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UNITED STATES DISTRICT COURT

EASTERN DISTRICT OF CALIFORNIA

THE DELTA SMELT CASES, SAN LUIS & DELTA-MENDOTA WATER AUTHORITY, *et al.* v. SALAZAR, *et al.* (Case No. 1:09-cv-407) STATE WATER CONTRACTORS v. SALAZAR, *et al.* (Case No. 1:09-cv-422) COALITION FOR A SUSTAINABLE DELTA, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-480) METROPOLITAN WATER DISTRICT v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-631) STEWART & JASPER ORCHARDS, *et al.* v. UNITED STATES FISH AND WILDLIFE SERVICE, *et al.* (Case No. 1:09-cv-892)	1:09-cv-407 OWW GSA 1:09-cv-422 OWW GSA 1:09-cv-631 OWW GSA 1:09-cv-892 OWW GSA PARTIALLY CONSOLIDATED WITH: 1:09-cv-480 OWW GSA **DECLARATION OF DR. RICHARD B. DERISO IN SUPPORT OF PLAINTIFFS' MOTION FOR INJUNCTIVE RELIEF** Ctrm: 3 Judge: Hon. Oliver W. Wanger

I, Dr. Richard B. Deriso declare:

I. INTRODUCTION

1. In my previous declarations, dated July 31, 2009, November 13, 2009, December 7, 2009, January 26, 2010, and March 1, 2010, I set forth my comprehensive explanation of the analysis that the United States Fish and Wildlife Service ("FWS") performed in its 2008 Delta Smelt Biological Opinion ("BiOp"), including its clear, fundamental errors in its analysis of OMR flows, Fall X2, and the incidental take levels. See Doc. 167; Doc. 401; Doc. 455; Doc. 508; Doc. 605.

2. In this declaration, I specifically focus on management measures for Old and Middle River ("OMR") flows that will reduce entrainment events during the smelt adult period from what has historically occurred. I have also developed revised incidental take limit ("ITL") calculations, based on these management measures, for the adult period. I also propose a revised ITL for juvenile smelt.

3. The management measures proposed are based on turbidity. The data reveals that turbidity measurements can be a powerful "trigger" for setting OMR flows to avoid entrainment. In other words, turbidity is used as the controlling factor for setting OMR flows because of the

strong relationship between turbidity and entrainment. I have developed a mathematical model (a formula) and fitted it to normalized delta smelt salvage (salvage/previous FMWT) for the period December through March 1988-2009 as a function of turbidity at Clifton Court and OMR flow.

4. In this declaration, I have provided results for a three-day model, in which the previous three-day average turbidity at Clifton Court is used to estimate the daily OMR flow limit for the current day that would provide substantial reduction in daily normalized salvage of adult delta smelt.

5. In developing the three-day model, predicted normalized salvage was highly statistically significantly correlated with observed normalized salvage (p-value < 0.00001). This means that the model performed very well in using prior data on turbidity and OMR flow to predict the historic entrainment events that occurred over the December through March 1988-2009 record. Because the model can predict entrainment events, it can be used in managing the projects to avoid or reduce such events in the future.

6. At the end of this declaration, I also introduce and explain the life cycle model that I developed with Dr. Mark Maunder, which shows that entrainment is not a significant factor impacting the smelt population growth rate, but that several other environmental factors are.

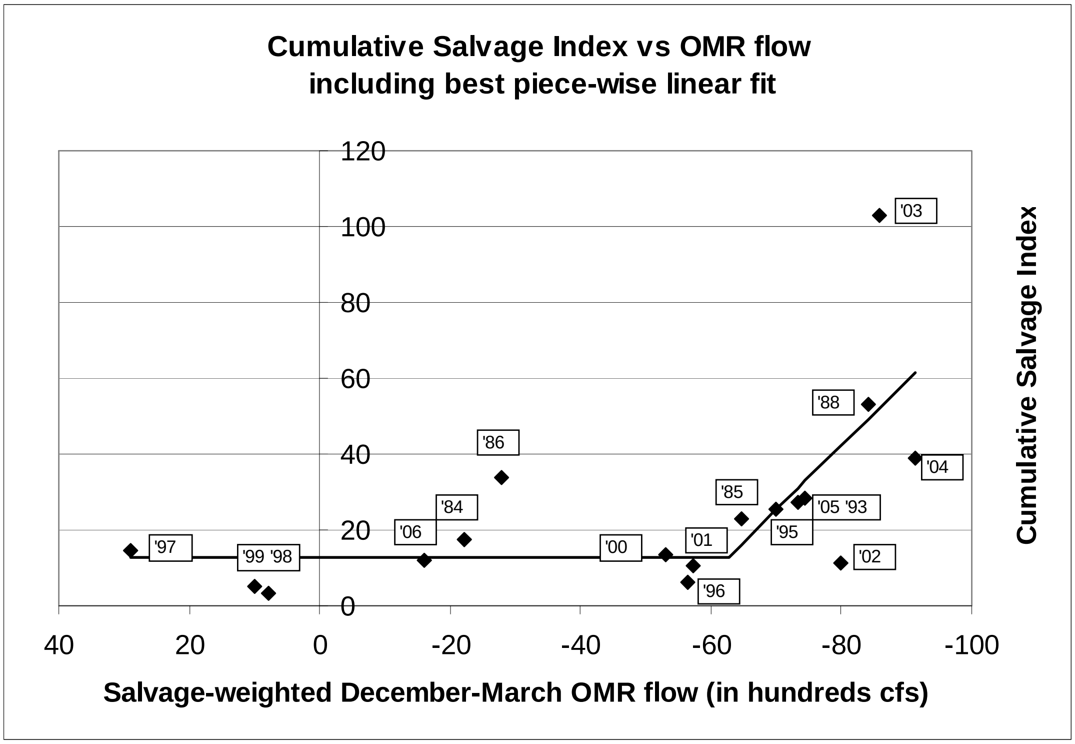
7. My qualifications and experience are set forth in my previous declaration, Doc. #401 ¶¶ 5-10 and Exhibits A and B thereto.

II. TURBIDITY AND OMR FLOW DATA CAN BE USED TO CONSTRUCT A NORMALIZED SALVAGE MODEL PREDICTING WINTER SALVAGE RATES

8. In developing the turbidity approach model for adult salvage, I modified the analysis from my previous declaration (Doc. 455 ¶ 16) that was presented as a prediction of normalized winter salvage (salvage/previous FMWT). That original analysis graphed adult normalized salvage (y-axis) against salvage-weighted average OMR flow for the December through March time period (x-axis). The graph consisted of a flat line for flows less negative than an OMR salvage-weighted average of -6,100 cfs, as shown below in Figure 1. Therefore, those results suggested that salvage rates, when graphed only against OMR flows, do not increase

until flows are more negative than -6,100 cfs; the OMR flow where salvage rates begin to increase is defined as the OMR trigger.

Figure 1.



9. That prior analysis only looked at two variables—OMR flow and normalized salvage.[1] The advanced approach that I have developed for this declaration allows the OMR trigger to be dependent on an additional variable—turbidity. A model utilizing OMR limits based on the level of turbidity predicts normalized salvage far better than a simple piece-wise model, such as Figure 1, which did not depend on turbidity. The model used in this analysis can be written as:

$$S = a + (1 - p)[b(OMR - OMR^{*})]$$

$$p = 1, OMR > OMR^{*};\ p = 0, otherwise.$$

$$OMR^{*} = a' + (1 - p')[b'(TUR - TUR^{*})]$$

$$p' = 1, TUR > TUR^{*};\ p' = 0, otherwise.$$

[1] I purposefully limited my prior declaration to reviewing the approach contained in the Smelt Biological Opinion.

where OMR^* is the OMR trigger, TUR^* is the turbidity trigger, (a, a', b, b') are constants, OMR is daily OMR flow, TUR is previous 3-day average Clifton Court turbidity, and *S* is the daily normalized salvage (specific parameter estimates used for the model set forth in this declaration are referenced below in ¶11, Table 2).

10. Parameters for the normalized salvage model were estimated by non-linear least-squares minimization of the difference between predicted and observed normalized salvage for each daily time period within the months of December through March of 1988-2009, provided that the data were available to the minimum specifications detailed below.[2]

III. THE MANAGEMENT OF OMR FLOWS BETWEEN DECEMBER AND MARCH TO PROTECT PRE-SPAWNING ADULT DELA SMELT SHOULD UTILIZE THREE-DAY AVERAGE TURBIDITY DATA AND CORRESPONDING OMR FLOW LIMITS

11. The results of the model show that predicted normalized salvage is highly correlated with observed normalized salvage using the previous three-day average turbidity (p-value < 0.00001). As a comparison, I also fitted a linear regression model of turbidity and OMR flow to normalized salvage, and the results of that model were also statistically significant. However, the three-day analysis that I ran performed measurably better. Comparing the three-day model to the linear model, the three-day model's Akaike Information Criteria (AIC) score was more that 400 lower than the linear fit.[3] Paraphrasing the seminal text on AIC scores by Burnham and Anderson,[4] models that are 10 or more AIC units above the best model have essentially no

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[2] Data on OMR flows, turbidity, and salvage were obtained by the Metropolitan Water District of Southern California ("MWD") from a Freedom of Information Act ("FOIA") request to FWS and from certain websites. The FOIA request was submitted by MWD to FWS on August 10, 2009. FWS responded to the FOIA request by providing data through March 2006 in an excel worksheet titled "Take Analysis.xls" (see Chart 3). Data for dates after March 2006 were obtained from the following websites: turbidity (http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=CLC); OMR (http://waterdata.usgs.gov/ca/nwis/sw; salvage: http://www.usbr.gov/mp/cvo/fishrpt.html); salvage (http://www.usbr.gov/mp/cvo/fishrpt.html). The FMWT data used to normalize salvage was obtained from http://www.dfg.ca.gov/delta/data/fmwt/charts.asp. Two days of Middle River flows were estimated using a correlation between Old and Middle River flows. See data points for 12/21 and 12/22 of the 2008 OMR data set at http://waterdata.usgs.gov/ca/nwis/sw.

[3] AIC represents a measure of the goodness of fit of an estimated statistical model and is utilized as a tool for model selection. To interpret AIC scores, one compares the AIC values for a set of models fit to the same data set. The model with the lowest AIC score (in this case, the 3-day model) is the preferred model.

[4] Burnham, K. P. and Anderson, D.A. 2004. Multimodel inference, understanding AIC and BIC in model selection, Socio. Methods & Res. 33(2): 261-304.

support. Therefore, the linear model has essentially no support when compared to the three-day model I developed, as it is more than 400 units above the three-day model. In simplest terms, the three-day turbidity model that I have presented here is far superior to a linear regression model of turbidity. Table 1, below, demonstrates the AIC score results between the linear regression model and the three-day model version. Table 2 contains the parameter estimates used for the coefficients in the three-day model formula.

Table 1. AIC score comparison: fits to daily normalized salvage

Model	**Linear**	**Three-day model version**
Number of Parameters	4	6
Number of observations	1880	1880
RSS	234	186
ln(likelihood)	-5,128	-4,914
AIC	**10,263**	**9,840**
Difference in AIC		**- 423**

Table 2.

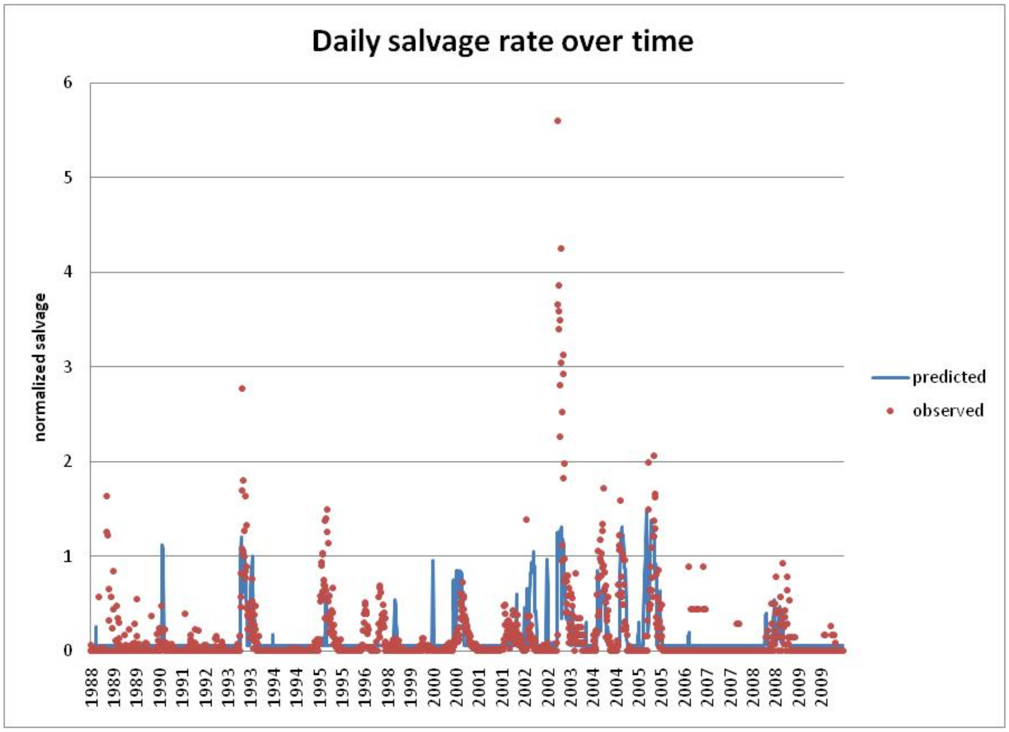
Coefficient	**Three-day average**
a	0.061
b	-0.00021
b'	402.21
TUR***	28.747
a'	-3590

12. Statistics fitting the three-day average turbidity and daily OMR flow in a multiple linear regression model to daily normalized salvage are calculated in Appendix 1. As seen in the tabled outputs, both turbidity and OMR flow are highly statistically significant covariates.

13. The huge improvement in AIC score (more than 600 units) by increasing model complexity (by adding the additional variable of turbidity and going non-linear) to the basic piece-wise approach described in paragraph 8 is statistically well-supported. Figure 2, below, plots both the actual observed daily normalized salvage of delta smelt for December-March 1988-2009, and also the normalized salvage that the three-day model would have predicted using the historic turbidity data. Predictions are based on the best fit of the model with prior three-day

average turbidity at Clifton Court and daily OMR flow to observed normalized salvage. As seen in Figure 2, the model predicts most of the days with increased normalized salvage (defined as salvage rate in the figure).

Figure 2.

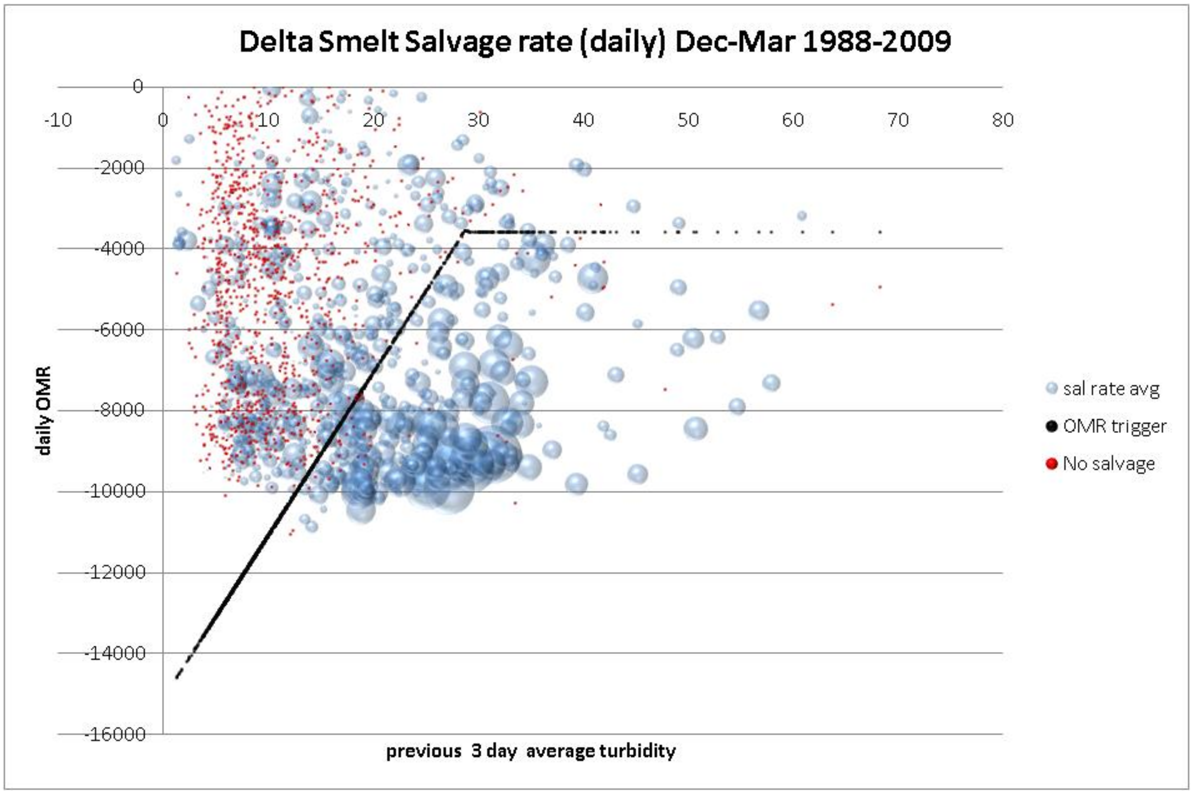


14. Figure 2 shows that the model using turbidity has a powerful ability to predict when salvage events will occur.

15. Figure 3, below, shows a bubble plot in which the OMR trigger is shown on the Y-axis as a function of prior three-day average turbidity on the X-axis, along with observed normalized salvage (the bubbles). Data is shown only if there are three previous days with turbidity estimates and it is restricted to days with negative daily OMR flow (for a total of 1880 days). The size of the bubbles is proportional to the amount of observed daily normalized salvage; the bigger the bubble, the larger the percentage of the population salvaged. As seen in Figure 3, most of the larger normalized salvage events (the larger bubbles) lie in the region that

the data suggests would be avoided by using the proposed OMR limits (i.e., the events in the region below and to the right of the OMR trigger would be avoided).

Figure 3.



16. Table 3, below, provides the specific numerical values of the proposed individual flow limits (based on the OMR trigger) for each unit of turbidity. The table also places the OMR flow limits in five-unit "bins." More specifically, a median OMR flow limit is shown for each five-unit range of turbidity levels greater than 15 and less than 30 (i.e., one flow limit is proposed for turbidity values of 16-20 and another for turbidity 21-25). These "bin" values are shown because it is my understanding they may be more operationally feasible than constantly changing flow limits with every single change in turbidity value. Limits are given for use with the previous three-day turbidity model, and the OMR flow limits were constrained at -9,000 for purposes of this table. While the OMR limit at turbidity levels of 15 and less would be more negative than -9000 cfs, this is based on an assumption that the projects would not be restricted in any other

way. I am informed, in fact, that there are a number of other limitations and practical restrictions that would necessarily limit OMR flows.[5] Thus, for purposes of Table 3, I constrained OMR limits to -9000 cfs for turbidity levels 1-15.

Table 3.

