

Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Individual-Based Modeling of Delta Smelt Population Dynamics in the Upper San Francisco Estuary: II. Alternative Baselines and Good versus Bad Years

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Published online: 01 Aug 2013.

To cite this article: Kenneth A. Rose, Wim J. Kimmerer, Karen P. Edwards & William A. Bennett (2013) Individual-Based Modeling of Delta Smelt Population Dynamics in the Upper San Francisco Estuary: II. Alternative Baselines and Good versus Bad Years, Transactions of the American Fisheries Society, 142:5, 1260-1272, DOI: [10.1080/00028487.2013.799519](https://doi.org/10.1080/00028487.2013.799519)

To link to this article: <http://dx.doi.org/10.1080/00028487.2013.799519>

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ARTICLE

Individual-Based Modeling of Delta Smelt Population Dynamics in the Upper San Francisco Estuary: II. Alternative Baselines and Good versus Bad Years

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Abstract

We used a previously described individual-based population model to further explore the population dynamics of Delta Smelt *Hypomesus transpacificus* in the upper San Francisco Estuary. We formulated four alternative baseline configurations of the model and used a factorial design to systematically isolate the effects of factors that determined a good versus bad year. The alternative baseline conditions were obtained by substituting different assumptions about growth, maturity, and mortality into the original baseline configuration. In the simulation experiment, we varied five factors by setting each value to its 1998 (best year) or 2001 (worst year) value: salinity, temperature, zooplankton densities, hydrodynamics, and eggs per age-1 individual at spawning. Although some of the alternative baselines resulted in lower January abundances, estimated finite population growth rates were very similar for all versions. The simulation experiment showed that juvenile growth in the winter prior to spawning (i.e., eggs per age-1 individual) was the most important single factor in making 2001 a bad year, although no single factor alone was sufficient to fully account for the poor conditions in 2001 relative to 1998. Temperature played an important secondary role, and hydrodynamics played a more minor role. The results of the simulation experiment were robust, as similar results were obtained under the four alternative baselines. We compare our results with previous modeling and statistical analyses of the long-term monitoring data; we also discuss some implications of our results for Delta Smelt management and suggest future directions for analyses.

The Delta Smelt *Hypomesus transpacificus* resides only in the San Francisco Estuary and is listed as threatened under the U.S. Endangered Species Act and as endangered under the California Endangered Species Act. Abundance of Delta Smelt

started to decline in the 1980s, and a sharp decrease starting in 2001 led to a series of management actions that were intended to benefit the species but that also involved reducing the water available to be diverted for irrigation and water supply (NRC

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Received November 9, 2012; accepted April 19, 2013

2012). The State Water Project and the Central Valley Project have exported an average of 30% of the freshwater flowing into the estuary during 1960–2000, with the percentage generally increasing through time and exceeding 60% in some years and seasons (Kimmerer 2004). The State Water Project facility provides drinking water for over 23 million Californians; combined, the two diversion facilities fuel an estimated $\$25 \times 10^9$ annual agricultural economy (Grimaldo et al. 2009).

A suite of factors has been identified as important in contributing to the decline of Delta Smelt. These factors include entrainment by water diversion facilities (Kimmerer 2008, 2011; Miller 2011), contaminant effects (Kuivila and Moon 2004; Cannon et al. 2009; Brooks et al. 2012), shifts in the zooplankton (prey) community (Nobriga 2002; Feyrer et al. 2003; Winder and Jassby 2011), and changes in physical habitat (Feyrer et al. 2007; Nobriga et al. 2008; Kimmerer et al. 2009). The role of these factors in contributing to the Delta Smelt's decline has been examined by using statistical analysis of long-term field data (Mac Nally et al. 2010; Thomson et al. 2010; Miller et al. 2012) and population dynamics modeling (Maunder and Deriso 2011). These analyses have led to what many consider to be contradictory conclusions about the relative importance of various factors in affecting Delta Smelt population dynamics (NRC 2010; Kimmerer 2011; Miller 2011).

Determining the factors that affect Delta Smelt population dynamics is critical for formulating effective remediation actions. Remediation actions under the federal Endangered Species Act are termed "reasonable and prudent alternatives" (RPAs), and specific actions were proposed as part of the recent biological opinion for Delta Smelt (USFWS 2008) and were subsequently argued in court (NRC 2010). One RPA restricts water diversions during the winter to limit losses of Delta Smelt at the diversion facilities (Grimaldo et al. 2009; Kimmerer 2011). Another controversial RPA was designed to protect fall habitat by using reservoir releases to maintain the estuarine salinity field in certain spatial regions (NRC 2010). The high economic costs of these various management actions, coupled with uncertainty about how they may affect Delta Smelt population dynamics, have led to controversy (NRC 2012).

In a companion paper (Rose et al. 2013, this issue), we described an individual-based population model of Delta Smelt and used a historical baseline simulation for 1995–2005 to identify the factors leading to good and bad years for Delta Smelt. In the present paper, we extend the analysis of Rose et al. (2013) by formulating alternative baseline configurations of the model and by using a factorial design to systematically isolate the effects of factors that determined a good year versus a bad year. We formulated four alternative baseline conditions by substituting different assumptions about growth, maturity, and mortality into the baseline configuration. The four alternative baselines were (1) fixed larval growth instead of food-dependent larval growth, (2) size-dependent mortality instead of stage-dependent mortality, (3) density-dependent mortality instead of density-independent mortality, and (4) length-dependent maturity rather than a length

threshold for maturity. Each of these assumptions was important to baseline dynamics, and each was uncertain. Our earlier identification of good and bad years was from the historical simulation, and the effects of some factors can be confounded by the autocorrelation that is inherent in a historical simulation. Here, we follow up with a designed simulation experiment in which we systematically varied the factors that are potentially important in determining good and bad years, and we further show the robustness of the simulation experiment results by repeating the experiment for each of the four alternative baseline conditions. We demonstrate that the results obtained under the original baseline conditions were similar under the four alternative baseline conditions (i.e., robust), and we further refine the role of various factors in determining good and bad years.

MODEL DESCRIPTION

Overview

The individual-based model followed the reproduction, growth, mortality, and movement of super-individuals over their entire life cycle (from eggs to age 3) on the same spatial grid as the Delta Simulation Model (DSM2) hydrodynamics model that was developed by and is widely used by the California Department of Water Resources (baydeltaoffice.water.ca.gov/modeling/deltamodeling/models/dsm2/dsm2.cfm). A model year was defined as a water year: October 1 of the previous year to September 30 (e.g., model year 2001 extends from October 1, 2000, to September 30, 2001). The model is described in detail by Rose et al. (2013) and is briefly summarized here.

The spatial grid was one-dimensional, with 517 channels and 5 reservoirs (Figure 1 in Rose et al. 2013). The DSM2 hydrodynamics model provided hourly values of water velocities and flows into and out of channels and reservoirs, which were used as inputs to a particle tracking model (PTM) that was embedded in the Delta Smelt individual-based model. A second grid of 11 coarser boxes was overlaid onto the channel grid, and values of daily temperature, salinity, and biomass densities of six zooplankton groups in each box were used to assign values to each channel.

For each super-individual, we tracked a suite of traits, including life stage, growth rate, weight, length, age, diet, location on the grid, maturity status, fecundity, and worth. Worth was the number of identical population individuals represented by the super-individual. Rather than following every individual and removing them upon death, we followed a fixed number of super-individuals and decreased their worth in each time step to account for mortality (Scheffer et al. 1995). All computations were scaled from the super-individuals to the population by multiplying by the worth of the super-individuals. Individuals were assigned to five life stages: egg, yolk sac larva, postlarva, juvenile, and adult. Advancement to the next life stage (development) was based on (1) temperature for egg to yolk sac larva

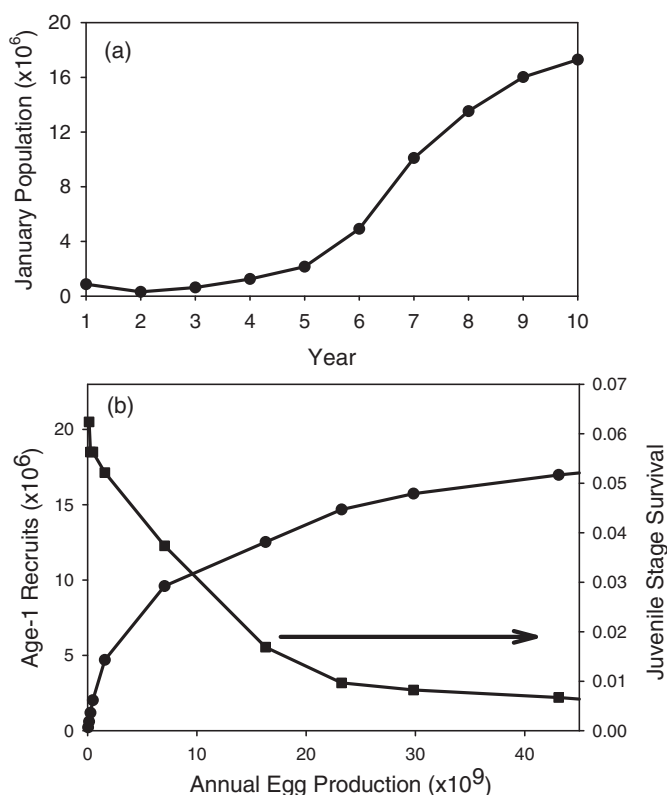


FIGURE 1. Simulated adult Delta Smelt abundance over time and juvenile survival from each year in a 15-year model run with artificially increasing egg production every year and density-dependent juvenile mortality: (a) adult abundance in January of each year and (b) age-1 recruits (circles, primary y-axis) and juvenile-stage survival (squares, secondary y-axis) versus annual egg production for each year.

to larva; (2) length for larva to postlarva to juvenile; and (3) date (January 1) for juvenile to age 1 and for age 1 to age 2.

