A state–space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt (*Hyposmesus transpacificus*)

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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 multistage life cycle model that allows for density dependence and environmental factors to impact different life stages. Models are ranked using a two-covariates-at-a-time stepwise procedure based on AIC$_c$ 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 (*Hyposmesus transpacificus*), 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.

Résumé : Les multiples facteurs qui agissent sur les différents stades du cycle biologique influencent la dynamique des populations et compliquent l'évaluation et la gestion des populations. Afin de fournir des avis de gestion appropriés, il faut utiliser les données pour déterminer quels facteurs sont importants et quels stades du cycle ils affectent. Il est aussi important de considérer la densité dépendance, car elle peut modifier l'impact de certains facteurs. Nous mettons au point un type de modèle état–espace à stades de vie multiples qui tient compte de l'impact de la densité dépendance et des facteurs du milieu sur les différents stades de vie. Les modèles sont placés par ordre à l'aide d'une procédure pas-à-pas de deux covariables à la fois basée sur l'établissement de la moyenne des modèles de type AIC$_c$ afin de réduire la possibilité d'exclure des facteurs décelables en combinaison, mais non isolément. Une analyse d'impacts sert à évaluer les effets des facteurs sur la population. Nous illustrons ce cadre d'analyse en l'appliquant à l'éperlan du delta (*Hyposmesus transpacificus*), une espèce menacée qui est potentiellement affectée par de multiples facteurs anthropiques. Nos résultats montrent que la densité dépendance et quelques facteurs clés affectent la population d'éperlans du delta. La température, les proies et les prédateurs dominent parmi les facteurs révélés par les données et ils agissent sur différents stades de vie. Les facteurs retenus expliquent les déclins récents de l'abondance de l'éperlan du delta et peuvent fournir une perspective sur la cause de la diminution des espèces pélagiques dans l'estuaire de San Francisco.

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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 (Rose et al. 2001). 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.

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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, 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 with 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 (*Hyposmesus transpacificus*). 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 because of 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 US 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, 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.

$$(1) \qquad N_{t,s} \sim \text{Lognormal}\left[f(N_{t,s-1}), \sigma^2_{s-1}\right]; \qquad s > 1$$

$$(2) \qquad N_{t,1} \sim \text{Lognormal}\left[f(N_{t-1,\text{nstages}}), \sigma^2_{\text{nstages}}\right]$$

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).

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

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.

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

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

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

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.,

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

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.,

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

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).

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

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 $\boldsymbol{a}$, $\boldsymbol{b}$, $\boldsymbol{\gamma}$; 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 $\boldsymbol{\nu}$. The observation error standard deviation, $\boldsymbol{\nu}$, 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 $N_{1,1}$, $\boldsymbol{a}$, $\boldsymbol{b}$, $\boldsymbol{\gamma}$, $\boldsymbol{\lambda}$, $\boldsymbol{\beta}$, $\boldsymbol{\sigma}$, and $\boldsymbol{\nu}$.

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 (ADMB; 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 at http://admb-project.org/.

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

$$N_{t,s} = f(N_{t,s-1})\exp\left(\sigma_{s-1}\varepsilon_{t,s-1} - 0.5\sigma_{s-1}^2\right) \tag{10}$$

$$N_{t,1} = f(N_{t-1,\mathrm{nstages}}) \times \exp\left(\sigma_{\mathrm{nstages}}\varepsilon_{t-1,\mathrm{nstages}} - 0.5\sigma_{\mathrm{nstages}}^2\right) \tag{11}$$

$$\varepsilon_{t,s} \sim N(0,1) \tag{12}$$

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

$$0.5\sum_{t,s}\varepsilon_{t,s}^2 \tag{13}$$

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

$$-\ln(L) = \sum_{t,s}\ln(\nu_{t,s}) + \frac{(I_{t,s} - qN_{t,s})^2}{2\nu_{t,s}^2} \tag{14}$$

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 whether $b = 0$. When $b = 0$, γ has no influence on the results, and unless a hypothesis about γ 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, γ). A factor has no influence on the model when its coefficient (λ, β) 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 criterion adjusted for sample size (AIC$_\mathrm{c}$) and AIC$_\mathrm{c}$ 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 (Anderson et al. 2000; Hobbs and Hilborn 2006).

The AIC$_\mathrm{c}$ is useful for ranking alternative hypotheses when multiple covariates and density dependence assumptions are being considered. The AIC$_\mathrm{c}$ (Burnham and Anderson 2002) is given by

$$\mathrm{AIC_c} = -2\ln L + 2K + \frac{2K(K+1)}{n-K-1} \tag{15}$$

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 AIC$_\mathrm{c}$ score.

AIC$_\mathrm{c}$ 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$_\mathrm{c}$ weights are essentially the rescaled likelihood penalized by the number of parameters, which is considered the likelihood for the model (Anderson et al. 2000).

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_j \exp(-0.5\Delta_j)} \tag{16}$$

where Δ is the difference in the AIC$_\mathrm{c}$ score from the minimum AIC$_\mathrm{c}$ 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 et 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 AIC$_\mathrm{c}$ model in the current iteration is at least four AIC$_\mathrm{c}$ units higher than the model with the lowest overall AIC$_\mathrm{c}$ (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 Kullback–Leibler (K–L) best model ($4 \leq \Delta$) and the fact that there is a maximum Δ when adding

Table 1. Algorithm for evaluating covariates for the delta smelt (*Hyposmesus transpacificus*) application.

1	Evaluate density dependence.
(a)	Calculate all combinations of density-dependent processes without the inclusion of factors. Combinations include (*i*) density independent; (*ii*) Beverton–Holt; (*iii*) Ricker; and (*iv*) estimate both b and γ. These can be at any of the three stages.
(b)	Choose the density dependence combination that has the lowest AIC_c, or if there are several that have similar support, choose multiple combinations.
2	Evaluate covariates.
(a)	For each density dependence scenario chosen in 1b, run all possible one- and two-covariate combinations.
(b)	For each combination, set the AIC_c 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 AIC_c weights for a given covariate across all models that include that covariate.
(d)	Select the two covariates with the highest summed AIC_c weights to retain for the next iteration.
(e)	Iterate *a–d* until the AIC_c value of the best model in the current iteration is more than four units higher than the lowest AIC_c 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 AIC_c is degraded. If the AIC_c is not degraded, exclude that covariate from the model.

covariates to the lowest AIC_c model. We have chosen to carry out the selection process by using the sum of the AIC_c 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 AIC_c model can be justified (their page 330) based on professional judgment, but only after the results of formal selection methods have been presented (their page 334). For example, model parameterizations that do not make sense biologically might be eliminated from consideration. Burnham and Anderson (2002) give an example (their page 197) where a quadratic model is rejected because it could not produce the monotonic increasing dose response that was desired. Sometimes AIC_c 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, Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, personal communication, 2010).

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 A). We assume that recruitment (or the individuals surviving) cannot 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).

