

1 State-space population dynamics 2 models: development and advantages 3 over simple log-linear regressions for 4 modeling survival illustrated with 5 application to longfin smelt (*Spirinchus* 6 *thaleichthys*)

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17 **Abstract**

18 Factors impacting the survival of individuals between two life stages have traditionally been evaluated
19 using log-linear regression of the ratio of abundance estimates for the two stages. These analyses
20 require simplifying assumptions that may impact the results of hypothesis tests and subsequent
21 conclusions about the factors impacting survival. Modern statistical methods can reduce the
22 dependence of analyses on these simplifying assumptions. State-space models and the related concept
23 of random effects allow the modeling of both process and observation error. Nonlinear models and
24 associated estimation techniques allow for flexibility in the system model, including density
25 dependence, and in error structure. Population dynamics models link information from one stage to the
26 next and over multiple time periods and automatically accommodate missing observations. We
27 investigate the impact of observation error, density dependence, population dynamics, and data for
28 multiple stages on hypothesis testing using data for longfin smelt in the San Francisco Bay-Delta.

29 **Highlights**

- 30 Modern statistical methods reduce the dependence on simplifying assumptions
- 31 State-space models allow the modeling of both process and observation error
- 32 Nonlinear models and associated estimation techniques allow flexibility in the model
- 33 Population dynamics models link information from one stage to the next and over time
- 34 Illustrated using hypothesis testing for longfin smelt in the San Francisco Bay-Delta

35 **Key words**

36 log-linear regression; longfin smelt; population dynamics; random effects; state-space model; survival;

37 **1 Introduction**

38 Estimation of survival and the factors influencing survival are vital in the research and management of
39 natural resources. Survival is a critical component of methods used to determine sustainable yields of
40 harvested resources (Quinn and Deriso, 1999). Managers need to know the most influential factors
41 effecting the survival of endangered species to focus limited financial resources on research and
42 management actions that obtain the most benefit. Anthropogenic effects have to be separated from
43 natural impacts to determine the relative importance of restricting human activities (e.g. Deriso et al.,
44 2008).

45 Survival can be estimated using a number of approaches ranging from field studies such as following
46 individuals using radio tracking and determining their fate (White and Garrott, 1990; Skalski et al., 2010)
47 to sophisticated statistical state-space population dynamics models that integrate multiple data types
48 including mark-recapture data (Besbeas et al., 2003; Maunder, 2004; Schaub and Abadi, 2010).
49 Facilitated by the availability of time series of relative abundance, log-linear modeling of the ratio of
50 relative abundance in two different life stages is a common approach to estimate relative survival and
51 evaluate the support for different hypotheses about the factors influencing survival. Log-linear modeling
52 is used because it is conveniently implemented in traditional software packages as a linear equation.
53 However, it restricts the analysis to a subset of models that are not necessarily the most appropriate for
54 the particular application. Log-linear modeling also aggregates process and observation error into a
55 single term limiting the ability to fully characterize uncertainty. Modern nonlinear modeling software
56 such as BUGS (Lunn et al., 2009) and AD Model Builder (Fournier et al., 2012) expand the modeling
57 options outside those covered by “fixed effects” log-linear models allowing flexibility in model and error
58 structure (Bolker et al., 2013).

59 Correctly dealing with both observation and process error is important for hypothesis testing and
60 evaluating data based support for alternative hypotheses (Maunder and Watters, 2003; Deriso et al.,
61 2008). Process error (also known as process noise or process variability) refers to stochasticity in
62 population dynamics, hence parameters as “random effects”, and observation error refers to inaccuracy

63 in observations (de Valpine, 2003). One approach for dealing with both observation and process error is
64 to ignore one or the other entirely. Polacheck et al. (1993) found that ignoring process error (an
65 observation error estimator) was superior to ignoring observation error (a process error estimator)
66 when estimating the parameters of a simple population dynamics model, but they did not evaluate
67 hypothesis testing. Ignoring process error biases likelihood ratio and Akaike information criterion (AIC;
68 Akaike, 1973) based tests towards incorrectly accepting covariates (Maunder and Watters, 2003). Other
69 tests such as analysis of deviance (Skalski, 1996) or randomization tests (Edgington, 1987; Deriso et al.,
70 2008) can be used, but they are less elegant and impractical in some situations. An alternative approach
71 is to include both process and observation error, but assume the ratio of the variances is known (e.g.
72 Walters and Ludwig, 1981) or that one of the variances is known (e.g. Maunder and Watters, 2003).
73 Incorrectly specifying the variance terms can bias hypothesis tests (Deriso et al., 2007). The preferred
74 approach is to use state-space models (e.g. Schnute, 1994; Newman, 1998; deValpine, 2002; Buckland et
75 al., 2004, 2007; Maunder and Deriso, 2011) that allow the estimation of the variance for both
76 observation and process error. It should be noted that state-space models are often described under a
77 different name such as random effect, hierarchical, or Bayesian models. De Valpine and Hastings (2002)
78 found that state-space models produced lower bias and often lower variance estimates than least
79 squares estimators that ignore either process noise or observation error. Traditionally, state-space
80 models have been used to model demographic variability such as the binomial probability of individuals
81 surviving given an average survival rate (Dupont, 1983; Besbeas et al., 2002). However, demographic
82 variability is typically overwhelmed by environmental variability (Buckland et al., 2007), so
83 environmental variability is often modeled instead of demographic variability or in addition to
84 demographic variability (e.g. Rivot et al., 2004; Newman and Lindley, 2006). Nonlinear, non-Gaussian
85 state-space models generally require computationally intensive high dimensional integrals that have no
86 closed form solution (de Valpine, 2003). The implementation of state-space models in a Bayesian
87 framework have been facilitated by the development of Markov chain Monte Carlo methods (Punt and
88 Hilborn, 1997; Newman et al., 2009; Lunn et al., 2009). Markov chain Monte Carlo methods have also
89 been adapted to implement state-space models in a classical framework (Lele et al., 2007). Alternatively
90 Laplace approximation (Skaug, 2002; Skaug and Fournier, 2006) or importance sampling (Maunder and
91 Deriso, 2003) can be used to implement the integration in a classical framework. Modern nonlinear
92 modeling software such as BUGS (Lunn et al., 2009) and AD Model Builder (Fournier et al., 2012) have
93 made state-space models practical for many applications (Bolker et al., 2013).

94 Density dependence is an important factor in the dynamics of many populations (Brook and Bradshaw,
95 2006) and can occur in multiple life stages (e.g. Ciannelli et al., 2004). It is important to consider density
96 dependence because it can modify the impact of factors (Rose et al., 2001; Maunder and Deriso, 2011).
97 Environmental factors and density dependence have been identified in numerous studies either
98 independently or in combination (e.g. Saether, 1997; Brook and Bradshaw, 2006; Ciannelli et al., 2004;
99 Deriso et al., 2008; Maunder and Deriso, 2011). Density dependence can easily be integrated into state-
100 space models (e.g. de Valpine and Hastings, 2002; Maunder and Deriso, 2011).

101 Log-linear models, like generalized linear models (GLMs), analysis of variance (ANOVA), and related
102 statistical methods, do not incorporate demographic relationships between abundances through time

103 (de Valpine, 2003). In contrast, lifecycle models link life-stages and time periods using population
104 dynamics propagating information and uncertainty (Buckland et al., 2007; Maunder and Deriso, 2011).
105 This link allows information related to one life-stage to inform processes influencing other life-stages
106 and is particularly important when data is not available for all life stages for all time periods. Hypotheses
107 that are difficult to consider with ANOVA and related methods can be simple to express with a
108 population dynamics model (De Valpine, 2003). De Valpine (2003) found that a population dynamics
109 model gave much higher statistical power than ANOVA and provided greater biological insight. Even
110 approximately correct population dynamics models provided higher power than omitting demographic
111 structure, but as the model structure becomes more incorrect, Type I error, power, or both is degraded
112 (De Valpine, 2003).

113 Hypothesis testing is an essential part of statistical analysis and is particularly important when
114 evaluating factors that are impacting survival. When we refer to hypothesis testing we are more
115 generally referring to the evaluation of the data based support for alternative configurations of the
116 model, where each configuration could represent an alternative hypothesis. Hypothesis testing can
117 easily become complex in population dynamics models because of the multiple factors operating on
118 different stages under the presence of density dependence. Deriso et al. (2008) present a framework for
119 evaluating alternative factors influencing survival and Maunder and Deriso (2011) extended the
120 framework to include density dependence in survival. The first step is to identify the factors to be
121 considered, including the life stages that are impacted by each factor and where density dependence
122 occurs. Next, develop a model to include these factors. Then conduct hypothesis tests to determine
123 which factors are important. Finally, conduct impact analysis to determine the impact of the factors on
124 quantities useful for management.

