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1 Temporally varying natural mortality: sensitivity of a virtual popu-
2 lation analysis and an exploration of alternatives

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- 35 1. age- and time-dependent models
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- 37 3. cohort reconstruction
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- 39 5. salmon stock assessment

40 *Highlights:*

- 41 1. Salmon cohort reconstructions (CR) commonly assume fixed, low adult natural mor-
42 tality rate.
- 43 2. CR estimate remaining vital rates well unless adult natural mortality rate is approxi-
44 mately twice that assumed.
- 45 3. Separable models make adult natural mortality rate identifiable through additive ef-
46 fects.
- 47 4. Separable models did not outperform CR and performed worse when assumptions
48 violated.
- 49 5. Some separable models estimated adult natural mortality rates with little bias under
50 conditions conducive to CR.

1 Abstract

Cohort reconstructions (CR) currently applied in Pacific salmon management estimate temporally variant exploitation, maturation, and juvenile natural mortality rates but require an assumed (typically invariant) adult natural mortality rate (d_A), resulting in unknown biases in the remaining vital rates. We explored the sensitivity of CR results to misspecification of the mean and/or variability of d_A , as well as the potential to estimate d_A directly using models that assumed separable year and age/cohort effects on vital rates (Separable Cohort Reconstruction, SCR). For CR, given the commonly assumed $d_A = 0.2$, the error (RMSE) in estimated vital rates is generally small (≤ 0.05) when annual values of d_A are low to moderate (≤ 0.4). The greatest absolute errors are in maturation rates, with large relative error in the juvenile survival rate. The ability of CR estimates to track temporal trends in the juvenile natural mortality rate is adequate (Pearson's correlation coefficient > 0.75) except for high d_A (≥ 0.6) and high variability ($CV > 0.35$). The alternative SCR models allowing estimation of time-varying d_A by assuming additive effects in natural mortality, fishing mortality, and/or maturation rates did not outperform CR across all simulated scenarios, and are less accurate when additivity assumptions are violated. Nevertheless an SCR model assuming additive effects on fishing and natural (juvenile and adult) mortality rates led to nearly unbiased estimates of all quantities estimated using CR, along with borderline acceptable estimates of the mean d_A under multiple sets of conditions conducive to CR. Adding an assumption of additive effects on the maturation rates allowed nearly unbiased estimates of the mean d_A as well. The SCR models performed slightly better than CR when the vital rates covaried as assumed. These separable models could serve as a partial check on the validity of CR assumptions about the adult natural mortality rate, or even a preferred alternative if there is strong reason to believe the vital rates, including juvenile and adult natural mortality rates, covary strongly across years or age classes as assumed.

2 Introduction

Fisheries stock assessments use a variety of statistical and mathematical tools in an attempt to understand the current abundance and dynamics of fished stocks. While the form of model employed in a stock assessment may vary considerably depending on scientific and management context, estimates of natural mortality are an integral component of stock assessment. It is known that many results from stock assessments can be heavily influenced by the choice of natural mortality (e.g., biological reference points, Goodyear, 1993). Yet, owing to the difficulty of directly estimating natural mortality, fixed external estimates or assumed values are frequently used. Temporal and/or age-dependent variation in natural mortality undoubtedly exists and the assumption of fixed natural mortality likely results in assessment errors. However, estimation of temporal variation in natural mortality in stock assessments is rare ([Brodziak et al., 2011](#)). While this is a topic of ongoing research and progress is being made (e.g., Hollowed et al., 2000; Lee et al., 2011; Deroba and Schueller, 2013), challenges remain (e.g., Maunder and Wong, 2011; Francis, 2012) and incorporation of time-varying mortality into stock assessments has been slow and largely limited to a few taxa (Deroba and Schueller, 2013).

Cohort reconstructions or virtual population analyses (Hilborn and Walters, 1992) performed on tagged cohorts of salmon are the backbone of salmon stock assessment (e.g., Mohr, 2006; O'Farrell et al., 2012; PSC CTC, 2014). Reconstruction of cohorts from coded wire tag recovery data (Nandor et al., 2010) allows estimation of age-specific abundance, harvest rates, maturation rates, and other vital rates used for salmon management. An assumption of known, and typically invariant, natural mortality rates for adult salmon is required for statistical identifiability when using current techniques that treat cohorts independently (Hankin et al., 2005). Unfortunately, this means that vital rate estimates are biased to an unknown extent by assumed and arbitrary values assigned to adult natural mortality rates. For example, a real increase in the natural mortality rate between age 2 and age 3 in a particular year could be erroneously interpreted instead as unusually high maturation at age 2

103 and low early life survival for the corresponding cohort.