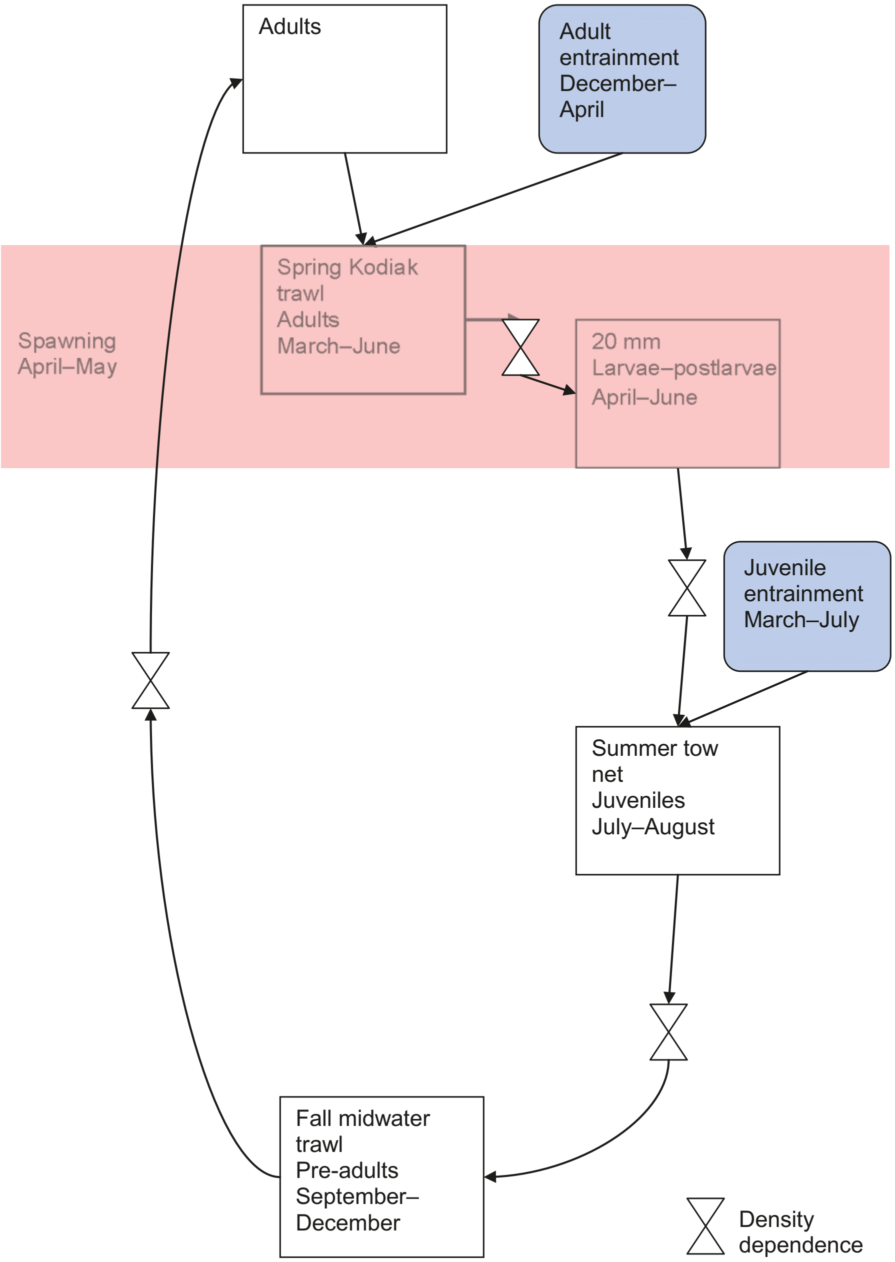
Impact analysis

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 multistage life cycle model is applied to delta smelt to illustrate the application of the model, covariate selection procedure, and impact analysis. Delta smelt effectively live for 1 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 (Fig. 1). The model stages are associated with the timing of the three main surveys, (*i*) 20 mm trawl (20 mm), (*ii*) summer tow net (STN), and (*iii*) fall midwater 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

Fig. 1. Life cycle diagram of delta smelt (*Hyposmesus transpacificus*) with survey, entrainment, and density dependence timing.



time period. The FMWT abundance index is available for the whole time period except for 1974 and 1979. The 20 mm 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 (2010*b*, tables 2.1 and 2.2). The standard errors were calculated by bootstrap procedures (Manly 2010*a*). The 20 mm survey index was taken from Nations (2007). The index values and standard errors are given in the supplementary material[1]. The results of the bootstrap analysis suggest that the abundance indices are normally distributed (Manly 2010*a*).

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 $1 - \mu = \exp(\beta x)$, and x will be used as a covariate in the model. Setting $\beta = 1$ gives $x = \ln(1 - \mu)$.

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 (2010*b*). The entrainment mortality rates are calculated based on Kimmerer (2008); the rates were obtained by fitting a piecewise linear

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[1] Supplementary data are available with the article through the journal Web site (http://www.nrcresearchpress.com/cjfas).

Table 2. The variables used as candidates to account for the changes in delta smelt abundance.

Factor	Name	Covariate	Stage	Before–After	Sign	Description	Data scaling	Justification
1	SpDys	1	A	Before	+	Days where temperature is in the range 11–20 °C	Norm	This measures the number of days of spawning — the longer the spawning season, presumably the better chance of survival
2	TpAJ	2	L	Before	– or +	Average water temperature in delta smelt habitat for April–June	Norm	Temperature affects growth rate and survival of early life stages
3	TpAJ	2	A	After	– or +			
4	TpJul	3	L	After	–	Average water temperature in delta smelt habitat for July	Norm	Higher water temperatures can be lethal; could also include August temperature
5	EPAJ	4	L	Before	+	Minimum eurytemora and pseudodiaptomus density for April–June	Norm	Measures height of food "gap" in spring, as eurytemora falls from spring maximum and pseudodiaptomus rises from ~0
6	EPAJ	4	A	After	+			
7	EPJul	5	L	After	+	Average eurytemora and pseudodiaptomus density for July	Norm	Measures food availability in summer until summer tow net survey, identified as problem by Bennett (2005) based on smelt condition
8	Pred1	6	J	After	–	September–December abundance of 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 Secchi depth
9	Pred1	6	A	Before	–			
10	Pred1	6	A	After	–			
11	StBass	7	J	After	–	September–December abundance of striped bass	Mean	A major predator, whose abundance is measured as actual number of adults
12	StBass	7	A	Before	–			
13	StBass	7	A	After	–			
14	DSLth	8	L	After	+	Delta smelt average length	Norm	See Bennett (2005) for length vs. fecundity relationship, linear for 1-year-olds
15	DSLth	8	J	After	+			
16	DSLth	8	A	After	+			
17	TpJS	9	J	After	–	Maximum 2-week average temperature for July–September	Norm	Measure of whether lethal temperature is reached in hot months
18	EPJA	10	J	After	+	Average eurytemora and pseudodiaptomus density for July–August	Norm	Measures food availability in summer between STN and FMWT surveys, identified as problem by Bennett (2005) based on smelt condition
19	Secchi	11	A	Before	–	January–February weighted Secchi depth	Norm	Protection from predators
20	Secchi	11	A	After	–			
21	Jent	12	L	After	+*	Juvenile entrainment	Raw	Entrained in by water pumps
22	Aent	13	A	Before	+*	Adult entrainment	Raw	Entrained in by water pumps
23	Pred2	14	L	Before	–	April–June abundance of 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 Secchi depth
24	Pred2	14	A	After	–			

Note: 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.

Table 3. AIC_c weights for all possible density dependence models without covariates.

		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

Note: 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).

regression model of winter Old Middle River flow to his adult entrainment estimates and his larval–juvenile entrainment estimates were fitted to a multiple linear regression model with spring Old Middle River flow and spring low salinity zone (as measured by X). 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 (2010*b*) 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 (2010*b*) 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 covariate values used in the model are given in the supplementary material[1]). 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 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.

