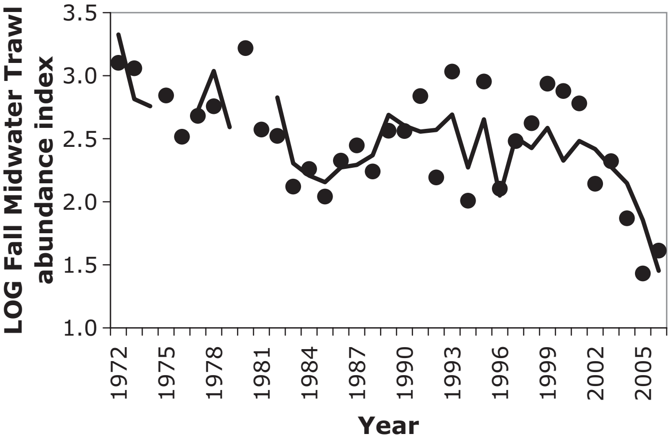


Figure 4 Actual and predicted values of the Fall Midwater Trawl index of abundance of sub-adult delta smelt. Circles are actual values. The line shows predicted values.

The best regression equation found for the fall-to-fall survival of delta smelt is

$$\begin{aligned}\mathrm{Ln}(\mathit{Survival}) = -0.246 - 2.781{*}\mathit{PFAb} + 1.048{*}\mathit{PFAb1}\\ + 0.997{*}\mathit{EPAJ} + 0.482{*}\mathit{EPSD},\end{aligned} \tag{11}$$

where survival is the ratio of the FMWT index, a measure of sub-adult abundance in the fall, to the previous year's FMWT index; *PFAb* is the FMWT index of the previous year divided by 1,000; *PFAb*1 is the FMWT index of the previous-previous year divided by 1,000; *EPAJ* is the minimum *Eurytemora* + *Pseudodiaptomus* density in April–June divided by 1,000; and *EPSD* is average *Eurytemora* + *Pseudodiaptomus* density in September–December divided by 1,000. Figure 4 shows actual abundance of sub-adult delta smelt (the FMWT index) and values predicted by equation 11.

These three equations each reflect a stock-recruitment relationship in which end-of-period abundance is proportional to

Table 6 Percentage of variation in Ln(*Survival*) explained and the contribution of each factor to that percentage

Period	% Ln(*Survival*)[a] variation explained	Important factors	Percent of variation explained[b]	Percent of variation explained[c]
Fall-to-summer	70.2%	*PFAb* = previous fall abundance/1,000	0.0%	38.3%
		*PFAb*1 = previous previous fall abundance/1,000	14.0%	7.7%
		EPAJ = minimum *Eury* + *Pseu*, Apr–Jun/1,000	39.0%	32.8%
		Entrain = proportional entrainment at export pumping plants, %/100	6.0%	9.1%
		EPJM = average *Eury* + *Pseu*, Jan–Mar/1,000	11.2%	11.2%
Summer-to-fall	67.6%	*JAb* = July abundance/10,000	47.0%	64.1%
		EPSD = average *Eury* + *Pseu*, Sep–Dec/1,000	20.6%	20.6%
Fall-to-fall	61.6%	*PFAb* = previous fall abundance/1,000	25.8%	61.6%
		*PFAb*1 = previous-previous fall abundance/1,000	15.2%	18.6%
		EPAJ = minimum *Eury* + *Pseu*, Apr–Jun/1,000	12.5%	8.0%
		EPSD = average *Eury* + *Pseu*, Sep–Dec/1,000	8.1%	8.1%

[a] For fall-to-summer and fall-to-fall analyses, "survival" means survival and reproduction.

[b] Percent of variation explained by the variables when added one at a time in order shown.

[c] Percent of variation explained when variable is added last into the equation.

beginning-of-period abundance. However, this proportional relationship is adjusted by a density-dependence term that causes abundance to be reduced when beginning-of-period abundance is high and is further adjusted by prey-density terms that cause delta smelt abundance to increase with availability of prey. In addition, summer abundance relative to previous fall abundance is reduced by entrainment. Both summer abundance and fall abundance, relative to previous fall abundance, are higher than expected when the abundance two-years previous is high.