	Three-day turbidity model	
Bin size:	1-unit	5-unit
Turbidity	OMR limit	OMR limit
1-15	-9,000	-9,000
16	-8,717	-7,913
17	-8,315	
18	-7,913	
19	-7,510	
20	-7,108	
21	-6,706	-5,902
22	-6,304	
23	-5,902	
24	-5,499	
25	-5,097	
26	-4,695	-4,012
27	-4,293	
28	-3,891	
29	-3,590	
30+	-3,590	-3,590

17. The expected salvage rate corresponding to all OMR limits in Table 3 is 5.02 (i.e., the median salvage rate for the years 1988-2009 using the turbidity model). That is, we expect that about half of the time salvage rates will be above 5.02 if the daily flow controls are followed.

18. The three-day operational approach provides an approximate 58% reduction in adult normalized salvage when compared to the historical average for 1988-2009 (December through March). Stated another way, assuming the projects had been run historically according to

[5] I also understand that there are instances where turbidity may be isolated in Clifton Court Forebay, and that in these particular conditions smelt may not arrive at the project pumps. For instance, current conditions at Clifton Court Forebay show high levels of turbidity but no salvage has been occurring. My understanding is that the proposed interim remedy order submitted by Plaintiffs deals with this circumstance by providing for specific turbidity levels to be met at Prisoner's Point, Victoria Canal, and Holland Cut, in keeping with the use of those three monitoring stations in the Biological Opinion.

this proposal, the model predicts that the normalized salvage would have been 58% lower than what did occur. For the purpose of comparison, this reduction is better than the estimated 57% reduction in normalized salvage that would have occurred if flows had been continually limited to a flat -3,000 cfs (based on the average normalized salvage for daily OMR flows between -2,500 cfs and -3,500 cfs during December through March of 1988-2009). Therefore, this proposal provides for much more water, but also substantially reduces and avoids entrainment.

19. Based on my analyses, the data persuasively demonstrates that daily OMR flow limits are accurately calculated by utilizing three-day turbidity data and corresponding OMR flow limits.

IV. AN INCIDENTAL TAKE LIMIT (ITL) FOR ADULT DELTA SMELT SHOULD BE SET AT THE 80% UPPER CONFIDENCE INTERVAL UNDER LOG-NORMAL DISTRIBUTION

20. An incidental take limit is an amount of salvage that is greater than what is expected under normal operations and which requires consultation with the agency when and if it is exceeded. This paper proposes a method for calculating a proper ITL for adult smelt. In developing the proposed limit, I followed a two-part approach: i) estimate what the expected salvage rate would be in the future, and ii) find an amount above the expected rate that could serve as a trigger for further consultation.

21. My adult Delta smelt ITL calculations are based on the assumption that future daily flow controls are limited to those specified in my OMR recommendations in Section III above. The estimated salvage rates that would have occurred by following the daily flow controls were calculated for a subset of days[6] in the December through March time frame for the years 1988-2009. The average of the daily estimated salvage rates for a given water year were then multiplied by the total number of days in the time period December-March to obtain a season total salvage rate. Those rates are listed below in Table 4.

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[6] The subset consisted of days in which the previous three days had turbidity measurements and the current day had negative OMR flow.

Table 4. Winter adult salvage rates obtained by following daily flow controls and that are used in the calculation of confidence intervals

Year	Estimated Salvage Rate
1988	1.67
1989	12.28
1990	3.67
1991	3.40
1992	2.37
1993	9.21
1994	0.54
1995	23.46
1996	8.98
1997	25.20
1998	3.30
1999	2.44
2000	8.13
2001	9.50
2002	4.90
2003	14.30
2004	8.84
2005	4.93
2006	9.30
2007	0.93
2008	9.00
2009	1.10
Median Salvage Rate	5.02

22. With respect to this proposal, the median salvage rate for those 22 years using the turbidity model is 5.02. Given that 5.02 is the median, we expect that about half of the time salvage rates will be above 5.02 if the daily flow controls are followed.[7] This median is lower than the median in the smelt BiOp (i.e., more protective) because the three-day turbidity model is more effective at reducing and avoiding entrainment.

23. In order to determine a reasonable incidental take limit based on salvage rates, I propose using an upper one-sided confidence interval of 80% as an acceptable level of risk. I

[7] The ITL in the 2008 smelt BiOp is calculated using the average cumulative salvage index (BiOp at 287). That means that consultation will be triggered about 50% of the time, or roughly every other year.

understand that in discussions over acceptable levels of risk for various species, NMFS has relied upon 80%, and that this is a conservative number that favors the species relative to higher confidence intervals.[8] Using an 80% confidence level results in a salvage rate of 12.4. Correspondingly, the likelihood that the salvage rate for any given future year will exceed 12.4 is about 20% of the time provided the daily flow limit proposal is implemented.

24. That leads to the following proposed ITL:

Adult Incidental Take Limit = 12.4 * Prior year's FMWT index

To calculate the percentage of the population entrained at this take limit, I conservatively relied on the same estimates from a publication that was relied on in the BiOp, namely the Kimmerer 2008 study. I took the ratio of Kimmerer's estimates of annual adult entrainment to the annual normalized salvage for the years 1995-2006 (following the date range he used in his study) and calculated the median of those annual ratios. That median ratio is the coefficient used to scale the salvage rates into a percentage entrainment of the adult population.[9] When this estimate is performed, the proposed take limit effectively equates to 4.80% of the smelt population.

25. The above analysis demonstrates that based on my estimates of what expected salvage rates will be in the future, an ITL for adult Delta smelt should be set at the 80% upper confidence interval under log-normal distribution. Using an 80% upper confidence level will result in monitoring take levels and initiating reconsultation action in instances where take exceeds a modest 4.80%.

V. AN INCIDENTAL TAKE LIMIT (ITL) FOR JUVENILE DELTA SMELT SHOULD BE SET AT THE 80% UPPER CONFIDENCE INTERVAL UNDER LOG-NORMAL DISTRIBUTION

26. In my previous declaration (Doc. #455, ¶¶ 23-29), I presented several analyses that demonstrate there is no statistically significant relationship between OMR flows and juvenile Delta smelt salvage rates (juvenile salvage/20-mm survey index). The graph from page 13 of my

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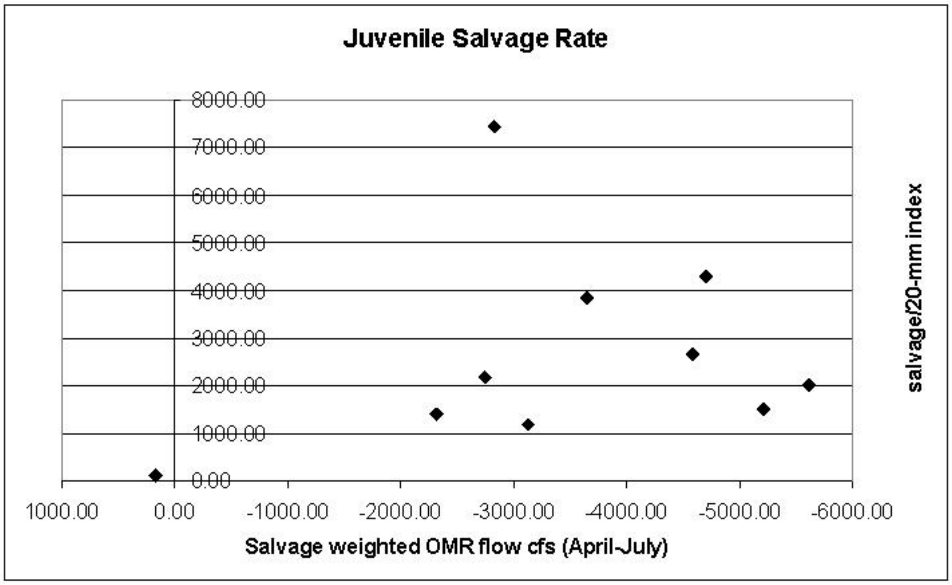
[8] Pers. comm. with Dr. Kenneth Burnham.

[9] While the underlying assumption of Kimmerer that entrainment is proportional to OMR flow remains unsupported for all the reasons set forth in my prior declarations (see Doc. 401 ¶¶ 71-76; Doc. 455 ¶16; Doc. 508 ¶¶ 10-22), Kimmerer's proportionality co-efficient, which contains expanded salvage data that includes other sources of mortality in Clifton Court Forebay, provides one way to translate the ITL into a percentage of the population.

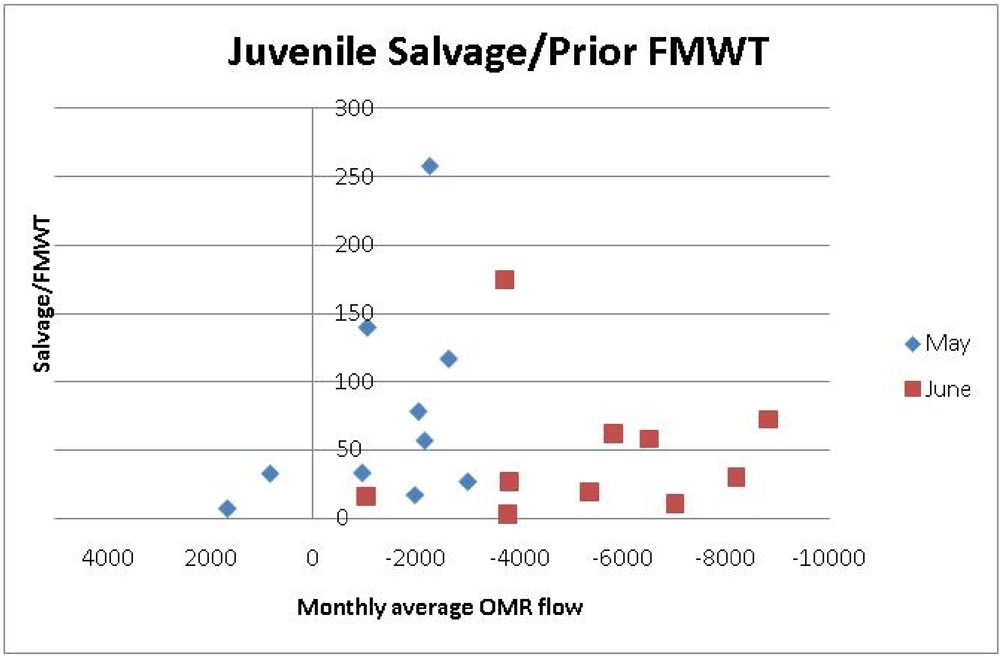
previous declaration is reproduced below as Figure 4 to show visually that there is no relationship between juvenile salvage rates and OMR flows.

Figure 4.



27. In Figure 5, below, I plotted monthly data for May and June, the two months where most salvage occurs. The y-axis is monthly salvage/previous FMWT (which is the juvenile salvage rate). OMR flows are given on the x-axis. As seen in Figure 5, there is no visual relationship between the monthly juvenile salvage rate and OMR.

Figure 5.



28. To calculate the Juvenile Salvage Index (JSI), I followed the approach discussed in the BiOp (page 389), which defined the Juvenile Salvage Index as:

Monthly Juvenile Salvage Index (JSI) = cumulative seasonal salvage ≥ 20 mm by month end divided by current WY FMWT Index

29. I constructed Table 5, below, to show the average JSI for years in which OMR flow in the spring was negative. Given that the data do not evidence a relationship between negative OMR flow and juvenile salvage rates, salvage rates located near the average value would be expected in the future, irrespective of any OMR flow controls that may be implemented. This leads to a proposed ITL calculation of:

Juvenile Incidental Take Limit = (upper 80% confidence interval JSI)* Prior year's FMWT index

Table 5. NOTE: The zero value for April 2005 was not used in the log-normal calculation.

Year	prior FMWT		Juvenile Salvage/prior FMWT				
			April	May	June	July	Apr-Jul
1995	102						
1996	899		0.12	33.81	10.50	0.16	44.60
1997	127		9.13	258.49	62.02	4.25	333.88
1998	303						
1999	420		1.02	140.31	174.69	47.20	363.21
2000	864		2.02	57.29	58.44	1.72	119.47
2001	756		0.69	17.42	3.20	0.01	21.31
2002	603		0.62	78.54	19.78	0.04	98.98
2003	139		3.63	117.33	72.63	0.09	193.68
2004	210		1.31	27.38	30.44	0.09	59.21
2005	74		0.00	7.39	15.96	0.00	23.35
2006	27						
2007	41		0.59	10.44	36.80	17.27	65.10
2008	28		0.14	33.21	27.04	0.50	60.89
2009	23		0.00	18.39	13.65	0.00	32.04
	Average		1.61	66.67	43.76	5.94	117.98
	stand dev		2.59	73.97	46.74	13.89	118.10
	JSI		1.61	68.27	112.03	117.98	117.98
			JSI for corresponding upper confidence interval of 80% under log-normal distribution				
	JSI Upper confidence interval of 80%		3.1	109.1	175.4	184.9	184.9
2011	Juvenile Incidental take limit based on 80% confidence interval and previous FMWT		89	3,164	5,087	5,362	5,362

30. All of the above analyses demonstrate that based on my estimates of what expected salvage rate will be in the future, and the calculation of a trigger for further consultation above that expected rate, ITLs for adult and juvenile Delta smelt should be set at the 80% upper confidence interval under log-normal distribution.

VI. LIFE CYCLE MODELING SHOWS THAT ENTRAINMENT IS NOT A SIGNIFICANT FACTOR IMPACTING THE SMELT POPULATION GROWTH RATE BUT THAT SEVERAL ENVIRONMENTAL FACTORS ARE

31. The foregoing discussion is designed to monitor and address entrainment of Delta smelt. The important issue remains over what is causing, and what may remedy, the population decline of the species. As both I and others have previously explained, a life cycle model is the common tool used for this type of population analysis.

32. Dr. Mark Maunder and I have used available data on the Delta smelt and developed a life cycle model; the results of the model provide important information that may be used for future management of the species. Specifically, the model indicates that food abundance, temperature, predator abundance, and density dependence are the most critical factors impacting the Delta smelt population—not entrainment from water export operations. See Exhibit A. (Mark Maunder and Richard Deriso, "A state-space multi-stage lifecycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt" (Dec. 27, 2010) (under review) (hereinafter "Maunder and Deriso")).

33. The model Dr. Maunder and I developed represents the different life cycle stages of the species (adult, larval, juvenile) and how the population abundance changes between stages. It models survival from one life stage to the next, as well as the stock-recruit relationship between adults and larvae. It allows multiple factors or covariates (including factors relating to environmental conditions and mortality rates based on entrainment) to influence the survival and stock-recruit relationships. Each factor represents a hypothesis about what conditions or events make a difference for smelt survival and recruitment.

34. The survey data upon which the model is based spans the period 1972 to 2006. It comes from Manly 2010[10] and Nations 2007,[11] and includes: the 20mm trawl survey (1995 to 2006) [larvae]; the Summer tow net survey (1972 to 2006) [juveniles]; and the Fall mid-water trawl survey (1972 to 2006, but no data for years 1974 and 1979) [pre-adults]. The Spring Kodiak trawl survey was not used because it was only recently initiated and does not go back enough years. The environmental data examined with the model were taken from Manly 2010, with the exception of secchi depth data, which Dr. Manly provided in a personal communication. All survey and environmental data is set forth in Tables S1 and S2 in Maunder and Deriso. Maunder and Deriso at pps. 69-74. Entrainment rates (i.e., normalized salvage) were

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[10] Manly, B.F.J. 2010. Initial analyses of delta smelt abundance changes from Fall to Summer, Summer to Fall, and Fall to Fall. Western EcoSystems Technology, Inc. 2003 Central Avenue, Cheyenne, Wyoming, 82001, unpublished report.

[11] Nations, C. 2007. Variance in Abundance of Delta Smelt from 20 mm Surveys. Western EcoSystems Technology, Inc. 2003 Central Avenue, Cheyenne, Wyoming, 82001, unpublished report.

conservatively estimated by fitting regression models based on OMR flow to the entrainment estimates in Kimmerer (2008).[12]

35. We fit the model to the data, and used a model selection procedure to determine which factors (covariates) are important for explaining changes in smelt survival and recruitment. That procedure involved using Akaike Information Criterion (AIC) to rank models that included different mixes of co-variates based on the strength of evidence in the data for including each co-variate in the better models.

36. Through this winnowing process, testing multiple co-variates and multiple combinations of co-variates, we determined that of all the factors we tested, food abundance, temperature, predator abundance, and density dependence are the most important factors controlling the population dynamics of delta smelt. Maunder & Deriso at p. 31. Survival is positively related to food abundance and negatively related to temperature and predator abundance. Maunder & Deriso at p. 31. The model selection procedure did not select entrainment in the larval-juvenile life stage as an important factor affecting the population growth rate. While we found some support for adult entrainment as a factor affecting the population growth rate, it was not one of the main factors and the coefficient was unrealistically high and highly negatively correlated with the coefficient for water clarity. Maunder & Deriso at p. 31. Impact analysis further showed that if adult entrainment has any effect on smelt population growth rate, it is minor. Maunder & Deriso at p. 24.

37. These results indicate that the use of the turbidity-based approach for limiting increases in the adult smelt entrainment rate, described above, is a conservative approach that errs on the side of protecting the species. More generally, the data shows that imposing restrictions on the projects to avoid entrainment is not a sensible approach to improving the smelt population and that, instead, efforts should be focused on addressing environmental conditions affecting the species, such as its food supply.

[12] 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 Watershed Science 6(2): 1-27.

I declare under penalty of perjury under the laws of the State of California and the United States that the foregoing is true and correct and that this declaration was executed on January 28, 2011 at Del Mar, California.

DR. RICHARD B. DERISO

Appendix

Appendix 1. Statistics Fitting the Average Turbidity and Daily OMR Flow in a Multiple Linear Regression Model to Daily Normalized Salvage

Statistics fitting the three-day average turbidity and daily OMR flow in a multiple linear regression model to daily normalized salvage are shown below in Table 1. As seen in the tabled outputs, both turbidity and OMR flow are highly statistically significant covariates.

Table 1. SUMMARY OUTPUT for linear regression of daily normalized salvage

Regression Statistics				
Multiple R	0.44		multiple linear regression	
R Square	0.20		for normalized salvage	
Adjusted R Square	0.20			
Standard Error	0.35			
Observations	1880			
ANOVA				
	df	*SS*	*MS*	*F*
Regression	2	57.16	28.58	229.33
Residual	1877	233.91	0.12	
Total	1879	291.07		
	Coefficients	*Standard Error*	*t Stat*	***P-value***
Intercept	-2.74E-01	2.25E-02	-1.22E+01	**6.78E-33**
turbidity 3-day average	1.69E-02	9.48E-04	1.78E+01	**6.87E-66**
Daily OMR	-3.29E-05	3.05E-06	-1.08E+01	**2.54E-26**

Appendix 2. Details on the Calculation of Upper Confidence Intervals

The one-sided confidence interval I calculated for the proposed ITL is based on a t-test statistic for testing whether the means of two distributions are equal. The test statistic is based on the assumptions that the two distributions have equal variances and samples are of different sample size. In this application, one of the distributions represents salvage rate in a future year for a single year. The other distributions are historical samples. The test statistic is:

$$t = \frac{(x_2 - \bar{x}_1)}{S\sqrt{1 + \frac{1}{N}}}$$

In the above calculation, the sample mean of the historical data is $\bar{x}_1$, the standard deviation of the historical data is *S*, the single sample from a future year is x_2, and sample size is *N*. The t-statistic has N-1 degrees of freedom. The application in this paper uses the equation above for a given *t* value to solve for the corresponding x_2. For example, with N=9 and upper one-sided confidence interval probability of 0.95, the *t* value is 1.86. Substitute 1.86 in the equation above along with estimates of the sample mean and standard deviation then solve for the x_2 which would be the salvage rate at the upper one-sided 95% confidence interval. For the log-normal distribution the data were log-transformed to calculated confidence intervals which were then back transformed.