125 Data from longfin smelt (*Spirinchus thaleichthys*) in the San Francisco Bay-Delta are used to illustrate the
126 development and advantages of using state-space population dynamics models over simple log-linear
127 regressions for modeling survival. The models are implemented in AD Model Builder (Fournier et al.,
128 2012) using the La Place approximation for random effects (Skaug and Fournier, 2006) under a classical
129 (frequentist) framework. Longfin smelt is of conservation concern because it is exposed to a variety of
130 anthropogenic factors (e.g. habitat modification, sewage outflow, farm runoff, and water diversions)
131 and survey data has shown a decline in abundance. Longfin smelt was listed as threatened under the
132 California Endangered Species Act in 2009 and was proposed but declined for federal listing (MacNally et
133 al., 2010). Several other species in the San Francisco Estuary have also experienced declines (Bennett,
134 2005; Sommer et al., 2007; MacNally et al., 2010; Thomson et al., 2010; Maunder and Deriso, 2011), but
135 the declines have yet to be fully explained.

136 **2 Theory**

137 State-space models (e.g. Newman, 1998; Buckland et al., 2004, 2007) appropriately accommodate both
138 observation and process error (De Valpine, 2002, 2003), which can be essential for unbiased hypothesis
139 testing (Maunder and Watters, 2003; Deriso et al., 2008). However, the concept of state-space models is
140 somewhat complicated. De Valpine (2002, 2003) provides a useful description of state-space models in
141 the context of population dynamics models, but further description may be beneficial and insightful to

142 the reader. Here we illustrate state-space models with a simple population dynamics model where the
143 abundance in the next time period is simply those that survive from the previous time period:

$$144 \quad E[X_{t+1}|X_t] = \mu_s X_t \quad \text{Eq. 1}$$

145 where X_t is the number of individuals at time t , which are the states; μ_s is the mean survival rate. The
146 observations of the population are estimates of absolute abundance from line transects and the
147 sampling variation in these estimates is assumed to be normally distributed:

$$148 \quad Y_t \sim N(X_t, \sigma^2) \quad \text{Eq. 2}$$

149 where Y_t is the line transect estimate of absolute abundance at time t and σ^2 is the sampling variance.

150 State-space population dynamics models have three main components: 1) states (\mathbf{X}), 2) parameters ($\boldsymbol{\theta}$),
151 and 3) observations (\mathbf{Y}). The states represent the population such as the abundance in a life stage at a
152 given time. The parameters describe the average relationship (transition) between the states (e.g. the
153 average survival rate), but also include the initial state (e.g. X_1) and the variance parameters (e.g. σ). The
154 observations are measurements of the states, or some function of the states. The states and parameters
155 are unknown and they, or a function of them, are the quantities of interest. The observations, which are
156 known, are used to provide information about the states and parameters. Observations are generally
157 not a census of the population, but a sample of the population and therefore contain sampling error
158 (e.g. if a line transect or trawl survey is used to estimate the abundance of a population). This sampling
159 error is the observation error and is generally represented by the likelihood function. In other words, the
160 observation is known, but there is uncertainty in how the observation relates to the true abundance.
161 There may also be additional error in making the observations over and above the sampling variability,
162 but for illustrative purposes we ignore this error.

163 In traditional maximum likelihood estimation, the parameters of the model are estimated by finding the
164 parameter values that, conditional on these values, give the highest probability (likelihood) that the
165 observations came from the model. Since the states (\mathbf{X}) are a direct function of the parameters ($\boldsymbol{\theta}$), for
166 known observations and given parameter values, the probability function described in equation 2 can be
167 evaluated. Equation 2 can be evaluated for all possible parameter values and the parameter values that
168 maximize equation 2 are those that most likely produced the observations. The likelihood function that
169 is maximized to estimate the parameters is proportional to the sampling distribution (equation 2). To
170 better illustrate state-space models, let

$$171 \quad f(\boldsymbol{\theta}, \mathbf{Y}) = f(\mathbf{X}, \mathbf{Y}), \quad \text{Eq. 3}$$

172 the joint distribution of the data and parameters, since the parameters determine the states, represent
173 the probability distribution in equation 2 and

$$174 \quad f_{\boldsymbol{\theta}}(\mathbf{Y}), \quad \text{Eq. 4}$$

175 the likelihood function, represents equation 3 evaluated at the parameter values $\boldsymbol{\theta}$. Traditional
176 maximum likelihood assumes that there is a single true value for each parameter. In a State-space

177 population dynamics model, it is assumed that the values of the parameters may change over time. This
178 is the process error. Before describing state-space models, consider the survival in each time period as a
179 separate model parameter s_t :

180

$$181 \quad E[X_{t+1}|X_t] = s_t X_t \quad \text{Eq. 5}$$

182

183 In this case, the likelihood function can be denoted $f_{\theta,s}(\mathbf{Y})$ and traditional maximum likelihood assumes
184 that there is a single true value for survival probability in each time period and for the other model
185 parameters (note that the average survival parameter is replaced with a set of survival parameters, one
186 for each time period) and the survival parameters are estimated along with the other model parameters
187 by maximizing the likelihood function. However, there is now one survival parameter for each
188 observation and each survival will be estimated to exactly match the observation. No other parameters
189 can be estimated (e.g. the observation error variance) and the process error cannot be separated from
190 the observation error.

191 Intuitively, the estimation procedure could be improved by adding information based on the form of the
192 process error probability distribution (e.g. if the temporal variability in survival is known to be low, a
193 survival parameter in one time period that is very different from the survival in the other time periods is
194 unlikely) and can be conceptualized as putting an informative prior, in the Bayesian sense, on the
195 process error (except that the mean and variance of the prior are unknown) (e.g. $s_t = \mu_s \exp(\varepsilon_t)$, where
196 $\varepsilon_t \sim N(0, v^2)$), which parallels the random effects approach in generalized linear mixed models
197 (GLMMs), or in alternative notation $\ln(X_{t+1}) \sim N(\ln(\mu_s X_t), v^2)$). In this
198 case, $f_{\theta,s}(\mathbf{Y}) = f(\mathbf{Y}|\mathbf{s}, \boldsymbol{\theta})f(\mathbf{s}|\boldsymbol{\theta}) = f(\mathbf{Y}|\boldsymbol{\varepsilon}, \boldsymbol{\theta})f(\boldsymbol{\varepsilon}|\boldsymbol{\theta})$, where $f(\boldsymbol{\varepsilon}|\boldsymbol{\theta})$ is the process error probability
199 distribution, and the resulting likelihood is often referred to as a penalized likelihood. The penalized
200 likelihood combines the sampling probability distribution of the observations with the probability
201 distribution of the states (recall that the parameters determine the state and similarly the process error
202 probability distribution also defines the state probability distribution). These methods estimate the
203 process errors (or states) along with the other model parameters while maximizing the joint probability
204 distribution of the process error and the observations. However, the MLE of the process error variance is
205 not statistically consistent (Seber and Wild, 1989) and the likelihood function is degenerative towards
206 zero variance (Maunder and Deriso, 2003). There is often a negatively biased local maximum that can be
207 used for inference, but the global maximum is at zero process error variance (Maunder and Deriso,
208 2003). Typically either the observation error variance or the process error variance has to be fixed or the
209 ratio between them fixed (Walters and Ludwig, 1981). In the case of evaluating multiple covariates that
210 explain the processes error, the process error variance will decrease as covariates are added and
211 therefore the process variance should be reduced appropriately, which can only be practically achieved
212 if the process variance is estimated.

213 In contrast to penalized maximum likelihood, state-space models, like random effect models,
 214 implemented in a classical (frequentist) framework treat the process error (or states) as random
 215 variables rather than parameters and when the process error is integrated out they produce a marginal
 216 likelihood or “true likelihood” function that is used for inference (e.g. equation 4 becomes $\int f_{\theta}(\mathbf{Y}, \boldsymbol{\varepsilon}) d\boldsymbol{\varepsilon}$
 217 or equivalently $\int f_{\theta}(\mathbf{Y}, \mathbf{X}) d\mathbf{X}$). Intuitively, this can be thought of as summing up the likelihood of the
 218 observations for each possible state weighted by the probability of that state (conditioned on the
 219 parameter values), which is related to model averaging. Each possible survival will give different
 220 population abundance (state). Hence the derivation of “state-space”, which refers to the whole range of
 221 possible trajectories through time of the population states (de Valpine, 2002). Integrating out the
 222 process error takes advantage of properties of random variables (e.g. the marginal distribution), which
 223 has the advantage that it provides a consistent non-degenerative MLE for the process error variance.
 224 Pawitan (2003) appropriately summarizes state-space models/random effects as a convenient way to
 225 deal with lots of parameters. In a Bayesian framework (Punt and Hilborn, 1997), parameters are also
 226 treated as random variables and integrated out (e.g. equation 4 becomes $\int \int f(\mathbf{Y}, \boldsymbol{\theta}, \boldsymbol{\varepsilon}) d\boldsymbol{\varepsilon} d\boldsymbol{\varphi}$ or
 227 equivalently $\int \int f(\mathbf{Y}, \boldsymbol{\theta}, \mathbf{X}) d\mathbf{X} d\boldsymbol{\varphi}$, where $\boldsymbol{\varphi}$ are the parameters that are not of interest) and the
 228 probability distribution is used for inference rather than the likelihood function. One advantage of the
 229 state-space modeling approach over penalized maximum likelihood is that the marginal likelihood is
 230 consistent with AIC theory, which can be used for hypothesis testing and model selection.