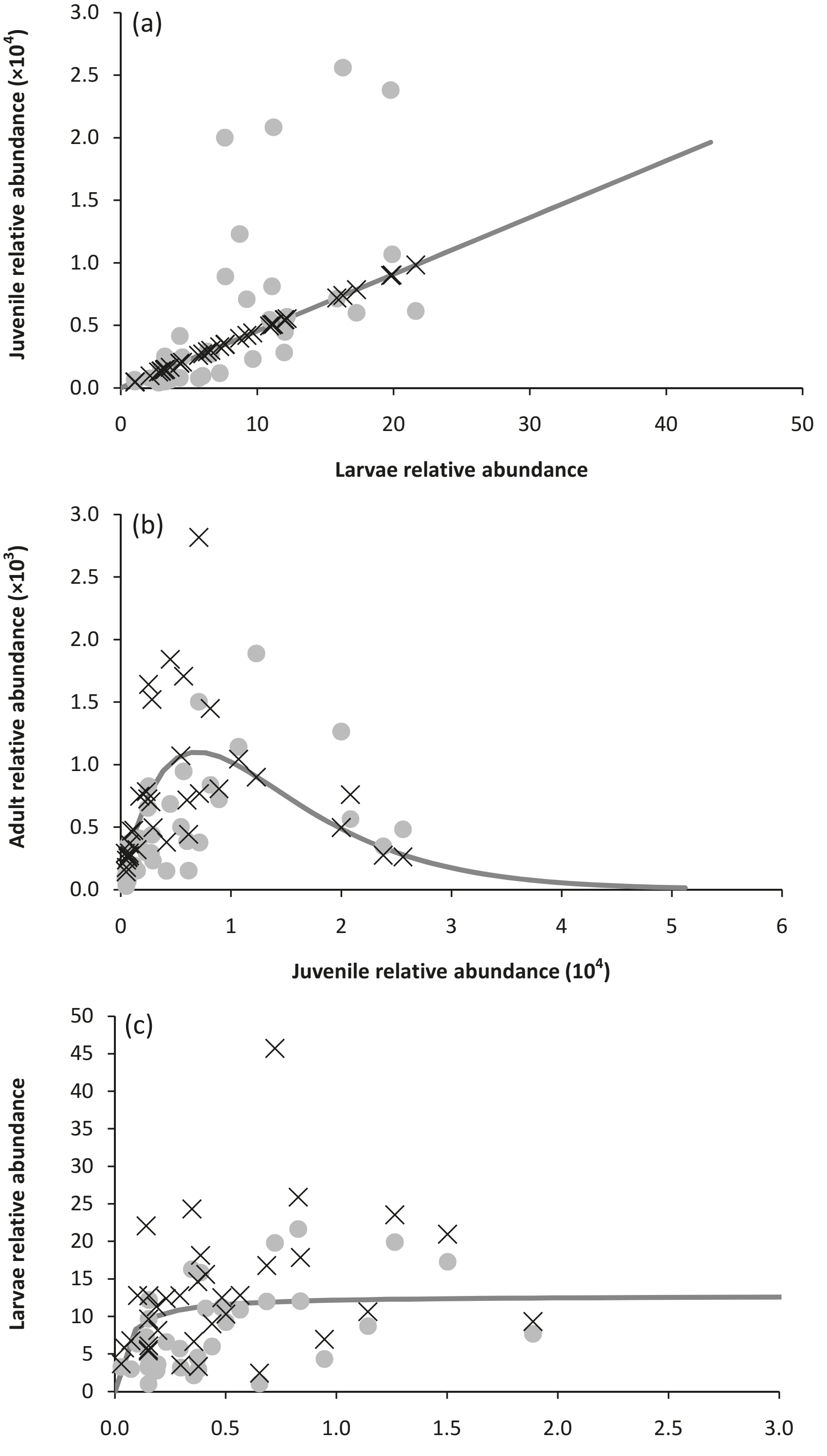
The standard approach outlined above and in Table 1 is applied to the delta smelt application. The Ricker model was approximated by setting $\gamma = -\exp(-10)$. We also constrained $\gamma < 0$ to avoid computational errors. It is difficult to scale the survey data to absolute abundance, so they are 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 were 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

AIC_c 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 (Figs. 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 (three to four times) higher than that for density dependence. Therefore, we proceed with four density dependence scenarios: (*i*) Beverton–Holt density dependence in survival from juveniles to adults (JBH); (*ii*) Beverton–Holt density dependence in survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship from adults to larvae (JBHABH); (*iii*) Ricker density dependence in survival from juveniles to adults (JR); and (*iv*) Ricker density dependence in survival from juveniles to adults and a Beverton–Holt stock–recruitment relationship from adults to larvae (JRABH).

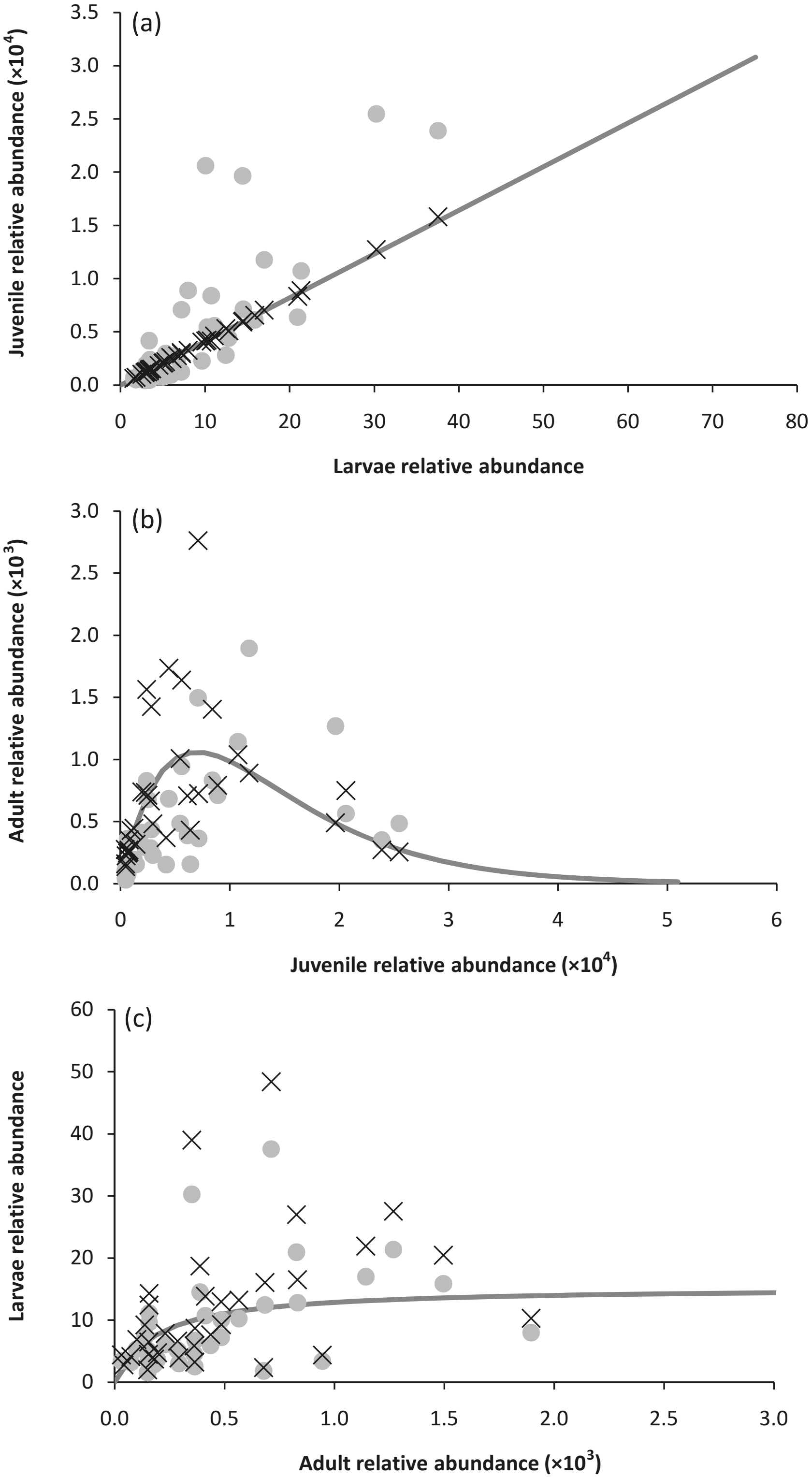
The number and the type of factors supported by the data

Fig. 2. Relationship among stages in the model for the lowest AIC$_c$ 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.



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 AIC$_c$ models (eight and nine 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 (five covariates each). Several temperature, prey, and predator covariates (TpAJ, EPAJ, EPJA, TpJul,

Fig. 3. Relationship among stages in the alternative model (the model that has the fewest covariates and the AIC is less than two 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.



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 $\mathrm{AIC_c}$ 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-

Table 4. Order of inclusion of factors into the analysis.