Comparing the Relative Contribution of Each Factor to the Explained Variation in Ln(**Survival**)

Table 6 shows the percentage of variation in Ln(*Survival*) that is explained by each equation and the contribution of each factor to that percentage. The density-dependence terms, *PFAb* or *JAb*, have relatively important contributions to variation in Ln(*Survival*) for all three periods, and, while *PFAb* is not important as an individual factor for fall-to-summer survival, its inclusion renders important the contribution of other factors once it is added to the equation. Prey-density terms have a relatively important contribution to variation in Ln(*Survival*), as does the previous-previous fall abundance, which accounts for the sawtooth survival pattern. The contribution of entrainment to variation in Ln(*Survival*) is not as important as the contribution of prey densities to fall-to-summer survival. Entrainment was not chosen for inclusion in the fall-to-fall equation because it did not meet the criteria for inclusion.

Testing Selected Factors with Indirect Effects on Survival

There was no evidence that any of six environmental factors with indirect effects, which were identified in previous studies, further explained changes in fall-to-fall delta smelt survival beyond those accounted for by factors with direct effects shown in equations 9, 10, and 11. It is noted that this does not necessarily mean that these or other factors with indirect effects might not have important effects on one or more factors that have direct effects.

Testing Effects of Measures of "Abiotic Habitat" Volume on the Best Fall-to-Fall Regression Equation

This study attempted to add estimates of the volume of water within the suitable range of conductivity, Secchi depth, and water temperature to the best regression equation, as well as suitable volumes weighted with prey density (densities of *Eurytemora* + *Pseudodiaptomus*), the values of which are in the supplemental material to this article. When adding volume weighted by prey density, prey density terms were first removed from the best regression equations. None of those measures met the criteria above for inclusion in the best regression equation for fall-to-fall survival.

DISCUSSION

The analyses presented here focused on environmental factors that have plausible mechanisms for direct effects on the survival of delta smelt, leaving identification of factors having important, indirect effects—that is, the factors that have important effects on important factors with direct effects—for subsequent analyses. Effects on delta smelt survival were analyzed from fall (when delta smelt are sub-adult or pre-spawning adults) to summer (when delta smelt are next-generation juveniles) and from fall to fall (addressing the life cycle across a single generation). The regression equations resulting from this latter analysis serve as a life-cycle model. Effects on survival from summer to fall were also analyzed, thereby allowing insight into sources of mortality during this delta smelt growth stage. Analyses indicate that prey density is the most important environmental factor affecting abundance and population trends in delta smelt over the period 1972 through 2006 and also that changes in prey density appear to best explain the sharp drop in delta smelt abundance in this century. Entrainment of delta smelt at state and federal export pumping plants in the Sacramento-San Joaquin Delta appears to contribute to survival rates from fall to summer and, therefore, to juvenile abundance in summer, but entrainment was not a statistically significant factor in survival from fall to fall—that is, to inter-annual changes in the size of the delta smelt population. Density dependence was an important factor affecting survival from fall to summer, summer to fall, and fall to fall. Its inclusion in the best regression equations was also important in revealing the effects of prey density and entrainment on delta smelt abundance. This finding indicates that density dependence must be accounted for in analyses directed at identifying factors that are important to the abundance of delta smelt. Delta smelt survival from fall to summer and fall to fall showed a persistent sawtooth pattern over much of the period analyzed, and this effect was captured by inclusion of a term for delta smelt abundance in fall of the year prior to beginning-of-period abundance in fall-to-summer and fall-to-fall survival analyses. It is noted that the best regression equations may not apply for values of factors outside the range of values actually observed.