231 3 Methods

232 3.1 Models

233 3.1.1 Log-linear regression

234 A common approach to model the survival of the number of individuals in a population from one
 235 life-stage to the next as a function of explanatory variables is a log-linear regression of the numbers
 236 in the second stage as a ratio of those in the first stage. A typical analysis models the reproductive
 237 output from adults (A_t) to the surviving juveniles in the next year (J_{t+1}).

$$238 \ln(J_{t+1}/A_t) \sim N(\alpha + \boldsymbol{\beta} \mathbf{I}_t, \sigma^2) \quad (\text{Eq. 6})$$

239 or equivalently in a different notation (the former notation is commonly used to describe state-space
 240 models and the latter notation commonly used to describe random effect models and can be a more
 241 useful description (de Valpine, 2003)).

$$242 \ln(J_{t+1}/A_t) = \alpha + \boldsymbol{\beta} \mathbf{I}_t + \varepsilon_t \quad (\text{Eq. 7})$$

243 where

$$244 \varepsilon_t \sim N(0, \sigma^2), \quad (\text{Eq. 8})$$

245 N represents a normal distribution, α and $\boldsymbol{\beta}$ are parameters of the linear model, \mathbf{I}_t is a matrix of
 246 covariates, and σ^2 is the variance of the error.

247 The observations are often only an index of relative abundance related to the absolute abundance by a
 248 constant q , often called catchability in the fisheries literature, such that

$$249 \ln(q_J J_{t+1}/q_A A_t) = \alpha + \beta \mathbf{I}_t + \varepsilon_t \quad (\text{Eq. 9})$$

250 and unless $q_J = q_A$, α no longer relates to survival (it also includes reproductive output in our example),
 251 but a combination of survival and differences in catchability. Never-the-less, this does not influence
 252 hypothesis tests of the covariates as long as the q 's are constant through time or their temporal
 253 variation is random and independent of the covariates.

254 The parameters can be estimate by maximizing the likelihood based on the assumed error distribution
 255 (equation 8). The likelihood function is typically used to represent observation error. However, ε in
 256 equation 9 includes both process and observation error and if J and A are known without error then ε
 257 describes the unexplained variation (process error) in the modeled relationship. If J and A are known
 258 with error (multiplicative and log-normal)

259

$$260 \ln\left(\left(J_{t+1} \exp(\varepsilon_{J,t+1})\right) / \left(A_t \exp(\varepsilon_{A,t})\right)\right) = \alpha + \beta \mathbf{I}_t + \varepsilon_t \quad (\text{Eq. 10})$$

261 where

$$\varepsilon_{A,t} \sim N(0, \sigma_{A,t}^2)$$

$$\varepsilon_{J,t+1} \sim N(0, \sigma_{J,t+1}^2)$$

262 Such that

$$263 \ln(J_{t+1}/A_t) = \alpha + \beta \mathbf{I}_t + \varepsilon_t - \varepsilon_{J,t+1} + \varepsilon_{A,t} \quad (\text{Eq. 11})$$

264

265 illustrating that equation 6 combines process error and observation error from both measures of
 266 abundance into a single error term $\varepsilon_t \sim N(0, \sigma_{J,t}^2 + \sigma_{A,t+1}^2 + \sigma_\varepsilon^2)$

267 It should be noted that often an estimate of the sampling precision of each observation is available
 268 (hence the time subscript on the variance terms), which eliminates the need to estimate the observation
 269 error variance, but this is generally not the case for the process error. If the observation error differs
 270 substantially among observations, ignoring the observation error may bias the results. Knowing the
 271 observation error variance facilitates the separation of process and observation error.

272 3.1.2 Alternative formulation

273 The log-linear regression is deterministically equivalent and, depending on assumptions,
 274 stochastically equivalent to an exponential growth model. The log-linear model assumes that the
 275 unexplained variation in the log of the abundance ratios is normally distributed while the

276 exponential growth model assumes that the unexplained variation in the abundance in the second
277 stage is log-normally distributed

278

$$279 \quad J_{t+1} = \acute{\alpha} A_t \exp(\beta \mathbf{I}_t + \varepsilon_t) \quad (\text{Eq. 12})$$

280 Where $\acute{\alpha} = \exp(a)$

281

282 **3.1.3 State-space model**

283 The estimates of abundance used in the regression are often known with error and this error should be
284 taken into consideration when doing the analysis. State-space models can be used to include both
285 observation (i.e. the uncertainty in the estimates of abundance) and process error (the process variation
286 not explained by the regression coefficients). In general, random effects are used to model process
287 error and are equivalent to integrating across the state-space in a state-space model.

288 An advantage of non-linear state-space models is the flexibility in representing process and observation
289 error. Equation 6 assumes log-normal multiplicative error for both the observation and process error
290 with constant variance. The log-normal assumption as implemented in Equation 6 will provide an
291 unbiased estimate of a , but the quantity of interest $\acute{\alpha} = \exp(a)$ will be biased such that the expected
292 value of $E[\acute{\alpha}] = \exp(a + 0.5\sigma^2)$ (Maunder and Deriso, 2011). Equation 12 could be modified to account
293 for the bias

294

$$295 \quad J_{t+1} = \acute{\alpha} A_t \exp(\beta \mathbf{I}_t + \varepsilon_t - 0.5\sigma^2) \quad (\text{Eq. 13})$$

296 Similarly the likelihood and random effects can be modified to deal with the log-normal bias correction
297 when implementing observation and process error. This may be particularly important when the
298 observations have different variances resulting in different bias correction factors for each time period.

299 Alternative error structures could also be used to implement the process and observation error and they
300 need not have the same error structure. For example, the process error may be log-normal, while the
301 observation error might be normal.

302 **3.1.4 Density dependence**

303 Population regulation is controlled by both density independent and density dependent factors. The log-
304 linear regression typically includes covariates representing density independent factors (e.g. the
305 environment). Density dependence can be included in the log-linear regression by adding additional
306 terms related to abundance into the regression. The Ricker model (Ricker, 1954)

$$307 \quad J_{t+1} = \acute{\alpha} A_t \exp(-bA_t + \beta \mathbf{I}_t + \varepsilon_t) \quad \text{Eq. 14}$$

308 is often used because it can be linearized by taking the natural logarithm and implemented using
309 multiple linear regression.

310

$$311 \quad \ln(J_{t+1}) = a + \ln(A_t) - bA_t + \beta \mathbf{I}_t + \varepsilon_t \quad \text{Eq. 15}$$

312 Where $a = \ln(\hat{a})$

313 However, the Beverton-Holt model (Beverton and Holt, 1957) is often more applicable for some
314 populations, but requires iterative non-linear estimation.

315

$$316 \quad J_{t+1} = \frac{aA_t}{1+bA_t} \exp(\beta \mathbf{I}_t + \varepsilon_t) \quad \text{Eq. 16}$$

317

318 **3.1.5 State-space population dynamics model**

319 The log-linear regression only models survival from one stage to the next. A sequence of separate log-
320 linear regressions can be used to model the survival between each stage, however this does not link
321 information among stages, which can be useful particularly if there is substantial error in the estimates
322 of abundance or if there are missing abundance estimates. In the case where adults are a year older
323 than juveniles and the juveniles are measured the year after spawning:

324

$$325 \quad J_{t+1} = \frac{a_J A_t}{1+b_J A_t} \exp(\beta_J \mathbf{I}_t + \varepsilon_{J,t}) \quad \text{Eq. 17}$$

$$326 \quad A_{t+1} = \frac{a_A J_t}{1+b_A J_t} \exp(\beta_A \mathbf{I}_t + \varepsilon_{A,t}) \quad \text{Eq. 18}$$

327 where the process errors $\varepsilon_A \sim N(0, \sigma_{\varepsilon_A}^2)$ and $\varepsilon_J \sim N(0, \sigma_{\varepsilon_J}^2)$ are treated as random effects and the
328 observation errors $\ln(J) \sim N(\ln(J), \sigma_J^2)$ and $\ln(A) \sim N(\ln(A), \sigma_A^2)$ are implemented using likelihoods.

329 In addition to the parameters of the two Beverton-Holt models, the covariate coefficients, and the
330 standard deviations of the random effects, the initial condition for the population dynamics model,
331 which are the abundance in the first time period for adults, J_1 , and abundance in the first time period for
332 adults, A_1 , in this case, have to be estimated as parameters. Figure 1 illustrates the difference between
333 the exponential model representation of the log-linear regression and the state-space population
334 dynamics model.