CERTIFICATE OF SERVICE

I hereby certify that on January 28, 2011, I electronically filed the foregoing with the Court by using the Court's CM/ECF system.

Participants in the case who are registered CM/ECF users will be served by the Court's CM/ECF system.

I further certify that the court-appointed experts are not registered CM/ECF users. I have emailed the foregoing document to the following:

DECLARATION OF DR. RICHARD B. DERISO IN SUPPORT OF PLAINTIFFS' MOTION FOR INJUNCTIVE RELIEF

SERVICE LIST

Dr. André Punt University of Washington School of Aquatic and Fishery Sciences P.O. Box 355020 Seattle, WA 98195 *ThePuntFam@aol.com*	Dr. Thomas Quinn University of Washington School of Aquatic and Fishery Sciences P.O. Box 355020 Seattle, WA 98195 *TQuinn@U.Washington.edu*

I declare under penalty of perjury under the laws of the State of California the foregoing is true and correct and that this declaration was executed on January 28, 2011, at San Francisco, California.

/s/ Jennifer P. Doctor
Jennifer P. Doctor
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Exhibit A

Exhibit A

A state-space multi-stage lifecycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt

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Abstract

Multiple factors acting on different life stages influence population dynamics and complicate the assessment and management of populations. To provide appropriate management advice, the data should be used to determine which factors are important and what life stages they impact. It is also important to consider density dependence because it can modify the impact of some factors. We develop a state-space multi-stage life cycle model that allows for density dependence and environmental factors to impact different life stages. Models are ranked using a two-covariate-at-a-time stepwise procedure based on AICc model averaging to reduce the possibility of excluding factors that are detectable in combination, but not alone. Impact analysis is used to evaluate the impact of factors on the population. The framework is illustrated by application to delta smelt, a threatened species that is potentially impacted by multiple anthropogenic factors. Our results indicate that density dependence and a few key factors impact the delta smelt population. Temperature, prey, and predators dominated the factors supported by the data and operated on different life stages. The included factors explain the recent declines in delta smelt abundance and may provide insight into the cause of the pelagic species decline in the San Francisco Estuary.

Key words: delta smelt; density dependence; model selection; population dynamics; state-space model;

Introduction

Multiple factors acting on different life stages influence population dynamics and complicate the assessment and management of natural populations. To provide appropriate management advice, the available data should be used to determine which factors are important and what life stages they impact. It is also important to consider density dependent processes because they can modify the impact of some factors and the strength of density dependence can vary among life stages. Management can then better target limited resources to actions that are most effective. Unfortunately, the relationships among potential factors, the life stages that they influence, and density dependence are often difficult to piece together through standard correlation or linear regression analyses.

Life cycle models are an essential tool in evaluating factors influencing populations of management concern (Buckland et al. 2007). They can evaluate multiple factors that simultaneously influence different stages in the presence of density dependence. They also link the population dynamics from one time period to the next propagating the information and uncertainty. This link allows information relating to one life stage (i.e., abundance estimates) to inform processes influencing other life stages and is particularly important when data is not available for all life stages for all time periods. The life cycle model should be fit to the available data to estimate the model parameters, including parameters that represent density dependence, and determine the data based evidence of the different factors that are thought to influence the population dynamics. Finally, the model should be used to direct research or provide management advice.

Deriso et al. (2008) present a framework for evaluating alternative factors influencing the dynamics of a population. It extends earlier work by Maunder and

Watters (2003), Maunder and Deriso (2003), and Maunder (2004) and is similar to approaches taken by others (e.g., Besbeas et al. 2002; Clark and Bjornstad 2004; Newman et al. 2006). The Deriso et al. framework involves several components. First, the factors to be considered are identified. Second, the population dynamics model is developed to include these factors and then fitted to the data. Third, hypothesis tests are performed to determine which factors are important. Finally, in order to provide management advice, the impact of the factors on quantities of management interest, are assessed. They illustrate their framework using an age-structured fisheries stock assessment model fit to multiple data sets. Their application did not allow for density dependence in the population dynamics, except through the effect of density on the temporal variation in which ages are available to the fishery.

Inclusion of density dependence is important in evaluating the impacts on populations. Without density dependence, modeled populations can increase exponentially. This is unrealistic and can also cause computational or convergence problems in fitting population dynamics models to data. Density dependence can also moderate the effects of covariates. This is important because factors affecting density independent survival may be much less influential in the presence of density dependence compared to factors that affect carrying capacity (e.g., habitat). It is also important to correctly identify the timing of when the factors influence the population with respect to the timing of density dependence processes and available data. The approach also provides a framework for amalgamating the two paradigms of investigating population regulation outlined by Krebs (2002); the density paradigm and the mechanistic paradigm.

Here we develop a life cycle model that allows for density dependence at multiple life stages and allows for factors to impact different life stages. We apply the framework of Deriso et al. (2008) where the first component also includes identifying the life stages that are impacted by each factor and where density dependence occurs. We illustrate the framework by applying it to Delta smelt. Delta smelt is an ideal candidate to illustrate the modeling approach because there are several long-term abundance time series for different life stages and a range of hypothesized factors influencing its survival for which covariate data is available. Life cycle models have been recommended to evaluate the factors effecting delta smelt (Bennett 2005; Mac Nally et al. 2010; Thomson et al. 2010).

Delta smelt is of particular management concern due to declines in abundance and the myriad of anthropogenic factors that could be causing the decline. Delta smelt is endemic to the San Francisco Estuary, which has multiple stressors including habitat modification, sewage outflow, farm runoff, and water diversions, to name just a few. Delta smelt was listed as threatened under the U.S. and California Endangered Species Acts in 1993. Several other pelagic species in the San Francisco Estuary have also experienced declines, but the factors causing the declines are still uncertain (Bennett 2005; Sommer et al. 2007). Recent studies have investigated the factors hypothesized to have caused the declines at both the species and ecosystem level, but the results were not conclusive (Mac Nally et al. 2010; Thomson et al. 2010).

Materials and Methods

Model

The model is stage based with consecutive stages being related through a function that incorporates density dependence. For simplicity and to be consistent with the predominant dynamics of delta smelt, we assume an annual life cycle. However, it is straightforward to extend the model to a multiple year life cycle or to stages that cover multiple years (i.e., adding age structure; e.g., Rivot et al. 2004; Newman and Lindley 2006). Within a year the number of individuals in each stage is a function of the numbers in the previous stage. The number of individuals in the first stage is a function of the numbers in the last stage in the previous year (i.e., the stock-recruitment relationship), except for the numbers in the first stage in the first year, which is estimated as a model parameter. The functions describing the transition from one stage to the next are modeled using covariates. A state space model (Newman 1998; Buckland et al. 2004; Buckland et al. 2007) is used to allow for annual variability in the equation describing the transition from one life stage to the next. Traditionally, state space models describe demographic variability (e.g., using a binomial probability distribution to represent the number of individuals surviving based on a given survival rate; e.g., Dupont 1983; Besbeas et al. 2002) however environmental variability generally overwhelms demographic variability (Buckland et al. 2007) so we model the process variability (e.g., Rivot et al. 2004; Newman and Lindley 2006) using a lognormal probability distribution (Maunder and Deriso 2003). Our approach differs from modeling the log abundance and assuming additive normal process variability (e.g., Quinn and Deriso 1999, page 103) and the population dynamics function models the expected value rather than the median. The difference in the expectation will simply be a scaling factor ($\exp[-0.5\sigma^2]$) unless the variance of the process variability changes with time.

(1) $$N_{t,s} \sim \text{Lognormal}\left(f\left(N_{t,s-1}\right), \sigma_{s-1}^2\right) \qquad s > 1$$

(2) $$N_{t,1} \sim \text{Lognormal}\left(f\left(N_{t-1,nstages}\right), \sigma_{nstages}^2\right)$$

Where t is time, s is stage, *nstages* is the number of stages in the model, and σ_s is the standard deviation of the variation not explained by the model (process variability) in the transition from stage s to the next stage.

The three parameter Deriso-Schnute stock-recruitment model (Deriso 1980; Schnute 1985) is used to model the transition from one stage to the next. The Deriso-Schnute model is a flexible stock-recruitment curve in which the third parameter (γ) can be set to represent the Beverton-Holt ($\gamma = -1$) and Ricker ($\gamma \to 0$) stock-recruitment models (Quinn and Deriso 1999, page 95).

(3) $$f\left(N\right) = aN\left(1 - b\gamma N\right)^{\frac{1}{\gamma}}$$

where the parameter a can be interpreted as the number of recruits per spawner at low spawner abundance or the survival fraction at low abundance levels. In cases for which only the relative abundance at each stage can be modeled (as in the delta smelt example), a also contains a scaling factor from one survey to the next. The parameter b determines how the number of recruits per spawner or the survival rate decreases with abundance. Constraints can be applied to the parameters to keep the relationship realistic: $a \geq 0$, b $\geq$

0. The additional constraint $a \leq 1$ can be applied when the relationship is used to describe survival and the consecutive stages are modeled in the same units.

Covariates are implemented to influence the abundance either before density dependence [$g(N,x)$] or after density dependence [$h(x)$]. Although, when no density dependence is present the two methods are identical.

(4) $$f(N) = ag(N,x)(1 - b\gamma g(N,x))^{\frac{1}{\gamma}} h(x)$$

(5) $$g(N,x) = N \exp\left[\sum \lambda x\right]$$

(6) $$h(x) = \exp\left[\sum \beta x\right]$$

Where λ and β are the coefficients of the covariate (x) for before and after density dependence, respectively, and are estimated as model parameters.

For survival it might be important to keep the impact of the environmental factors within the range 0 to 1 and the logistic transformation can be used, e.g.,

(7) $$ag(N,x) = N \frac{\exp\left[a' + \sum \lambda x\right]}{1 + \exp\left[a' + \sum \lambda x\right]}$$

Where the parameter a' defines the base level of survival (i.e. $a = \frac{\exp[a']}{1 + \exp[a']}$) and replaces a of the density dependence function.

If the covariate values are all positive, the negative exponential can be used, e.g.,

$$(8) \qquad g(N,x) = N\exp\left[-\sum \lambda x\right] \qquad\qquad \lambda \geq 0 \quad x \geq 0$$

A combination of the above three options may be appropriate depending on the application.

The importance of the placement of the covariates (i.e., before or after density dependence) relates to both the timing of density dependence and the timing of the surveys, which provide information on abundance. Covariates could be applied to the other model parameters. For example, covariates that are thought to be related to the carrying capacity (e.g., habitat) could be used to model *b*.

The model is fit to indices of abundance ($I_{t,s}$). The abundance indices are assumed to be normally distributed, but other sampling distributions could be assumed if appropriate. Typically, if the index of abundance is a relative index and not an estimate of the absolute abundance, the model is fit to the index by scaling the model's estimate of abundance using a proportionality constant (*q*, often called the catchability coefficient) (Maunder and Starr 2003).

$$(9) \qquad I_{t,s} \sim \text{Normal}\left(qN_{t,s}, \nu_{t,s}^2\right)$$

However, the scaling factor is completely confounded with the *a* parameter of the Deriso-Schnute model and therefore the population is modeled in terms of relative abundance that is related to the scale of the abundance indices for each life stage and only makes sense in terms of total abundance if the abundance indices are also in terms of total abundance. Therefore, the proportionality constant (q) should be set to one. Other data could also be used in the analysis if appropriate (e.g., information on survival from mark-recapture studies; Besbeas et al. 2002; Maunder 2004).

Model parameters to estimate

The model parameters estimated include the initial abundance of the first stage $N_{1,1}$, the parameters of the stock-recruitment model for each stage $\mathbf{a}, \mathbf{b}, \boldsymbol{\gamma}$, the coefficients of the covariates $\boldsymbol{\lambda}, \boldsymbol{\beta}$, the standard deviation of the process variability for each stage $\boldsymbol{\sigma}$, and the standard deviation of the observation error (used in defining the likelihood function) for each index of abundance $\mathbf{v}$. The observation error standard deviation, $\mathbf{v}$, is often fixed based on the survey design or restricted so that there is not a parameter to estimate for each survey and time period (e.g. Maunder and Starr 2003). The state space model can be implemented by treating the process variability as random effect parameters (de Valpine 2002). The likelihood function that is optimized is calculated by integrating over these parameters (Skaug 2002; Maunder and Deriso 2003). Therefore, they are not treated as parameters to estimate. However, realizations of the random effects can be estimated by using empirical Bayes methods (Skaug and Fournier 2006) so that the unexplained process variation can be visualized. The estimated parameters of the model are:

$$\text{Parameters} = \{N_{1,1}, \mathbf{a}, \mathbf{b}, \boldsymbol{\gamma}, \boldsymbol{\lambda}, \boldsymbol{\beta}, \boldsymbol{\sigma}, \mathbf{v}\}$$

Implementation in AD Model Builder

Dynamic models like the multistage life cycle model described here can be computationally burdensome if they are carried out in a state-space modeling framework (i.e., integrating over the state-space or equivalently the process variability) and efficient parameter estimation is needed if multiple hypotheses are being tested. Implementation is facilitated by the use of Markov chain Monte Carlo and related methods (Newman et al. 2009) and their use has increased in recent years (Lunn et al. 2009). In particular, authors have found a Bayesian framework convenient for implementation (Punt and Hilborn 1997). An alternative approach is to use the Laplace approximation to implement the integration (Skaug 2002). AD Model Builder (http://admb-project.org/) has an efficient implementation of the Laplace approximation using automatic differentiation (Skaug and Fournier 2006). The realizations of the random effects are estimated by using empirical Bayes methods adjusted for the uncertainty in the fixed effects (Skaug and Fournier 2006). ADMB was originally designed as a function minimizer and therefore likelihoods are implemented in terms of negative log-likelihoods and probability distributions are implemented in terms of negative log-probabilities. A more complete description of ADMB and its implementation of random effects can be found in Fournier et al. (in review).

The population is modeled using random effects to implement the state space model (de Valpine 2002)

(12) $$N_{t,s} = f\left(N_{t,s-1}\right)\exp\left[\sigma_{s-1}\varepsilon_{t,s-1} - 0.5\sigma_{s-1}^{2}\right]$$

(13) $$N_{t,1} = f\left(N_{t-1,nstages}\right)\exp\left[\sigma_{nstages}\varepsilon_{t-1,nstages} - 0.5\sigma^2_{nstages}\right]$$

(14) $$\varepsilon_{t,s} \sim N(0,1)$$

A penalty is added to the objective function to implement the random effects,

(15) $$\sum_{t,s}\varepsilon^2_{t,s} .$$

The negative log-likelihood function for the abundance indices ignoring constants is

(16) $$-\ln[L] = \sum_{t,s}\ln[v_{t,s}] + \frac{\left(I_{t,s} - qN_{t,s}\right)^2}{2v^2_{t,s}}$$

Model selection

Model selection (Hilborn and Mangel 1997) can be used to determine if the data supports density dependence for a particular stage or the factors that impact the population dynamics. In our analysis different models are represented by different values of the model parameters. The relationship between one stage and the next is density independent if $b = 0$. Therefore, a test for density dependence tests if $b = 0$. When $b = 0$, $\boldsymbol{\gamma}$ has no influence on the results and unless a hypothesis about $\boldsymbol{\gamma}$ is made (i.e., Beverton-Holt, $\gamma = -1$ or Ricker, $\gamma \to 0$), testing between density independence and density dependence requires the estimation of two additional parameters ($b, \boldsymbol{\gamma}$). A factor has no influence on the model when its coefficient ($\boldsymbol{\lambda}, \boldsymbol{\beta}$) is fixed at zero. Therefore, testing a factor requires estimating one parameter for each factor tested. There are a variety of methods available for model selection and hypothesis testing, each with their own set of issues (e.g., Burnham and Anderson 1998; Hobbs and Hilborn 2006). Given these issues, we rely on Akaike information criteria adjusted for sample size (AICc) and AICc weights to rank models and provide an idea of the strength of evidence in the data about an a priori set of alternative hypotheses (factors) but they are not used as strict hypothesis tests (Andersen et al. 2000; Hobbs and Hilborn 2006).

The AIC is useful for ranking alternative hypotheses when multiple covariates and density dependence assumptions are being considered. The AICc (Burnham and Anderson 2002), is given by

(10) $$AIC_c = -2\ln L + 2K + \frac{2K(K+1)}{n-K-1}$$

where L is the likelihood function evaluated at its maximum, K is the number of parameters, and n is the number of observations. A better model fit is one with a smaller AICc score.

AIC weights are often used to provide a measure of the relative support for a model and to conduct model averaging (Hobbs and Hilborn 2006). AIC weights are essentially the rescaled likelihood penalized by the number of parameters, which is considered the likelihood for the model (Anderson et al. 2000).

(11) $$w_i = \frac{\exp[-0.5\Delta_i]}{\sum_j \exp[-0.5\Delta_j]}$$

Where Δ is the difference in the AICc score from the minimum AICc score.

The correct modeling of observation and process variability (error) is important for hypothesis testing. If process variability is not modeled, likelihood ratio and AIC based tests are biased towards incorrectly accepting covariates (Maunder and Watters 2003). Other tests, such as randomization tests, should be used if it is not possible to model the additional process variability (e.g., Deriso et al. 2008). Incorrect sampling distribution assumptions (e.g., assumed values for the variance) can influence the covariate selection process and the weighting given to each data set can change which covariates are chosen (Deriso et al 2007). If data based estimates of the variance are not available, estimating the variances as model parameters or using concentrated likelihoods is appropriate (Deriso et al. 2007). Missing covariate data need to be dealt with appropriately, such as by using the methods described in Gimenez et al. (2009) and Maunder and Deriso (2010).

Parameter estimation of population dynamics models generally requires iterative methods, which take longer than calculations based on algebraic solutions, and therefore limit the number of models that can be tested (Maunder at al. 2009). This is problematic when testing hypotheses because, arguably, all possible combinations of the covariates and density dependent possibilities should be evaluated. All possible combinations should be used because a covariate by itself may not significantly explain process variation, but in combination they do (Deriso et al. 2008) and some covariates may only be significant if density dependence is taken into consideration. However, modeling of process variability, as we suggest, may minimize this possibility. In many cases, time and computational resource limitations may prevent testing all possible combinations and therefore we suggest the strategy described in Table 1.