The regression equations can be interpreted as follows, using the fall-to-fall equation as an example. Delta smelt survival is the ratio *FMWT*/*PFAb*, where *PFAb* is the previous year's FMWT index. So, equation 11 can be written as

$$\frac{FAb}{PFAb} = e^{-0.246-(2.781\times10^{-3}PFAb)+(1.048\times10^{-3}PFAb1)+(0.997\times10^{-3}EPAJ)+(0.482\times10^{-3}EPSD)}$$

or

$$\begin{aligned} FAb &= 0.782 PFAb\, e^{-(2.781\times10^{-3}PFAb)} e^{(1.048\times10^{-3}PFAb1)} \\ &\quad e^{(0.997\times10^{-3}EPAJ)} e^{(0.482\times10^{-3}EPSD)}, \end{aligned}$$

where *PFAb1* is the previous-previous FMWT index, *EPAJ* is the minimum *Eurytemora* + *Pseudodiaptomus* density in April–June, and *EPSD* is the average *Eurytemora* + *Pseudodiaptomus* density in September–December. Assuming that the number of delta smelt eggs in spring is proportional to the previous abundance index derived from the FMWT, this equation can be interpreted as follows:

$$\begin{aligned}
&FMWT = [\text{eggs in spring} = 0.782PFAb]\\
&\times[\text{survival reduction related to density dependence}\\
&\text{from previous FMWT} = e^{-(2.781\times10^{-3}PFAb)}]\\
&\times[\text{survival increase from contribution of previous}-\\
&\text{previous abundance} = e^{(1.048\times10^{-3}PFAb1)}]\\
&\times[\text{survival increase from high minimum food density in}\\
&\text{April} - \text{June} = e^{(0.997\times10^{-3}EPAJ)}]\\
&\times[\text{survival increase from high September}-\\
&\text{December food density} = e^{(0.482\times10^{-3}EPSD)}],
\end{aligned}$$

with the negative constant term in equation 11 indicating that survival (that is, the combined effects of survival and reproduction) from fall to fall is less than one—typical of a species experiencing an extended decline in abundance.

There was some indication that average water temperature and calanoid copepod biomass (a general measure of prey density) in April–June were important contributors to survival of delta smelt from fall to summer. Furthermore, predation in April–June, representing the combined effects of water clarity and abundance of the predators, inland silversides, largemouth bass, crappie, and sunfish, was important to delta smelt survival from fall to fall. Numerous factors with direct effects on delta smelt survival did not have statistically significant effects on the subsequent abundance of delta smelt, including the length of the spawning period as determined by water temperature; turbidity as an individual factor affecting larval feeding success in spring as measured by Secchi depth; average or maximum water temperature in summer; deviations of water temperature from optimum values in spring; predation in summer and fall by predators other than striped bass and predation in all seasons by striped bass; delta smelt fecundity, as measured by the size (average length) of delta smelt in December; and the average density of *Limnoithona*, an invasive zooplankton that has become the most abundant potential prey species in the estuary.

The effects of factors that might have indirect effects on survival were analyzed using factors that were identified by previous studies as potentially important in determining delta smelt population trends. These factors are the average value of X2 (a measure of western Delta salinity) in the previous fall ("fall X2"), turbidity in winter as measured by Secchi depth, ammonium concentration in spring in downstream sub-regions of the Delta, and flows that feed the Delta's export pumps in winter and spring. None of these factors met the criteria for inclusion in the best regression equations based on factors with direct effects on delta smelt survival. It is noted that these factors and other factors with indirect effects could have important effects on factors that have direct effects on delta smelt, as suggested in Figure 2, but there was no attempt to identify those relationships here, although it is noted that Delta water flows to the export pumps were incorporated in estimates of proportional entrainment.

Results indicate that delta smelt survival was more sensitive to measures of the effects of individually specified factors with direct effects on fish than to measures of the volume of water within suitable ranges of conductivity, Secchi depth, and temperature (abiotic habitat, the term used in Feyrer et al. [2007]). Once the effects of individually specified factors were accounted for, with attention to their co-occurrence with delta smelt, the volume of water with conductivity, Secchi depth, and temperature in the suitable ranges for each of those three variables did not meet the criteria for inclusion in the best regression equation for fall-to-fall survival, nor did such volumes weighted with prey density, even after prey density terms were removed from the best regression equations for fall-to-fall survival based on factors with direct effect.