335 **3.2 Hypothesis testing and model selection**

336 There are various methods that can be used for hypothesis testing and evaluating the data based
337 evidence of support for alternative hypotheses, or, perhaps more accurately, evaluating the measure of

338 evidence from data about alternative models (Hilborn and Mangel, 1997; Hobbs and Hilborn, 2006). The
339 influence of a covariate can be eliminated from the model by fixing the associated coefficient at zero.
340 This produces a nested model, and model selection can be conducted using likelihood ratio tests. In the
341 case of a two sided hypothesis test, two times the difference in the negative log-likelihood is compared
342 with 3.84 based on $\Pr\{\chi_1^2 < 3.84\} = 0.95$. If the test is a one sided hypothesis test with significance
343 level of 5% then two times the difference in the negative log-likelihood is compared with 2.71 based on
344 $\Pr\{\chi_1^2 < 2.71\} = 0.90$ and the constraint that the sign of the coefficient has to be correct.

345 The likelihood ratio test is not appropriate for non-nested models. For example, when comparing
346 between two models that include different covariates or two different density dependence
347 assumptions. In this case, information theory-based methods such as the Akaike information criterion
348 (AIC; Akaike, 1973) are appropriate. They are also appropriate for nested models. We use the AIC
349 adjusted for small sample size (AIC_c) (Burnham and Anderson, 2002)

$$350 \quad AIC_c = -2\ln L + 2K + \frac{2K(K+1)}{n-K-1} \quad (\text{Eq. 19})$$

351 Where L is the likelihood function evaluated at its maximum, K is the number of estimated parameters,
352 and n is the number of observations. The difference between a given model and the model with the
353 lowest AIC_c value, Δ , is used for comparing models. For model comparison, Burnham and Anderson
354 (1998) recommend: “For any model with $\Delta \leq 2$ there is no credible evidence that the model should be
355 ruled out For a model with $2 \leq \Delta \leq 4$ there is weak evidence that the model is not the K-L [Kullback-
356 Leibler] best model. If a model has $4 \leq \Delta \leq 7$ there is definite evidence that the model is not the K-L
357 best model, and if $7 \leq \Delta \leq 10$, there is strong evidence that the model is not the K-L best model.
358 Finally, if $\Delta > 10$, there is very strong evidence that the model is not the K-L best model.”

359 **3.3 Application**

360 Data from longfin smelt in the San Francisco Bay-Delta are used to show the development and
361 advantages of using state-space population dynamics models over simple log-linear regressions for
362 modeling survival. We implement a range of models to determine the difference between the modeling
363 approaches (Table 1). A conceptual model of the San Francisco Bay longfin smelt population was used as
364 a basis for identifying potential environmental covariates considered in model development (Hanson,
365 2013; see also Rosenfield and Baxter, 2007; Baxter et al., 2008; Rosenfield, 2010). The covariates
366 reflected various geographic regions of the estuary and seasonal periods based on the life history and
367 seasonality of each lifestage of longfin smelt. A total of 36 potential covariates were identified in the
368 initial selection process. The covariates included various flow variables (e.g., spring X2 location, winter-
369 spring Delta outflow, winter-spring Napa River flow, spring outflow thresholds of 34,500 cfs and 44,500
370 cfs, spring Sacramento River inflow in addition to various variations of Sacramento and San Joaquin
371 River runoff), zooplankton (prey) densities (e.g., mysid, *Eurytemora*, and *Pseudodiaptomus* densities
372 over various seasonal time periods), predators and competitors (e.g., juvenile Chinook salmon densities
373 in the spring, predators in various regions, and the Asian overbite clam *Potamocorbula*), and a variety of
374 abiotic environmental variables (e.g., Secchi depth as an index of turbidity, water temperature,

375 ammonium loading to various regions of the estuary, and the ratio of ammonium loading to Delta
376 inflow). Based on the conceptual model the sign (positive or negative) in the relationship between each
377 covariate and the predicted longfin smelt population response was also assigned to each covariate. All
378 of the environmental covariates were then entered into two formulations of the longfin smelt lifecycle
379 model (a model in which spawners are the adult lifestage (November-March) ages 1 and 2 and an
380 alternative model in which pre-adults (October-March) ages 0 and 1 and adults (November-March) ages
381 1 and 2 were equally weighted in the model as spawners) and a series of statistical analyses were
382 performed to identify those covariates with the greatest contribution to the model development
383 (Maunder and Deriso, 2013). The covariates that explained the most variation from each category of
384 covariate (e.g. flow, prey, predators, environmental conditions) were then used in the application below
385 that illustrates the benefits of state-space models.

386 AIC_C was used to conduct forward stepwise covariate selection. The procedure selects the covariate with
387 the best AIC_C improvement conditional on the inclusion of all previous selected covariates. The
388 procedure is stopped when there are no further improvements to AIC_C . The covariates selected and the
389 ΔAIC_C are used to compare methods. The covariates were normalized (mean subtracted and divided by
390 the standard deviation) to improve model performance. Several factors were chosen as candidates for
391 the model selection procedure (Table 2 and 3), these factors were chosen based on initial analysis of the
392 wider range of factors in supplemental table 1 (Maunder and Deriso, 2013; Hanson et al., 2013). Many
393 of the factors in the larger set were highly correlated, most of which were eliminated. We kept two flow
394 variables that were highly correlated to illustrate some of the difficulties in hypothesis testing. The
395 model is fit to relative abundance indices for each stage (Table 4 and Maunder and Deriso 2013b), as
396 appropriate. The models are implemented using AD Model builder (Fournier et al., 2012) and the
397 Laplace approximation in used for random effects (Skaug and Fournier, 2006). The observation error in
398 equation 10 is implemented by treating the true population abundance as a random effect and using the
399 sampling distribution as the likelihood for abundance. The true abundance is then used in the
400 calculation of the regression model and the likelihoods for the observations are combined with the
401 likelihood for the regression equation. We do not include the lognormal bias correction since α is not of
402 interest and the temporal variation in the observation error is low.

403 **4 Results**

404 In general, all scenarios support the two flow related covariates when a single covariate is tested (Figure
405 2) followed closely by the prey species *Eurytemora*. However, after including a flow covariate, support
406 for *Eurytemora* is lost and it is not selected in any of the final models. In all models, ammonia is the
407 second covariate selected and temperature is the third covariate selected (Table 5). Adding density
408 dependence (models JLRRL and JLRBH) results in more support for Sacramento runoff over Napa river
409 runoff, and over the other covariates in general, when comparing single covariate models. Using
410 observation error only for juveniles and no process error (model J-L--) creates greater differences in the
411 likelihood between covariates and gives increased relative support to temperature and ammonia.

412 The likelihood values from the log-linear model (model J/A--L-) and the exponential model (model J--L-)
413 are identical as expected (Figure 3). The results from the log-linear model with observation error (model

414 J/ARRL-), which implies both observation error and process error, and the exponential model with both
415 observation error and process error (model JRLR-) are identical despite the likelihood and random
416 effects representing different error components.

417 Adding observation error makes little difference in relative likelihoods (Figure 3), but changes the
418 variables selected (Table 5). Sacramento runoff is selected in the first stage of the stepwise regression in
419 place of Napa river runoff. This is in part because Napa river runoff and Sacramento River runoff are
420 highly correlated. The stepwise procedure also selects Napa river runoff as a fourth covariate. However,
421 if Sacramento River runoff is dropped from the final model (that is the model chosen by the step-wise
422 procedure that includes both flow variables) the AIC_c drops by 2.58 units. The alternative model which
423 only includes Napa river runoff as the flow variable is 5.39 units lower than the model which only
424 includes Sacramento river run off as the flow variable (Figure 4) providing “definite” evidence of Napa
425 river runoff over Sacramento river runoff in models that do not include density-dependence; evidence
426 favors Napa river runoff over Sacramento river runoff in all the different model configurations, but not
427 as definitive as the ones above (Table 6).

428 Ignoring process error and including observation error only for the juvenile abundance produces much
429 greater changes in the likelihood causing all covariates to be selected except for those that are rejected
430 because the coefficient is the wrong sign.

431 The Ricker (model JLRRL) and Beverton-Holt (model JLRBH) forms of density dependence produce
432 different results with the Beverton-Holt model including Napa outflow as a fourth covariate resulting in a
433 better AIC_c, but it is only 1.65 units lower than the Ricker model providing “no credible” evidence to
434 differentiate between the two forms of density dependence. The AIC_c is 4.19 units less than the
435 exponential model with observation error providing only “weak” evidence for density dependence. If
436 the Sacramento outflow is discarded from the Beverton-Holt model, the AIC_c is only 0.25 units less than
437 the final model, and is only 1.21 units lower than if Napa runoff is not included and Sacramento runoff is
438 included (Figure 4). So there is “no credible” evidence supporting one runoff covariate over the other in
439 the presence of density dependence. This differs from the result without density dependence, which
440 shows “definite” evidence of Napa river runoff over Sacramento runoff.