We stop evaluating covariates when the lowest AICc model in the current iteration is at least 4 AICc units higher than the model with the lowest overall AICc (step 2e). The approach is based on a compromise between eliminating models for which *there is definite, strong, or very strong evidence that the model is not the K-L best model* ($4 \leq \Delta$)) and the fact that there is a maximum Δ when adding covariates to the lowest AICc model. We have chosen to carry out the selection process by using the sum of the AICc weights over all models that include the corresponding factor (step 2d). This selection process chooses factors that have high support in general, work in combination with other factors, and are therefore less likely to preclude additional factors in subsequent steps. This approach embraces the multiple hypothesis weight of evidence framework and is somewhat consistent with model averaging. We also remove models for which any of the estimated covariate coefficients are the incorrect sign as assumed a priori (step 2b). Modification of this procedure may be needed depending on the available computational resources, the number of covariates and model stages, and the relative difference in the weight of evidence among models.

Burnham and Anderson (2002) note that in general, there are situations where choosing to make inferences using a model other than the lowest AICc model can be justified (page 330) based on professional judgment, but only after the results of formal selection methods have been presented (page 334). For example, model parameterizations that do not make sense biologically might be eliminated from consideration. Burnham and Anderson (2002) give an example (page 197) where a quadratic model is rejected because it could not produce the monotonic increasing dose response that was desired. Sometimes AICc will select a model that fits to quirks or noise in the data but does not provide a useful model. The selected best model is a type of estimate, and so like a parameter estimate it can sometimes be a poor estimate (Ken Burnham, Colorado State University, personal communication).

Parameter estimates from stock recruitment models in integrated assessments are often biased towards extremely strong density dependent survival (recruitment is independent of stock size) (Conn et al. 2010) and this is unrealistic for stocks that have obtained very low population sizes. We therefore identify values of the Deriso-Shnute stock-recruitment relationship (for the Beverton-Holt and Ricker special cases) *b* parameter that are realistic (see Appendix). We assume that recruitment (or the individuals surviving) can’t be greater than 80% of that expected from the average population size when the population is at 5% of the average population size seen in the surveys during the period studied. Models with unrealistic density dependence are given zero weight in that step of the model selection prodecure (step 2b).

Impact analysis

To determine the impact of the different factors on the stock, we conducted analyses using values of the covariates modified to represent a desired (e.g. null) effect. Following Deriso et al. (2008) these analyses were conducted simultaneously within the code of the original analyses so that the impact assessments shared all parameter values with the original analyses. This allowed estimation of uncertainty in the difference between the models with the covariate included and with the desired values of the covariate. The results are then compared for the quantities of interest, which may be a derived quantity other than the covariate's coefficients. For example, if a covariate is related to some form of mortality, the coefficient is set to zero to determine what the abundance would have been in the absence of that mortality (e.g., Wang et al. 2009).

Application to Delta smelt

The multi-stage lifecycle model is applied to delta smelt to illustrate the application of the model, covariate selection procedure, and impact analysis. Delta smelt effectively live for one year and one spawning season. Some adults do survive to spawn a second year, but the proportion is low (Bennett 2005) and we ignore them in this illustration of the modeling approach. The delta smelt life cycle is broken into three stages (Figure 1). The model stages are associated with the timing of the three main surveys, (1) 20mm trawl (20mm), (2) summer tow net (STN), and (3) fall mid-water tow (FMWT), and roughly correspond to the life stages larvae, juveniles, and adults, respectively. The reason for associating the model stages with the surveys is because the surveys are the only data used in the model and therefore information is only available on processes operating between the surveys. The population is modeled from 1972 to 2006 because these are the years for which data for most of the factors are available. The STN abundance index is available for the whole time period. The FMWT abundance index is available for the whole time period except for 1974 and 1979. The 20mm abundance index is only available starting in 1995. Other survey data are available (e.g., the Spring Kodiak trawl survey), but they are not used in this analysis.

The FMWT and STN survey indices of abundance are the estimates taken from Manly (2010b) tables 2.1 and 2.2. The standard errors were calculated by bootstrap procedures (Manly, 2010a). The 20mm survey index was taken from Nations (2007). The index values and standard errors are given in the supplementary material. The results of the bootstrap analysis suggest that the abundance indices are normally distributed (Manly 2010a).

Two types of factors are used in the model (Table 2). The first are standard factors relating to environmental conditions. The second are mortality rates based on estimates of entrainment at the water pumps. The mortality rates are converted to the appropriate scale to use in the model. Let u represent the mortality fraction such that the survival fraction is $1-u=\exp[\beta x]$ and x will be used as a covariate in the model. Setting $\beta=1$ gives $x=\ln[1-u]$.

Several factors were chosen for inclusion in the model (Table 3). These factors are used for illustrative purposes only and they may differ in a more rigorous investigation of the factors influencing delta smelt. The environmental factors are taken as those proposed by Manly (2010b). The entrainment mortality rates are calculated based on Kimmerer (2008); the rates were obtained by fitting a piece-wise linear regression model of winter Old Middle River (OMR) flow to his adult entrainment estimates and his larval/juvenile entrainment estimates were fitted to a multiple linear regression model with spring OMR flow and spring low salinity zone (as measured by X2). The values from Kimmerer (2008) were used for years in which they are available and the linear regression predictions were used for the remaining years. Manly (2010b) provided several variables as candidates to account for the changes in delta smelt abundance from fall to summer and summer to fall. The fall to summer covariates could influence the adult and larvae stages, while the summer to fall covariates could influence the juvenile stage. The factors proposed by Manly (2010b) are those that are considered to act directly on delta smelt. There are many other proposed factors that act indirectly through these factors. We also include secchi disc depth as a covariate for water turbidity/clarity since it was identified as a factor by Thomson et al. (2010). Exports were also identified as an important factor and were assumed to be related to entrainment. However, we chose to use direct measures of entrainment. Interactions among the factors were not considered in the application. However, some of the covariates implicitly include interactions in their definition and construction.

Some manipulation of the data was carried out before use in the model (the untransformed covariates values used in the model are given in the supplementary material). Delta smelt average length was missing for 1972-1974, 1976, and 1979, and was set to the mean based on Maunder and Deriso (2010). The factors were normalized (mean subtracted and divided by standard deviation) to improve model performance, except for the covariates relating to predator abundance, which were just divided by the mean, and the entrainment mortality rates, which were not transformed. These exceptions are factors that are hypothesized to have a have a unidirectional impact and setting their coefficients to zero is needed for impact analysis. Setting the coefficient for the entrainment mortality rate covariates to one can be used to determine the impact if the entrainment estimates are assumed to be correct.

The standard approach outlined above and in table 1 is applied to the delta-smelt application. The Ricker model was approximated by setting $\gamma = -\exp[-10]$. We also constrained $\gamma < 0$ to avoid computational errors. It is difficult to scale the survey data to absolute abundance, so they are all treated as relative abundance and are not on the same scale. The scaling parameter a is not limited to $a \leq 1$ and the exponential model is used for all covariates. To illustrate the impact analysis, we implement three scenarios. In the first scenario, the covariates are all set to zero. This means that environmental conditions are average, predation is zero, and entrainment is zero. We implement the second scenario if one or both of the entrainment covariates are selected for inclusion in the model. In this case, only the entrainment coefficients are set to zero. In the third scenario we take the final set of covariates and add the entrainment covariates (or substitute them if they we already included in the model) with their coefficients set to one and rerun the model. In this case, only the entrainment coefficients are set to zero in the impact analysis.

Results

AICc values and weights were calculated for all possible combinations of density dependence that included no density dependence (No), a Beverton-Holt Model (BH), a Ricker model (R), and estimation of both b and γ (DD) (Table 3). Density dependence was clearly preferred for survival from juveniles to adults (J), but it is not clear if the density dependence is Beverton-Holt, Ricker, or somewhere in between. The Beverton-Holt and Ricker models for juvenile survival appear to be influenced by three consecutive data points (years 1976-1978) of high juvenile abundance with corresponding average adult abundance (Figures 2 and 3). The evidence for and against density dependence is about the same for the stock-recruitment relationship from adults to larvae (A). With slightly more evidence for no density dependence if survival from juveniles to adults is Beverton-Holt and slightly more evidence for Beverton-Holt density dependence if the survival from juveniles to adults is Ricker. The evidence for no density dependence in survival from larvae to juveniles (L) is moderately (3 to 4 times) higher than for density dependence. Therefore, we proceed with four density dependence scenarios: (1) Beverton-Holt density dependence in survival from juveniles to adults (JBH); and (2) Beverton-Holt density dependence in survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship from adults to larvae (JBHABH); (3) Ricker density dependence in survival from juveniles to adults (JR); and (4) Ricker density dependence in survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship from adults to larvae (JRABH).

The number and the type of factors supported by the data depended on the assumptions made about density dependence (Tables 4 and 5). The models with density dependence for both survival from juveniles to adults and a stock recruitment relationship for adults to larvae included more covariates in the lowest AICc models (8 and 9 covariates for Beverton-Holt and Ricker density dependence in survival from juveniles to adults, respectively) than the models that included only density dependence for survival from juveniles to adults (5 covariates each). Several temperature, prey and predator covariates (TpAJ, EPAJ, EPJA, TpJul, Pred1) were selected in the first few steps and were included in all models. The April-June abundance of predators (Pred2) was selected in the first few steps in one model, but not selected at all in the others.

Overall, the model with Ricker density dependence in survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship from adults to larvae had better AICc scores than the other models (Table 5). This differs from the similarity in scores obtained when no covariates were included in the models (Table 3). For all density dependent assumptions, there were alternatives with more (or less) covariates than the lowest AICc model (within the models for that density dependence assumption), for which there was not *definite, strong, or very strong evidence that the model is not the K-L best model* ($4 \le \Delta$) suggesting that these factors should also be considered as possible factors that influence the population dynamics of delta smelt (Table 5). Although, the asymmetrical nature of the AICc scores for nested models should be kept in mind.

The magnitude and the sign of the covariate coefficients are generally consistent across models (Table 6). The covariates were standardized so that the size of the coefficients are generally comparable across covariates. The coefficients are similar magnitudes for most covariates except those for water clarity (Secchi) and, particularly, adult entrainment (Aent), which had much larger effects. These both occurred before the stock-recruitment relationship from adults to larvae, which had a very strong density dependence effect. Pred2 had a small effect. The confidence intervals on the coefficients support inclusion of the covariates in the lowest AICc models except for Pred2 (Table 6). The effects for Secchi and Aent appear to be unrealistically large and their coefficients have a moderately high negative correlation. This appears to be a consequence of the unrealistically strong density dependence estimated in the stock-recruitment relationship from adults to larvae for those models (see Table S6).

The five lowest AIC_c models in iteration 6 of the two factors at a time procedure had a *b* parameter of the Beverton-Holt stock recruitment relationship from adult to larvae that was substantially greater than the critical value used to define realistic values of the parameter. The sixth model had an AIC of 812.53, which is worse than the lowest AICc model of iteration 5. The lowest AICc model with Beverton-Holt survival from juveniles to adults and Beverton-Holt stock recruitment relationship from adult to larvae also had an unrealistic *b* parameter and the next lowest AICc model had an AIC of 812.33. Therefore, the lowest AICc model after accounting for realistic parameter values is the lowest AICc model from iteration 5 with Ricker survival from juveniles to adults and Beverton-Holt stock recruitment relationship from adult to larvae with one additional covariate (Table 5, AICc = 808.47). The confidence intervals for the pred2 covariate for this model contained zero and removing the Pred2 covariate essentially had no effect on the likelihood. Therefore, we chose this model without the Pred2 covariate as the lowest AICc model (AICc = 806.63). Several models had an AICc score within 2 units of this model, which according to the Burnham and Anderson guidelines "*there is no credible evidence that the model should be ruled out*". Therefore, to illustrate the sensitivity of results to the model choice we also provide results for the model with the fewest parameters that was within 2 AICc units of the lowest AICc model. This alternative model is that selected with two additional parameters in iteration 3 of the selection procedure (Table 5, AICc=810.20). Removing the Pred2 covariate improved the AICc score (808.63) so we also eliminated the Pred2 covariate from this model.

The models fit the survey data well (Figures 4 and 5), in fact better than expected from the survey standard errors, indicating that most of the variation in abundance was modeled by the covariates or unexplained process variability. The unexplained process variability differed among the stages (Figure 6; Table 7). Essentially all the variability in survival between larvae and juveniles was explained by the covariates. The amount of variability in the survival from juveniles to adults explained was higher than in the stock-recruitment relationship, but they show similar patterns (Figure 6; Table 7).

The impact analysis of the selected covariates shows that the adult abundance under average conditions, with no predators, and entrainment mortality set to zero, differs moderately from that estimated in the original model (Figure 7). In particular, the recent decline is not as substantial under average conditions indicating that the covariates describe some of the decline, although there is still substantial unexplained variation and a large amount of uncertainty in the recent abundance estimates. Entrainment is estimated to have only a small impact on the adult abundance in either the lowest AICc model, which uses the estimated adult entrainment coefficient and the juvenile entrainment coefficient is zero, or the alternative model, in which both the juvenile and adult entrainment coefficients are set to one (Figure 8). The lowest AICc model with the two entrainment coefficients set at 1 did not converge and results are not shown for that analysis, although the results are expected to be similar.

Discussion

We developed a state-space multi-stage lifecycle model to evaluate population impacts in the presence of density dependence. Application to delta-smelt detected strong evidence for a few key factors and density dependence operating on the population. Both environmental factors (e.g., Deriso et al. 2008) and density dependence (e.g., Brook and

Bradshaw 2006) have been detected in a multitude of studies either independently or in combination (e.g., Sæther 1997; Ciannelli et al. 2004). Brook and Bradshaw (2006) used long-term abundance data for 1198 species to show that density dependence was a pervasive feature of population dynamics that holds across a range of taxa. However, the data they used did not allow them to identify what life stages the density dependence operates on. Ciannelli et al. (2004) found density dependence in different stages of walleye Pollock. In our application we found evidence against density dependent survival from larvae to juveniles, strong evidence for density dependence in survival from juveniles to adults, and weak evidence for density dependence in the stock-recruitment relationship from adults to larvae, which includes egg and early larval survival. Other studies have suggested that density dependence is more predominant at earlier life stages (e.g., Fowler 1987; Gaillard et al. 1998), although the life history of these species differs substantially from delta smelt. The density dependence in survival from juveniles to adults found in our study was probably heavily influenced by three consecutive years of data. Unfortunately, this is a common occurrence in which autocorrelated environmental factors cause autocorrelation in abundance within a stage and this likely influences other studies as well. We only allowed factors to influence density independent survival, either before or after density dependence, however the factors could also influence the strength or form of the density dependence (Walters 1987). For example, Ciannelli et al. (2004) found that high wind speed induced negative density dependence in the survival of walleye Pollock eggs. Our analysis is one of the few, but expanding, applications investigating both density dependent and density independent factors in a rigorous statistical framework that integrates multiple data sets within a life cycle model. The framework amalgamates the density and the mechanistic paradigms of investigating population regulation outlined by Krebs (2002) while accommodating the fact that most available data is observational rather than experimental. More detailed mechanistic processes could be included in the model if the appropriate observational or experimental data are available.

One factor is often erroneously singled out as the only major cause of population decline (e.g., over fishing; Sibert et al. 2006). However, there is a substantial accumulation of evidence that multiple factors interact to cause population declines. Our analysis found support for a variety of factors that influence delta smelt population dynamics. We also showed that together these factors explain the decline in the delta smelt population. Deriso et al. (2008) also found support that multiple factors influenced the decline and suppression of the Prince William Sound herring population, including one or more unidentified factors related to a particular year.

Three of the first four factors included in the delta smelt application acted on the survival between larvae and juveniles. This is also the period where no density dependence in survival occurred. The final model estimates that the factors explain all the variability in survival from larvae to Juveniles. The 20mm trawl survey, which provides information on juvenile abundance, only starts in 1995 so there is less data to explain and this may be partly why the unexplained process variability variance goes to zero. The process variability for the other stages may partly absorb the variability in survival from larvae to juveniles.

Deriso et al. (2008) showed that multiple factors influence populations and that analysis of factors in isolation can be misleading. We also found that multiple factors influence the dynamics of delta smelt and that evaluating factors in isolation can produce different results than evaluating them in combination. The type of density dependence assumed also impacted what factors were selected. Specifically, one predator covariate (Pred2) would be the first selected covariate based simply on AICc for two of the density dependent assumptions, but was not selected by the two factor stepwise procedure (see supplementary material). However, this covariate was selected in the first step of the two factor stepwise procedure for another density dependent assumption, which happened to be the final model with the lowest AICc. In the final model the confidence intervals on the coefficient indicate that this factor should not be included in the model. Exploratory analysis showed that this covariate had about a 0.6 correlation with a temperature (TpAJ) and a prey covariate (EPAJ) that were consistently selected in the first or seconds steps, which operated on the same stage (larvae), when these covariates were combined together. The covariate was also highly correlated with time (see supplementary material). We did find, to some extent, which other covariates were included in the model and the order in which they were included changed depending on the density dependence assumptions. However, apart from the one predator covariate, the four density dependence assumptions tended to select the same factors in the first few steps of the model selection procedure, although the order of selection differed.

There was substantial correlation among estimated parameters (see supplementary material). The parameters of the density dependence function were highly positively correlated as previously observed for stock-recruitment relationships (Quinn and Deriso 1999) and reparameterization might improve the estimation algorithm. The relative number of larvae in the first year is negatively correlated with parameters influencing larval survival including the survival fraction at low abundance (*a*), the standard deviation of the process variability, and the prey covariate coefficients. The coefficients for the prey and temperature covariates influencing larval survival are correlated. This is partly related to the fact that some of these covariates are also correlated. The coefficients for water clarity (Secchi) and adult entrainment (Aent) in the lowest AIC model were highly negatively correlated and were correlated with the parameters of the adult density dependence survival function. The coefficient for adult entrainment is also unrealistically large suggesting that the model including water clarity and adult entrainment is unreliable.

The covariates were included in the model as simple log-linear terms. There may be more appropriate relationships between survival and the covariates. For example, good survival may be limited to a range of covariate values so a polynomial that describes a dome shape cure may be more appropriate. There may also be interactions among the covariates. Neither of these was considered in the delta smelt application. Although, some of the covariates were developed based on combining different factors such as water clarity and predator abundance. Some of the covariates were highly correlated (see supplementary material), but those with the highest correlations were either for different stages or not selected in the final models.

Density dependence and environmental factors could influence other population processes (e.g. growth rates) or the ability (catchability) of the survey to catch delta smelt. Modeling of catchability has been extensively researched for indices of abundance based on commercial catch data (Maunder and Punt 2004) and results have shown that the relationship between catch-per-unit-effort and abundance can be nonlinear (Harley et al. 2001; Walters 2003). Rigorous statistical methods have been developed to account for habitat quality in the development of indices of abundance from catch and effort data (Maunder et al. 2006). Methods have been developed to integrate the modeling of catchability within population dynamics models as a random walk (Fournier et al. 1998) or as a function of covariates (Maunder 2001; Maunder and Langley 2004). Surveys are less likely to be effected by systematic changes in catchability because sampling effort and survey design tend to be more consistent over time than effort conducted by commercial fishing fleets. Most fisheries stock assessments assume that there are no systematic changes in survey catchability unless there is an obvious change (e.g. change in survey vessel). However, catchability may changes due to factors such as changes in the spatial distribution of the species or population density. Similar methods as used for survival can be used to model catchability as a function of density or environmental factors. Random influences on catchability beyond those caused by simple random sampling can be accommodated by estimating the standard deviation of the likelihood function used to fit the model to the survey data (Maunder and Starr 2003). However, the fit to the delta smelt data appears better than expected from the bootstrap confidence intervals suggesting that the observation error is smaller than estimated by the bootstrap procedure. Systematic and additional random variation in catchability could bias the evaluation of strength and statistical significance of density dependence and environmental factors (Deriso et al. 2007).