Some caution should be taken in interpreting results pertaining to entrainment of delta smelt at state and federal Delta export pumping plants. Estimates of delta smelt entrainment are based on those used in a previous modeling exercise (Kimmerer, 2008). Those methods of estimating proportional entrainment provide a more rational conceptual framework than other methods that have been used (see Grimaldo et al. [2009], for example), because Kimmerer estimated entrainment relative to population size, attempted to estimate the standing crop of delta smelt at the time of entrainment (rather than using abundance estimates derived from samples collected several months earlier), and attempted to overcome uncertainties associated with the fact that larval delta smelt are not actually incorporated in fish salvage data from pumping plants. However, Kimmerer's model estimates are based on a number of assumptions. Of 18 assumptions underlying estimates, Miller (2011) concluded that at least 12 of these assumptions introduced bias, and 11 of those 12 introduced an upward bias in the putative effects of export pumps on delta smelt mortality. This study attempted to correct Kimmerer's estimates to account for that bias, but could do so for just three of the 12 assumptions. The corrections reduced Kimmerer's annual estimates of proportional entrainment by about half, and Miller (2011) concluded that further reductions would be appropriate if other assumptions could be quantified. Furthermore, Kimmerer did not estimate proportional entrainment prior to 1995; however, his estimates were extended back to 1972 using correlations with X2, flow, and Secchi depth measures for those years (as described in supplemental material) and Kimmerer's 1995–2006 estimates and those hind-cast estimates were adjusted to account for bias that could be quantified. Therefore, the role of entrainment as a contributing factor to population trends from fall to summer that are largely determined by density-dependence factors and availability of the preferred foods used by delta smelt is uncertain and likely (still) biased upward.

Ascertaining the importance of prey density in determining population trends in delta smelt in part resulted from attentive specification of factor values. The densities of the two prey species, *Eurytemora* and *Pseudodiaptomus*, were used, summed as the measure of prey density, reflecting findings in several previous studies that explicitly reference consumption of these zooplankton by delta smelt (see supplemental material). There was also an attempt to account for the location of delta smelt when estimating prey density, because prey densities in subregions that are not occupied by delta smelt cannot be relevant to delta smelt survival. Moreover, there was an attempt to measure the seasonal low point in prey density in the spring of recent years, when the favored prey *Eurytemora* rises from near zero in late winter and then declines to near zero in May or June, at approximately the same time that other suitable prey species *Pseudodiaptomus* increases in numbers from essentially zero and persists at greater numbers until the following winter (see supplemental material).

It is noted that the importance of the factor, minimum *Eurytemora* plus *Pseudodiaptomus* in April–June, which measures the low point in the food availability for young delta smelt, provides a plausible mechanism for Bennett's observation that almost no early-hatch larvae of delta smelt have survived until later life stages in recent years (Bennett, 2005; USFWS 2009). That spring low point appeared in the mid 1980s; since then, if larval delta smelt hatch prior to the occurrence of this low point in densities of the two zooplankton species, larval survival might exhibit a pattern of low returns.