441 Using a population dynamics model by linking both stages using a Beverton-Holt relationship (model
442 PLLRBH) produces nearly identical support for the covariates compared to the Beverton-Holt model
443 when evaluating single covariate models. The final selected model adds the additional prey covariate for
444 survival from Juveniles to adults.

445 **5 Discussion**

446 We have illustrated the progression from traditional log-linear models for estimating the factors
447 influencing survival to state-space population dynamics life-cycle models. State-space models
448 accommodate both observation and process error, both of which can be vital to avoid bias in parameter
449 estimates, confidence intervals, and hypothesis tests (De Valpine and Hastings, 2002; Maunder and
450 Watters, 2003; Deriso et al., 2007). Our model that ignored process error selected prey as an additional

451 covariate, which was not selected by any other model, and would have selected additional covariates if
452 they had not been discarded because the coefficient was the wrong sign. In our application, ignoring
453 observation error did not have a large impact on the relative support for the different covariates.
454 However, it did change what covariates were selected because the two flow covariates were highly
455 correlated. In other applications, where observation error is larger and particularly if it varies among
456 data points, the influence of including observation error is likely to be greater. Explicitly modeling
457 process error and separating it from observation error is also important in estimating the probability of
458 future events such as extinction (Maunder, 2004) and evaluating the uncertainty in the relationships
459 between survival and covariates so this uncertainty can be included in management advice (Maunder
460 and Deriso, 2011).

461 The observation error standard deviations used in our application, calculated from bootstrap analysis of
462 the survey data, were assumed known and to represent the random sampling error. They do not include
463 variation due to other factors such as annual changes in survey catchability. This additional observation
464 error may influence hypothesis testing. The standard deviation representing additional variation in the
465 observation process could be estimated analytically (Maunder and Starr, 2003; Deriso et al., 2007) or
466 covariates added to the observation model, perhaps using finer scale data (e.g. Maunder, 2001; Besbeas
467 and Freeman, 2006). Estimating the additional observation error variance adds one more parameter,
468 which will increase the variance of parameter estimates and will probably reduce the statistical
469 significance of covariates.

470 The estimated observation error (sampling) variance often assumes the process error. This is essentially
471 what the log-linear and simple exponential models do. They do not explicitly model the process error,
472 but by ignoring the observation error variances in the likelihood and estimating the variance of the
473 likelihood function, which formally represents the observation error, they accommodate the process
474 error. However, it is important to understand that the variance estimates from these models represent a
475 combination of process error and observation error, particularly for making predictions since predictions
476 are desired for true abundance and not observed abundance. In more complex population dynamics
477 models, like those used in fisheries stock assessment (Maunder and Punt, 2013; Punt et al., 2013,
478 Methot and Wetzel, 2013), which model many processes, only one type of process error is typically
479 modeled (e.g. annual recruitment variability) and estimation of the observation error variance for a
480 variety of data types or the modeled process error may accommodate the unmodeled process error.

481 Contemporary fisheries stock assessment models (Maunder and Punt, 2013; Punt et al., 2013; Methot
482 and Wetzel, 2013) are often too complicated to model in a state-space framework, although some
483 success has been achieved (McAllister and Ianelli, 1997; Maunder and Deriso, 2003), particularly in a
484 Bayesian context (Punt and Hilborn, 1997). The standard approach is to use penalized likelihood with the
485 variance of the process error for annual recruitment fixed at a pre-determined value (Maunder and
486 Deriso, 2003). Misspecified process error variance will bias confidence intervals and hypothesis tests.
487 Adding covariates to explain process error will reduce the process error variance, and the variance
488 needs to be adjusted for this. Hopefully, as computers and estimation algorithms get more efficient,
489 fisheries stock assessment models can be implemented in the state-space framework so the process
490 error variance can be estimated. In the meantime, it might be prudent to estimate the parameters and

491 conduct hypothesis tests under different assumptions about the process error variance to ensure that
492 results are consistent.

493 We found that modeling either process error or observation error as random effects or likelihood
494 functions gave the same results. This was an interesting result and it is not clear if this is a general
495 phenomena or if it is a consequence of comparing linear Gaussian models.

496 Our results corroborate other studies that have found that evaluating factors in isolation can produce
497 different results than evaluating them in combination (e.g. Deriso et al., 2008; Maunder and Deriso,
498 2011). Similarly, our results parallel those of Maunder and Deriso (2011) who found that some final
499 models had a coefficient with confidence intervals that cover zero and removing that covariate
500 improved the AIC_c. As with Maunder and Deriso's (2011) study, the covariate in question (Sacramento
501 River flow) was highly correlated with another covariate (Napa river flow) included in the model.

502 Maunder and Deriso (2011) recommend that all possible combinations of covariates and density
503 dependent factors, which we did not do in our illustration, should be evaluated because some factors
504 may only be detected in combination with other factors or in the presence of density dependence.
505 Conducting analyses of all possible combinations can be computationally demanding. To reduce the
506 computational time, Maunder and Deriso (2011) applied a strategy that evaluates two covariates at a
507 time and uses AIC_c summed over all possible one and two covariate combinations to select a covariate
508 that has general support. In contrast, Anderson et al. (2000) warn against testing all possible
509 combinations unless using model averaging. Practical advice is to ensure that covariates included in the
510 model have *a priori* support and that the framework of Maunder and Deriso (2011) is followed to
511 identify the life stage and the relationship to density dependence before conducting an all combinations
512 analysis. Given the availability of distributed computing resources, all combinations analysis should be
513 practical, but care needs to be taken to ensure that all models have converged on the optimal solution,
514 since this is may be difficult to do on a large number of model runs. Results should be used to rank
515 models and provide an idea of the data based evidence for alternative hypotheses rather than strict
516 acceptance-rejection hypothesis testing (Maunder and Deriso, 2011).

517 We illustrated how multiple stages, each with their own data sets, can be integrated into a population
518 dynamics model. This is an elementary form of the contemporary integrated analysis, which attempts to
519 include all relevant data into a single analysis (Maunder, 2003; Buckland et al., 2007; Schaub and Abadi,
520 2010; Maunder and Punt, 2013; Methot and Wetzel, 2013). The potential for integrated analysis is
521 limitless with different data types, sampling distributions, and processes being modeled. For example,
522 information on survival from mark-recapture data could be included in the population dynamics models
523 either by directly integrating the mark-recapture data into the model (Maunder, 2004) or by
524 approximating the likelihood (Besbeas et al., 2002). Integrated analysis facilitates the propagation of
525 information and uncertainty, particularly when states are linked from one time period to the next in a
526 population dynamics model. For example, one life stage in the analysis of Maunder and Deriso (2011)
527 did not have an abundance index until partway through the modeling time frame and the processes
528 related to this stage were informed by the indices of abundance for other stages. However, the years
529 that the index was available were enough to help determine which stages the covariates influenced.

530 Similarly, Tenan et al. (2012) showed how integrating different types of data allowed for the estimation
531 of population processes not directly measured in the field. We found that adding data and a covariate
532 for survival from juveniles to adults did not influence the support for the covariates of survival from
533 Adults to Juveniles. This is somewhat reassuring since the application had good data for all time periods
534 and therefore it would not be desirable for the results of one stage to influence those of another. If
535 process error was not modeled, the added data may have inadvertently influenced the covariate
536 selection. If the data was poor or missing for some time periods, then it would be reasonable and
537 desirable for data for one stage to influence the other stages.

538 The models we used to illustrate state-space models were simple compared to those used in many real
539 applications (e.g. fisheries stock assessment; see Maunder and Punt, 2013; Methot and Wetzel, 2013;
540 Punt et al., 2013). Alternative functions could be used to model the transition among stages. For
541 example, Maunder and Deriso (2011) used the three-parameter Deriso-Schnute stock-recruitment
542 model (Deriso, 1980; Schnute, 1985). The Deriso-Schnute stock-recruitment model has a third
543 parameter than can be set to represent either the Beverton-Holt or Ricker stock-recruitment models.
544 Maunder and Deriso (2011) also allow the flexibility to implement covariates before or after density
545 dependence. Covariates could influence the strength or form of the density dependence (Walters, 1987;
546 Ciannelli et al., 2004). The covariates were included as simple log linear terms and there may be more
547 appropriate relationships between survival and covariates. For example there may be a dome shape
548 relationship between survival and temperature with lower survival at lower and higher temperature or
549 temperature may interact with prey availability.