The estimates of the *b* parameter of the Beverton-Holt stock-recruitment relationship between adults and larvae produced density dependence that was unrealistically strong in a few models. Consequently, this caused estimates of some coefficients that were also unrealistic (e.g., the coefficient for adult entrainment was nearly two orders of magnitude higher than expected). Even when a model was selected for which the *b* parameter was considered reasonable, the coefficient for adult entrainment was still an order of magnitude greater than expected. This illustrates that naively following AICc model selection without use of professional judgment is not recommended. We could have included all models in the sum of the AICc weights by bounding the *b* parameter in the parameter estimation process (the parameter would probably be at the bound), but we considered inference based on models with a parameter at the bound inappropriate. An alternative approach would be to use an informative prior for *b* (Punt and Hilborn 1997) to pull it away from unrealistic values, but we did not have any prior information that was considered appropriate.

Andersen et al. (2000) warn against data dredging as a method to test factors that influence population dynamics. In their definition of data dredging they include the testing of all possible models, unless, perhaps, if model averaging is used. This provides somewhat of a dilemma when using a multi-stage life cycle model because there are often multiple candidate factors for each life stage and they may only be detectable if included in the model together. For this reason, we use an approximation to all possible models and rely on AICc and AICc weights to rank models and provide an idea of the strength of evidence in the data about the models and do not apply strict hypothesis tests. Some form of model averaging using AICc weights might be applicable to the impact analysis, although the estimates of uncertainty would have to include both model and parameter uncertainty. The estimates of uncertainty in our impact analysis under estimate uncertainty because they do not include model selection uncertainty and use of model averaging might provide better estimates of uncertainty (Burnham and Anderson 2002). In addition, we use symmetric confidence intervals and approaches that provide asymmetric confidence intervals may be more appropriate (e.g., based on profile likelihood or Bayesian posterior distribution).

Our results suggest that of all the factors that we tested, food abundance, temperature, predator abundance and density dependence are the most important factors controlling the population dynamics of delta smelt. Survival is positively related to food abundance and negatively related to temperature and predator abundance. There was also some support for a negative relationship with water clarity and adult entrainment, and a positive relationship with the number of days where the water temperature was appropriate for spawning. The first variables to be included in the model were those related to survival from larvae to juveniles, followed by survival from juveniles to adults, and finally the stock-recruitment relationship. Mac Nally et al. (2010) also found that high summer water temperatures had an inverse relationship with delta smelt abundance. Thomson et al. (2010) found exports and water clarity as important factors. We did not include exports, but included explicit estimates of entrainment. We found some support for adult entrainment, but it was not one of the main factors and the coefficient was unrealistically high and highly correlated with the coefficient for water clarity. Mac Nally et al. (2010) and Thomson et al. (2010) only used the FMWT data and did not look at the different life stages, which probably explains why the factors supported by their analyses differ from what we found.

We found strong evidence for density dependence in survival from juveniles to adults, some evidence for density dependence for the stock-recruitment relationship from adults to larvae and evidence against density dependence in survival from larvae to juveniles. This might be surprising since the population is of conservation concern due to low abundance levels. However, the available data covers years, particularly in the 1970s, where the abundance was high and data for these years provide information on the form and strength of the density dependence. At the recent levels of abundance, density dependence is probably not having a substantial impact on the population and survival is impacted mainly by density independent factors. Previous studies only found weak evidence for a stock-recruitment relationship and suggested that density independent factors regulate the delta smelt population (e.g., Moyle et al. 1992). Bennett (2005) found that the strongest evidence for density dependence was between juveniles and pre-adults. Mac Nally et al. (2010) found strong support for density dependence, but Thomson et al. (2010) did not.

Several pelagic species in the San Francisco Estuary have also experienced declines, but the factors causing the declines are still uncertain (Bennett 2005; Sommer et al. 2007). Thomson et al. (2010) used Bayesian change point analysis to determine when the declines occurred and included covariates to investigate what caused the declines. They were unable to fully explain the decline and unexplained declines were still apparent in the early 2000s. The impact analysis we applied to delta smelt suggests that the factors included in the model explain the low levels of delta smelt in the mid 2000s. Although, there is still substantial annual variation in the delta smelt abundance and uncertainty in the estimates of abundance for these years.

The theory for state-space stage-structured life cycle models is well developed (Newman 1998; de Valpine, P. 2002; Maunder 2004), they have been promoted

(Thomson et al. 2010; Mac Nally et al. 2010), they facilitate the use of multiple data sets (Maunder 2003), provide more detailed information about how factors impact a population, and we have shown that they can be implemented. Therefore, we recommend that they are an essential tool for evaluating factors impacting species of concern such as delta smelt.

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Appendix: Calculating realistic values for the *b* parameter of the Beverton-Holt and Ricker versions of the Deriso-Schnute stock-recruitment model.

The third parameter (γ) of the Deriso-Schnute stock-recruitment model (Deriso 1980; Schnute 1985)

$$f(N) = aN(1 - b\gamma N)^{\frac{1}{\gamma}}$$

can be set to represent the Beverton-Holt ($\gamma = -1$) and Ricker ($\gamma \to 0$) models (Quinn and Deriso 1999, page 95), which correspond to

$$f(N) = \frac{aN}{1 + bN} \text{ and } f(N) = aN\exp[-bN]$$

The recruitment at a given reference abundance level (e.g., the carrying capacity N_0) can be calculated as

$$R_0 = \frac{aN_0}{1 + bN_0} \text{ and } R_0 = aN_0\exp[-bN_0]$$

The recruitment when the abundance is at a certain fraction (p) of this reference level can be calculated as

$$R_p = \frac{apN_0}{1 + bpN_0} \text{ and } R_p = aN_0 \exp[-bpN_0]$$

A standard reference in fisheries is the recruitment as a fraction of the recruitment in the absence of fishing (the carrying capacity) that is achieved when the abundance is 20% of the abundance in the absence of fishing (steepness).

$$h = \frac{R_{0.2}}{R_0} = \frac{1/N_0 + b}{5/N_0 + b} \text{ and } h = \frac{R_{0.2}}{R_0} = 0.2\exp[0.8bN_0]$$

To set b for a given steepness

$$b = \frac{5h - 1}{N_0 - hN_0} \text{ and } b = \frac{\ln[5h]}{0.8N_0}$$

The 20% reference level was probably chosen because the objective of fisheries management has traditionally been to maximize yield and it is generally considered that when a population falls below 20% of its unexploited level the stock cannot sustain that level of yield. In the delta smelt application the concern is about low levels of population abundance and we do not estimate the unexploited population size. Therefore, a more appropriate reference level might be 5% of the average level observed in the surveys.

$$h_{0.05} = \frac{R_{0.05}}{R_{ave}} = \frac{1/N_{ave} + b}{20/N_{ave} + b} \text{ and } h_{0.05} = \frac{R_{0.05}}{R_{ave}} = 0.05\exp[0.95bN_{ave}]$$

$$b = \frac{20h_{0.05} - 1}{N_{ave} - h_{0.05}N_{ave}} \text{ and } b = \frac{\ln[20h_{0.05}]}{0.95N_{0.05}}$$

This specification is also more appropriate when considering both the Beverton-Holt and Ricker models because the Ricker model reduces at high abundance levels and the recruitment at an abundance level that is 20% of the carrying capacity could be higher than the recruitment at carrying capacity. We restrict the models to those that have *b* estimates such that the expected recruitment when the population is at 5% of its average level (over the survey period) is equal to or less than 80% of the recruitment expected when the population is at its average level (Table A1). This is equivalent to a Beverton-Holt $h_{0.2}$ = 0.95 based on the abundance reference level being the average abundance from the surveys, which is probably conservative is the sense of not rejecting high values of *b*.

Appendix References

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Table A1. Maximum values of the parameter *b* for inclusion of models in the model selection process.

		Maximum *b*	
	Average abundance	Beverton-Holt	Ricker
20mm (larvae)	7.99	9.3867	0.3653
STN (juveniles)	6140	0.0122	0.0005
FMWT (adults)	459	0.1634	0.0064

Table 1. Algorithm for evaluating covariates for the delta smelt application.

1) Evaluate density dependence

a) Calculate all combinations of density dependent processes without the inclusion of factors.

Combinations include: a) density independent; b) Beverton-Holt; c) Ricker; and d) estimate both b and γ. These can be at any of the three stages.

b) Choose the density dependence combination that has the lowest AICc or if there are several that have similar support, choose multiple combinations.

2) Evaluate covariates

a) For each densitity dependence scenario chosen in (1b) run all possible one and two covariate combinations

b) For each combination, set the AICc weight to zero if the sign is wrong for either of the coefficients in the combination or if the b parameter of a density dependence function is unrealistically high.

c) Sum AICc weights for a given covariate across all models that include that covariate

d) Select the two covariates with the highest summed AICc weights to retain for the next iteration

e) Iterate a-d until the AICc value of the best model in the current iteration is more than 4 units higher than the lowest AICc model

3) Double check all included covariates

a. Check confidence intervals of the estimated coefficients for all included covariates to see if they contain zero.

b. For all coefficients that contain zero remove the associated covariate and see if the AICc is degraded. If the AICc is not degraded, exclude that covariate from the model.

Table 2. The variables used as candidates to account for the changes in delta smelt abundance. A = occurs between adult and larval stages, L = occurs between larval and juvenile stages, J = occurs between juvenile and adult stages. Norm = subtract mean and divide by standard deviation, Mean = divide by mean, Raw = not scaled. The covariate is attributed to after density dependence unless it is known to occur before density dependence. This is because density dependence generally reduces the influence of the covariate. *= the effect of entrainment on survival is negative, but the covariate is formulated so setting the coefficient to 1 implies the assumption that entrainment is known without error, so the coefficient should be positive.

Factor	Name	Covar	Stage	B(efore)/ A(fter)	Sign	Description	Data scaling	Justification
1	SpDys	1	A	B	+	Days where temperature is in	Norm	This measures the number of days of

						the range 11-20C		spawning—the longer the spawning season, presumably the better chance of survival.
2	TpAJ	2	L	B	- or +	Average water temperature Apr-Jun in delta smelt habitat	Norm	Temperature affects growth rate and survival of early life stages.
3	TpAJ	2	A	A	- or +			
4	TpJul	3	L	A	-	Average water temperature July in delta smelt habitat	Norm	Higher water temperatures can be lethal. Could also include August temperature.
5	EPAJ	4	L	B	+	Minimum eurytemora and pseudodiaptomus density April-Jun	Norm	Measures height of food "gap" in spring, as eurytemora falls from spring maximum and pseudodiaptomus rises from ~0.
6	EPAJ	4	A	A	+			
7	EPJul	5	L	A	+	Average eurytemora and pseudodiaptomus density July	Norm	Measures food availability in summer until STN survey, identified as problem by Bennett based on smelt condition.
8	Pred1	6	J	A	-	Sep-Dec abundance other	Mean	Predation is a source of direct mortality,

						predators		measured as the product of relative density from beach seine data with the square of average sechi depth
9	Pred1	6	A	B	-			
10	Pred1	6	A	A	-			
11	StBass	7	J	A	-	Sep-Dec abundance striped bass	Mean	A major predator, whose abundance is measured as actual number of adults.
12	StBass	7	A	B	-			
13	StBass	7	A	A	-			
14	DSLth	8	L	A	+	Delta smelt average length	Norm	See Bennett (2005) for length vs fecundity relationship, linear for 1-year-olds.
15	DSLth	8	J	A	+			
16	DSLth	8	A	A	+			
17	TpJS	9	J	A	-	Maximum 2-week average temperature Jul-Sep	Norm	Measure of whether lethal temperature is reached in hot months.
18	EPJA	10	J	A	+	Average eurytemora	Norm	Measures food availability in summer between

						and pseudodiaptomus density July-August		STN and FMWT surveys, identified as problem by Bennett based on smelt condition.
19	Secchi	11	A	B	-	Jan-Feb Weighted Secchi depth	Norm	Protection from predators
20	Secchi	11	A	A	-			
21	Jent	12	L	A	+ *	Juvenile entrainment	Raw	Entrained in by water pumps
22	Aent	13	A	B	+ *	Adult entrainment	Raw	Entrained in by water pumps
23	Pred2	14	L	B	-	Apr-Jun abundance other predators	Mean	Predation is a source of direct mortality, measured as the product of relative density from beach seine data with the square of average sechi depth
24	Pred2	14	A	A	-			

Table 3. AICc weights for all possible density dependence models without covariates. L = survival from larvae to juveniles; J = survival from juveniles to larvae; A = the stock recruitment relationship from adults to larvae; No = no density dependence, BH = Beverton-Holt density dependence; R = Ricker density dependence; DD = Deriso-Schnute density dependence (i.e. estimate γ)

		J-No	J-BH	J-R	J-DD	Sum
L-No	A-No	0.000	0.079	0.062	0.027	0.168
	A-BH	0.000	0.075	0.067	0.026	0.168
	A-R	0.000	0.059	0.052	0.020	0.131
	A-DD	0.000	0.069	0.064	0.023	0.156
	Sum	0.000	0.281	0.245	0.096	0.622
L-BH	A-No	0.000	0.022	0.017	0.007	0.047
	A-BH	0.000	0.020	0.018	0.007	0.045

	A-R	0.000	0.016	0.014	0.005	0.035
	A-DD	0.000	0.018	0.017	0.006	0.040
	Sum	0.000	0.076	0.066	0.025	0.167
L-R	A-No	0.000	0.022	0.017	0.007	0.047
	A-BH	0.000	0.020	0.018	0.007	0.045
	A-R	0.000	0.016	0.014	0.005	0.035
	A-DD	0.000	0.018	0.017	0.006	0.040
	Sum	0.000	0.076	0.066	0.025	0.167
L-DD	A-No	0.000	0.006	0.005	0.002	0.013
	A-BH	0.000	0.005	0.005	0.002	0.012
	A-R	0.000	0.004	0.004	0.001	0.009
	A-DD	0.000	0.004	0.004	0.001	0.010
	Sum	0.000	0.020	0.017	0.006	0.043

Table 4.

Order of inclusion of factors into the analysis. JBH = Beverton-Holt density dependence from the Juvenile to Adult stage; JBHABH = Beverton-Holt density dependence from the juvenile to adult stage and Beverton-Holt density dependence from the adult to larvae stage (the stock-recruitment relationship); JR = Ricker density dependence from the Juvenile to Adult stage; JRBH = Ricker density dependence from the juvenile to adult stage and Beverton-Holt density dependence from the adult to larvae stage (the stock-recruitment relationship). See Tables 2 and 3 for definitions. *This covariate was excluded from the final model because the confidence interval of its coefficient included zero and including the covariate degraded the AICc.

Factor	name	Stage	B(efore)/A(fter)	JBH	JBHABH	JR	JRABH
2	TpAJ	L	B	1	1	2	2
4	TpJul	L	A	2	2	2	3
5	EPAJ	L	B	1	1	1	1
7	EPJul	L	A		4		5
8	Pred1	J	A	2	2	3	3
18	EPJA	J	A	3	3	1	2
19	Secchi	A	B		3		4
22	Aent	A	B		4		4
23	Pred2	L	B				1*

Table 5. AICc values for each step in the model selection process. Shaded values are the lowest AICc for that density dependence configuration. See Table 4 for definitions.

	Step 1		Step 2		Step 3		Step 4		Step 5		Step 6		Step 7	
	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
JBH	841.06	833.44	827.58	824.00	823.01	823.30	824.61	825.95	828.28	831.08				
JBHABH	832.46	824.68	818.25	815.18	813.92	814.32	814.17	811.85	812.33	814.75				
JR	841.80	833.67	826.25	821.40	820.00	821.10	822.58	823.71	826.26	828.86				
JRBH	833.16	824.93	817.96	814.72	811.60	810.20	810.72	810.38	808.47	809.23	810.86	813.39	817.03	820.83

Table 6. Estimates of coefficients (and 95% confidence intervals) from the lowest AICc models for each density dependence assumption. Definitions of abbreviations and a description of the covariates can be found in Table 2 and the density dependence configurations in Table 4. The alternative model is the model that has the fewest covariates and the AICc is less than 2 AICc units greater than the lowest AICc model.

Factor	name	Stage	B/A	JBH	JBHABH	JR	JRABH	JRABH no Pred2	Alternative
2	TpAJ	L	B	-0.32 (-0.46, -0.18)	-0.21 (-0.36, -0.07)	-0.32 (-0.45, -0.19)	-0.20 (-0.34, -0.06)	-0.22 (-0.36, -0.09)	-0.31 (-0.44, -0.18)
4	TpJul	L	A	-0.29 (-0.50, -0.08)	-0.30 (-0.49, -0.12)	-0.28 (-0.49, -0.07)	-0.28 (-0.47, -0.09)	-0.32 (-0.50, -0.13)	-0.30 (-0.50, -0.11)
5	EPAJ	L	B	0.39 (0.15, 0.63)	0.40 (0.18, 0.62)	0.37 (0.13, 0.61)	0.32 (0.09, 0.55)	0.36 (0.14, 0.58)	0.47 (0.23, 0.71)
7	EPJul	L	A		0.32 (0.07, 0.58)		0.31 (0.05, 0.56)	0.33 (0.07, 0.59)	
8	Pred1	J	A	-0.45 (-0.84, -0.06)	-0.49 (-0.90, -0.08)	-0.37 (-0.71, -0.03)	-0.42 (-0.77, -0.07)	-0.44 (-0.78, -0.09)	-0.40 (-0.75, -0.05)
18	EPJA	J	A	0.21 (0.00, 0.42)	0.22 (0.00, 0.45)	0.44 (0.21, 0.66)	0.46 (0.22, 0.69)	0.46 (0.22, 0.69)	0.46 (0.23, 0.69)
19	Secchi	A	B		-1.08 (-1.97, -0.19)		-1.24 (-2.27, -0.22)	-1.15 (-2.11, -0.20)	
22	Aent	A	B		9.50 (0.62, 18.38)		10.97 (0.93, 21.01)	10.32 (0.99, 19.65)	
23	Pred2	L	B				-0.19 (-0.52, 0.13)		
	a	L		396 (334, 458)	451 (373, 529)	396 (337, 456)	593 (307, 879)	454 (376, 532)	410 (340, 481)
	a	J		0.74 (0.01, 1.48)	0.77 (-0.02, 1.56)	0.39 (0.18, 0.6)	0.42 (0.19, 0.65)	0.43 (0.2, 0.66)	0.41 (0.19, 0.63)
	a	A		0.03 (0.02, 0.04)	0.2 (-0.13, 0.53)	0.03 (0.02, 0.04)	0.27 (-0.24, 0.78)	0.25 (-0.18, 0.67)	0.08 (0, 0.16)
	b	L		0	0	0	0	0	0
	$b\ (10^{-4})$	J		8.38 (-0.19, 16.95)	7.95 (-0.57, 16.48)	1.43 (1.01, 1.84)	1.42 (1.01, 1.84)	1.44 (1.02, 1.85)	1.43 (1.01, 1.84)

b (10^{-2})	A	0	1.48 (-1.41, 4.38)	0	2.35 (-2.77, 7.47)	1.93 (-1.96, 5.81)	0.52 (-0.34, 1.39)
γ	L						
γ	J	-1	-1	0	0	0	0
γ	A		-1		-1	-1	-1
σ	L	0.07 (-0.32, 0.45)	0 (-0.35, 0.35)	0.04 (-0.5, 0.59)	0 (-0.35, 0.35)	0 (-0.26, 0.26)	0.1 (-0.2, 0.39)
σ	J	0.52 (0.36, 0.67)	0.55 (0.39, 0.71)	0.46 (0.31, 0.6)	0.48 (0.32, 0.63)	0.48 (0.32, 0.63)	0.47 (0.32, 0.62)
σ	A	0.79 (0.57, 1.01)	0.61 (0.45, 0.77)	0.82 (0.59, 1.04)	0.61 (0.45, 0.77)	0.62 (0.46, 0.78)	0.71 (0.52, 0.9)
$h_{0.05}$	L	1	1	1	1	1	1
$h_{0.05}$	J	0.24 (0.09, 0.4)	0.24 (0.08, 0.4)	0.11 (0.09, 0.14)	0.11 (0.09, 0.14)	0.12 (0.09, 0.14)	0.11 (0.09, 0.14)
$h_{0.05}$	A	1	0.29 (-0.06, 0.64)	1	0.38 (-0.09, 0.85)	0.34 (-0.07, 0.75)	0.15 (0, 0.3)

Table 7. Estimates of standard deviation of the process variation and the percentage of the process variation explained by the covariates for the lowest AICc model.