This study's findings are consistent with recent assertions that contaminant-mediated prey availability shows dominant effects on patterns of the abundance of delta smelt and several other fish in the Delta (Glibert, 2010), although the analysis did not attempt to identify the causes of the substantial changes in prey densities in recent years. Furthermore, the analyses address an observation by Feyrer et al. (2007), who concluded that their analyses of just several physical factors as determinants of delta smelt abundance would have been improved by consideration of other factors, particularly prey density. Without carrying out analyses that accounted for density dependence and included such essential variables as prey availability and predation on delta smelt, they concluded that the average value of X2 in the previous fall was the essential causative agent of subsequent summer juvenile abundance (see Feyrer et al., 2007, and USFWS, 2009). The analyses of this study considered the effects of density dependence and prey density, as well as numerous other factors in addition to average X2 position in the previous fall, and once the effects of prey density were accounted for, no evidence was found of effects of average X2 value in the previous fall on delta smelt population dynamics. Thomson et al. (2009) found that water clarity, position of X2 in winter–spring, and the volume of water exports were important to long-term abundance of delta smelt and other fish but could not explain the recent decline in abundance of delta smelt to record low levels. Mac Nally et al. (2010) found that the position of X2 in the spring in the estuary and increased water clarity were important to delta smelt abundance. Differences between the present findings and those of Thomson et al. and Mac Nally et al. are attributed to this study's focus on those factors that specifically should have direct effects on abundance and to a more precise quantification of environmental factors—including explicitly considering spatial and temporal aspects of prey availability, integrating the specific locations of different life stages of delta smelt in average values of variables, and expressing prey availabilities in terms of densities of zooplankton species known to be preferred by delta smelt. Grimaldo et al. (2009) attributed demographic trend effects to entrainment of delta smelt at the export pumping plants (measured as the number of fish salvaged there) and to export volumes by virtue of the relationship of those flows to rates of fish salvage. While some effect of entrainment (which incorporated effects of export flows) was found on delta smelt survival from fall to summer, entrainment of fish at the export pumps did not exhibit a significant relationship with the population dynamics of the fish over its entire life cycle. Assessment of the relative importance of entrainment in determining delta smelt survival, as well as that of several other factors, during various periods in the past and for various future management actions, awaits further analysis.

It is believed that this study's analysis is the first to combine careful quantification of variables, based on publicly available agency data, with wildlife agency-derived conceptual models transformed to represent the hierarchical manner in which environmental factors interact to affect abundance and survival of delta smelt. The benefits of this approach included a reduction in the occurrence of correlations that might arise by chance, due to the inclusion of many variables relative to the number of years of data, and identification of environmental factors on which future studies can focus in order to elucidate the ecological mechanisms as a basis for management actions, thereby providing a sound basis for agency determinations and policy decisions.

Nonetheless, limitations in the presented analyses are acknowledged. Time-series index values of delta smelt abundance are based on data from surveys that were not explicitly designed to sample that fish species, and more recently initiated surveys that are designed to sample delta smelt more efficiently suffer from lack of longer time series and from the challenges of sampling for a species that now is scarce. In addition there are no data on disease, a factor with a potentially important, direct effect on delta smelt abundance and, with the exception of ammonia, almost no data on contaminants that act directly on delta smelt. Some comfort can be taken in findings that 60 to 70% of the variation in delta smelt survival can be explained by factors included in the analyses, but that finding cannot rule out the importance of disease and contaminants. Further limitations to clearer resolution of the causative factors in the decline of delta smelt include the infrequency with which some environmental factors are being measured. For example, zooplankton samples were taken once or twice per month beginning in 1972 and in the separate, 20-mm survey (CDFG, http://www.dfg.ca.gov/delta/projects.asp?ProjectID=20mm), every two weeks in spring beginning in 1995. Hourly water temperature data are not available prior to the mid 1990s, requiring reliance on correlations with air temperature, which, fortunately, is highly related to water temperature. These limitations are offset somewhat by the large variations in delta smelt abundance from year to year, and the 95% decline in abundance from 1999 to 2006, suggesting that the signals of environmental effects that have been identified are not subtle and that the current lack of desired levels of precision in and frequency of sampling for underlying data for environmental variables can be tolerated.

The present results, indicating that the importance of prey density as measured by the sum of *Eurytemora* + *Pseudodiaptomus* densities, are supported by observed recent sharp declines in the abundance of two other pelagic fish that share at least partial reliance on the same prey—longfin smelt and young striped bass (Armor et al., 2005; Baxter et al., 2008). Slater (2008) concluded from diet studies that young longfin smelt rely heavily on *Eurytemora* in spring, and Moyle (2002) reported that striped bass larvae frequently feed on *Eurytemora*.