550 It is important to evaluate the impact of covariates so that management advice can be provided.
551 Extending the approach of Wang et al. (2009), Deriso et al. (2008) and Maunder and Deriso (2011)
552 carried out impact analysis retrospectively by simultaneously running a model that shared parameters
553 and fixed covariates at null values to ensure that uncertainty was maintained. This method calculates
554 the impact on quantities of interest and the effect size, which is much more informative than simply
555 determining what covariates are statistically significant. The separation of process error from
556 observation error using state-space models allows better characterization of uncertainty in future
557 projections. Although, trends in population processes, perhaps related to covariates, can be more
558 important for predicting extinction (Maunder, 2004) and it may be difficult to model the covariates into
559 the future.

560 We found that multiple factors and density dependence influenced the survival of longfin smelt. The
561 AIC_c was over four units higher for the Beverton-Holt model compared to the exponential model
562 suggesting there is “definite” evidence for density dependence. The level of evidence is less if the
563 models with Napa river flow are used. Maunder and Deriso (2011) also found multiple factors and
564 density dependence influenced the survival of delta smelt. Similarly, Deriso et al. (2008) found support
565 for multiple factors and density dependence influencing Prince William Sound herring (*Clupea pallasii*).
566 As in this study, Maunder and Deriso (2011) found that many of the covariates selected were robust to
567 the form of the density dependence, although, density dependence reduced the ability of the model to
568 differentiate between Napa River flow and Sacramento River flow. In the absence of density
569 dependence there was “definite” evidence of Napa river runoff over Sacramento runoff but when

570 density dependence was added there was “no credible” evidence supporting one runoff covariate over
571 the other.

572 We found that flow, ammonia, and temperature were consistently supported by the data for longfin
573 smelt. Thomson et al. (2010) found that X2 (a measure of the spatial extent of salinity: position of the
574 2% isohaline), which is related to flow, and water clarity explained longfin abundance. MacNally et al.
575 (2010) also found that X2 explained longfin abundance, but in addition found a correlation with prey
576 species. Among candidate flow variables, we did not find either X2, OMR flow, or the two outflow
577 threshold variables in supplemental Table 1 to be important covariates in our initial screening after the
578 inclusion of flow variables that had higher support in the data (Maunder and Deriso, 2013) and
579 therefore they were not included in the covariate lists in Table 2. Maunder and Deriso (2011) did not
580 find that flow variables explained the survival of delta smelt, which inhabits the same system as longfin
581 smelt. They found that temperature, prey, and predators dominated the covariates that were supported
582 by data. Several other pelagic species in the San Francisco Estuary have also experienced declines, but
583 the cause is still uncertain (Bennett, 2005; Sommer et al., 2007; Mac Nally et al., 2010; Thomson et al.,
584 2010; Maunder and Deriso, 2011).

585 The theory for state-space life cycle population dynamics models is well developed (Newman, 1998; de
586 Valpine, 2002; Maunder, 2004) and software to implement them is available (Lunn et al., 2009; Fournier
587 et al., 2012; Bolker et al., 2013). State-space models have been shown to be superior to other methods
588 (de Valpine and Hastings, 2002; de Valpine, 2003) and applied in a variety of situations (e.g. Millar and
589 Meyer, 2000; Buckland et al., 2004; McAllister and Ianelli, 1997; Maunder and Deriso, 2011). Therefore,
590 we recommend that they are an essential tool for evaluating factors impacting species of concern and
591 encourage further research to facilitate their use.

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746

747 Table 1. Description of modeling scenarios. RE = random effect. The name is based on the entries in the
 748 other columns.

Name	Dependent variable	Adult observation error	Juvenile observation error	Process error	Density dependence	Equation
J/A--L-	J/A	None	None	Likelihood	None	7
J--L-	J	None	None	Likelihood	None	12
J/ARRL-	J/A	RE	RE	Likelihood	None	7
J-L--	J	None	Likelihood	None	None	12
J-LR-	J	None	Likelihood	RE	None	12
JRLR-	J	RE	Likelihood	RE	None	12
JRLRR	J	RE	Likelihood	RE	Ricker	14
JRLRBH	J	RE	Likelihood	RE	B-H	16
PLLRBH	J and A	Likelihood	Likelihood	RE for both A and J	B-H	17 and 18

749

750 Table 2. Covariates

751

Factor	Time	Stage	sign of coefficient
Mysid	May to June	Adult to Juveniles	positive
Secchi depth	April to June	Adult to Juveniles	negative
Eurytemera	April to May	Adult to Juveniles	positive
Napa River flow	Jan-Mar	Adult to Juveniles	positive
Predators central +San Pablo	Annual	Adult to Juveniles	negative
Average temperature	April to June	Adult to Juveniles	negative
San Pablo ammonium	April to June	Adult to Juveniles	negative
Sacramento River runoff	prev Oct to July	Adult to Juveniles	positive
Overbite clam presence	year round	Adult to Juveniles	negative
Mysid	July to September	Juveniles to pre-adult	positive

752

Table 3. Normalized covariates used in the models

Year	Mysid	Secchi depth	Eurytemera	Napa River flow	Predators central + San Pablo	Average temperature	San Pablo ammonium	Sacramento River runoff	Overbite clam presence	Mysid2
1980	0.853718	1.132715	1.080842	-0.53318	-1.00832	1.000508	-0.49261	-0.81876	-1.82153	0.19676
1981	0.008556	-0.38085	1.563369	0.942767	-0.73836	-1.07541	-1.07396	1.717238	-1.82153	0.066562
1982	-0.57054	-0.47351	1.13467	1.605906	-0.81277	-0.70393	1.154556	2.202613	-1.82153	4.98957
1983	1.294227	0.876522	0.081392	-0.13147	-0.75301	-0.5933	-1.17085	0.460037	-1.82153	0.274976
1984	2.456133	2.069006	-0.55701	-0.59147	-0.76796	-0.35928	0.185635	-0.82558	-1.82153	-0.02174
1985	3.304004	-0.91878	1.685837	0.907025	-0.47223	0.672727	-0.27897	0.855612	-1.82153	-0.01752
1986	0.818859	1.863066	-0.53119	-1.25034	-0.7215	1.877846	-1.26775	-1.02678	0.53128	1.529492
1987	-0.22898	-1.13284	-0.69825	-0.76187	-0.83145	-0.14351	1.057664	-1.03133	0.53128	-0.38099
1988	-0.39433	-1.65546	-0.60016	-1.1355	-0.31977	0.618684	0.214993	-0.39591	0.53128	-0.49302
1989	-0.51841	-0.93892	-0.69613	-1.118	-0.75124	1.215098	1.352603	-1.02792	0.53128	-0.42254
1990	-0.58082	-1.44758	-0.5917	-2.28245	-0.10439	-1.39273	0.240282	-1.12113	0.53128	-0.46772
1991	-0.53252	1.137815	-0.68111	-0.92498	-0.46803	2.259919	-0.84297	-1.07225	0.53128	-0.40537
1992	-0.48866	0.330416	-0.07055	1.075703	-0.21676	0.012591	-1.11001	0.444124	0.53128	-0.49349
1993	-0.69768	-0.5702	-0.70014	-1.16338	-0.39592	-0.60919	1.248929	-1.19274	0.53128	-0.41223
1994	-0.73336	1.35507	2.518919	1.348697	-0.52902	-0.7761	-1.11059	1.846823	0.53128	-0.15803
1995	-0.68224	-0.07661	-0.7433	0.658241	-0.42458	0.682527	0.869306	0.453217	0.53128	-0.391
1996	-0.28661	-0.5692	-0.719	0.509216	-0.14333	0.855629	3.141715	0.809007	0.53128	-0.34611
1997	0.23437	-0.62056	0.617156	1.339571	-0.69596	-1.44204	-0.56712	1.48876	0.53128	-0.25294
1998	-0.60568	-0.67723	0.041468	0.409611	0.004222	-1.22387	-0.4494	0.328179	0.53128	-0.35382
1999	0.488225	1.119202	0.313572	0.039809	0.330112	0.014348	0.246096	0.067873	0.53128	-0.22533
2000	-0.41639	1.365879	-0.7372	-0.60789	1.841149	0.795584	-0.59938	-0.9654	0.53128	-0.11864
2001	-0.4009	0.208726	-0.73971	0.198123	2.578221	0.086682	0.454607	-0.42091	0.53128	-0.3559
2002	-0.57373	0.301604	-0.7808	0.474233	1.235607	1.471128	-0.33894	0.114478	0.53128	-0.09974
2003	-0.27168	-0.10606	-0.81838	0.533286	0.43951	0.276905	1.033635	-0.25723	0.53128	-0.38441
2004	-0.70805	-0.11766	-0.77685	0.808158	-0.71743	0.072677	-0.6497	0.028088	0.53128	-0.16125

2005	-0.50008	0.386148	1.257426	1.246163	-0.29197	0.327947	-0.77243	1.567193	0.53128	-0.15728
2006	-0.76575	-1.13876	-0.7933	-1.05727	0.62834	-0.16466	0.719187	-0.91197	0.53128	-0.34049
2007	0.147108	-0.91678	-0.57735	-0.00905	1.433459	-1.91036	0.346218	-0.91197	0.53128	-0.30393
2008	-0.74928	-1.09509	-0.73349	-1.52307	0.770768	-0.83802	-0.42892	-0.60051	0.53128	0.053042
2009	-0.63695	-0.00317	-4.72E-17	0.13014	2.654387	-0.09821	0.142357	-0.26064	0.53128	-0.42238

Table 4. Relative abundance indices and their standard deviations.