Growth increments at each time step were determined from body weight, temperature, and the biomass densities of the six zooplankton groups (adult *Limnithona* spp.; calanoid copepods; other calanoid adults; adult *Eurytemora*; adult *Acanthocyclops vernalis*; and adult *Pseudodiaptomus*). Length was then increased if fish weight had increased sufficiently. Mortality was a stage-specific, fixed rate plus starvation (if the weight of an individual fell below 50% of the weight expected for its length) and entrainment by the two water diversion facilities. Movement on the spatial grid was by physical transport using a PTM for yolk sac larvae, larvae, and postlarvae; movement was behavioral (in response to salinity) for juveniles and adults. Development, reproduction, growth, and mortality were updated daily, whereas movement of eggs and all larval stages was updated hourly and movement of juveniles and adults was updated every 12 h.

Model Outputs

In our companion paper (Rose et al. 2013), we presented a detailed comparison between individual-based model outputs

and data. We focus here on model predictions involving a small subset of those output variables. The major outputs presented for all simulations in this paper are the annual adult abundance in January and the annual finite population growth rate (λ). Annual adult abundance in January was computed as the summed worth of all individuals on January 1, including the young of the year that just became age 1 and the age-1 fish that just became age 2; it did not include age-2 fish that were just removed as they became age 3. We used the individual-based model output to estimate a Leslie age-based matrix model for each year to summarize the complicated individual-based model results with a single variable, λ . The value of λ was based on the detailed dynamics of the individual-based model but allowed for easier comparison among years. A 2×2 matrix model was estimated each year by computing the average maturity, fecundity, and age-specific survival rates and by using eigenvalue analysis to determine λ (see Supplement F in the online version of Rose et al. 2013).

Additional model outputs were used selectively to configure or confirm the alternative baselines and to provide some explanation for how the factors in the simulation experiment (described below) affected Delta Smelt. These outputs were defined and their calculations were described by Rose et al. (2013): stage-specific survival rates, recruitment (number of entering age-1 individuals on January 1), fraction of entering age-1 fish that were mature at the time of spawning, number of eggs per entering age-1 individual, percentage of individuals in and seaward of the Sacramento River–San Joaquin River confluence box at various times during the year (together with monthly average Sacramento–San Joaquin River Delta [hereafter, “Delta”] outflows), average daily fraction of larvae that were entrained in water diversions during a year, and annual fraction of adults that were entrained. Finally, we used a Lagrangian approach and reported the averaged values of p (proportion of maximum consumption) and temperature experienced by individuals for selected time periods in the simulations.

MODEL SIMULATIONS

Alternative Baselines

We configured four additional versions of the baseline model: fixed larval growth, size-dependent mortality, density-dependent mortality, and length-dependent maturity. We used the historical baseline simulation of 1995–2005 to help configure and calibrate the alternative baselines.

Fixed larval growth.—Model predictions of Delta Smelt abundance in the historical simulation were sensitive to larval growth rates, and we were uncertain about our formulation of larval feeding and bioenergetics. Use of a fixed duration for the larval stage eliminated variation in larval growth as a factor in year-to-year differences. Larval growth was fixed by specifying the larval duration in days rather than letting the transition from larva to juvenile be determined by length. We used the average

larval duration over years from the baseline simulation (26 d) for all simulations with the fixed larval growth rate.

Size-dependent mortality.—Mortality in the original baseline version was constant within each stage but decreased with successive stages, so penalties in survival for slow growth occurred only through the delay in transition from larvae to postlarvae and from postlarvae to juveniles. Making mortality length dependent reflected the idea that vulnerability to predation mortality decreases with increasing size (Sogard 1997; Bailey and Duffy-Anderson 2010; Gislason et al. 2010), so that faster growth would increase cumulative survival regardless of how stage transitions were triggered. We assumed that mortality rate was a function of length (M_L ; d^{-1}) for larvae through adults; we then fit the function to the constant stage-specific mortality rates from the baseline simulation, associating the rate with the midpoint length of each stage:

$$M_L = -0.034 + 0.165 \cdot L^{-0.322}. \quad (1)$$

We re-ran the 1995–2005 simulation and compared averaged annual stage-specific fractional survival rates between the baseline and the alternative with size-dependent mortality (Table 1) to confirm that this alternative produced mortality rates that were generally similar to those from the original baseline. Survival from yolk sac larva through age 2 was similar (4.4×10^{-5} in the baseline versus 3.5×10^{-5} under size-dependent mortality); juvenile survival increased (0.054 in the baseline; 0.073 under size-dependent mortality), and age-1 survival was approximately halved (0.092 in the baseline; 0.044 under size-dependent mortality).

Density-dependent mortality.—The original baseline version was set up as density independent because the recent Delta Smelt population is at such a low level that density-dependent effects seem unlikely. To allow for subsequent simulations at higher Delta Smelt densities, we included an alternative baseline with density-dependent mortality. The juvenile stage is the likely stage for density dependence based on general theory (Rothschild 1986; Cowan et al. 2000). Bennett (2005) and Maunder

and Deriso (2011) found evidence for a density-dependent relationship between summer and fall Delta Smelt indices, and this relationship occurs in our simulation for the juvenile life stage. We assumed a multiplier of the juvenile daily mortality rate based on the normalized density of juveniles in each box on each day,

$$M' = M \cdot e^{3.0 \left(\frac{D_t}{0.005} \right)}, \quad (2)$$

where D_t is the density of juveniles (number/ m^3) and 0.005 is an average juvenile density (number/ m^3).

We calibrated the value of 3.0 in equation (2) to obtain realistic maximum January adult abundances of about 20–25 million; the highest abundance estimate from the spring Kodiak trawl and fall midwater trawl (MWT) data during 1968–2006 was 24.3 million in 1981. We ran the model by repeating 1995 conditions from the historical simulation (high Delta Smelt survival) but with artificially increased egg production each year to generate a spawner–recruit curve under ever-increasing January adult abundances. We adjusted the multiplier in the exponent within equation (2) (final value = 3.0) until it generated a leveling off at high egg production that occurred roughly with about 20–25 million adults in January (Figure 1a). Juvenile-stage survival decreased with increasing population abundance from 0.06 to less than 0.01, resulting in a leveling off of age-1 recruits at about 20 million (Figure 1b). Abundance of age-1 recruits was similar to January adult abundance because most of the adults were age-1 individuals.

Length-dependent maturity.—The simple maturity rule (fish > 60 mm TL are mature) in the original baseline was substituted with a smoother, length-dependent maturity relationship (Figure 2). Model results were potentially sensitive to small

TABLE 1. Stage-specific durations (d) and survival (fraction) of Delta Smelt averaged over the 1995–2005 simulations for the original baseline and the alternative baseline that used size-dependent mortality.

Stage	Duration (d)		Survival (fraction)	
	Baseline	Size dependent	Baseline	Size dependent
Eggs	10.5	10.4	0.56	0.57
Yolk sac larvae	4.88	4.87	0.82	0.71
Larvae	26.3	26.0	0.23	0.25
Postlarvae	21.7	22.2	0.49	0.50
Juveniles	186	187	0.054	0.073
Age 1	365	365	0.092	0.044
Age 2	365	365	0.088	0.11

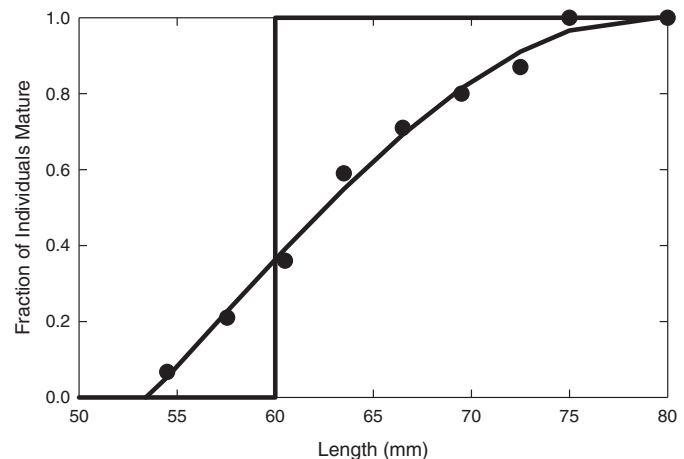


FIGURE 2. Fraction of Delta Smelt individuals that were mature as function of length for the baseline (60-mm cutoff) and the length-dependent maturity alternative. The points (circles) represent the fractions mature by length, estimated by assigning females (from the spring Kodiak trawl survey for 2002–2010) to 3-mm length bins and using ripe or spent individuals (condition codes 4–6) as mature.

changes in length of young of the year causing large changes in the mature fraction of individuals because typical lengths varied around 60 mm when maturity was determined. The relationship between fraction mature and fish length was fitted by allocating females that were sampled in the spring Kodiak trawl survey during 2002–2010 into 3-mm length bins and using ripe or spent individuals (codes 4–6) as mature. This resulted in an asymmetric relationship of fraction mature at around 60 mm (Figure 2). Use of other definitions for maturity resulted in relationships that were more symmetric at around 55–65 mm. We used the asymmetric relationship because it was justifiable based on the data and it provided a better test of model robustness.