104 Biased vital rates are an obvious problem for management models. In addition, such
105 biases may impair ecological or evolutionary insights when cohort reconstruction results are
106 used, for example, to explore putative drivers of variation in maturation rates (e.g., Hankin
107 and Logan, 2010) or juvenile survival (Sharma et al., 2013; Kilduff et al., 2014). In addition, it
108 is of course impossible to explore the role of environmental conditions or predators (Hilborn
109 et al., 2012) in driving variation in adult natural mortality if such mortality is *a priori*
110 assumed to be constant.

111 This paper therefore has two major goals. First, we use simulation studies to thoroughly
112 explore the sensitivity of results from traditional cohort reconstructions assuming known,
113 temporally invariant adult natural mortality to misspecification of mean mortality rates and
114 to variability in mortality rates. Second, we explore the potential for direct estimation of
115 time-varying adult natural mortality rates for a range of biological scenarios. The existing
116 literature on salmon population dynamics uses the terms “rate”, “fraction”, “probability”,
117 and “proportion” in ways that are not always consistent. Unless we make specific reference to
118 instantaneous rates when referring to other studies, the word “rate” is used throughout this
119 paper, along with a unitless number, to represent the conditional probability or proportion of
120 fish making a specified transition over one time step of the model. This is consistent with use
121 of the term “rate” in cohort reconstruction models used by the Pacific Salmon Commission
122 (e.g., PSC CTC 2014) and Pacific Fishery Management Council (e.g., O’Farrell et al. 2012).

123 **3 Methods**

124 Virtual population analysis (or cohort analysis) is applied to catch-at-age data to back cal-
125 culate the number of individuals alive prior to a mortality event, with the goal of obtaining
126 abundance estimates and mortality rates (e.g., Fry, 1949; Pope, 1972). This method requires
127 a known terminal fishing mortality rate for the maximum age and specified natural mortal-

128 ity rates. Classical analyses of this type are deterministic in that the stochastic variation
129 inherent in the data is not accounted for, and the accompanying model is fully saturated
130 (no degrees of freedom); thus measures of statistical uncertainty are not readily available
131 (Megrey, 1989).

132 A model resembling the classical virtual population analysis of Pope (1972) is applied
133 to the management of Pacific Salmon stocks (e.g., Mohr, 2006; O’Farrell et al., 2012; PSC
134 CTC, 2014). This model, termed cohort reconstruction, employs a monthly rather than
135 annual time step, but similar to Pope (1972), a pulse fishery occurs at the start of each time
136 step followed by natural mortality (Xiao and Wang, 2007). For the cohort reconstruction,
137 the final time step in each year includes an additional mortality event, maturation, and a
138 terminal maturation rate of 1.0 is required as opposed to a specified terminal fishing mortality
139 rate. Additionally, cohort reconstruction methods estimate monthly or annual, rather than
140 instantaneous, mortality rates and include an accounting for incidental fishing mortality.

141 Since the monthly models simply apportion a constant annual natural mortality rate
142 across months, and depend on detailed month-specific harvest data and assumed mortality
143 of discards, we chose an annual model for tractability, interpretability, and faster simulation.
144 We did not explicitly model incidental fishing mortality, assuming it was incorporated into
145 catch estimates. This cohort reconstruction (CR, abbreviations are defined in Table 1) as-
146 sumes an annual sequence of discrete mortality events: ocean fishery mortality followed by
147 maturation followed by ocean natural mortality. (Fish that mature return to the river where
148 they are either caught in river fisheries or spawn and die shortly thereafter.) This recon-
149 struction, in common with similar methods, requires a fixed age 2, 3, and 4 (“adult”) natural
150 mortality rate specified *a priori*. It is equivalent to Pope’s (1972) cohort analysis when catch
151 also includes escapement and fish are instantaneously removed from the population at the
152 beginning of the year (Xiao and Wang, 2007).