Year	Juveniles		Adults	
	Index	sd	Index	sd
1980	5.147645	1.540905	0.671315	0.147691
1981	0.054695	0.011506	2.028516	0.500702
1982	6.811693	1.338478	1.789226	0.375208
1983	0.762013	0.223661	4.703123	0.83494
1984	0.903832	0.288505	1.00861	0.214744
1985	0.112521	0.031633	1.54415	0.293123
1986	0.306562	0.027569	0.850549	0.107033
1987	0.056342	0.013876	3.128023	0.350311
1988	0.039315	0.010529	0.999951	0.130288
1989	0.032967	0.006855	0.522527	0.122224
1990	0.015897	0.004812	0.246579	0.062757
1991	0.00576	0.001925	0.147667	0.082057
1992	0.025127	0.00702	0.051506	0.023044
1993	0.138967	0.03988	0.377306	0.089155
1994	0.043509	0.011538	0.75603	0.2145
1995	10.73554	2.403421	0.158759	0.045147
1996	0.029749	0.007081	3.440189	0.42718
1997	0.073301	0.013608	0.567071	0.101007
1998	1.387879	0.420226	0.61144	0.098984
1999	2.561377	0.471928	0.917655	0.122052
2000	0.344826	0.072434	1.297423	0.180564
2001	0.033508	0.009184	1.427239	0.203511
2002	0.114351	0.027719	0.695358	0.177047
2003	0.095383	0.0378	0.719237	0.120373
2004	0.054189	0.012327	0.586214	0.096707
2005	0.1773	0.048076	0.498012	0.111741
2006	0.270357	0.083662	0.457178	0.102388
2007	0.074141	0.026098	0.185869	0.042095

2008	0.06446	0.014879	0.479959	0.108918
2009	0.023163	0.00668	0.292118	0.082641

Table 5. Order of covariates chosen by the forward step-wise procedure.

Covars	J/A--								
	L-	J/ARRL-	J--L-	J-L--	J-LR-	JRLR-	JRLRR	JRLRBH	PLLRBH
Mysid									
Secchi depth									
Eurytemera									
Napa River flow	1	4		1	4	1	4	4	5
Predators central									
+San Pablo				5					
Average									3
temperature	3	3		3	3	3	3	3	
San Pablo ammonium	2	2		2	2	2	2	2	2
Sacramento River									
runoff		1		1		1	1	1	1
Overbite clam									
presence									
Mysid July-Sept									4

Table 6. AIC_c values for the steps in the forward stepwise selection procedure (see Table 5 for selection order) and for models with no covariates and with different combinations of flow variables (temperature and ammonia included). AIC_c scores cannot be compared among some models because the data used to fit the model is different. Models with observation error in both abundances time series fit to both abundance time series are comparable (models J/ARRL-, JRLR-, JRLRR, and JRLRBH) but cannot be compared to models that fit to only the juvenile abundance time series (models J/A--L-, J--L-, and J-L--). The two stage model includes two random effects (PLLRBH) and due to the method used to model random effects cannot be compared to the other models.

Covariates	J/A--L-	J/ARRL-	J--L-	J-L--	J-LR-	JRLR-	JRLRR	JRLRBH	PLLRBH
Mysid May-June									
Secchi depth									
Eurytemera									
Napa River flow	105.14	-19.46		105.14	359.95	50.32		-23.64	41.33
Predators central +San Pablo				351.12					
Average temperature	88.53	-16.65		88.53	405.73	33.44	-16.65	-21.99	-22.68
San Pablo ammonium	95.23	-13.10		95.23	650.94	40.28	-13.10	-17.39	-18.98
Sacramento River runoff		-4.72			1006.95		-4.72	-10.84	-12.17
Overbite clam presence									
Mysid July-Sept									42.16
No covariates	121.29	11.11		121.29	1573.34	66.27	11.11	12.49	12.45
Napa River runoff	88.53	-22.04		88.53	365.05	33.44	-22.04	-23.59	-23.89
Sacramento River runoff	94.07	-16.65		94.07	405.73	38.89	-16.65	-21.99	-22.68
Both flow variables	91.23	-19.46		91.23	359.95	36.10	-19.46	-23.01	-23.64
Best forward stepwise	88.53	-19.46		88.53	351.12	33.44	-19.46	-21.99	-23.64

Figure captions

Figure 1. Conceptual diagram illustrating the differences between a) the exponential model representation of the log-linear regression and b) the full state-space population dynamics model. The shaded (red) solid arrows represent forcing functions and the dashed arrows represent predictions of the observations used in the likelihood functions.

Figure 2. Difference in negative log-likelihood from the model with no covariates to the model with the covariate with lowest negative log-likelihood for each scenario. Model J-L-- is on the second Y axis. The covariates are presented in the same order as they are defined in Table 2.

Figure 3. Difference in AIC_c from the selected model compared to the model without covariates for each scenario. The value for model J-L-- is truncated.

Figure 4. Difference in AIC_c between the models with different flow variables. The blue histogram includes only SacNapa River runoff and the models with Sacramento River Runoff and between the models with Napa River runoff and both Sacramento River Runoff and Napa River runoff. The Sacramento River Runoff value for model J-L-- is truncated.

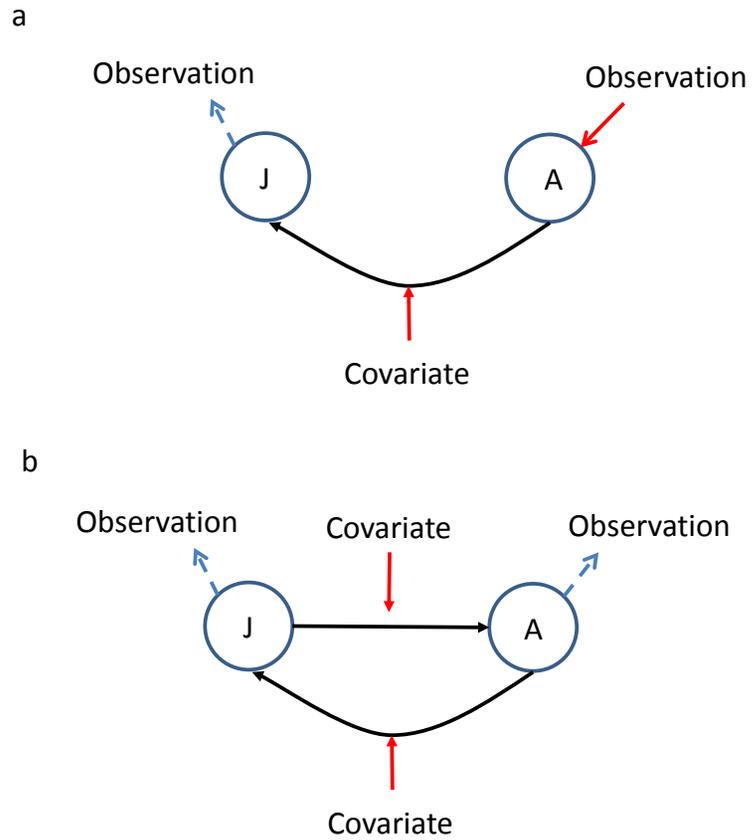


Figure 1. Conceptual diagram illustrating the differences between a) the exponential model representation of the log-linear regression and b) the full state-space population dynamics model. The shaded (red) solid arrows represent forcing functions and the dashed arrows represent predictions of the observations used in the likelihood functions.