Simulations under alternative baselines.—The 1995–2005 historical simulation with the original baseline (analyzed by Rose et al. 2013) was repeated with each of the four alternative baselines. We compared simulated January adult abundances and λ values among the original baseline and the four alternative versions. Results from a single simulation are presented. The individual-based model has stochastic aspects in assigning zooplankton biomass densities to channels and spawning temperatures to females, the y and z movements of the PTM, and the random component of behavioral movement. Because of the summing and averaging over many individuals and over time, population-level outputs (e.g., mean length at age, spatial distributions, and λ) varied by less than 5%—and often by less than 2%—among replicate simulations.

Good versus Bad Years

In this paper, we further explore the factors affecting the good year (1998) and bad year (2001) for Delta Smelt recruitment as identified in the analysis of the historical simulation (Rose et al. 2013). We performed a factorial simulation experiment to identify the conditions that caused the differences between water year 1998, which had the largest λ (2.45) within the baseline historical simulation, and water year 2001, which had the smallest λ (0.33) in the simulation. We varied five factors: salinity (S), temperature (T), zooplankton densities (Z), hydrodynamics (H), and eggs per entering age-1 individual (i.e., recruit) on January 1 (E). Each of these five factors was set to either its 1998 value or its 2001 value, resulting in a total of 32 (2^5) combinations.

Salinity.—Salinity affected the movement patterns of juveniles and adults and thus affected their spatial distribution and vulnerability to entrainment. The year 1998 was a high-outflow year, and salinities were very low for the modeled area from roughly March to August, after which salinity increased but remained below 5 psu (Figure 2b in Rose et al. 2013). Salinity in boxes down-estuary from the confluence was higher during the low-outflow year, 2001, than during 1998; this higher salinity occurred throughout 2001 except for a short period in March (Figure 2d in Rose et al. 2013). In the original baseline historical simulation, adults were located farther seaward with the salinity distribution in 1998. Average August outflow was 568 m³/s in 1998 versus 90 m³/s in 2001, and the percentage of adults that

were in or seaward of the confluence box on September 1 was 97% during 1998 versus 67% during 2001 of the original baseline simulation (Figure 10e in Rose et al. 2013). The fraction of January adults that were entrained was 0.05 in 1998 versus 0.14 in 2001.

Temperature.—Temperature affected the initial date and duration of the spawning period; the egg and yolk sac development and mortality rates; and the bioenergetics (growth) of larvae, postlarvae, juveniles, and adults. When viewed systemwide, differences in temperature between 1998 and 2001 were not obvious (Figure 2a, c in Rose et al. 2013). More detailed analysis of the historical simulation using the average temperature experienced by model individuals showed two major differences between 1998 and 2001: (1) warmer fall and winter at the beginning of the water year and (2) cooler and delayed warming in the spring. Fall 1997 and winter 1998 were warmer than fall 2000 and winter 2001. During October 1–December 30, juveniles experienced an average temperature of 15.9°C in 1997 versus 15.0°C in 2000. Mean temperature experienced by these individuals (which became adults after January 1) during February 27–June 7 (the spawning period) was 14.8°C in 1998 versus 16.4°C in 2001. The warming in the spring also occurred later in 1998, and the average day of spawning was April 28 in 1998 versus April 6 in 2001.

Zooplankton.—The effect of switching 1998 and 2001 zooplankton densities would seem to be the simplest to interpret because this factor only affected feeding rate and therefore growth rate; however, the use of multiple prey groups made interpretation difficult. Dominant prey groups in the annual diets of postlarval, juvenile, and adult Delta Smelt in the baseline simulation were other calanoid adults and adult *Pseudodiaptomus*. The differences between 1998 and 2001 in the biomass densities of these two key prey groups were complicated (see Figure 3c versus 4c and Figure 3f versus 4f in Rose et al. 2013). Although adult *Pseudodiaptomus* biomasses were generally higher during summer and fall in 1998 than in 2001, biomasses of other calanoid adults during summer and fall were higher in 2001 and biomass in the southwest Suisun Bay box during winter and spring was much higher in 2001. Biomass densities of the other zooplankton groups also showed complicated differences. For example, the biomass density of adult *A. vernalis* was higher (and occurred at high levels for a longer period) in the Suisun Marsh box during 1998, but adult *Eurytemora* biomass density was higher in the southern Delta and eastern Delta boxes during 2001 (see Figure 3d versus 4d and Figure 3e versus 4e in Rose et al. 2013).

We relied on the p -value from the bioenergetics model to infer prey availability. The p -value reflects prey availability scaled for maximum consumption rate, which also depends on temperature. The historical simulation using the original baseline version showed that average p -values experienced by juveniles during the faster fall–winter growth (October 1–December 30) was 0.76 in 1997–1998 versus 0.68 in 2000–2001. This difference, in combination with warmer temperatures, led to longer recruits

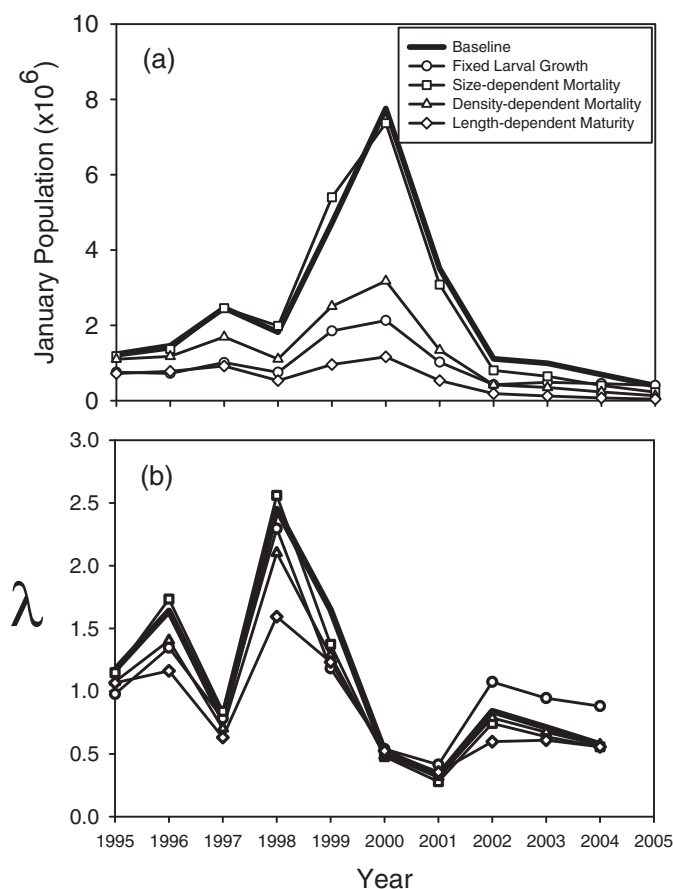


FIGURE 3. Simulated (a) annual adult Delta Smelt abundance in January and (b) finite population growth rate (λ ; fraction per year), 1995–2005, for the original baseline simulation and the four alternative baseline simulations. The values of λ were determined by using an age-based Leslie matrix model applied to individual-based model output for each year. No value for 2005 is possible because the simulations ended on September 30, 2005; information through December 31, 2005, would be needed to estimate the matrix model for 2005.

on January 1 in 1998 than in 2001 (mean TL = 61.4 mm versus 56.5 mm). Averaged p -values in 1998 were also somewhat higher during the summer growth period (April 18–October 1) for young of the year (0.89 in 1998 versus 0.84 in 2001), although by October the mean lengths of young of the year were only slightly greater in 1998 than in 2001 (54 mm versus 52 mm).