153 We develop our example based on a subset of the data available on cohorts of hatchery-
154 reared salmon tagged in distinct release groups using a coded wire tag (Nandor et al., 2010),

155 specifically yearling releases of Klamath River fall Chinook salmon produced at Iron Gate
 156 Hatchery, California. We assume that a single cohort of age 1 coded wire tagged fish is
 157 released annually, that these fish are not subject to the ocean fishery or maturation at
 158 age 1, and that fish live a maximum of five years (all age 5 fish that survive the ocean
 159 fishery mature). Fish age increments by one year following the ocean natural mortality
 160 period. We index cohorts by i , $i = 1, 2, \dots, I$, for I years of releases, with i equal to the
 161 birth year of a cohort (i.e., cohort i is released at age 1 in year $i + 1$). For cohort i , with
 162 R_i tagged fish released in October, fish first face juvenile mortality risk until April, then
 163 mortality from fishing, then removals for maturation in September, and then the cycle of
 164 potential mortality sources repeats annually for adults, with natural mortality now reflecting
 165 over-winter natural mortality in the ocean. This model structure implies a sequence of
 166 mortality outcomes at age a : the number caught in the ocean fishery, C_{ia} ; the number that
 167 matured and returned to freshwater, M_{ia} ; and the number that died from natural mortality,
 168 D_{ia} (symbols are defined in Table 2). However, $\{C_{ia}, M_{ia}, a = 2, 3, 4, 5\}$ are observable,
 169 whereas $\{D_{ia}, a = 1, 2, 3, 4\}$ are not; only the total natural mortality across ages is indirectly
 170 observable as $D_{i+} = \sum_{a=1}^4 D_{ia} = R_i - \sum_{a=2}^5 (C_{ia} + M_{ia})$. Although observable, the C_{ia} and
 171 M_{ia} quantities themselves are estimated, denoted by \hat{C}_{ia} and \hat{M}_{ia} , by expanding the observed
 172 number of tag recoveries in a sampling stratum by the inverse of the sampling fraction and
 173 summing over the strata involved, respectively. \hat{C}_{ia} can also include an accounting for
 174 incidental fishing mortality.

175 3.1 Cohort reconstruction

176 Given the estimates $\{\hat{C}_{ia}, \hat{M}_{ia}, a = 2, 3, 4, 5\}$ for cohort i , abundance is reconstructed from
 177 the oldest age to the youngest age by assuming that the adult natural mortality rates at
 178 age 2, 3, and 4 are known ($\tilde{d}_{i2} = \tilde{d}_{i3} = \tilde{d}_{i4} = 0.2$), and estimating the number alive at the

179 beginning of age a as

$$(1) \quad \hat{N}_{ia} = \begin{cases} \hat{C}_{ia} + \hat{M}_{ia} + \frac{\hat{N}_{i\ a+1}}{1 - \hat{d}_{ia}}, & a = 2, 3, 4 \\ \hat{C}_{ia} + \hat{M}_{ia} & a = 5. \end{cases}$$

180 The $\{\hat{N}_{ia}\}$ estimates then permit estimation of the age-specific ocean exploitation (c_{ia}) and
 181 maturation (m_{ia}) rates for the cohort, along with the juvenile natural mortality rate (d_{i1}):

$$(2) \quad \hat{c}_{ia} = \frac{\hat{C}_{ia}}{\hat{N}_{ia}}, \quad \hat{m}_{ia} = \frac{\hat{M}_{ia}}{\hat{N}_{ia} - \hat{C}_{ia}}, \quad a = 2, 3, 4, 5$$

182 and

$$(3) \quad \hat{d}_{i1} = 1 - \frac{\hat{N}_{i2}}{R_i},$$

183 respectively. Abundances and vital rates are estimated separately for each cohort, $i =$
 184 $1, 2, \dots, I$.

185 We explore the sensitivity of the above CR model estimates to assumptions about adult
 186 natural mortality using methods described in Section 3.3 and present the results in Sec-
 187 tion 4.1.

188 3.2 Separable cohort reconstruction

189 To estimate temporally varying natural mortality, we extend previous work by Hankin and
 190 Mohr (1993), which was based on band recovery models (e.g., Seber, 1970; Brownie et al.,
 191 1985) and a separable model decomposing vital rates into year and age effects (Pope, 1974;
 192 Doubleday, 1976; Kope, 1987). This approach is broadly applicable to any population where
 193 the recovery of individuals that share vital rates is tracked across a progression of possible
 194 fates and this progression can be reasonably approximated as a series of conditionally in-
 195 dependent binomial processes. Through the sharing of certain year and age effects across

196 cohorts, or cohort and age effects across years, it is possible with this stochastic, separable
 197 cohort reconstruction (SCR) model to estimate adult natural mortality rates in addition to
 198 the exploitation, maturation, and juvenile natural mortality rates by reducing the number of
 199 parameters to be estimated. Note that the CR model is normally applied to a single cohort,
 200 or as in this case, applied independently to multiple cohorts. The SCR models, in contrast,
 201 link cohorts across years and cannot be applied independently to a single cohort.