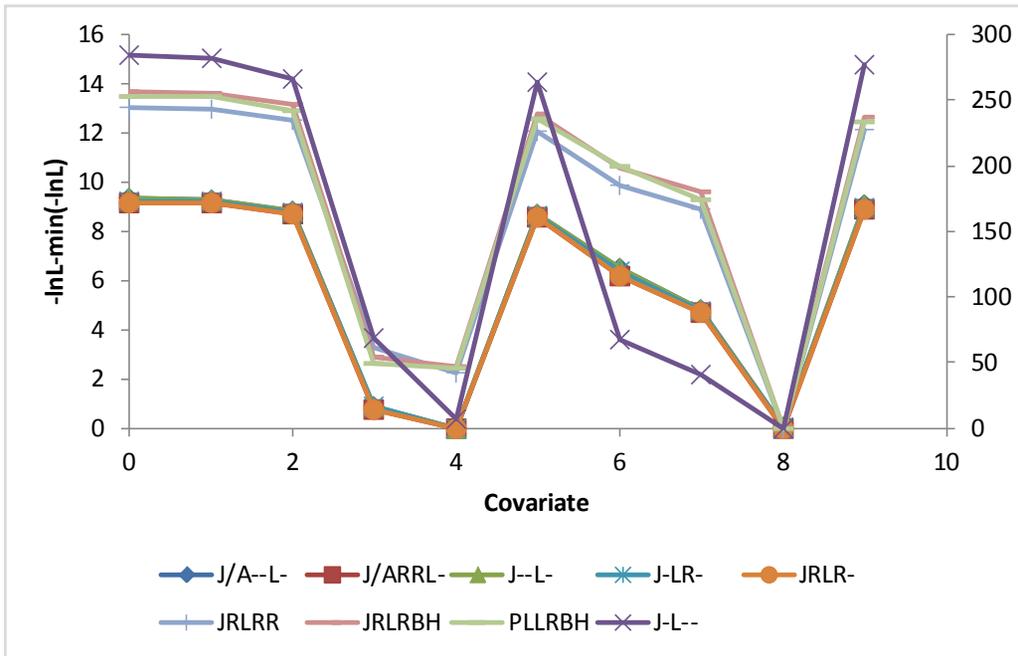


Figure 2. Difference in negative log-likelihood from the model with no covariates to the model with the covariate with lowest negative log-likelihood for each scenario. Model J-L-- is on the second Y axis. The covariates are presented in the same order as they are defined in Table 2.

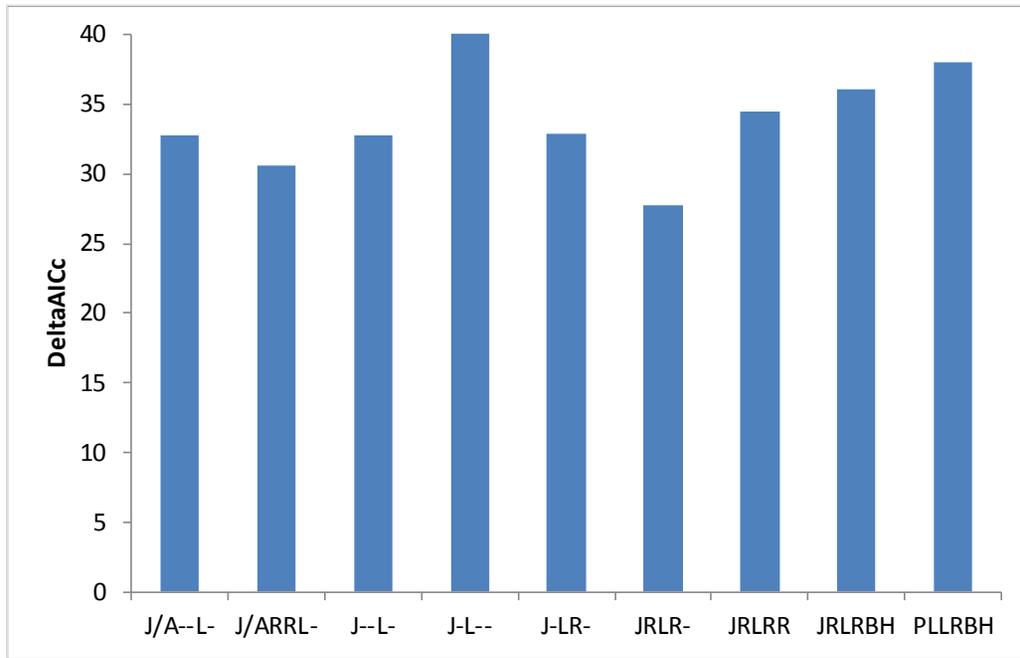


Figure 3. Difference in AICc from the selected model compared to the model without covariates for each scenario. The value for model J-L-- is truncated.

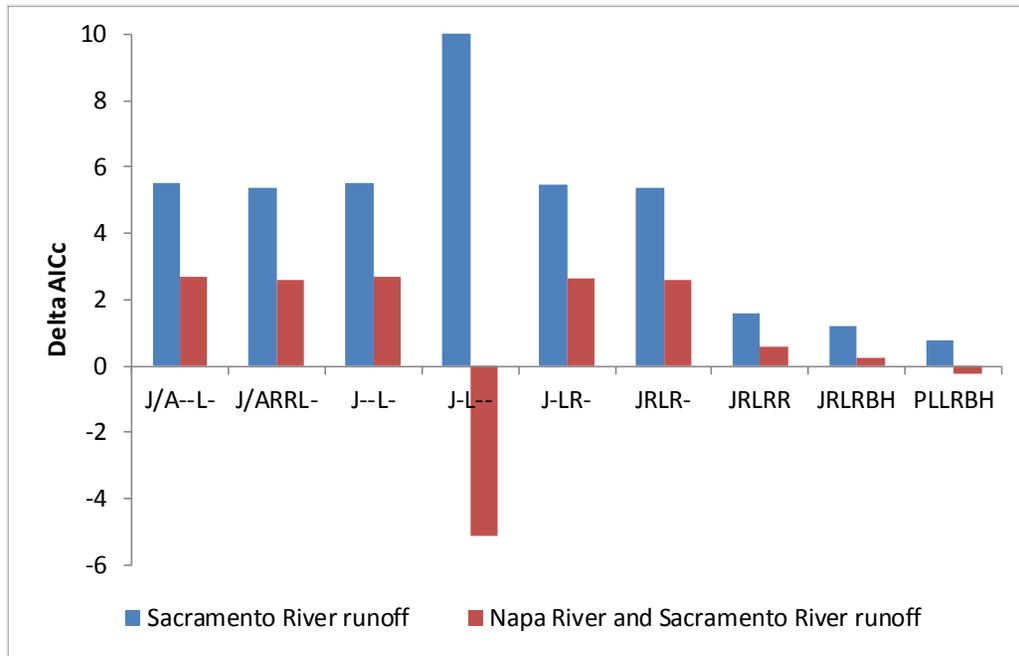


Figure 4. Difference in AIC_c between the models with different flow variables. The blue histogram includes only Sacramento River runoff and the red histogram includes both Napa River and Sacramento River runoff. The DeltaAICc values are the AIC_c values for these models minus the AIC_c values for the model with only Napa River runoff. The Sacramento River Runoff value for model J-L-- is truncated.

Supplemental Table 1. Covariates evaluated for inclusion in the life cycle model for longfin smelt in Maunder and Deriso 2013.

Factor	Time	Stage	sign of coefficient
Mysid	July to September	Juveniles to pre-adult	positive
Mysid	May to June	Adult to Juveniles	positive
OMR	January to March	Adult to Juveniles	positive
X2	April to June	Adult to Juveniles	negative
Secchi	April to June	Adult to Juveniles	negative
Secchi	August to September	Juveniles to pre-adult	negative
Outflow	January to March	Adult to Juveniles	positive
Eury	April to May	Adult to Juveniles	positive
Napa R	Jan-Mar	Adult to Juveniles	positive
outflow threshold indicator at 34500 cfs	Mar-May	Adult to Juveniles	positive
outflow threshold indicator at 44500 cfs	Mar-May	Adult to Juveniles	positive
chinook salmon Chipps Island trawl	Apr-May	Adult to Juveniles	negative
predators central +San pablo	Annual	all stages	negative
predators suisun Bay	Jan-Mar	Adult to Juveniles	negative
predators suisun	Mar-Jul	Adult to Juveniles	negative
avg MWT temperature	January to March	Adult to Juveniles	negative
avg MWT temperature	April to June	Adult to Juveniles	negative
avg MWT temperature	July	Adult to Juveniles	negative
area weighted ammonium	April to June	Adult to Juveniles	negative
Central Bay ammonium	April to June	Adult to Juveniles	negative
San Pablo ammonium	April to June	Adult to Juveniles	negative
Suisun Bay ammonium	April to June	Adult to Juveniles	negative
Pseudodiaptomus	April to July	Adult to Juveniles	positive
Water Temperature where smelt occur	spring	Adult to Juveniles	negative
Secchi Depth where smelt occur	spring	Adult to Juveniles	negative

predators where smelt occur total 12 months	year round	all stages	negative
Metric Tons of Ammonium discharged Sacramento	April to June	Adult to Juveniles	negative
Sacramento River Inflow	April to June	Adult to Juveniles	positive
Ammonium/inflow	April to June	Adult to Juveniles	negative
Sacramento River Runoff	prev Oct to March	Adult to Juveniles	positive
Sacramento Runoff	April to June	Adult to Juveniles	positive
Sacramento Runoff	prev Oct to July	Adult to Juveniles	positive
Sacramento + San Joaquin Runoff	prev Oct to March	Adult to Juveniles	positive
Sacramento + San Joaquin Runoff	April to July	Adult to Juveniles	positive
Sacramento + San Joaquin Runoff	year round	all stages	positive
overbite clam presence	year round	all stages	negative