Hydrodynamics.—Hydrodynamics affected the entrainment of yolk sac larvae, larvae, and postlarvae via the PTM; the entrainment of juveniles and adults; and the starting locations of new juveniles by determining the transport of larval life stages. Average May outflow was 1,922 m³/s in 1998 versus 273 m³/s in 2001, and the percentage of postlarvae that were in or seaward of the confluence box after transport (June 24) was 84% in 1998 versus 24% in 2001. Almost no larvae were predicted to be entrained during 1998, whereas the daily average entrainment loss was 1.2% in 2001.

Eggs per age-1 individual.—Unlike the other factors, which had readily available values for 1998 and 2001, the number of eggs per age-1 individual required additional calculations in the model to achieve 1998 or 2001 values in the factorial simulation experiment. The number of eggs per age-1 fish reflected growth that occurred in the fall and winter leading up to spawning. In the original historical simulation, the mean length of young of the year on October 1 was somewhat greater in 1997 (starting value for 1998) than in 2000 (54.0 mm versus 52.0 mm) due to the more favorable summer conditions in 1997 than in 2000. This small difference was amplified by warmer temperature and higher prey densities in the fall and winter of 1997, resulting in a mean length of 61.4 mm on January 1, 1998, versus 56.5 mm on January 1, 2001. These lengths straddled the 60-mm maturity cutoff, and whereas 72% of entering age-1 individuals were mature in 1998, only 15% of entering age-1 fish were mature in 2001 of the historical baseline simulation. Thus, although there were fewer recruits on January 1, 1998, than on January 1, 2001 (0.159×10^7 versus 0.258×10^7), the number of mature age-1 female spawners was greater in 1998 (0.287×10^6 versus 0.1105×10^6) and egg production was about 1.5 times higher in 1998 (0.942×10^9 versus 0.641×10^9).

In the historical baseline simulation, the average number of eggs per age-1 individual was 491.8 for 1998 versus 89.3 for 2001. We did not explicitly simulate the previous year's conditions for the simulation experiment, in which either 1998 or 2001 conditions were repeated year after year. Rather, we adjusted the fecundity of entering age-1 individuals each year when we projected spawning so that the total projected number of eggs divided by the number of simulated entering age-1 individuals would be either 491.8 or 89.3.

Simulations in the good year versus bad year experiment.—Simulations were for 15 years, with 4 years of spin-up using 1999 conditions as in the baseline simulations, followed by 11 years of 1 of the 32 combinations of 1998 or 2001 conditions repeated every year. We used the two extreme years because they provided the best contrast for separating out the effects of multiple factors and thus for identifying which factors were most important in determining year-class strength. Eleven years of repeated conditions were simulated in order to ensure that we had the long-term (equilibrium) population responses to the specified conditions; shorter simulations could be affected by initial conditions and still reflect aspects of the transient solutions. We refer to the 32 combinations by using the letters of the factors that were set to 2001 values (i.e., S for salinity, T for temperature, Z for zooplankton, H for hydrodynamics, and E for eggs per entering age-1 individual). For example, in the simulation labeled “ EH ,” eggs per age-1 fish and hydrodynamics were set at 2001 values, while salinity, temperature, and zooplankton were set at 1998 values. We report λ averaged over years 10–14 of each 15-year simulation. As with the baseline simulations, results from a single simulation are presented because replicate simulations differed by less than 5% in their population-level outputs. Values of λ that were 25% and 50% higher than the

2001 value are shown for reference to aid in judging how close the other λ values were to the 2001 value.

Robustness

To confirm the robustness of results based on the original baseline, we also repeated all of the 32 simulation combinations under each of the four alternative baseline conditions. We only report the averaged λ for years 10–14 for four combinations (*ET*, *EH*, *ETH*, and *ETHS*) that resulted in low λ values to illustrate that the full set of combinations was robust to the alternative baselines. We focused on these four combinations because they resulted in low λ values near the 2001 value and because their robustness is particularly important, as they form the basis for identifying which factors determine how a good year differs from a bad year.

RESULTS

Alternative Baselines

The use of size-dependent mortality resulted in January adult abundances similar to those in the original baseline, while the alternative baselines with fixed larval growth, density-dependent mortality, and length-dependent maturity resulted in January abundances that were lower than those in the original baseline (Figure 3a). Lower peak abundances were expected for the density-dependent mortality version because juvenile survival was specified to decrease under high abundances. Larval growth (and therefore larval-stage survival) had an important influence on both good and bad years. Lower abundances under length-dependent maturity occurred because the maturity relationship was not symmetric around 60 mm (Figure 2) and thus would, on average, result in a lower fraction of young of the year becoming mature than was observed with the simple 60-mm rule in the original baseline.

Despite these differences in January abundances, λ values were very similar for all versions of the baseline, with the length-dependent maturity alternative differing the most from the original baseline (Figure 3b). Relatively high January adult abundance occurred in 2001 (Figure 3a), despite the lowest λ being observed in that year, because January abundance was related to conditions in the previous summer and fall and was not reflective of the spring and summer conditions in 2001. The high λ values during years prior to 2001 led to high January adult abundance in 2001. The temporal pattern in λ values for length-dependent maturity was the same as that for the original baseline, but values in all years were lower than baseline values, with the largest difference occurring in 1998 ($\lambda = 1.59$ for length-dependent maturity versus 2.45 for the original baseline). The original baseline and the four alternatives all identified 1998 as the best model year and 2001 as the worst model year for Delta Smelt.

Systematic Comparison of Best versus Worst Years

The intersimulation variability in λ values decreased and more combinations approached the 2001 value as the number of factors set to 2001 values increased (Figure 4). The percentage of combinations that resulted in λ values within 50% of the 2001 λ value increased from 0% when one factor was set to the 2001 value to 10% for two factors at 2001 values, 50% for three factors at 2001 values, and 60% for four factors at 2001 values. All but one of the combinations that generated a λ value within 50% of the 2001 value involved either eggs per age-1 individual or temperature being set at the 2001 value.

Juvenile growth in the fall prior to spawning (i.e., as reflected by the number of eggs per age-1 fish) was the most important single factor in making 2001 a bad year, although no single factor alone was sufficient to fully account for the poor conditions in 2001 relative to 1998 (Figure 4). Temperature (*T*) played an important secondary role (Figure 4, shaded circles), and hydrodynamics (*H*) played a more minor role; salinity (*S*) and zooplankton (*Z*) as single factors were unimportant. When one factor at a time was switched from 1998 to 2001 values (Figure 4, leftmost section), only eggs per age-1 fish (*E*) resulted in a λ value less than 1.0. The single factors *T* and *H* (each at the 2001 value) generated the second- and third-lowest λ values (1.1 and 1.5). As a single factor, *Z* (which determined

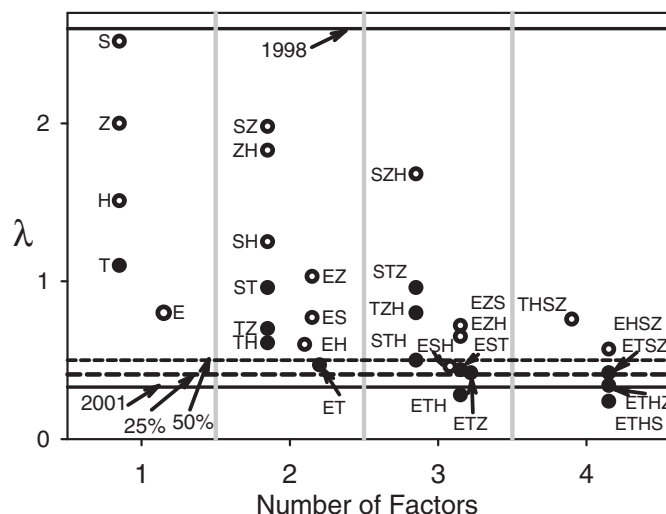


FIGURE 4. Contributions of five factors to differences between the best year (1998) and worst year (2001) for Delta Smelt. Each circle represents the mean finite population growth rate (λ) for years 10–14 of a 15-year simulation of repeated conditions for each factor (salinity [*S*], temperature [*T*], zooplankton [*Z*], hydrodynamics [*H*], and number of eggs per age-1 individual [*E*]) at either 1998 or 2001 values. Results are organized by the number of factors that were set to 2001 values (i.e., 1–4 factors; each combination code [e.g., “STZ”] lists the factors set at 2001 values); within each section, results with the number of eggs per age-1 individual at its 1998 value are shown on the left and results with that factor at its 2001 value are shown on the right. Shaded circles denote all combinations that included the 2001 temperature. The 1998 and 2001 values of λ are indicated by solid horizontal lines; the dotted horizontal lines represent λ values that are 25% and 50% higher than the 2001 value.

growth) generated a λ of 2.0, which was lower than the value for 1998 ($\lambda = 2.6$) but still much higher than the value for 2001 ($\lambda = 0.33$). When only S was set to the 2001 value, there was almost no effect on λ (2.52 versus 2.60).