	Standard deviation without covariates	Standard deviation with covariates	%variation explained
Larvae	0.72	0.00	100%
Juvenile	0.63	0.48	43%
Adult	0.71	0.62	24%

Figure captions

Figure 1. Life cycle diagram of delta smelt with survey, entrainment, and density dependence timing.

Figure 2. Relationship among stages in the model for the lowest AICc model that has Ricker survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship. Points are the model estimates of abundance, lines are the estimates from the stock recruitment models without covariates or process variation, crosses are the estimates without covariates.

Figure 3. Relationship among stages in the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model). Points are the model estimates of abundance, lines are the estimates from the stock recruitment models without covariates or process variation, crosses are the estimates without covariates.

Figure 4. Fit (line) to the survey abundance data (circles) for the lowest AICc model that includes Ricker survival between juveniles and adults and a Beverton-Holt stock-recruitment relationship. Confidence intervals are the survey observations plus and minus two standard deviations as estimated from bootstrap analysis.

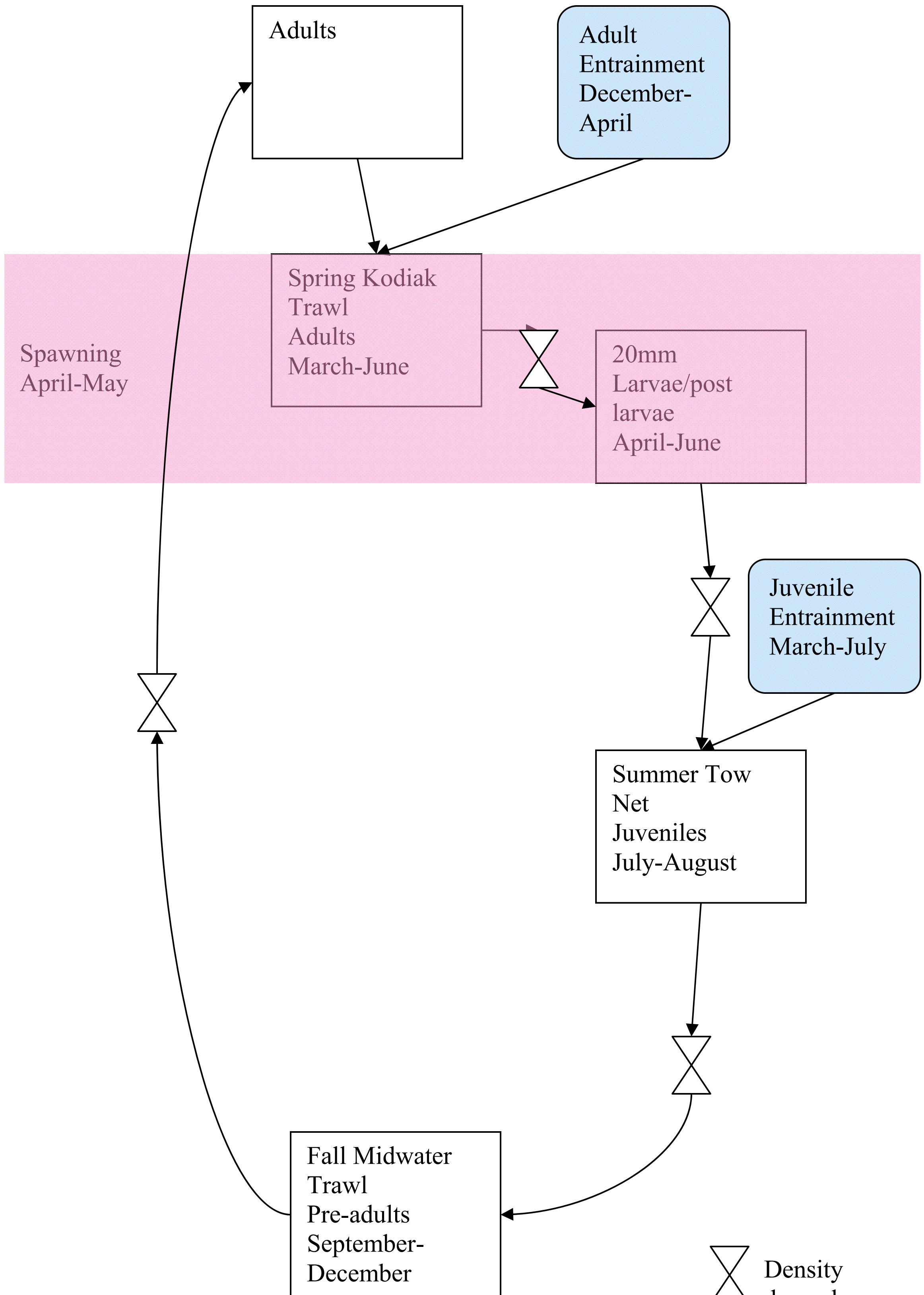
Figure 5. Fit (line) to the survey abundance data (circles) for the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) that includes Ricker survival from juveniles to adults and a Beverton-Holt stock recruitment relationship. Confidence intervals are the survey observations plus and minus two standard deviations as estimated from bootstrap analysis.

Figure 6. Estimates of the realizations of the process variation random effects ($\exp\left[\sigma_s \varepsilon_{t,s} - 0.5\sigma_s^2\right]$) for the lowest AICc model that includes Ricker survival between juveniles and adults and a Beverton-Holt stock-recruitment relationship (top) and the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) (bottom).

Figure 7. Estimates of abundance with and without covariates (coefficients of the covariates set to zero) (top) and ratio of the two with 95% confidence intervals (bottom, y-axis limited to show details) from the lowest AICc (left panels) model that has Ricker survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship and the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) (right panels).

Figure 8. Estimates of the adult abundance with and without adult entrainment (top) and the ratio of adult abundance without adult entrainment to with adult entrainment (bottom, y-axis limited to show details) from the lowest AICc model (left panels) with Ricker

survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship and the alterative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model) (right panels).


Adults
Adult Entrainment December-April
Spawning April-May
Spring Kodiak Trawl Adults March-June
20mm Larvae/post larvae April-June
Juvenile Entrainment March-July
Summer Tow Net Juveniles July-August
Fall Midwater Trawl Pre-adults September-December
Density dependence

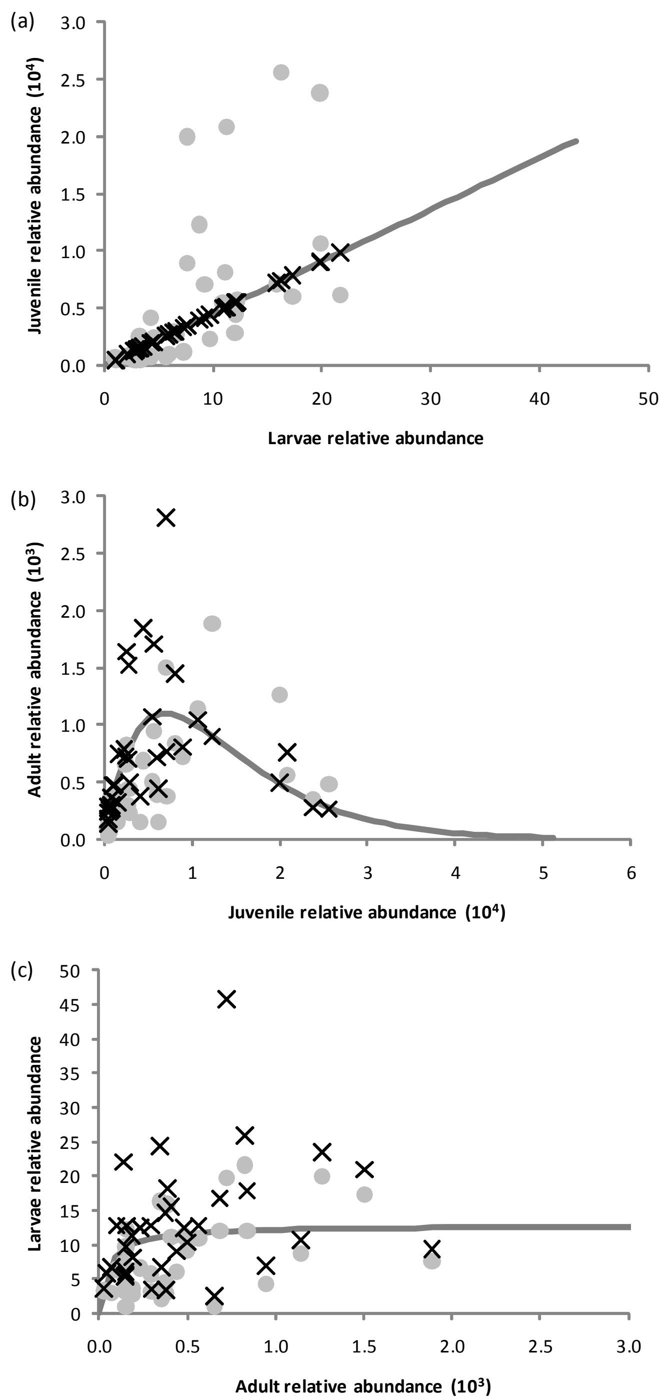

(a)
Juvenile relative abundance (10⁴)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
10
20
30
40
50
Larvae relative abundance
(b)
Adult relative abundance (10³)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6
Juvenile relative abundance (10⁴)
(c)
Larvae relative abundance
50
45
40
35
30
25
20
15
10
5
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Adult relative abundance (10³)

Figure 2.

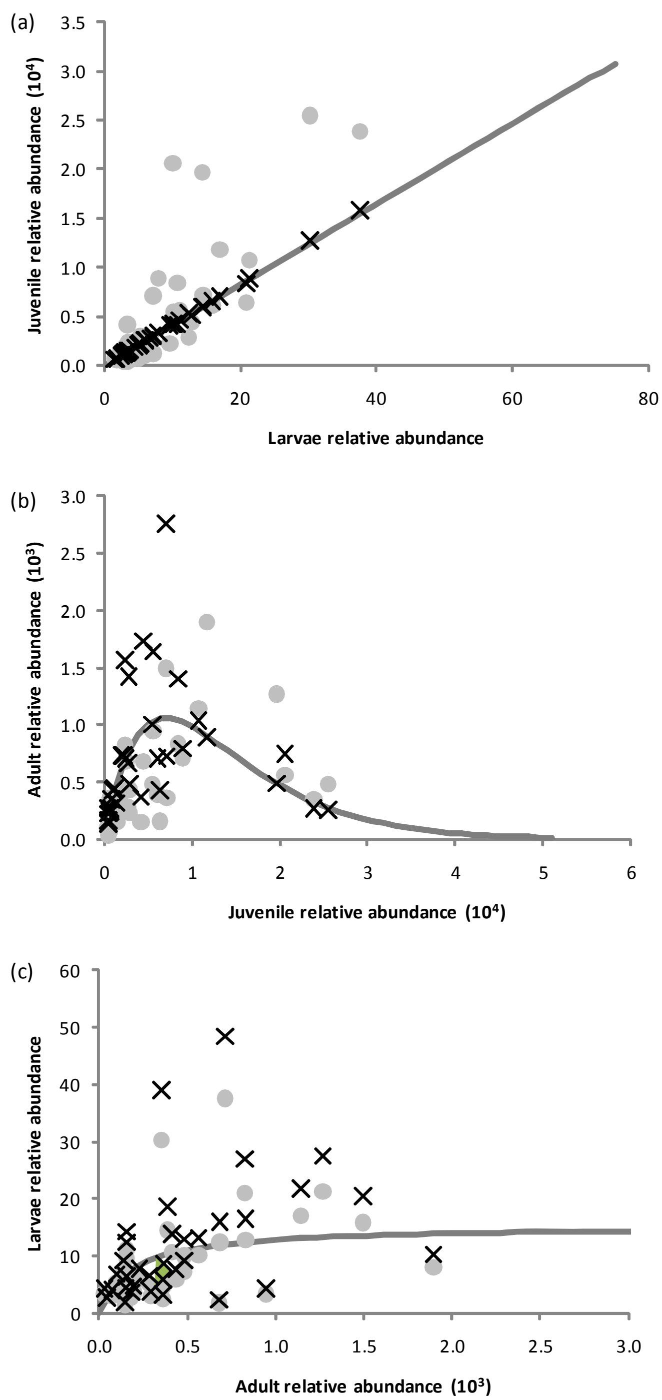

(a)
Juvenile relative abundance (10⁴)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
Larvae relative abundance
(b)
Adult relative abundance (10³)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6
Juvenile relative abundance (10⁴)
(c)
Larvae relative abundance
60
50
40
30
20
10
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Adult relative abundance (10³)

Figure 3.

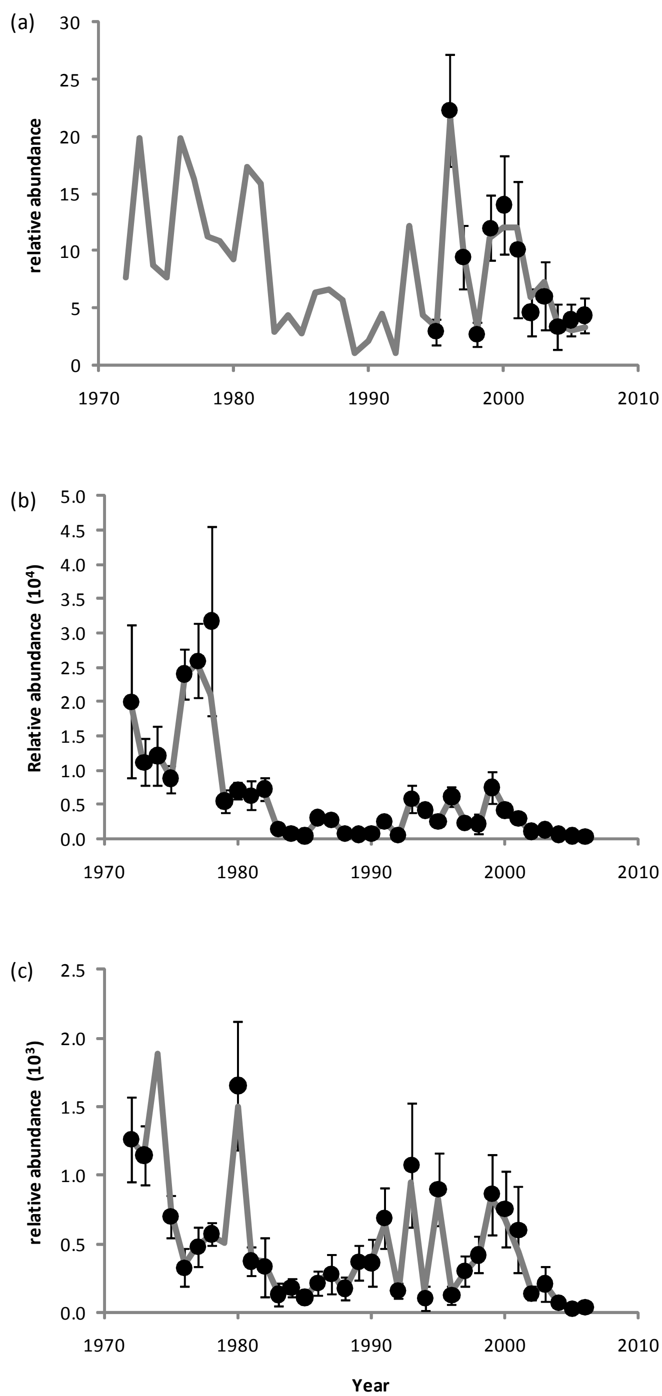

(a)
relative abundance
30
25
20
15
10
5
0
1970
1980
1990
2000
2010
(b)
Relative abundance (10⁴)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
(c)
relative abundance (10³)
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
Year

Figure 4.

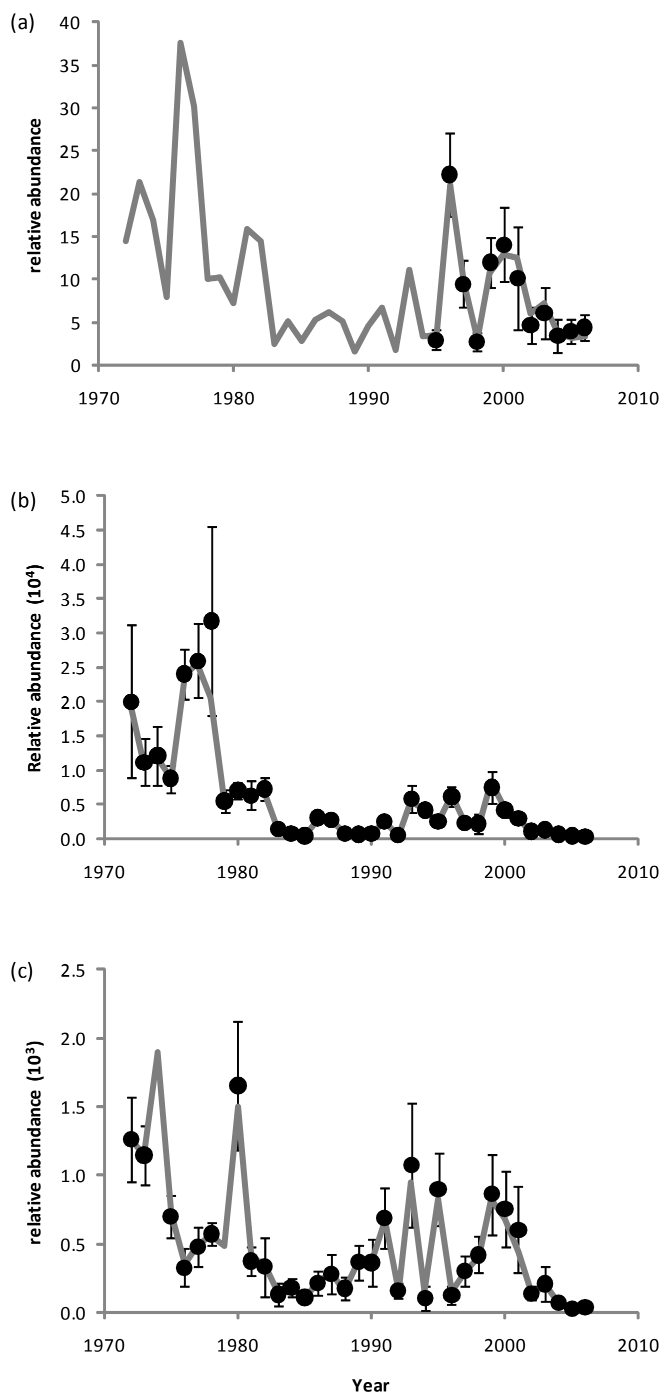

(a)
relative abundance
40
35
30
25
20
15
10
5
0
1970
1980
1990
2000
2010
(b)
Relative abundance (10⁴)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
(c)
relative abundance (10³)
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
Year

Figure 5.