Factor	Name	Stage	Before–After	JBH	JBHABH	JR	JRABH
2	TpAJ	L	Before	1	1	2	2
4	TpJul	L	After	2	2	2	3
5	EPAJ	L	Before	1	1	1	1
7	EPJul	L	After	—	4	—	5
8	Pred1	J	After	2	2	3	3
18	EPJA	J	After	3	3	1	2
19	Secchi	A	Before	—	3	—	4
22	Aent	A	Before	—	4	—	4
23	Pred2	L	Before	—	—	—	1*

Note: JBH = Beverton–Holt density dependence from the juvenile (J) to adult (A) stage; JBHABH = Beverton–Holt density dependence from the juvenile to adult stage and Beverton–Holt density dependence from the adult to larvae (L) 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 $\mathrm{AIC_c}$.

dependent assumptions, there were alternatives with more (or less) covariates than the lowest $\mathrm{AIC_c}$ 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 ($4 \leq \Delta$), suggesting that these factors should also be considered as possible factors that influence the population dynamics of delta smelt (Table 5). However, the asymmetrical nature of the $\mathrm{AIC_c}$ 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 $\mathrm{AIC_c}$ 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 Supplemental Table S6 online[1]).

The five lowest $\mathrm{AIC_c}$ 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 $\mathrm{AIC_c}$ model of iteration 5. The lowest $\mathrm{AIC_c}$ 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 $\mathrm{AIC_c}$ model had an AIC of 812.33. Therefore, the lowest $\mathrm{AIC_c}$ model after accounting for realistic parameter values is the lowest $\mathrm{AIC_c}$ 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, $\mathrm{AIC_c} = 808.47$). 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 $\mathrm{AIC_c}$ model ($\mathrm{AIC_c} = 806.63$). Several models had an $\mathrm{AIC_c}$ score within two units of this model; according to the Burnham and Anderson (1998, p. 128) 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 two $\mathrm{AIC_c}$ units of the lowest $\mathrm{AIC_c}$ model. This alternative model is that selected with two additional parameters in iteration 3 of the selection procedure (Table 5, $\mathrm{AIC_c} = 810.20$). Removing the Pred2 covariate improved the $\mathrm{AIC_c}$ score (808.63), so we also eliminated the Pred2 covariate from this model.

The models fit the survey data well (Figs. 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 (Fig. 6; Table 7). Essentially all the variability in survival between larvae and juveniles was explained by the covariates. The amount of variability explained in the survival from juveniles to adults was higher than that in the stock–recruitment relationship, but they show similar patterns (Fig. 6; Table 7).

There was substantial correlation among estimated parameters (see supplementary material[1]). The lowest AIC model has moderate and high correlation between the covariate coefficients and several model parameters and also among the covariate coefficients themselves (Supplemental Table S6[1]). The alternative model has fewer parameter correlations (Supplemental Table S7[1]). The parameters of the density dependence function were highly positively correlated. 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

Table 5. AIC_c values for each step in the model selection process.

	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

Note: Shaded values are the lowest AIC_c for that density dependence configuration. See Table 4 for definitions.

to the fact that some of these covariates are also correlated (Supplemental Table S5[1]). 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 density dependence survival function that relates adults and larvae. The coefficient for Aent is also unrealistically large. The coefficient for Pred1 is correlated with the parameters of the density dependence relationship for juvenile survival and is also highly positively correlated with year. The coefficient for EPJA is positively correlated with the parameter that controls density dependence for juvenile survival. The coefficient for EPJul in the lowest AIC model is correlated with several parameters.

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 (Fig. 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 AIC_c 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 (Fig. 8). The lowest AIC_c model with the two entrainment coefficients set at one 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 multistage life cycle 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 (*Theragra chalcogramma*). 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

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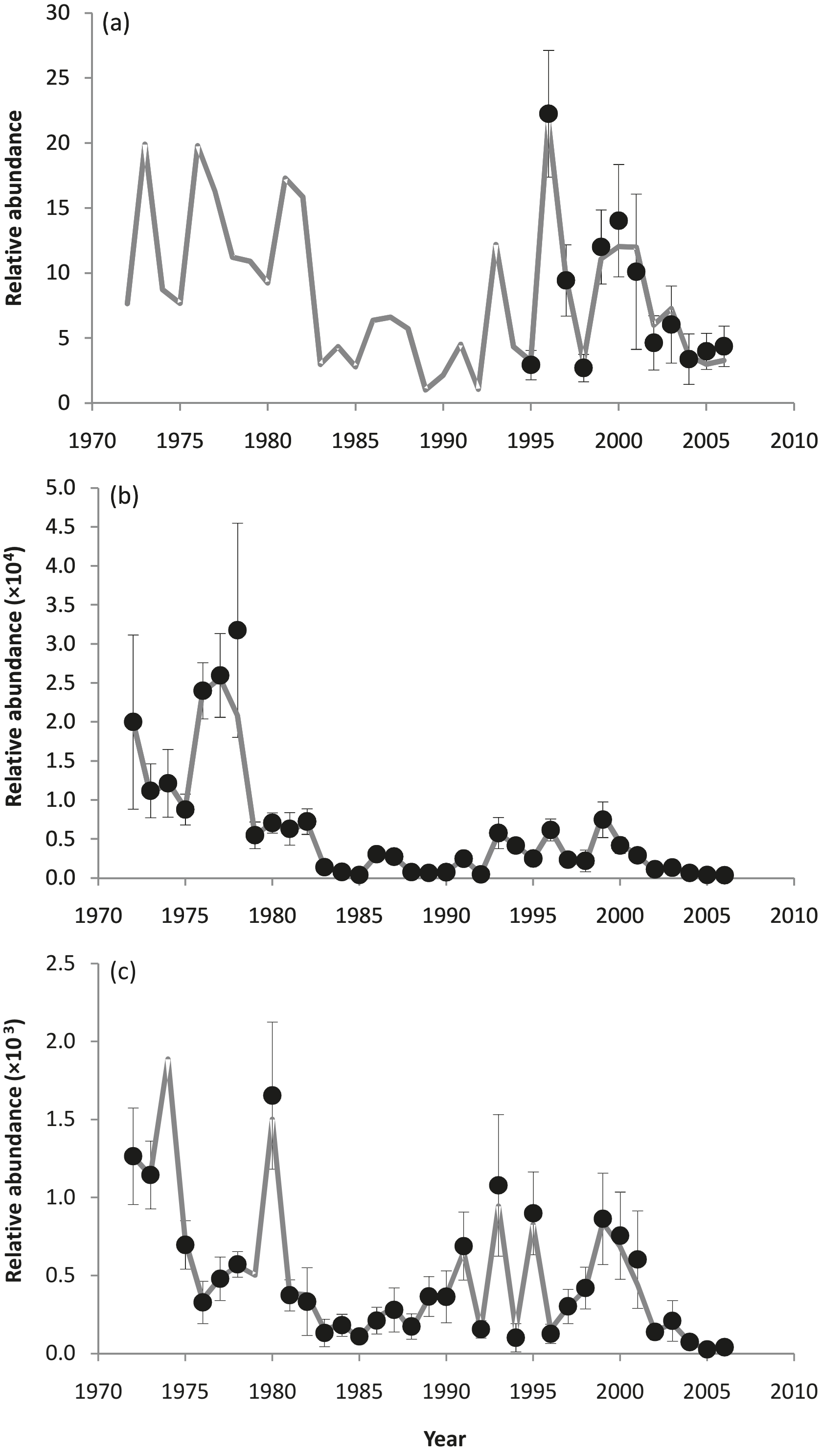
Table 6. Estimates of coefficients (and 95% confidence intervals) from the lowest AIC$_c$ models for each density dependence assumption.