All combinations of two factors set at 2001 values with eggs per age-1 individual at its higher 1998 value (left-side points in Figure 4, second section) generated λ values above 0.6; among these two-factor combinations, temperature and hydrodynamics at 2001 values together (TH) resulted in the lowest λ (0.61). The three lowest λ values all included 2001 temperature (Figure 4, shaded circles). The two-factor combinations that included the 2001 value for eggs per age-1 fish (right-side points in Figure 4, second section) resulted in λ values less than 1.0, and the ET and EH combinations produced λ values less than 0.6. Again, the lowest of these λ values was from the combination ET (Figure 4, shaded circle) and approached the λ value predicted for 2001 (0.47 versus 0.33).

Among the three-factor combinations set at 2001 values with eggs per age-1 individual set at the 1998 value (left-side points in Figure 4, third section), temperature and hydrodynamics were important. The highest λ (1.68) was predicted for the one combination that did not include 2001 temperature (SZH). The combinations with the three lowest λ values included the 2001 value for temperature (STZ , TZH , and STH ; Figure 4, shaded circles); the two lowest of these λ values were from combinations that also included 2001 hydrodynamics ($\lambda = 0.8$ for TZH and 0.5 for STH).

When the number of eggs per age-1 fish was included as one of the three factors set at 2001 values (right-side points in Figure 4, third section), all λ values were less than 1.0. The combinations also including 2001 temperature (ETH , ETZ , and EST) generated the lowest λ values (0.28, 0.42, and 0.44, respectively), which were close to the λ value for 2001. The combinations that did not include 2001 temperature (Figure 4, open circles) generally had higher λ values (0.72 for EZS and 0.65 for EZH); the exception was ESH , which yielded a λ value (0.46) similar to those from the three combinations that included the 2001 temperature.

The number of eggs per age-1 individual and temperature continued to be very important in four-factor combinations. All four-factor combinations that included the 2001 value for eggs per age-1 fish (right-side points in Figure 4, fourth section) resulted in λ values less than 0.5, and those combinations that also included 2001 temperature (Figure 4, shaded circles) generated λ values that were close to the 2001 value. Of the four combinations that included the 2001 value for eggs per age-1 fish, the three combinations that also included 2001 temperature ($ETSZ$, $ETHZ$, and $ETHS$) all generated λ values less than 0.45, whereas the combination without temperature ($EHSZ$) generated the highest λ value (0.60). The remaining four-factor combination ($THSZ$; left-side point in Figure 4, fourth section), in which the number of eggs per age-1 individual was set at the 1998 value, generated the highest λ (0.85) observed for any four-factor combination.

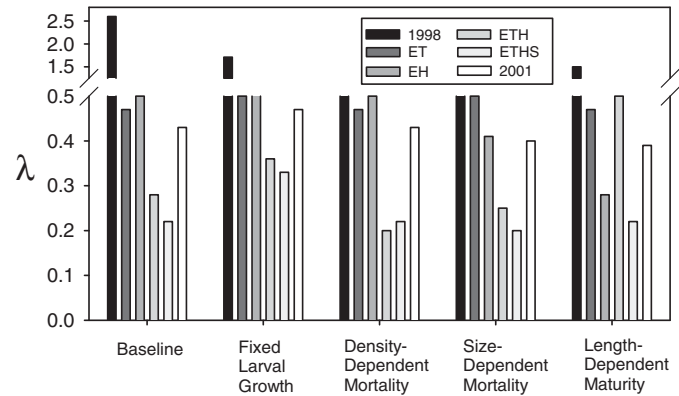


FIGURE 5. Averaged finite population growth rate (λ ; years 10–14) of Delta Smelt under the four alternative baselines and the four factor combinations that resulted in low λ values near the value for 2001. Factors are salinity (S), temperature (T), zooplankton (Z), hydrodynamics (H), and number of eggs per age-1 individual (E); each combination code (e.g., “ ETH ”) lists the factors that were set at 2001 values, and the remaining factors (i.e., with letters not shown) were set at 1998 values.

Robustness

The conditions leading to the good year (1998) were more sensitive to alternative baselines than the poor conditions leading to the bad year (2001; Figure 5). The four combinations (i.e., selected from Figure 4) that produced low λ values when set to their 2001 values under the original baseline generated similarly low λ values under the four alternative baselines. In contrast, the λ values varied more among the 1998 simulations. The alternative of density-dependent mortality produced the greatest reduction in λ for 1998 (λ decreased from 2.45 to 1.00). Larval growth and length-dependent maturity were also important in attaining the high λ predicted for 1998 in the original baseline. When larval growth was fixed at the overall average value (fixed duration), λ was reduced from 2.45 in the original baseline to 1.7; under length-based maturity, λ was reduced to 1.5. Size-dependent mortality was associated with the smallest reduction in the λ value for 1998 (λ decreased from 2.45 to 2.13).

DISCUSSION

Our analysis using a simulation experiment approach further clarified the relative influence of factors affecting Delta Smelt recruitment and population dynamics. In our companion paper (Rose et al. 2013), we compared conditions in 1998 with those in 2001 by using the 1995–2005 historical simulation. The five factors analyzed were inferred to be important in the historical simulation because their values differed, at least in some ways, between the best year and the worst year. In this paper, we systematically varied the five factors in a factorial simulation experiment to look for main and interaction effects. We moved away from the historical sequence of years and performed 15-year simulations with either 1998 or 2001 values repeated every year to allow the simulated population to reach a quasi-steady-state response. We also showed that our results, when viewed

in a comparative mode, were generally robust to alternative versions of the baseline model.

Our results demonstrated that among the factors we examined, no single factor completely accounted for the difference between the high λ in the best year (1998) and the low λ in the worst year (2001). Growth of juveniles in the fall–winter, temperature, and hydrodynamics clearly had the strongest effects, but λ could not be brought down from its 1998 value to near its 2001 value without some combination of factors. Thus, our results support the growing consensus that no single factor explains the Delta Smelt decline that occurred during 1995–2005 (Bennett and Moyle 1996; Bennett 2005; Baxter et al. 2010; Thomson et al. 2010).

Although we have shown that growth conditions in fall–winter were an important factor, there are many ways to achieve the faster growth that was predicted for 1998 relative to 2001. The growth conditions in winter affected the lengths of entering age-1 fish on January 1, with a 1998 value of 60.2 mm versus a 2001 value of 58.8 mm, and consequently affected the fraction mature (0.55 versus 0.41) and the egg production per entering age-1 fish (502.6 versus 107.6). These values for 1998 and 2001 differ from those reported in Rose et al. (2013) because the present values are averaged from the repeated years in the simulation experiment, whereas in our other paper (Rose et al. 2013) we reported values for 1998 and 2001 within the historical simulation. The difference in predicted mean lengths between 1998 and 2001 was well within the range of observed interannual values (see Figure 6 in Rose et al. 2013). Our analysis did not, however, distinguish how juveniles attained greater lengths prior to becoming age 1 and spawning. We used 1998 and 2001 conditions, but other years can also generate similar differences in growth based on combinations of zooplankton conditions and temperature; essentially, any mechanism that allows new age-1 recruits to have a greater length prior to spawning would result in a high number of eggs per age-1 fish and would set the stage for a good year. This can be achieved via warmer winter temperature (as in 1998) or by higher zooplankton densities causing faster growth at any time from the previous summer through early spring. If zooplankton conditions are better at higher salinity (seaward), then hydrodynamics (via its effect on transport) or salinity could also produce faster growth by putting individuals in boxes with higher prey biomass densities. We did not systematically examine how temperature, zooplankton, hydrodynamics, and salinity during the growing season of the year before or during the winter–spring period could potentially combine to promote faster growth and larger spawners in the spring. Rather, we used the suite of conditions for 1998 and 2001 to contrast a good year with a bad year.

A second way to increase egg production without faster growth of spawners would be to increase young-of-the-year survival prior to spawning. Total egg production was calculated as the number of eggs per entering age-1 fish times the number of age-1 fish. Our results were robust to the size-dependent mortality and length-based maturity versions of the baseline, so the

growth of adults affected the number of eggs per age-1 individual but not the abundance of age-1 fish. Higher Delta outflow at key times resulted in reduced entrainment, and hydrodynamics were consistently an important factor. Further analysis should explore spatial (box-scale) differences in mortality, which, if sufficient, could benefit the Delta Smelt via management manipulation of hydrodynamics and salinity, generating differences in starting age-1 abundances for spawning. We assumed that except for entrainment losses, mortality was stage dependent but not spatially variable.

Our results for the importance of food (zooplankton) are similar to those of Maunder and Deriso (2011), but we disagree about the roles of entrainment and density dependence. Maunder and Deriso (2011) used a stage-based life cycle model, and by introducing covariates into life stage survival (spawner–recruit) relationships, they determined that food abundance, temperature, predator abundance, and density dependence were the most important factors controlling the population dynamics of Delta Smelt. They further stated that there was some support for negative effects of water clarity and adult entrainment.