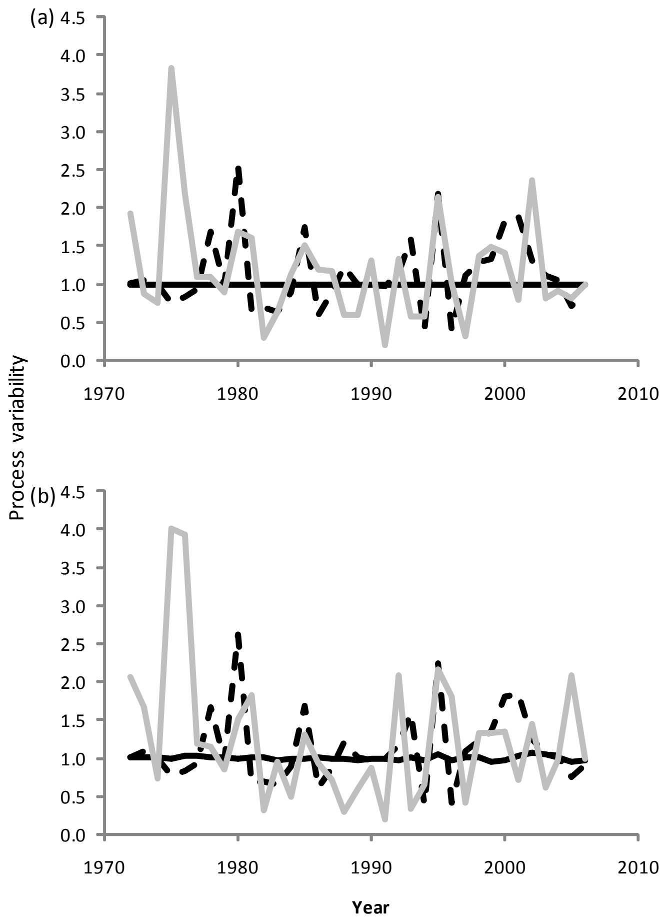

(a)
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
Process variability
(b)
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
Year

Figure 6.

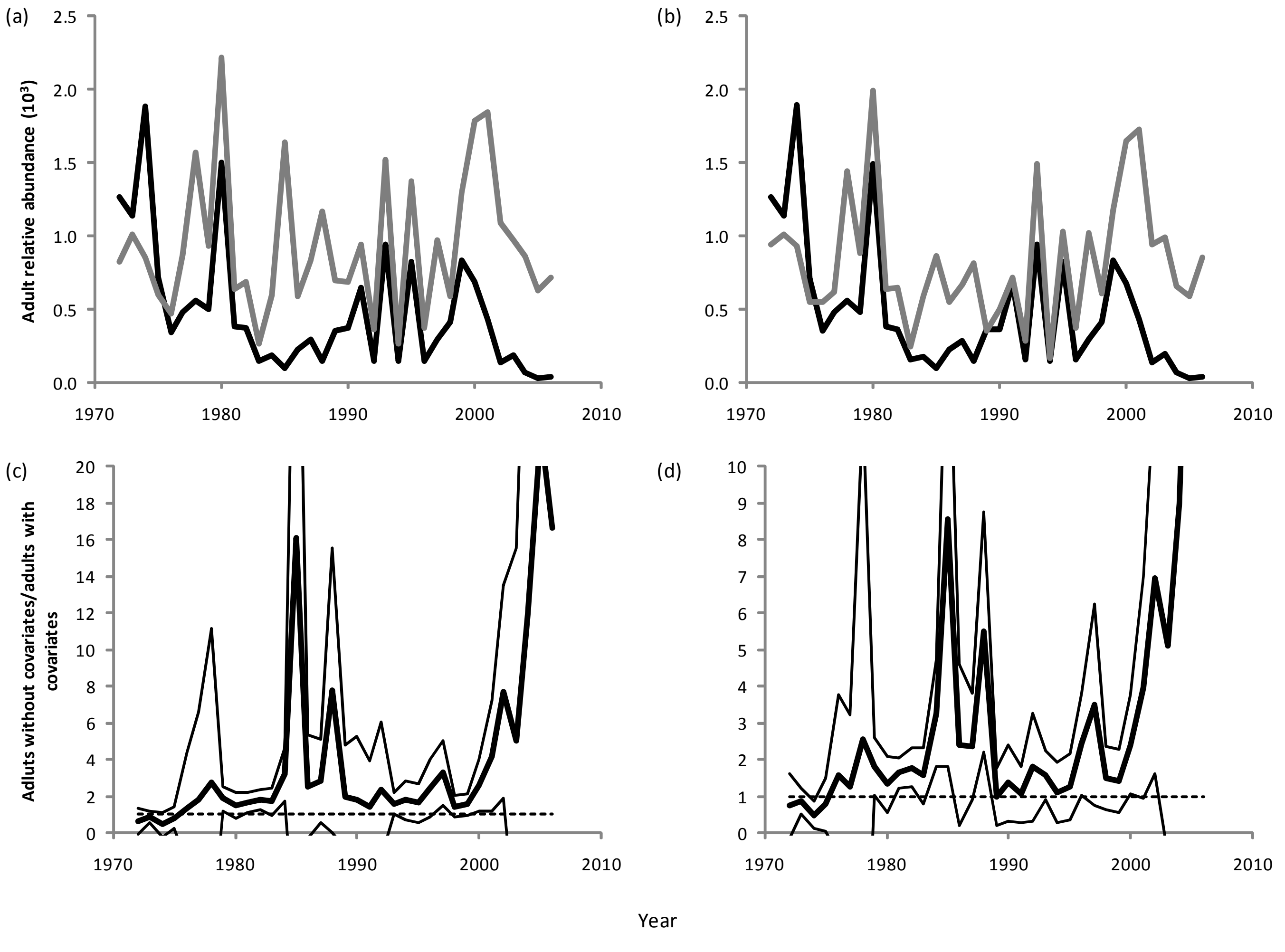

(a)
(b)
(c)
(d)
Adult relative abundance (10³)
Adluts without covariates/adults with covariates
Year
2.5
2.0
1.5
1.0
0.5
0.0
20
18
16
14
12
10
8
6
4
2
0
10
9
7
5
3
1
1970
1980
1990
2000
2010

Figure 7.

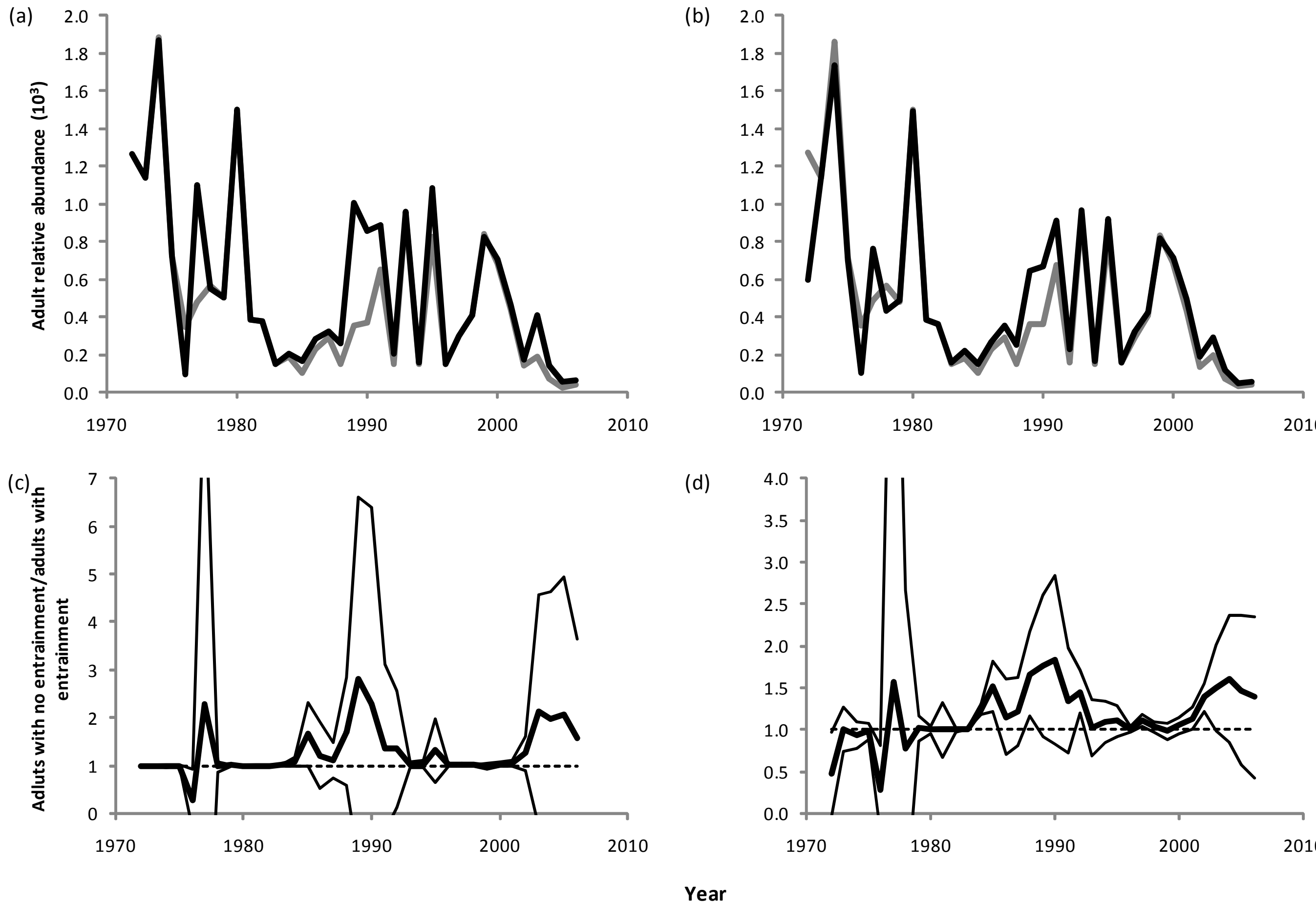

(a)
Adult relative abundance (10³)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1970
1980
1990
2000
2010
(b)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1970
1980
1990
2000
2010
(c)
Adluts with no entrainment/adults with entrainment
7
6
5
4
3
2
1
0
1970
1980
1990
2000
2010
(d)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1970
1980
1990
2000
2010
Year

Figure 8.

Supplementary material

The following tables provide the data used in the analysis, a complete set of results for all the covariates evaluated in the analysis, and correlation matrices for the factors and estimated parameters.

Table S1. Indices of abundance and standard errors used in the delta smelt application.

	20mm		STN		FMWT	
Year	value	SE	value	SE	value	SE
1972			20005	5577	1265	155
1973			11185	1722	1145	108.7
1974			12147	2175		
1975			8786	989	697	77.8
1976			24000	1802	328	67.7
1977			25965	2681	480	69.7
1978			31758	6867	572	41.2

1979	5484	853		
1980	7068	646	1654	235.6
1981	6300	1043	374	49.9
1982	7242	820	333	108.5
1983	1390	279	132	43.6
1984	779	147	182	35.2
1985	387	67	110	21.6
1986	3057	406	212	42.7
1987	2743	227	280	71
1988	764	129	174	40.7
1989	647	52	366	63.7
1990	747	125	364	83.3
1991	2486	334	689	108.8
1992	471	68	156	27.8
1993	5763	996	1078	226.6
1994	4156	380	102	45.4

1995	2.933692	0.563774	2490	307	899	132.6
1996	22.25453	2.437344	6162	701	127	31
1997	9.437214	1.371236	2362	353	303	55
1998	2.704639	0.526823	2209	694	420	67
1999	12.00716	1.428904	7478	1142	864	146.2
2000	14.02919	2.160034	4178	519	756	139.9
2001	10.10347	2.983169	2897	332	603	156.2
2002	4.63569	1.04671	1115	163	139	25.2
2003	6.043828	1.479269	1329	174	210	64.9
2004	3.380115	0.967356	649	113	74	19
2005	3.981609	0.693923	393	97	27	6.6
2006	4.372327	0.779492	352	117	41	11.9

Table S2. Untransformed covariate values. See Table 2 for definitions.

Year	SpDys	TpAJ	TpJul	EPAJ	EPJul	Preds1	StBass	DSLth	TpJS	EPJA	Secci	JEnt	AEnt	Preds2
1972	110	17.8	21.3	1243.77	4725	586	36498		21.8	4303	50	0.28136	0.02626	354
1973	104	18.6	21.3	754.234	1547	1041	27596		21.9	2082	26	0.1174	0.02626	793
1974	85	17.7	21.0	614.313	4202	850	32314		22.5	3799	44	0.0814	0.02626	446
1975	92	17.2	20.1	479.507	1520	735	41650	65.1	21.5	1545	44	0.06449	0.02626	280
1976	130	17.6	21.4	666.081	4125	19410	65427		21.9	2895	74	0.31567	0.0952	6118
1977	118	17.0	21.1	581.151	4194	22324	40655	65.6	21.5	3972	59	0.35274	0.02626	7095
1978	110	17.8	21.1	1457.95	2082	14726	28399	65.3	22.4	1391	13	0	0.02626	8423
1979	90	18.0	21.0	516.84	947	37712	25761		22.1	722	34	0.15945	0.02626	18631
1980	137	16.8	20.5	428.147	548	20360	20254	70.3	22.5	647	11	0.03108	0.02626	15120
1981	108	18.7	21.8	787.671	922	22248	20621	67.2	22.8	724	42	0.22261	0.02626	17070
1982	105	17.0	20.6	19.4272	636	30605	21560	66.2	21.4	670	31	0.00746	0.02626	23570
1983	102	17.3	20.7	271.066	530	28422	31059	62.2	22.2	544	28	0	0.02626	13957
1984	100	18.3	22.4	251.49	1560	29082	35459	69.5	22.8	1545	50	0.20125	0.02626	20444

1985	105	18.5	22.0	134.587	548	62483	46997	69.1	22.5	543	76	0.26546	0.06687	30364
1986	122	18.1	21.2	648.516	626	30255	22752	68.1	21.5	534	60	0	0.02626	22921
1987	102	19.0	20.6	534.328	392	42089	41144	64.8	21.3	519	65	0.26078	0.02626	26771
1988	125	17.8	22.4	119.215	364	36828	30207	69.5	23.1	360	46	0.3583	0.16922	26668
1989	108	17.9	21.1	383.708	2558	38551	29441	67.8	21.7	3641	67	0.27032	0.13226	24067
1990	100	18.4	22.0	200.219	3616	57128	32336	63.9	22.7	3837	46	0.36378	0.22385	26671
1991	108	17.2	21.3	150.931	2542	63209	39881	62.5	21.8	3059	87	0.3181	0.02626	23754
1992	99	19.2	21.3	531.604	2733	89736	44102	57.9	22.5	2828	82	0.28653	0.04369	42138
1993	112	17.8	21.5	602.607	1184	48487	27938	54.7	22.2	1425	23	0.06506	0.05702	25301
1994	102	17.8	21.1	1112	965	61942	32635	62.9	21.4	856	75	0.21454	0.02626	53729
1995	142	17.0	21.5	573.935	2366	59091	34966	58.5	22.0	1431	27	0	0.18	38412
1996	115	18.3	21.4	380.924	533	72056	44927	55.1	22.6	731	38	0.01	0.025	52547
1997	104	19.3	21.2	369.14	590	64436	56551	57.6	21.8	800	22	0.14	0.025	33056
1998	117	16.3	21.3	271.886	1002	25623	32979	59.3	22.6	842	30	0	0.01	21106
1999	112	17.3	21.3	751.657	1308	29853	42465	59.1	22.0	1091	56	0.07	0.03	21961
2000	118	18.9	20.8	411.035	825	74907	60639	59.3	22.2	1007	64	0.13	0.05	50114
2001	73	19.5	21.3	423.892	758	81186	48811	63.5	22.0	484	57	0.19	0.05	50992

2002	108	18.6	21.8	105.105	641	75565	32632	62.2	22.2	462	36	0.26	0.16	59540
2003	106	18.0	22.2	136.244	787	86509	40081	58.6	23.2	1525	35	0.17	0.22	56424
2004	108	19.1	21.3	153.943	354	109036	82253	62.0	22.3	1012	37	0.21	0.19	50151
2005	123	18.1	22.0	57.0556	849	119419	58943	59.6	22.8	466	49	0.03	0.09	68310
2006	95	17.8	22.6	121.846	1321	116848	41977	58.0	23.7	884	39	0	0.03	53328

Table S3a. AICc weights for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	Name	Stage	B/A	1st	2nd	3rd	4th	5th
1	SpDys	A	B	0.01	0.05	0.17	0.33	#
2	TpAJ	L	B	0.63	#	#	#	#
3	TpAJ	A	A	0.02	0.04	0.08	0.15	0.25
4	TpJul	L	A	0.31	0.68	#	#	#
5	EPAJ	L	B	0.56	#	#	#	#
6	EPAJ	A	A	0.01	0.00	0.00	0.00	0.00
7	EPJul	L	A	0.01	0.03	0.12	0.30	#
8	Pred1	J	A	0.13	0.43	#	#	#
9	Pred1	A	B	0.00	0.00	0.00	0.00	0.00

10	Pred1	A	A	0.00	0.00	0.00	0.00	0.00
11	StBass	J	A	0.01	0.06	0.08	0.17	0.25
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.03	0.09	0.19	0.24
15	DSLth	J	A	0.00	0.03	0.00	0.00	0.00
16	DSLth	A	A	0.00	0.00	0.00	0.00	0.00
17	TpJS	J	A	0.00	0.02	0.06	0.00	0.00
18	EPJA	J	A	0.06	0.27	0.41	#	#
19	Secchi	A	B	0.01	0.08	0.23	#	#
20	Secchi	A	A	0.01	0.08	0.23	*	*
21	Jent	L	A	0.01	0.00	0.00	0.00	0.00
22	Aent	A	B	0.01	0.03	0.08	0.16	0.33
23	Pred2	L	B	0.18	0.06	0.10	0.18	0.25
24	Pred2	A	A	0.00	0.03	0.06	0.00	0.00