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 ($\times 10^{-4}$)	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 ($\times 10^{-2}$)	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)

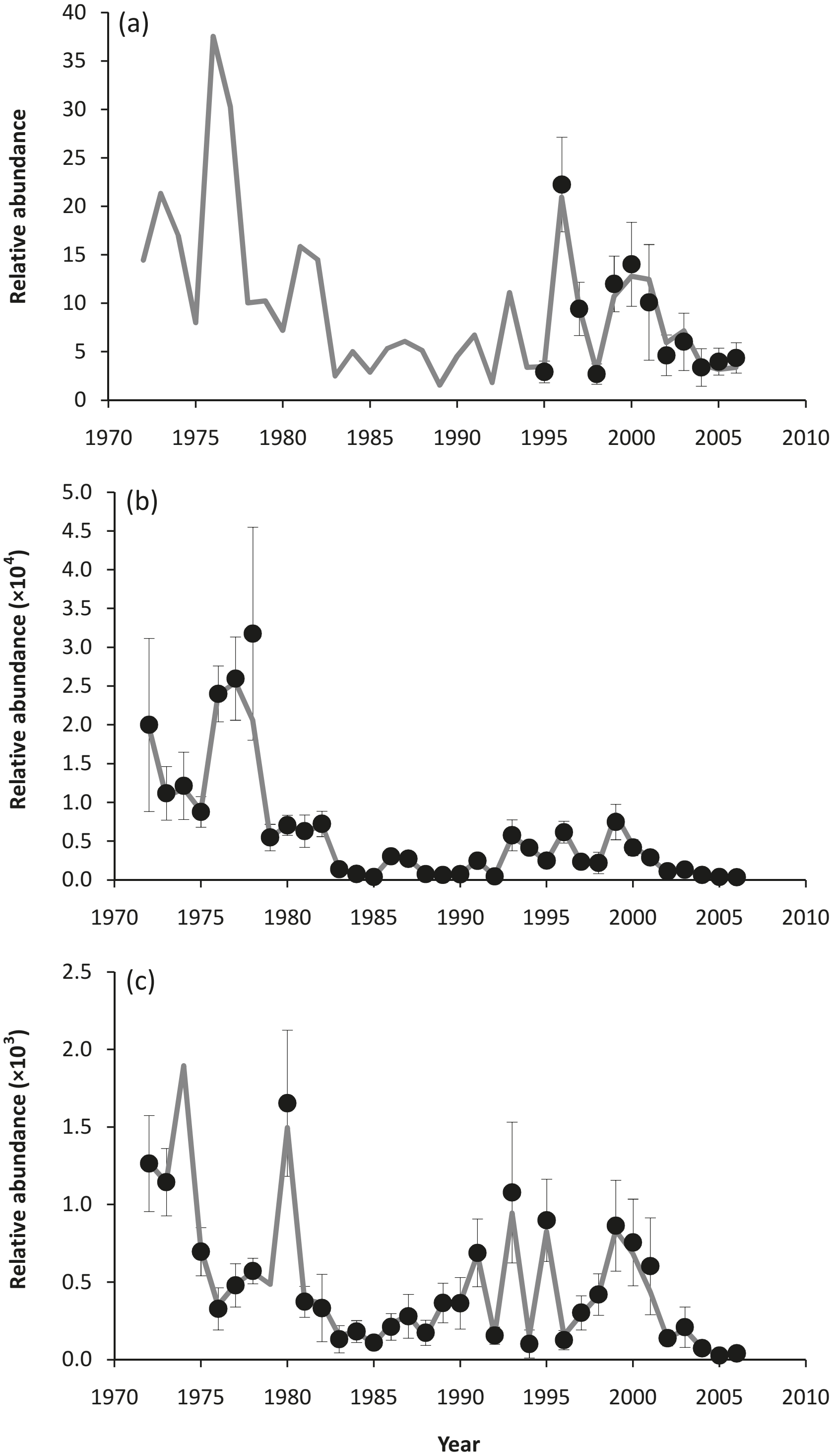
Note: Definitions of abbreviations and a description of the covariates can be found in Table 2 and the density dependence configurations in Table 4; B–A, before–after. The alternative model is the model that has the fewest covariates and the AIC$_c$ is less than two AIC$_c$ units greater than the lowest AIC$_c$ model.

Fig. 4. Fit (line) to the survey abundance data (circles) for the lowest AIC$_c$ 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.



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 regula-

Fig. 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 two 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.



tion 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., overfishing; 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

Fig. 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 AIC$_c$ model that includes Ricker survival between juveniles and adults and a Beverton–Holt stock–recruitment relationship (*a*) and the alternative model (the model that has the fewest covariates and the AIC is less than two AIC units greater than the lowest AIC model) (*b*).

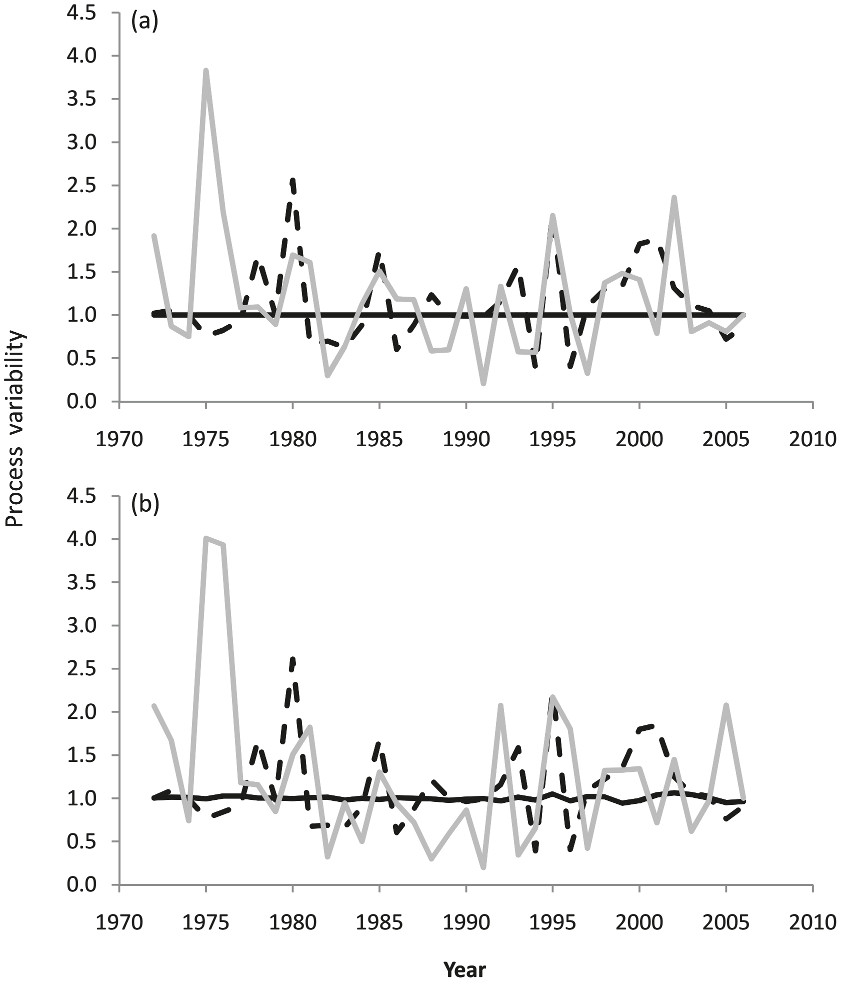


Table 7. Estimates of standard deviation of the process variation and the percentage of the process variation explained by the covariates for the lowest AIC$_c$ model.