Our simulation experiment contrasting the best year versus the worst year agrees with the important role of temperature and zooplankton, but we did not examine the effects of predator abundance or water clarity. Maunder and Deriso (2011) used spring and summer zooplankton conditions: minimum *Eurytemora* and *Pseudodiaptomus* densities for April–June; average *Eurytemora* density for July; and average *Pseudodiaptomus* density for July–August. We found that fall, winter, and early spring growth was potentially important, at least for the comparison between 1998 and 2001. Maunder and Deriso (2011) examined a longer time period (1970–2006) that covered larger changes in the zooplankton community, and this could emphasize the importance of spring and summertime zooplankton relative to other factors, such as winter growth and its consequences for spring reproduction. We recommend that conditions in the winter and early spring and conditions from the year before be further evaluated for their potential to benefit Delta Smelt.

We disagree to some extent with Maunder and Deriso (2011) about the role of entrainment and density dependence. Examination of Figure 8 of Maunder and Deriso (2011) to assess the role of entrainment showed more agreement with our analysis than did their general statement of “some support for a negative relationship with . . . adult entrainment.” They showed an approximately twofold increase in adults during 2002–2006 by eliminating entrainment. This agrees with our analysis, showing higher entrainment mortality during the same years as in our simulation; however, we would term their Figure 8 results as providing more than “some” support for a negative effect of adult entrainment. The Maunder and Deriso (2011) analysis covered a longer time period (1970–2006) than our analysis (1995–2005); thus, the role of covariates can differ and density dependence likely played a larger role at the earlier, higher abundance levels (see Bennett 2005). In addition, direct comparisons between the models are somewhat confounded because our analysis and the

Maunder and Deriso (2011) analysis shared some information, such as the entrainment estimates from Kimmerer (2008) and the spawner–recruit information from long-term monitoring.

Several statistical analyses of similar monitoring and covariate data as used by Maunder and Deriso (2011) also implicated various indicators of spring and summer zooplankton food availability as being important. Thomson et al. (2010) used Bayesian change point analysis to examine variation in the fall MWT index; Mac Nally et al. (2010) used multivariate autoregressive modeling to analyze the fall MWT index in a multispecies approach; and Miller et al. (2012) used Ricker spawner–recruit relationships to analyze the ratio of indices as survival indicators. These analyses all inferred that various combinations of water temperature, water clarity, zooplankton indicators, and entrainment were correlated to various degrees with the historical pattern in the Delta Smelt abundance indices.

Other assumptions that are inherent in our modeling merit further analyses as possible alternative versions of baseline conditions. The representation of predation on Delta Smelt was partially explored by using size-dependent mortality, but there are also temporal trends and spatial patterns to the key predators of Delta Smelt that could be important. Striped Bass *Morone saxatilis* and Largemouth Bass *Micropterus salmoides* show distinct spatial distributions within the San Francisco Estuary and have also exhibited recent temporal trends, with young Striped Bass declining and Largemouth Bass increasing (Nobriga and Feyrer 2007). Furthermore, exotic Mississippi Silversides *Menidia audens* are known to readily consume larval Delta Smelt and have increased substantially in recent years (Baerwald et al. 2012).

Another assumption worthy of investigation is that the Delta Smelt population in the individual-based model consisted of individuals that all exhibit the same migratory behavior. Limited field data indicate that there is partial or divergent migration (Secor 1999; Chapman et al. 2012) within the Delta Smelt population, with some individuals possibly remaining year-round in the Cache Slough region, which is located in the southwestern portion of our Sacramento River model box (Merz et al. 2011; Sommer et al. 2011). An alternative version of the baseline individual-based model could include some proportion of individuals that remain resident in some areas. Resident individuals, or individuals with reduced or altered migrations, could exhibit different growth because of spatial variation in temperature, zooplankton, and susceptibility to entrainment.

Our detailed individual-based approach is not commonly used to simulate the population dynamics of endangered fish species, although it can be adapted for use in the more traditional population viability analysis (PVA) and risk framework. The individual-based approach is increasingly being used to simulate fish population and community dynamics for purposes of answering ecological and fisheries management questions (DeAngelis and Mooij 2005). However, although the individual-based approach is usually mentioned in reviews of PVA approaches (e.g., Akçakaya and Sjögren-Gulve 2000; Morris et al. 2002; Petersen et al. 2008), the number of examples

of its use specifically for PVA remains quite limited. Some commonly used general models apply an individual-based approach, but they employ a very simple representation of processes (e.g., Jarić et al. 2010). Examples in which a more mechanistic individual-based model approach was used include models of endangered birds (Letcher et al. 1998), turtles (Mazaris et al. 2005), and recruitment of Colorado Pikeminnow *Ptychocheilus lucius*. Using an individual-based approach very similar to our Delta Smelt modeling, Jager et al. (2001) analyzed the effects of habitat fragmentation by dams on the White Sturgeon *Acipenser transmontanus*, which is a species of concern and has been listed as endangered elsewhere. Population viability analysis usually involves many realizations of a modeled population trajectory to generate risk values. Our individual-based model cannot easily be used to perform thousands of simulations. A possible link to a PVA-type analysis of Delta Smelt would be to (1) use the individual-based model in a systematic way to create crude probability distributions for the elements of the Leslie matrix model (which can generate λ values with Monte Carlo simulation) or (2) use the coupled individual-based model and Leslie model to directly generate distributions of λ values. Once sets of λ values are obtained for a variety of environmental and biological conditions, they can be used in more traditional PVA projections of long-term persistence (see Morris et al. 2002).

Our analysis addresses several ongoing methodological issues in fish population dynamics: spatial dynamics in complex habitats, coupled biological–physical modeling, and recruitment and population dynamics at low abundances. The need for studies of long-term population dynamics to deal with spatial dynamics has recently been discussed (Giske et al. 1998; Struve et al. 2010), and approaches that deal with spatial variation explicitly are receiving greater attention (e.g., Kerr et al. 2010). Increasingly, fish-related management issues require an integrated approach that combines the physics of water with the biology of the fish and other biota (Shenton et al. 2012), and one method is the direct coupling of fine-scale hydrodynamics with long-term fish population dynamics (Buckley and Buckley 2010; Rose et al. 2010; Hinrichsen et al. 2011; Stock et al. 2011).

Our model expands on the classical particle tracking approach by simulating detailed biological processes, relatively complicated behavioral movement, and multiple generations. Our Delta Smelt model simulated growth, survival, reproduction, and movement of individual fish on the same spatial grid as the hydrodynamics, and the super-individual method allowed for 15-year simulations. Although PTMs are commonly embedded within hydrodynamics models (North et al. 2009; Hinrichsen et al. 2011), the PTMs typically do not include detailed descriptions of growth and reproduction. Rather, these studies usually invoke, at most, simple movement behavior as an addition to passive transport and are mostly used for short-term (<1 year) simulations (Miller 2007; Lett et al. 2009; Gallego 2011). However, a consequence of full life cycle modeling that includes juveniles and adults within a detailed

spatial grid is that now we must simulate behavioral movement on relatively fine scales. Modeling behavioral movement is critical to ensure that individuals experience the appropriate conditions over time, but this remains a challenge (Watkins and Rose 2013). Delta Smelt movement patterns in our simulations were generally realistic but require further refinement.

Finally, much fish population modeling has focused on the effects of harvesting from high-number populations, whereas there is an increasing need to examine dynamics of fish populations at low abundances due to overharvest and in support of recovery plans for listed species (Keith and Hutchings 2012). The focus on harvesting leads to an emphasis on density-dependent mortality, often via the spawner–recruit relationship (Rose et al. 2001). Our approach differs from this by focusing on Delta Smelt population dynamics under density-independent conditions. We emphasized how individuals were transported through or navigated through their spatially complex and temporally varying habitat. Our analysis can be viewed as part of the broader idea of multiple factors within the match–mismatch theory of controls on young-of-the-year survival and therefore recruitment (Peck et al. 2012), coupled with the idea that adult bioenergetics are important for determining maturity and annual egg production (Neil et al. 1994; Rose et al. 2001). Because our model was density independent, all of the predicted variation in stage-specific survival rates was due to variation in how spatial distributions interacted with dynamic environmental conditions. Our results showed how the spatial and temporal positioning of all life stages each year (based on physical transport and salinity), combined with the pattern in daily water temperature and the amount of Delta outflow, affected the magnitude and location of egg production and the subsequent dynamic matching of larval and juveniles with their prey types, thus affecting recruitment success. However, even our modeling results were not simple to interpret, and therefore they also illustrate how spatially and temporally dynamic habitat can create complicated match–mismatch situations.