The results presented here suggest several areas for further study. Identification of the environmental factors that determine prey density leads the list. There is a need to elucidate and quantify that part of the effects hierarchy related to prey density. Strong inference can be drawn from this study—if the densities of the favored prey species consumed by delta smelt were to increase substantially, delta smelt abundance should increase. Under that circumstance, whatever the effects of entrainment from fall to summer, those effects would become less important because of density dependence. It would appear, therefore, that the key to recovery of delta smelt to levels of abundance that would reduce conservation concern is increased prey density.

Another area for further study relates to the cause of density dependence. Bennett (2005) suggested that density dependence was important based on his observation that, when comparing two poor stock-recruitment relationships—one with and one without density dependence—the one with density dependence appeared to be a better predictor. The present analysis, incorporating effects of many other factors, provides more convincing evidence that density-dependence effects act on delta smelt from fall to summer, summer to fall, and fall to fall, and it has demonstrated effects at low levels of abundance and reveals effects of other factors. Density dependence from summer to fall, as represented by terms for previous abundance in regression equations for survival, is one reason, along with variation in prey density, why entrainment, while contributing to the best regression equation that describes delta smelt survival from fall to summer, did not meet the criteria for inclusion in the best regression equation that explains survival from fall to fall, that is, from one generation to the next. The cause of density dependence in delta smelt deserves further study. This analysis suggests that it arises from some factor that was not considered here, or from a factor that was considered but was not specified adequately, such that its effects would be revealed. Delta smelt spawn most successfully on cobble or clean sand (J. Lindberg, University of California at Davis, personal communication), and meager sediment data (see http://www.water.ca.gov/bdma/meta/benthic.cfm) suggest that few stations in areas occupied by delta smelt show evidence of cobble or clean sand substrate. Nor was the possibility considered that the contemporary relatively small numbers of fish have led to stochastic demographic phenomena, such as difficulty in finding mates or some other manifestation of Allee effects (Allee et al., 1949). Identifying the cause of density dependence on delta smelt could provide a basis for actions to lessen its effects.

Further study is recommended of the inter-year sawtooth pattern in the abundance of delta smelt. This, too, is an important factor in these regression equations. Failure to identify an environmental factor or factors causing this pattern suggests that its cause may be inherent in the reproductive biology of delta smelt. Approximately 5% of delta smelt live for two years and spawn in the second year, producing a large number of eggs because of their larger size (Bennett, 2005). The existence of distinct demographic units of delta smelt that spawn every two years could explain the sawtooth pattern, but the absence of larger fish in the FMWT and STN argues against this possible explanation.

Predation also deserves more study. The identification of predation as a factor of some importance must be confirmed by more careful studies to overcome the general conclusion drawn by Moyle (2002) that there was little evidence of important predation effects, even when delta smelt were abundant relative to other prey fish many years ago. It is possible that the arrival and proliferation of invasive predators alters Moyle's conclusion.

There was some indication that water temperature is important, but water temperature, depending almost entirely on air temperature, cannot be controlled. However, the increasing trend in water temperature could affect various factors that are important to the abundance of delta smelt, including prey density, and such effects deserve study.

Results also indicate that the development of an effects hierarchy can provide an important framework on which to base analyses designed to assess the relative importance of multiple factors affecting the population dynamics of at-risk species. The findings presented here suggest that multiple environmental factors were responsible for the decline in abundance of delta smelt to record low levels, but that multiplicity is vertical with respect to the effects hierarchy, primarily extending down the hierarchy below prey density rather than horizontally across the hierarchy, as others have surmised (Baxter et al., 2010).

Furthermore, in the case of delta smelt, not only does an effects hierarchy suggest the use of simple linear regression models, but the low sampling errors in abundance relative to process errors indicates that this simple and transparent method of analysis is an appropriate method for identifying environmental factors with direct effects. Therefore, at least for delta smelt and perhaps for other fish for which sampling errors in abundance are relatively low, simple linear regression, as an alternative to more complex life-cycle models, can produce informative results.

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