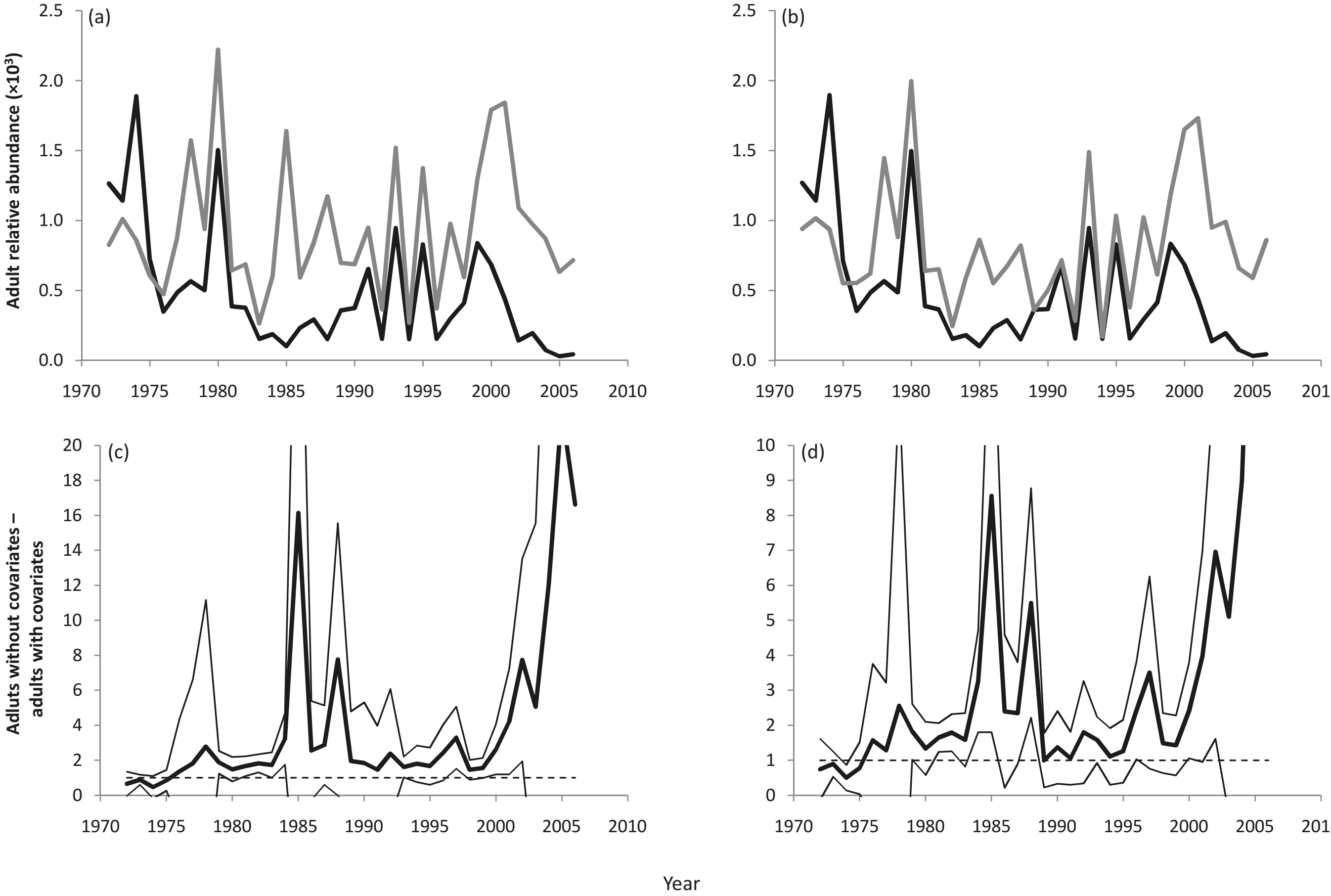
	Standard deviation		
	Without covariates	With covariates	% variation explained
Larvae	0.72	0.00	100
Juvenile	0.63	0.48	43
Adult	0.71	0.62	24

delta smelt population. Deriso et al. (2008) also found support that multiple factors influenced the decline and suppression of the Prince William Sound herring (*Clupea pallasii*) 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 20 mm 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 AIC$_c$ for two of the density-dependent assumptions, but was not selected by the two-factor stepwise procedure (see supplementary material[1]). 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 AIC$_c$. 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 (EPAJ) covariate that were consistently selected in the first or seconds steps, which operated on the same stage (larvae), when these

Fig. 7. Estimates of abundance with and without covariates (coefficients of the covariates set to zero) (top panels) and ratio of the two with 95% confidence intervals (bottom panels, *y* axis limited to show details) from the lowest AIC$_c$ (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 two AIC units greater than the lowest AIC model) (right panels).

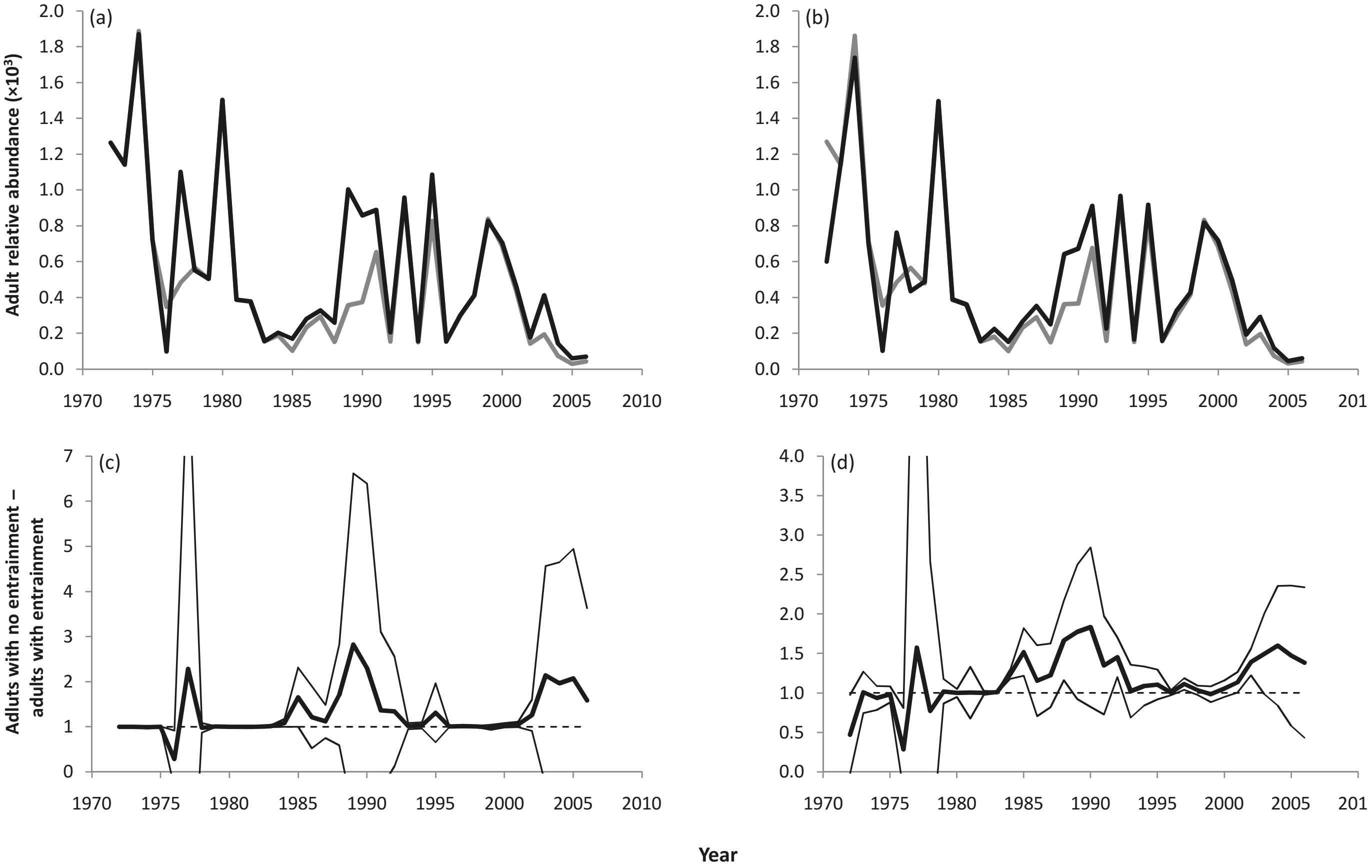


covariates were combined together. The covariate was also highly correlated with time (see supplementary material[1]). We did find, to some extent, which other covariates were included in the model, and the order in which they were included changed depending on the density dependence assumptions. However, 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.