Delta Smelt have been at the center of escalating controversy in the San Francisco Estuary region for several decades (NRC 2010; Kimmerer 2011; Miller 2011). What initially arose as a conflict between water demands for export versus for the environment (including Delta Smelt) has metastasized as the number of ostensible factors behind the decline of Delta Smelt has grown (e.g., Mac Nally et al. 2010; Maunder and Deriso 2011; Miller et al. 2012). The conflict has now evolved into a complicated situation in which multiple factors operate in interactive ways and are continually being argued over in court (Delta Smelt Consolidated Cases 2010). Our results contribute to the growing number of examples showing that multiple factors affect aquatic ecosystems (Breitburg and Riedel 2005; Ormerod et al. 2010; Cloern and Jassby 2012) and that the search for a single factor controlling fish population dynamics is unlikely to be successful (e.g., Rose 2000; Krebs 2002; Hecky et al. 2010; Lindegren et al. 2011).

Our results to date suggest that management actions to benefit Delta Smelt must deal with multiple stressors that occur at different points in the life cycle. An increase in prey would induce relatively large responses in reproduction but may not be feasible. We showed that growth leading up to spawning was important for subsequent population growth; it remains to be seen whether it is possible to promote growth of Delta Smelt or higher young-of-the-year survival prior to spawning (fall–spring) via management actions. We also showed that no single factor can alone account for the differences between good and bad years and that promoting growth should be done in combination with other actions (if feasible) to (1) ensure good temperatures for summer growth and delayed spawning and (2) ensure sufficient outflow and avoidance of high entrainment (see results in Rose et al. 2013). Our results also demonstrate that expectations should be clearly stated, as most management actions are unlikely to generate large, immediate responses because the influence of stressors varies from year to year and because the reduction in a single stressor during any one year may be moderated by the conditions in other, non-manipulated stressors occurring in that year.

We envision two other areas for future analyses using the individual-based model. First, extending the model simulations for the periods before 1995 and after 2005 would allow for more comparisons and contrasts of good versus bad years to determine other combinations of factors that may be important; climate change scenarios should be included in these simulations to allow for future-looking comparisons. This would require use of the DSM2 hydrodynamic model or another hydrodynamic model and the development of synthetic temperature, salinity, and zooplankton data. Second, a more rigorous side-by-side comparison of the Maunder and Deriso (2011) model and our individual-based model would facilitate an understanding of the relative effects of key stressors on Delta Smelt population dynamics. The population dynamics and reasons for the decline of Delta Smelt are complex. However, complexity is not a reason to avoid rigorous quantitative analyses—indeed, it is perhaps the best reason to develop and compare alternative modeling approaches.

ACKNOWLEDGMENTS

This project was funded by a grant from the CALFED Science Program (SCI-05-C106). The comments of two reviewers and the Associate Editor helped us greatly clarify the manuscript.

REFERENCES

- Akçakaya, H. R., and P. Sjögren-Gulve. 2000. Population viability analyses in conservation planning: an overview. *Ecological Bulletins* 48:9–21.
- Baerwald, M. R., B. M. Schreier, G. Schumer, and B. May. 2012. Detection of threatened Delta Smelt in the gut contents of the invasive Mississippi Silverside in the San Francisco Estuary using TaqMan assays. *Transactions of the American Fisheries Society* 141:1600–1607.

- Bailey, K. M., and J. T. Duffy-Anderson. 2010. Fish predation and mortality. Pages 322–329 in J. H. Steele, S. A. Thorpe, and K. K. Turekian, editors. *Marine biology: a derivative of the encyclopedia of ocean sciences*. Academic Press, San Diego, California.
- Baxter, R., R. Breuer, L. Brown, L. Conroy, F. Feyrer, S. Fong, K. Gehrts, L. Grimaldo, B. Herbold, P. Hrodey, A. Mueller-Solger, T. Sommer, and K. Souza. 2010. 2010 pelagic organism decline work plan and synthesis of results. Interagency Ecological Program for the San Francisco Estuary, California Department of Water Resources, Sacramento.
- Bennett, W. A. 2005. Critical assessment of the Delta Smelt population in the San Francisco Estuary, California. *San Francisco Estuary and Watershed Science* [online serial] 3(2):article 1.
- Bennett, W. A., and P. B. Moyle. 1996. Where have all the fishes gone? interactive factors producing fish declines in the Sacramento–San Joaquin Estuary. Pages 519–542 in J. T. Hollibaugh, editor. *San Francisco Bay: the ecosystem*. American Association for the Advancement of Science, San Francisco.
- Breitburg, D. L., and G. F. Riedel. 2005. Multiple stressors in marine systems. Pages 167–182 in E. A. Norse and L. B. Crowder, editors. *Marine conservation biology: the science of maintaining the sea's biodiversity*. Island Press, Washington, D.C.
- Brooks, M. L., E. Fleishman, L. R. Brown, P. W. Lehman, I. Werner, N. Scholz, C. Mitchelmore, J. R. Lovvorn, M. L. Johnson, D. Schlenk, S. van Drunick, J. I. Drever, D. M. Stoms, A. E. Parker, and R. Dugdale. 2012. Life histories, salinity zones, and sublethal contributions of contaminants to pelagic fish declines illustrated with a case study of San Francisco Estuary, California, USA. *Estuaries and Coasts* 35:603–621.
- Buckley, L. J., and L. B. Buckley. 2010. Toward linking ocean models to fish population dynamics. *Progress in Oceanography* 54:85–88.
- Chapman, B. B., K. Hulthén, J. Brodersen, P. A. Nilsson, C. Skov, L. A. Hansson, and C. Brönmark. 2012. Partial migration in fishes: causes and consequences. *Journal of Fish Biology* 81:456–478.
- Cloern, J. E., and A. D. Jassby. 2012. Drivers of change in estuarine-coastal ecosystems: discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics* 50:RG4001. DOI: 10.1029/2012RG000397.
- Connon, R. E., J. Geist, J. Pfeiff, A. V. Loguinov, L. S. D'Abronzio, H. Wintz, C. D. Vulpe, and I. Werner. 2009. Linking mechanistic and behavioral responses to sublethal esfenvalerate exposure in the endangered Delta Smelt *Hypomesus transpacificus* (fam. Osmeridae). *BMC Genomics* [online serial] 10:608. DOI: 10.1186/1471-2164-10-608.
- Cowan, J. H. Jr., K. A. Rose, and D. R. DeVries. 2000. Is density-dependent growth in young-of-the-year fishes a question of critical weight? *Reviews in Fish Biology and Fisheries* 10:61–89.
- DeAngelis, D. L., and W. M. Mooij. 2005. Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics* 36:147–168.
- Delta Smelt Consolidated Cases. 2010. F. Supp. 2d-2010 WL 2195960 at pp. 24, 26, 44. Eastern District of California.
- Feyrer, F., B. Herbold, S. A. Matern, and P. B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67:277–288.
- Feyrer, F., M. L. Nobriga, and T. R. Sommer. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 64:723–734.
- Gallego, A. 2011. Biophysical models: an evolving tool in marine ecological research. Pages 279–290 in F. Jopp, H. Reuter, and B. Breckling, editors. *Modelling complex ecological dynamics*. Springer-Verlag, Berlin.
- Giske, J., G. Huse, and Ø. Fiksen. 1998. Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries* 8:57–91.
- Gislason, H., N. Daan, J. C. Rice, and J. G. Pope. 2010. Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries* 11:149–158.
- Grimaldo, L. F., T. Sommer, N. Van Ark, G. Jones, E. Holland, P. B. Moyle, B. Herbold, and P. Smith. 2009. Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary: can fish losses be managed? *North American Journal of Fisheries Management* 29:1253–1270.
- Hecky, R. E., R. Mugidde, P. S. Ramlal, M. R. Talbot, and G. W. Kling. 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. *Freshwater Biology* 55(Supplement 1):19–42.
- Hinrichsen, H. H., M. Dickey-Collas, M. Huret, M. A. Peck, and F. B. Vikebø. 2011. Evaluating the suitability of coupled biophysical models for fishery management. *ICES Journal of Marine Science* 68:1478–1487.
- Jager, H. I., J. A. Chandler, K. B. Leppla, and W. Van Winkle. 2001. A theoretical study of river fragmentation by dams and its effects on White Sturgeon populations. *Environmental Biology of Fishes* 60:347–361.
- Jarić, I., T. Ebenhard, and M. Lenhardt. 2010. Population viability analysis of the Danube sturgeon populations in a Vortex simulation model. *Reviews in Fish Biology and Fisheries* 20:219–237.
- Keith, D. M., and J. A. Hutchings. 2012. Population dynamics of marine fishes at low abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1150–1163.
- Kerr, L. A., S. X. Cadrin, and D. H. Secor. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecological Applications* 20:497–507.
- Kimmerer, W. J. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological responses. *San Francisco Estuary and Watershed Science* [online serial] 2(1):article 1.
- Kimmerer, W. J. 2008. Losses of Sacramento River Chinook Salmon and Delta Smelt to entrainment in water diversions in the Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science* [online serial] 6(2): article 2.
- Kimmerer, W. J. 2011. Modeling Delta Smelt losses at the south Delta export facilities. *San Francisco Estuary and Watershed Science* [online serial] 9(1):article 5.
- Kimmerer, W. J., E. S. Gross, and M. L. MacWilliams. 2009. Is the response of estuarine nekton to freshwater flow in the San Francisco Estuary explained by variation in habitat volume? *Estuaries and Coasts* 32:375–389.
- Kimmerer, W. J., and M. L. Nobriga. 2008. Investigating particle transport and fate in the Sacramento–San Joaquin Delta using a particle tracking model. *San Francisco Estuary and Watershed Science* [online serial] 6(1):article 4.
- Krebs, C. J. 2002. Two complementary paradigms for analysing population dynamics. *Philosophical Transactions of the Royal Society of London B* 357: 1211–1219.
- Kuivila, K. M., and G. E. Moon. 2004. Potential exposure of larval and juvenile Delta Smelt to dissolved pesticides in the Sacramento–San Joaquin Delta, California. Pages 229–241 in F. Feyrer, L. R. Brown, R. L. Brown, and J. J. Orsi, editors. *Early life history of fishes in the San Francisco Estuary and watershed*. American Fisheries Society, Symposium 39, Bethesda, Maryland.
- Letcher, B. H., J. A. Priddy, J. R. Walters, and L. B. Crowder. 1998. An individual-based, spatially explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. *Biological Conservation* 86:1–14.
- Lett, C., K. A. Rose, and B. A. Megrey. 2009. Biophysical models. Pages 88–111 in D. Checkley, J. Alheit, Y. Oozeki, and C. Roy, editors. *Climate change and small pelagic fish*. Cambridge University Press, Cambridge, UK.
- Lindegren, M., Ö. Östman, and A. Gårdmark. 2011. Interacting trophic forcing and the population dynamics of herring. *Ecology* 92:1407–1413.
- Mac Nally, R., J. R. Thomson, W. J. Kimmerer, F. Feyrer, K. B. Newman, A. Sih, W. A. Bennett, L. Brown, E. Fleishman, S. D. Culbertson, and G. Castillo. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). *Ecological Applications* 20:1417–1430.
- Maunder, M. N., and R. B. Deriso. 2011. A state-space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to Delta Smelt (*Hypomesus transpacificus*). *Canadian Journal of Fisheries and Aquatic Sciences* 68:1285–1306.