202 3.2.1 Stochastic basis

203 We begin by recasting the CR model for cohort i as a sequence of conditionally independent
 204 binomial events that results in the $\{C_{ia}\}, \{M_{ia}\}, \{D_{ia}\}$ outcomes given the number alive at
 205 the beginning of the respective period:

$$(4) \quad \begin{aligned} C_{ia} &\sim \text{binomial}(N_{ia}, c_{ia}), & a = 2, 3, 4, 5 \\ M_{ia} &\sim \text{binomial}(N_{ia} - C_{ia}, m_{ia}), & a = 2, 3, 4, 5 \\ D_{ia} &\sim \text{binomial}(N_{ia} - C_{ia} - M_{ia}, d_{ia}), & a = 1, 2, 3, 4 \end{aligned}$$

206 with $N_{i1} = R_i$, $C_{i1} = M_{i1} = 0$, $N_{i a+1} = N_{ia} - C_{ia} - M_{ia} - D_{ia}$, and $m_{i5} = 1$. This is
 207 equivalent to a multinomial distribution for the overall set of cohort i outcomes given the
 208 number initially released (Zippin, 1956):

$$(5) \quad (\{C_{ia}\}, \{M_{ia}\}, \{D_{ia}\}) \sim \text{multinomial}(R_i; \{\pi_{C_{ia}}\}, \{\pi_{M_{ia}}\}, \{\pi_{D_{ia}}\}), \quad i = 1, 2, \dots, I$$

209 with the unconditional rates being defined as

$$(6) \quad \pi_{C_{ia}} = S_{i a-1} c_{ia}, \quad \pi_{M_{ia}} = S_{i a-1} (1 - c_{ia}) m_{ia}, \quad \pi_{D_{ia}} = S_{i a-1} (1 - c_{ia}) (1 - m_{ia}) d_{ia},$$

210 where S_{ia} is the probability that a cohort i fish survives all events from the time of release
 211 at age 1 through the end of age a :

$$(7) \quad S_{ia} = \begin{cases} 1 - d_{ia}, & a = 1 \\ S_{i, a-1} (1 - c_{ia}) (1 - m_{ia}) (1 - d_{ia}), & a = 2, 3, 4. \end{cases}$$

212 This result leads directly to the distribution for the observable cohort i data:

$$(8) \quad (\{C_{ia}\}, \{M_{ia}\}, D_{i+}) \sim \text{multinomial}(R_i; \{\pi_{C_{ia}}\}, \{\pi_{M_{ia}}\}, \pi_{D_{i+}}), \quad i = 1, 2, \dots, I$$

213 where $\pi_{D_{i+}} = \sum_{a=1}^4 \pi_{D_{ia}} = 1 - \sum_{a=2}^5 (\pi_{C_{ia}} + \pi_{M_{ia}})$. However, because R_i is large (typi-
 214 cally $R_i > 10^5$) and $\pi_{D_{i+}}$ is close to one (typically $\pi_{D_{i+}} > 0.95$) this distribution can be
 215 approximated as a product of independent Poisson distributions having an equivalent set of
 216 expectations (McDonald, 1980):

$$(9) \quad (\{C_{ia}\}, \{M_{ia}\}) \sim \prod_{a=2}^5 \text{Poisson}(R_i \pi_{C_{ia}}) \cdot \text{Poisson}(R_i \pi_{M_{ia}}), \quad i = 1, 2, \dots, I,$$

217 with $D_{i+} = R_i - \sum_{a=2}^5 (C_{ia} + M_{ia})$. Finally, assuming statistically independent outcomes
 218 among cohorts, the overall catch and maturation dataset is distributed approximately as

$$(10) \quad (\{C_{ia}\}, \{M_{ia}\}) \sim \prod_{i=1}^I \prod_{a=2}^5 \text{Poisson}(R_i \pi_{C_{ia}}) \cdot \text{Poisson}(R_i \pi_{M_{ia}}),$$

219 with the $\{\pi_{C_{ia}}\}$ and $\{\pi_{M_{ia}}\}$ being functions of the $\{c_{ia}\}$, $\{m_{ia}\}$, and $\{d_{ia}\}$ vital rates (equa-
 220 tions (6) and (7)).