Several of the model parameters show moderate to strong correlations. The three covariates included in the lowest AIC model, but not in the alternative model (EPJul, Secchi, and Aent), are highly correlated with other model parameters. The only coefficients that show strong correlation with each other in the alternative model are EPAJ and TPJul. These covariates have a moderate negative correlation, while the coefficients have a positive correlation and therefore offset each other. High correlation may indicate that the data do not provide enough information to separate the effects represented by the two parameters. However, hypothesis tests and the confidence intervals of the coefficients are used to judge if a particular hypothesis (covariate) is supported by the data. If there is not enough information in the data to separate two hypotheses, the hypothesis tests will fail to include one of the covariates or the confidence interval of the covariate's coefficient will contain zero. 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 inclusion of several covariates (TpAJ, EPAJ, EPJA, TpJul, Pred1) were robust to the form of density dependence and only showed low to moderate correlation among their coefficients. The predator covariate coefficient was highly correlated with the juvenile survival density dependence parameters, making the inclusion of this covariate less convincing. The predator covariate was also positively correlated with year. The coefficients for water clarity and adult entrainment, which were included in the lowest AIC model but excluded from the alternative model, were highly confounded with density dependence and required constraining the density dependence to reasonable parameter space. This may indicate that the effect of adult entrainment only shows up when abundance is very low. A model within two AIC units of the lowest AIC model did not contain either adult entrainment or water clarity, but did include all the robust factors. 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-

Fig. 8. Estimates of the adult abundance with and without adult entrainment (top panels) and the ratio of adult abundance without adult entrainment to that with adult entrainment (bottom panels, *y* axis limited to show details) from the lowest AIC$_c$ 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 two AIC units greater than the lowest AIC model) (right panels).



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-shaped curve 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[1]), 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). Previous studies using the data in this study have also assumed that catchability is constant over time (Mac Nally et al. 2010; Thomson et al. 2010). However, catchability may change because of 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. The standard deviations used in the likelihood functions are based on bootstrap analysis that takes the within-year sampling variability into consideration, but does not account for between-year variation in catchability. 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 $\mathrm{AIC_c}$ model selection without use of professional judgment is not recommended. We could have included all models in the sum of the $\mathrm{AIC_c}$ 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.

Anderson 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 multistage 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 $\mathrm{AIC_c}$ and $\mathrm{AIC_c}$ 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 $\mathrm{AIC_c}$ 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 underestimate 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 owing 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 from 2002 to 2006. However, 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 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), they provide more detailed information about how factors impact a population, they encompass all the statistical modeling advances advocated by Rose et al. 2001, 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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References

Anderson, D.R., Burnham, K.P., and Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. J. Wildl. Manage. **64**(4): 912–923. doi:10.2307/3803199.

Bennett, W.A. 2005. Critical assessment of the delta smelt population in the San Francisco estuary, California. San Francisco Estuary and Watershed Science, **3**(2): 1–71.

Besbeas, P., Freeman, S.N., Morgan, B.J.T., and Catchpole, E.A. 2002. Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics, **58**(3): 540–547. doi:10.1111/j.0006-341X.2002.00540.x. PMID:12229988.

Brook, B.W., and Bradshaw, C.J.A. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology, **87**(6): 1445–1451. doi:10.1890/0012-9658(2006)87[1445:SOEFDD]2.0.CO;2. PMID:16869419.

Buckland, S.T., Newman, K.B., Thomas, L., and Koesters, N.B. 2004. State–space models for the dynamics of wild animal populations. Ecol. Model. **171**(1–2): 157–175. doi:10.1016/j.ecolmodel.2003.08.002.

Buckland, S.T., Newman, K.B., Fernandez, C., Thomas, L., and Harwood, J. 2007. Embedding population dynamics models in inference. Stat. Sci. **22**(1): 44–58. doi:10.1214/088342306000000673.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and multimodel inference: a practical information-theoretic approach. 1st ed. Springer, New York.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.

Ciannelli, L., Chan, K.-S., Bailey, K.M., and Stenseth, N.C. 2004. Nonadditive effects of the environment on the survival of a large marine fish population. Ecology, **85**(12): 3418–3427. doi:10.1890/03-0755.

Clark, J.S., and Bjornstad, O.N. 2004. Population time series: process variability, observation errors, missing variables, lags, and hidden states. Ecology, **85**(11): 3140–3150. doi:10.1890/03-0520.

Conn, P.B., Williams, E.H., and Shertzer, K.W. 2010. When can we reliably estimate the productivity of fish stocks? Can. J. Fish. Aquat. Sci. **67**(3): 511–523. doi:10.1139/F09-194.

de Valpine, P. 2002. Review of methods for fitting time-series models with process and observation error and likelihood calculations for nonlinear, non-Gaussian state–space models. Bull. Mar. Sci. **70**: 455–471.

Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. **37**(2): 268–282. doi:10.1139/f80-034.

Deriso, R.B., Maunder, M.N., and Skalski, J.R. 2007. Variance estimation in integrated assessment models and its importance for hypothesis testing. Can. J. Fish. Aquat. Sci. **64**(2): 187–197. doi:10.1139/f06-178.

Deriso, R.B., Maunder, M.N., and Pearson, W.H. 2008. Incorporating covariates into fisheries stock assessment models with application to Pacific herring. Ecol. Appl. **18**(5): 1270–1286. doi:10.1890/07-0708.1. PMID:18686586.

Dupont, W.D. 1983. A stochastic catch–effort method for estimating animal abundance. Biometrics, **39**(4): 1021–1033. doi:10.2307/2531336. PMID:6689474.

Fournier, D.A., Hampton, J., and Sibert, J.R. 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. Can. J. Fish. Aquat. Sci. **55**(9): 2105–2116. doi:10.1139/f98-100.

Fowler, C.W. 1987. A review of density dependence in populations of large mammals. *In* Current mammalogy. *Edited by* H.H. Genoways. Plenum Press, New York. pp. 401–441.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol. Evol. **13**(2): 58–63. doi:10.1016/S0169-5347(97)01237-8. PMID:21238201.

Gimenez, O., Bonner, S., King, R., Parker, R.A., Brooks, S., Jamieson, L.E., Grosbois, V., Morgan, B.J.T., and Thomas, L. 2009. WinBUGS for population ecologists: Bayesian modeling using Markov chain Monte Carlo methods. *In* Modeling demographic processes in marked populations. *Edited by* D.L. Thomson, E.G. Cooch, and M.J. Conroy. Environ. Ecol. Stat. 3: 883–916.

Harley, S.J., Myers, R.A., and Dunn, A. 2001. Is catch-per-unit effort proportional to abundance? Can. J. Fish. Aquat. Sci. **58**(9): 1760–1772. doi:10.1139/f01-112.

Hilborn, R., and Mangel, M. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, N.J.

Hobbs, N.T., and Hilborn, R. 2006. Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. Ecol. Appl. **16**(1): 5–19. doi:10.1890/04-0645. PMID:16705957.

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.

Krebs, C.J. 2002. Two complementary paradigms for analysing population dynamics. Philos. Trans. R. Soc. Lond. B Biol Sci. **357**(1425): 1211–1219. doi:10.1098/rstb.2002.1122. PMID:12396513.

Lunn, D., Spiegelhalter, D., Thomas, A., and Best, N. 2009. The BUGS project: evolution, critique and future directions. Stat. Med. **28**(25): 3049–3067. doi:10.1002/sim.3680. PMID:19630097.

Mac Nally, R., Thomson, J.R., Kimmerer, W., Feyrer, F., Newman, K.B., Sih, A., Bennett, W., Brown, L., Fleishman, E., Culberson, S.D., and Castillo, G. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecol. Appl. **20**(5): 1417–1430. doi:10.1890/09-1724.1. PMID:20666258.

Manly, B.F.J. 2010*a*. Bootstrapping the July summer townet trawl data. Report available from Western EcoSystems Technology, Inc., Cheyenne, Wyo.

Manly, B.F.J. 2010*b*. Initial analyses of delta smelt abundance changes from fall to summer, summer to fall, and fall to fall. Report available from Western EcoSystems Technology, Inc., Cheyenne, Wyo.

Maunder, M.N. 2001. A general framework for integrating the standardization of catch per unit of effort into stock assessment models. Can. J. Fish. Aquat. Sci. **58**(4): 795–803. doi:10.1139/f01-029.

Maunder, M.N. 2003. Paradigm shifts in fisheries stock assessment: from integrated analysis to Bayesian analysis and back again. Nat. Resour. Model. **16**(4): 465–475. doi:10.1111/j.1939-7445.2003.tb00123.x.