Table S3b. AICc weights for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	name	Stage	B/A	1st	2nd	3rd	4th	5th
1	SpDys	A	B	0.00	0.01	0.04	0.08	0.26
2	TpAJ	L	B	0.40	#	#	#	#
3	TpAJ	A	A	0.02	0.03	0.06	0.07	0.14
4	TpJul	L	A	0.05	0.71	#	#	#
5	EPAJ	L	B	0.89	#	#	#	#
6	EPAJ	A	A	0.04	0.03	0.11	0.13	0.17
7	EPJul	L	A	0.01	0.03	0.15	0.37	#
8	Pred1	J	A	0.09	0.32	#	#	#
9	Pred1	A	B	0.00	0.00	0.01	0.05	0.04
10	Pred1	A	A	0.01	0.04	0.10	0.22	0.23

11	StBass	J	A	0.01	0.06	0.07	0.09	0.15
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.02	0.07	0.09	0.18
15	DSLth	J	A	0.00	0.02	0.00	0.00	0.00
16	DSLth	A	A	0.00	0.00	0.00	0.01	0.08
17	TpJS	J	A	0.00	0.02	0.05	0.00	0.00
18	EPJA	J	A	0.04	0.28	0.36	#	#
19	Secchi	A	B	0.01	0.06	0.24	#	#
20	Secchi	A	A	0.01	0.06	0.16	*	*
21	Jent	L	A	0.01	0.00	0.00	0.00	0.00
22	Aent	A	B	0.01	0.07	0.14	0.37	#
23	Pred2	L	B	0.34	0.10	0.11	0.13	0.19
24	Pred2	A	A	0.02	0.06	0.12	0.12	0.10

Table S3c. AICc weights for each step in the two factor analysis for the model with Ricker survival from juvenile to adult. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	name	Stage	B/A	1st	2nd	3rd	4th	5th
1	SpDys	A	B	0.01	0.03	0.18	#	#
2	TpAJ	L	B	0.39	0.91	#	#	#
3	TpAJ	A	A	0.01	0.04	0.08	0.13	0.26
4	TpJul	L	A	0.17	0.50	#	#	#
5	EPAJ	L	B	0.44	#	#	#	#
6	EPAJ	A	A	0.00	0.00	0.00	0.00	0.00
7	EPJul	L	A	0.01	0.02	0.11	0.24	#
8	Pred1	J	A	0.02	0.16	0.38	#	#
9	Pred1	A	B	0.00	0.00	0.00	0.00	0.00
10	Pred1	A	A	0.00	0.00	0.00	0.00	0.00

11	StBass	J	A	0.01	0.03	0.09	0.00	0.00
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.02	0.11	0.17	0.27
15	DSLth	J	A	0.00	0.04	0.17	0.15	0.26
16	DSLth	A	A	0.00	0.00	0.00	0.00	0.00
17	TpJS	J	A	0.00	0.00	0.00	0.00	0.00
18	EPJA	J	A	0.53	#	#	#	#
19	Secchi	A	B	0.01	0.04	0.18	0.26	#
20	Secchi	A	A	0.01	0.04	0.18	0.26	*
21	Jent	L	A	0.01	0.01	0.00	0.00	0.00
22	Aent	A	B	0.01	0.02	0.08	0.14	0.30
23	Pred2	L	B	0.37	0.09	0.11	0.18	0.26
24	Pred2	A	A	0.00	0.01	0.04	0.00	0.00

Table S3d. AICc weights for each step in the two factor analysis for the model with Ricker survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. In the Stage column A=Adults, L=Larvae, and J=Juveniles. In the B/A column B=before density dependence and A=after density dependence. # = not included in AICc weights calculation because it was selected in previous step. * = not included in AICc weights calculation because a similar covariate was selected in previous step. The shaded cells indicate the two models chosen to retain in subsequent tests.

Run	name	Stage	B/A	1st	2nd	3rd	4th	5th	6th	7th
1	SpDys	A	B	0.00	0.02	0.04	0.03	0.23	#	#
2	TpAJ	L	B	0.32	0.38	#	#	#	#	#
3	TpAJ	A	A	0.01	0.04	0.05	0.08	0.12	0.48	#
4	TpJul	L	A	0.04	0.09	0.61	#	#	#	#
5	EPAJ	L	B	0.78	#	#	#	#	#	#
6	EPAJ	A	A	0.03	0.02	0.07	0.19	0.18	0.00	0.00
7	EPJul	L	A	0.01	0.03	0.06	0.21	0.61	#	#
8	Pred1	J	A	0.01	0.13	0.30	#	#	#	#
9	Pred1	A	B	0.00	0.00	0.00	0.00	0.06	0.00	
10	Pred1	A	A	0.01	0.00	0.04	0.11	0.10	0.00	

11	StBass	J	A	0.00	0.04	0.08	0.00	0.00	0.00	0.00
12	StBass	A	B	0.00	0.00	0.00	0.00	0.00	0.17	0.00
13	StBass	A	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	DSLth	L	A	0.00	0.00	0.02	0.08	0.12	0.23	#
15	DSLth	J	A	0.00	0.04	0.09	0.09	0.10	0.20	0.54
16	DSLth	A	A	0.00	0.00	0.00	0.00	0.00	0.17	0.00
17	TpJS	J	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00
18	EPJA	J	A	0.35	0.89	#	#	#	#	#
19	Secchi	A	B	0.01	0.09	0.17	0.37	#	#	#
20	Secchi	A	A	0.00	0.04	0.09	0.15	*	*	*
21	Jent	L	A	0.00	0.03	0.00	0.00	0.00	0.00	0.00
22	Aent	A	B	0.01	0.07	0.15	0.23	#	#	#
23	Pred2	L	B	0.39	#	#	#	#	#	#
24	Pred2	A	A	0.01	0.00	0.05	0.10	0.04	0.05	0.53

Table S4a. AICc values and covariates included for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult. y = covariate included in lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate.

					test1		test2		test3		test4		test5	
					covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
				AICc	841.06	833.44	827.58	824.00	823.01	823.30	824.61	825.95	828.28	831.08
				Δ	18.05	10.43	4.57	0.99	0.00	0.28	1.60	2.94	5.27	8.07
Run	Name	Stage	B/A											
1	SpDys	A	B								y	y	#	#
2	TpAJ	L	B			Y	#	#	#	#	#	#	#	#
3	TpAJ	A	A											y
4	TpJul	L	A				y	y	#	#	#	#	#	#
5	EPAJ	L	B			Y	#	#	#	#	#	#	#	#
6	EPAJ	A	A											
7	EPJul	L	A									y	#	#
8	Pred1	J	A					y	#	#	#	#	#	#
9	Pred1	A	B											
10	Pred1	A	A											
11	StBass	J	A											
12	StBass	A	B											

13	StBass	A	A										
14	DSLth	L	A										
15	DSLth	J	A										
16	DSLth	A	A										
17	TpJS	J	A										
18	EPJA	J	A					y	y	#	#	#	#
19	Secchi	A	B						y	#	#	#	#
20	Secchi	A	A						*	*	*	*	*
21	Jent	L	A										
22	Aent	A	B									y	y
23	Pred2	L	B	y									
24	Pred2	A	A										

Table S4b. AICc values and covariates included for each step in the two factor analysis for the model with Beverton-Holt survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. y = covariate included in the lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate.

					test1		test2		test3		test4		test5	
					covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
				AICc	832.46	824.68	818.25	815.18	813.92	814.32	814.17	811.85	812.33	814.75
				AICc-min(AICc)	20.60	12.83	6.40	3.33	2.06	2.46	2.32	0.00	0.48	2.90
Run	Name	Stage	B/A											
1	SpDys	A	B											y
2	TpAJ	L	B			y	#	#	#	#	#	#	#	#
3	TpAJ	A	A											y
4	TpJul	L	A				y	y	#	#	#	#	#	#
5	EPAJ	L	B		Y	y	#	#	#	#	#	#	#	#
6	EPAJ	A	A											
7	EPJul	L	A								y	y	#	#
8	Pred1	J	A					y	#	#	#	#	#	#
9	Pred1	A	B											
10	Pred1	A	A										y	
11	StBass	J	A											
12	StBass	A	B											
13	StBass	A	A											

14	DSLth	L	A						
15	DSLth	J	A						
16	DSLth	A	A						
17	TpJS	J	A						
18	EPJA	J	A	y	y	#	#	#	#
19	Secchi	A	B		y	#	#	#	#
20	Secchi	A	A			*	*	*	*
21	Jent	L	A						
22	Aent	A	B				y	#	#
23	Pred2	L	B						
24	Pred2	A	A						

Table S4c. AICc values and covariates included for each step in the two factor analysis for the model with Ricker survival from juvenile to adult. y = covariate included in lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate.

					test1		test2		test3		test4		test5	
					covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
				AICc	841.80	833.67	826.25	821.40	820.00	821.10	822.58	823.71	826.26	828.86
				Δ	21.81	13.68	6.25	1.40	0.00	1.11	2.58	3.72	6.26	8.86
Run	name	Stage	B/A											
1	SpDys	A	B							y	#	#	#	#
2	TpAJ	L	B				y	y	#	#	#	#	#	#
3	TpAJ	A	A											y
4	TpJul	L	A					y	#	#	#	#	#	#
5	EPAJ	L	B				#	#	#	#	#	#	#	#
6	EPAJ	A	A											
7	EPJul	L	A									y	#	#
8	Pred1	J	A						y	y	#	#	#	#
9	Pred1	A	B											
10	Pred1	A	A											
11	StBass	J	A											
12	StBass	A	B											

13	StBass	A	A										
14	DSLth	L	A										
15	DSLth	J	A										
16	DSLth	A	A										
17	TpJS	J	A										
18	EPJA	J	A		Y	#	#	#	#	#	#	#	#
19	Secchi	A	B							y	y	#	#
20	Secchi	A	A							*	*	*	*
21	Jent	L	A										
22	Aent	A	B									y	y
23	Pred2	L	B	y	Y								
24	Pred2	A	A										

Table S4d. AICc values and covariates included for each step in the two factor analysis for the model with Ricker survival from juvenile to adult and a Beverton-Holt stock-recruitment relationship. y = covariate included in lowest AICc model, # = covariate selected in previous step, * = covariate not considered because it is similar to another covariate. Additional covariates increased the AICc by more than 4 units and are not shown.

					test1		test2		test3		test4		test5		test6		test7	
					covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2	covar1	covar2
				AICc	833.16	824.93	817.96	814.72	811.60	810.20	810.72	810.38	808.47	809.23	810.86	813.39	817.03	820.83
				AICc-min(AICc)	24.68	16.46	9.49	6.25	3.12	1.73	2.25	1.91	0.00	0.75	2.38	4.92	8.55	12.36
Run	name	Stage	B/A															
1	SpDys	A	B											y	#	#	#	#
2	TpAJ	L	B			y		y	#	#	#	#	#	#	#	#	#	#
3	TpAJ	A	A												y	y	#	#
4	TpJul	L	A						y	y	#	#	#	#	#	#	#	#
5	EPAJ	L	B		Y	y	#	#	#	#	#	#	#	#	#	#	#	#
6	EPAJ	A	A															
7	EPJul	L	A										y	y	#	#	#	#
8	Pred1	J	A							y	#	#	#	#	#	#	#	#
9	Pred1	A	B															
10	Pred1	A	A															

11	StBass	J	A												
12	StBass	A	B												
13	StBass	A	A												
14	DSLth	L	A										y	#	#
15	DSLth	J	A											y	y
16	DSLth	A	A												
17	TpJS	J	A												
18	EPJA	J	A	y	y	#	#	#	#	#	#	#	#	#	#
19	Secchi	A	B					y	y	#	#	#	#	#	#
20	Secchi	A	A							*	*	*	*	*	*
21	Jent	L	A												
22	Aent	A	B						y	#	#	#	#	#	#
23	Pred2	L	B	#	#	#	#	#	#	#	#	#	#	#	#
24	Pred2	A	A												y

Table S5. Correlation matrix for the covariates used in the analysis. See table 2 for definitions.

	Year	SpDys	TpAJ	TpJul	EPAJ	EPJul	Preds1	StBass	DSLth	TpJS	EPJA	Secci	JEnt	AEnt	Preds2
Year	1.00														
SpDys	0.03	1.00													
TpAJ	0.28	-0.41	1.00												
TpJul	0.41	0.06	0.21	1.00											
EPAJ	-0.48	0.03	-0.04	-0.31	1.00										
EPJul	-0.47	0.01	-0.23	-0.02	0.38	1.00									
Preds1	0.87	-0.06	0.44	0.45	-0.51	-0.36	1.00								
StBass	0.44	0.01	0.40	0.08	-0.23	0.00	0.54	1.00							
DSLth	-0.67	0.03	-0.10	-0.08	0.03	0.01	-0.53	-0.40	1.00						
TpJS	0.36	0.01	0.08	0.73	-0.35	-0.14	0.40	0.04	-0.16	1.00					
EPJA	-0.42	-0.07	-0.15	-0.04	0.27	0.94	-0.31	0.00	0.02	-0.16	1.00				
Secci	0.04	-0.13	0.21	0.06	-0.03	0.28	0.17	0.30	0.15	-0.26	0.31	1.00			
JEnt	-0.13	-0.11	0.33	0.25	-0.05	0.38	0.03	0.19	0.32	-0.09	0.47	0.60	1.00		
AEnt	0.38	0.22	0.15	0.45	-0.38	0.03	0.40	0.23	-0.04	0.30	0.10	-0.04	0.35	1.00	
Preds2	0.90	0.00	0.41	0.41	-0.44	-0.49	0.93	0.40	-0.50	0.33	-0.46	0.12	-0.05	0.39	1.00

Table S6. Correlation matrix for the parameters estimated in the model for the lowest AICc model that has Ricker survival from juveniles to adults and a Beverton-Holt stock-recruitment relationship. Many parameters are estimated on the log scale. See table 2 for covariate definitions.

			Correlation																
Parameter	Value	SD	$\ln(a_L)$	$\ln(a_J)$	$Ln(b_J)$	$Ln(a_A)$	$Ln(b_A)$	$Ln(N_{init})$	$Ln(\sigma_L)$	$Ln(\sigma_J)$	$Ln(\sigma_A)$	TpAJ	TpJul	EPAJ	EPJul	Pred1	EPJA	Secchi	Aent
$\ln(a_L)$	6.12	0.09	1.00																
$\ln(a_J)$	-0.84	0.27	-0.02	1.00															
$Ln(b_J)$	-8.85	0.15	-0.03	0.74	1.00														
$Ln(a_A)$	-1.40	0.87	0.12	0.06	0.05	1.00													
$Ln(b_A)$	-3.95	1.01	0.19	0.06	0.06	0.98	1.00												
$Ln(N_{init})$	2.03	0.42	-0.55	0.01	-0.02	-0.14	-0.17	1.00											
$Ln(\sigma_L)$	-10.30	3891.30	0.00	0.00	0.00	0.00	0.00	0.00	1.00										
$Ln(\sigma_J)$	-0.74	0.16	-0.03	0.06	-0.12	-0.01	-0.02	-0.01	0.00	1.00									
$Ln(\sigma_A)$	-0.48	0.13	-0.03	0.03	0.03	0.08	0.02	0.07	0.00	-0.03	1.00								
TpAJ	-0.22	0.07	0.07	0.07	0.03	0.06	0.04	-0.38	0.00	0.03	-0.01	1.00							
TpJul	-0.32	0.09	-0.22	0.02	-0.02	-0.24	-0.27	-0.07	0.00	0.05	-0.08	0.16	1.00						
EPAJ	0.36	0.11	-0.05	-0.02	-0.06	-0.05	-0.03	-0.30	0.00	0.05	-0.08	0.14	0.46	1.00					
EPJul	0.33	0.13	0.51	0.02	0.00	0.19	0.20	-0.64	0.00	0.00	-0.02	0.44	-0.17	-0.35	1.00				
Pred1	-0.44	0.17	-0.01	-0.86	-0.53	-0.07	-0.07	-0.02	0.00	0.04	-0.01	-0.07	-0.03	0.03	-0.03	1.00			
EPJA	0.46	0.12	-0.01	0.22	0.42	0.04	0.04	0.15	0.00	-0.06	0.04	-0.02	-0.02	-0.04	-0.03	-0.06	1.00		
Secchi	-1.15	0.48	-0.27	-0.08	-0.06	-0.81	-0.80	0.25	0.00	0.01	-0.01	-0.13	0.25	0.10	-0.35	0.08	-0.04	1.00	
Aent	10.32	4.67	0.18	0.07	0.06	0.89	0.85	-0.17	0.00	-0.01	0.01	0.11	-0.15	-0.13	0.29	-0.07	0.04	-0.71	1.00

Table S7. Correlation matrix for the parameters estimated in the alternative model (the model that has the fewest covariates and the AIC is less than 2 AIC units greater than the lowest AIC model). Many parameters are estimated on the log scale. See table 2 for covariate definitions.

			Correlation													
Parameter	Value	SD	$\ln(a_L)$	$\ln(a_J)$	$Ln(b_J)$	$Ln(a_A)$	$Ln(b_A)$	$Ln(N_{init})$	$Ln(\sigma_L)$	$Ln(\sigma_J)$	$Ln(\sigma_A)$	TpAJ	TpJul	EPAJ	Pred1	EPJA
$\ln(a_L)$	6.02	0.09	1.00													
$\ln(a_J)$	-0.89	0.27	-0.08	1.00												
$Ln(b_J)$	-8.85	0.15	-0.07	0.74	1.00											
$Ln(a_A)$	-2.52	0.52	0.05	0.04	0.02	1.00										
$Ln(b_A)$	-5.25	0.83	0.19	0.03	0.02	0.95	1.00									
$Ln(N_{init})$	2.67	0.39	-0.45	0.07	0.00	-0.13	-0.20	1.00								
$Ln(\sigma_L)$	-2.32	1.50	0.35	-0.14	-0.11	0.11	0.16	-0.34	1.00							
$Ln(\sigma_J)$	-0.76	0.16	-0.03	0.05	-0.12	0.03	0.02	0.00	-0.02	1.00						
$Ln(\sigma_A)$	-0.34	0.13	-0.08	0.08	0.05	0.14	0.01	0.13	-0.18	0.00	1.00					
TpAJ	-0.31	0.07	-0.19	0.09	0.04	0.04	0.00	-0.11	-0.10	0.03	0.06	1.00				
TpJul	-0.30	0.10	-0.16	0.05	0.00	-0.16	-0.19	-0.20	-0.13	0.02	-0.05	0.27	1.00			
EPAJ	0.47	0.12	0.28	-0.04	-0.08	0.16	0.21	-0.76	0.27	0.03	-0.14	0.29	0.40	1.00		
Pred1	-0.40	0.17	0.04	-0.87	-0.54	-0.05	-0.03	-0.08	0.13	0.05	-0.06	-0.08	-0.07	0.05	1.00	
EPJA	0.46	0.12	-0.02	0.22	0.41	0.01	0.01	0.17	-0.06	-0.07	0.03	0.00	-0.01	-0.07	-0.07	1.00