- Mazaris, A. D., Ø. Fiksen, and Y. G. Matsinos. 2005. Using an individual-based model for assessment of sea turtle population viability. *Population Ecology* 47:179–191.
- Merz, J. E., S. Hamilton, P. S. Bergman, and B. Cavallo. 2011. Spatial perspective for Delta Smelt: a summary of contemporary survey data. *California Fish and Game* 97:164–189.
- Miller, T. J. 2007. Contribution of individual-based coupled physical–biological models to understanding recruitment in marine fish populations. *Marine Ecology Progress Series* 347:127–138.
- Miller, W. J. 2011. Revisiting assumptions that underlie estimates of proportional entrainment of Delta Smelt by state and federal water diversions from the Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science* [online serial] 9(1):article 4.
- Miller, W. J., B. F. J. Manly, D. D. Murphy, D. Fullerton, and R. R. Ramey. 2012. An investigation of factors affecting the decline of Delta Smelt (*Hypomesus transpacificus*) in the Sacramento–San Joaquin Estuary. *Reviews in Fisheries Science* 20:1–19.
- Morris, W. F., P. L. Bloch, B. R. Hudgens, L. C. Moyle, and J. R. Stinchcombe. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. *Ecological Applications* 12:708–712.
- Neill, W. H., J. M. Miller, H. W. Van Der Veer, and K. O. Winemiller. 1994. Ecophysiology of marine fish recruitment: a conceptual framework for understanding interannual variability. *Netherlands Journal of Sea Research* 32:135–152.
- Nobriga, M. L. 2002. Larval Delta Smelt diet composition and feeding incidence: environmental and ontogenetic influences. *California Fish and Game* 88:149–164.
- Nobriga, M. L., and F. Feyrer. 2007. Shallow-water piscivore–prey dynamics in California's Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science* [online serial] 5(2):article 4.
- Nobriga, M. L., T. R. Sommer, F. Feyrer, and K. Fleming. 2008. Long-term trends in summertime habitat suitability for Delta Smelt (*Hypomesus transpacificus*). *San Francisco Estuary and Watershed Science* [online serial] 6(1):article 1.
- North, E. W., A. Gallego, and P. Petitgas, editors. 2009. Manual of recommended practices for modelling physical–biological interactions during fish early life. ICES Cooperative Research Report 295.
- NRC (National Research Council). 2010. A scientific assessment of alternatives for reducing water management effects on threatened and endangered fishes in California's Bay–Delta. National Academies Press, Washington, D.C.
- NRC (National Research Council). 2012. Sustainable water and environmental management in the California Bay–Delta. National Academies Press, Washington, D.C.
- Ormerod, S. J., M. Dobson, A. G. Hildrew, and C. R. Townsend. 2010. Multiple stressors in freshwater ecosystems. *Freshwater Biology* 55(Supplement 1): 1–4.
- Peck, M. A., K. B. Huebert, and J. K. Llopiz. 2012. Intrinsic and extrinsic factors driving match–mismatch dynamics during the early life history of marine fishes. *Advances in Ecological Research* 47:177–302.
- Petersen, J. H., D. L. DeAngelis, and C. P. Paukert. 2008. An overview of methods for developing bioenergetic and life history models for rare and endangered species. *Transactions of the American Fisheries Society* 137:244–253.
- Rose, K. A. 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecological Applications* 10:367–385.
- Rose, K. A., J. I. Allen, Y. Artioli, M. Barange, J. Blackford, F. Carlotti, R. Cropp, U. Daewel, K. Edwards, K. Flynn, S. L. Hill, R. HilleRisLambers, G. Huse, S. Mackinson, B. Megrey, A. Moll, R. Rivkin, B. Salihoglu, C. Schrum, L. Shannon, Y.-J. Shin, S. L. Smith, C. Smith, C. Solidoro, M. St. John, and M. Zhou. 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 2:115–130.
- Rose, K. A., J. H. Cowan Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2:293–327.
- Rose, K. A., W. J. Kimmerer, K. P. Edwards, and W. A. Bennett. 2013. Individual-based modeling of Delta Smelt population dynamics in the upper San Francisco Estuary: I. Model description and baseline results. *Transactions of the American Fisheries Society* 142:1238–1259.
- Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, Massachusetts.
- Scheffer, M., J. M. Baveco, D. L. DeAngelis, K. A. Rose, and E. H. van Nes. 1995. Super-individuals: a simple solution for modelling large populations on an individual basis. *Ecological Modelling* 80:161–170.
- Secor, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research* 43:13–34.
- Shenton, W., N. R. Bond, J. D. L. Yen, and R. Mac Nally. 2012. Putting the “ecology” into environmental flows: ecological dynamics and demographic modelling. *Environmental Management* 50:1–10.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60:1129–1157.
- Sommer, T., F. Mejia, M. Nobriga, F. Feyrer, and L. Grimaldo. 2011. The spawning migration of Delta Smelt in the upper San Francisco Estuary. *San Francisco Estuary and Watershed Science* [online serial] 9(2): article 2.
- Stock, C. A., M. A. Alexander, N. A. Bond, K. Brander, W. W. L. Cheung, E. N. Curchitser, T. L. Delworth, J. P. Dunne, S. M. Griffies, M. A. Haltuch, J. A. Hare, A. B. Hollowed, P. Lehodey, S. A. Levin, J. S. Link, K. A. Rose, R. Rykaczewski, J. L. Sarmiento, R. J. Stouffer, F. B. Schwing, G. A. Vecchi, and F. E. Werner. 2011. On the use of IPCC-class models to assess the impact of climate on living marine resources. *Progress in Oceanography* 58:1–27.
- Struve, J., K. Lorenzen, J. Blanchard, L. Börger, N. Bunnefeld, C. Edwards, C. Joaquín Hortal, A. MacCall, J. Matthiopoulos, B. Van Moorter, A. Ozgul, F. Royer, N. Singh, C. Yesson, and R. Bernard. 2010. Lost in space? Searching for directions in the spatial modelling of individuals, populations and species ranges. *Biology Letters* 6:575–578.
- Thomson, J. R., W. J. Kimmerer, L. R. Brown, K. B. Newman, R. Mac Nally, W. A. Bennett, F. Feyrer, and E. Fleishman. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications* 20:1431–1448.
- USFWS (U.S. Fish and Wildlife Service). 2008. Biological opinion (BO) on the long-term operational criteria and plan (OCAP) for coordination of the Central Valley project and state water project. USFWS, California and Nevada Region, Sacramento, California.
- Watkins, K. S., and K. A. Rose. 2013. Evaluating the performance of individual-based animal movement models in novel environments. *Ecological Modelling* 250:214–234.
- Winder, M., and A. D. Jassby. 2011. Shifts in zooplankton community structure: implications for food web processes in the upper San Francisco Estuary. *Estuaries and Coasts* 34:675–690.