Maunder, M.N. 2004. Population viability analysis based on combining Bayesian, integrated, and hierarchical analyses. Acta Oecol. **26**(2): 85–94. doi:10.1016/j.actao.2003.11.008.

Maunder, M.N., and Deriso, R.B. 2003. Estimation of recruitment in catch-at-age models. Can. J. Fish. Aquat. Sci. **60**(10): 1204–1216. doi:10.1139/f03-104.

Maunder, M.N., and Deriso, R.B. 2010. Dealing with missing covariate data in fishery stock assessment models. Fish. Res. **101**(1–2): 80–86. doi:10.1016/j.fishres.2009.09.009.

Maunder, M.N., and Langley, A.D. 2004. Integrating the standardization of catch-per-unit-of-effort into stock assessment models: testing a population dynamics model and using multiple data types. Fish. Res. **70**(2–3): 389–395. doi:10.1016/j.fishres.2004.08.015.

Maunder, M.N., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. **70**(2–3): 141–159. doi:10.1016/j.fishres.2004.08.002.

Maunder, M.N., and Starr, P.J. 2003. Fitting fisheries models to standardised CPUE abundance indices. Fish. Res. **63**: 43–50.

Maunder, M.N., and Watters, G.M. 2003. A general framework for integrating environmental time series into stock assessment models: model description, simulation testing, and example. Fish. Bull. **101**: 89–99.

Maunder, M.N., Hinton, M.G., Bigelow, K.A., and Langley, A.D. 2006. Developing indices of abundance using habitat data in a statistical framework. Bull. Mar. Sci. **79**: 545–559.

Maunder, M.N., Schnute, J.T., and Ianelli, J. 2009. Computers in fisheries population dynamics. *In* Computers in fisheries research. 2nd ed. *Edited by* B.A. Megrey and E. Moksness. Springer Science +Business Media B.V. pp. 337–372.

Moyle, P.B., Herbold, B., Stevens, D.E., and Miller, L.W. 1992. Life history and status of delta smelt in the Sacramento – San Joaquin estuary, California. Trans. Am. Fish. Soc. **121**(1): 67–77. doi:10.1577/1548-8659(1992)121<0067:LHASOD>2.3.CO;2.

Nations, C. 2007. Variance in abundance of delta smelt from 20 mm surveys. Report available from Western EcoSystems Technology, Inc., Cheyenne, Wyo.

Newman, K.B. 1998. State–space modeling of animal movement and mortality with application to salmon. Biometrics, **54**(4): 1290–1314. doi:10.2307/2533659.

Newman, K.B., and Lindley, S.T. 2006. Accounting for demographic and environmental stochasticity, observation error and parameter uncertainty in fish population dynamics models. N. Am. J. Fish. Manage. **26**(3): 685–701. doi:10.1577/M05-009.1.

Newman, K.B., Buckland, S.T., Lindley, S.T., Thomas, L., and Fernandez, C. 2006. Hidden process models for aninmal population dynamics. Ecol. Appl. **16**(1): 74–86. doi:10.1890/04-0592. PMID:16705962.

Newman, K.B., Fernandez, C., Thomas, L., and Buckland, S.T. 2009. Monte Carlo inference for state–space models of wild animal populations. Biometrics, **65**(2): 572–583. doi:10.1111/j.1541-0420.2008.01073.x. PMID:18565166.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. **7**(1): 35–63. doi:10.1023/A:1018419207494.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Rivot, E., Prevost, E., Parent, E., and Bagliniere, J.L. 2004. A Bayesian state–space modelling framework for fitting a salmon stage-structured population dynamic model to multiple time series of field data. Ecol. Model. **179**(4): 463–485. doi:10.1016/j.ecolmodel.2004.05.011.

Rose, K.A., Cowan, J.H., Jr, Winemiller, K.O., Myers, R.A., and Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish Fish. **2**: 293–327. doi:10.1046/j.1467-2960.2001.00056.x.

Sæther, B.E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends Ecol. Evol. **12**(4): 143–149. doi:10.1016/S0169-5347(96)10068-9. PMID:21238011.

Schnute, J. 1985. A general theory for the analysis of catch and effort data. Can. J. Fish. Aquat. Sci. **42**(3): 414–429. doi:10.1139/f85-057.

Sibert, J., Hampton, J., Kleiber, P., and Maunder, M.N. 2006. Biomass, size, and trophic status of top predators in the Pacific Ocean. Science (Washington, D.C.), **314**(5806): 1773–1776. doi:10.1126/science.1135347. PMID:17170304.

Skaug, H.J. 2002. Automatic differentiation to facilitate maximum likelihood estimation in nonlinear random effects models. J. Comput. Graph. Statist. **11**(2): 458–470. doi:10.1198/106186002760180617.

Skaug, H., and Fournier, D. 2006. Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models. Comput. Stat. Data Anal. **51**(2): 699–709. doi:10.1016/j.csda.2006.03.005.

Sommer, T., Armor, C., Baxter, R., Breuer, R., Brown, L., Chotkowski, M., Culberson, S., Feyrer, F., Gingras, M., Herbold, B., Kimmerer, W., Mueller-Solger, A., Nobriga, M., and Souz, K. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary: El colapso de los peces pelagicos en la cabecera del Estuario San Francisco. Fisheries, **32**: 270–277.

Thomson, J.R., Kimmerer, W.J., Brown, L.R., Newman, K.B., Mac Nally, R., Bennett, W.A., Feyrer, F., and Fleishman, E. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. Ecol. Appl. **20**(5): 1431–1448. doi:10.1890/09-0998.1. PMID:20666259.

Walters, C. 1987. Nonstationarity of production relationships in exploited populations. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 156–165. doi:10.1139/f87-319.

Walters, C.J. 2003. Folly and fantasy in the analysis of spatial catch rate data. Can. J. Fish. Aquat. Sci. **60**(12): 1433–1436. doi:10.1139/f03-152.

Wang, S.-P., Maunder, M.N., Aires-da-Silva, A., and Bayliff, W.H. 2009. Evaluating fishery impacts: application to bigeye tuna (*Thunnus obesus*) in the eastern Pacific Ocean. Fish. Res. **99**(2): 106–111. doi:10.1016/j.fishres.2009.05.010.

Appendix A. 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

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

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

$$R_0 = \frac{aN_0}{1 + bN_0} \quad \text{and} \quad R_0 = aN_0\exp(-bN_0)$$

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

$$R_p = \frac{apN_0}{1 + bpN_0} \quad \text{and} \quad R_p = aN_0\exp(-bpN_0)$$

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).

$$h = \frac{R_{0.2}}{R_0} = \frac{\frac{1}{N_0} + b}{\frac{5}{N_0} + b} \quad \text{and} \quad h = \frac{R_{0.2}}{R_0} = 0.2\exp(0.8bN_0)$$

To set b for a given steepness

$$b = \frac{5h - 1}{N_0 - hN_0} \quad \text{and} \quad b = \frac{\ln(5h)}{0.8N_0}$$

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.

$$h_{0.05} = \frac{R_{0.05}}{R_{\text{avg}}} = \frac{\frac{1}{N_{\text{avg}}} + b}{\frac{20}{N_{\text{avg}}} + b} \quad \text{and} \quad h_{0.05} = \frac{R_{0.05}}{R_{\text{avg}}} = 0.05\exp(0.95bN_{\text{avg}})$$

$$b = \frac{20h_{0.05} - 1}{N_{\text{avg}} - h_{0.05}N_{\text{avg}}} \quad \text{and} \quad b = \frac{\ln(20h_{0.05})}{0.95N_{0.05}}$$

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 in the sense of not rejecting high values of b.

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

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

Note: STN, summer tow net; FMWT, fall midwater tow.

References

Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. **37**(2): 268–282. doi:10.1139/f80-034.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Schnute, J. 1985. A general theory for the analysis of catch and effort data. Can. J. Fish. Aquat. Sci. **42**(3): 414–429. doi:10.1139/f85-057.