221 3.2.2 Model identifiability

222 For some models, speaking generally, it is not possible to estimate all of the parameters
 223 due to the structure of the model, and such models are said to be non-identifiable. Non-

224 identifiability can occur if a model is over-parameterized, where the model contains more
225 parameters than there are observed variables. In addition, non-identifiability can occur due
226 to parameter redundancy, where two or more parameters are confounded (they appear only
227 as a product), in which case the model could be rewritten in terms of a smaller number of
228 compounded parameters (see e.g. Cole et al., 2010, their example 1).

229 Various methods exist for detecting non-identifiability if it is not obvious. A numeric
230 method exists that involves examining the rank of the Hessian matrix (Viallefont et al.,
231 1998), and it is easily implemented since software packages often find the Hessian matrix
232 numerically as part of the process of estimating the standard errors of parameters. However,
233 this method can lead to incorrect conclusions, as demonstrated by Cole and Morgan (2010).
234 To accurately determine whether or not a model is identifiable, symbolic algebra can be
235 used (Cole et al., 2010) but this is complicated for complex models such as the SCR models
236 evaluated in this paper. Instead we use a hybrid symbolic-numerical method (Choquet and
237 Cole, 2012) to determine identifiability of the SCR models presented in this paper. It is both
238 accurate and relatively straightforward to use.

239 Even in the absence of over-parameterization or parameter redundancy, non-identifiability
240 can be caused by datasets with zero values (Cole et al., 2012). For all of the SCR models
241 described in Section 3.2.3 below, we found that as long as the dataset contains no zero values,
242 all parameters are identifiable.

243 3.2.3 Separable model variants

244 The CR model assumes that the vital rates $\{c_{ia}\}$, $\{m_{ia}\}$, and $\{d_{ia}\}$ are all cohort-age-specific
245 (or year-age-specific), and thus is over-parameterized given that the $\{D_{ia}\}$ are unobservable.
246 The CR estimation approach of treating the $\{d_{ia}\}$ as known is one way of reducing the
247 number of parameters to be estimated from the dataset. Alternatively, one might assume
248 that certain vital rates are shared among cohorts, years, or ages, or that the vital rates are
249 a function of a reduced number of separable effects regarding cohort, year or age. With this

250 additional imposed structure, it is possible to directly estimate the natural mortality rate.

251 The separable model form that we adopt presumes that the effects of cohort and age,
 252 or year and age on a vital rate are additive on the complementary log-log scale (McCullagh
 253 and Nelder, 1989). That is, for a particular vital rate p we assume that

$$(11) \quad g(p) = \log(-\log(1 - p))$$

254 is an additive function of these effects. The complementary log-log scale was adopted for
 255 two reasons. First, its use guarantees that the estimated vital rates will satisfy $0 < \hat{p} < 1$.
 256 Second, an additive model on this scale corresponds to the standard fishery mortality model
 257 for a Type 1 fishery (Ricker, 1975): $u_{ya} = 1 - \exp(-q_a f_y)$, where u_{ya} is the exploitation rate
 258 in year y of age a , f_y is the fishing effort in year y , and q_a is the catchability of age a . Thus,
 259 $g(u_{ya}) = \log(f_y) + \log(q_a)$ is an additive function of year and age effects.

260 We evaluated four SCR model variants (SCR-1, SCR-2, SCR-3, SCR-4) that imposed
 261 this additional structure on the $\{c_{ia}\}$, $\{m_{ia}\}$, and $\{d_{ia}\}$ rates. All four variants assumed
 262 that certain vital rates are shared among ages in a given year, or among years at a given
 263 age, and were based on our experience with Chinook salmon life history and fisheries, and
 264 the results of previous CR analyses of Chinook salmon. Specifically, we assume that: (1)
 265 age 4 and age 5 fish are fully vulnerable to the fishery, and experience the same exploitation
 266 rate in any given year; (2) the age 4 maturation rate is time invariant; and (3) the natural
 267 mortality rate in any given year is equal among adults (ages 2, 3, 4) but differs from that of
 268 the juveniles (age 1), letting a' denote the juvenile (J) and adult (A) age-classes:

$$(12) \quad a' = \begin{cases} J, & a = 1 \\ A, & a = 2, 3, 4. \end{cases}$$

269 All four SCR model variants also include separable age and year effects on $\{c_{ia}\}$, but differ
 270 depending on whether separable age and year or cohort effects were imposed on the $\{m_{ia}\}$

271 and/or $\{d_{ia}\}$.

272 SCR-1

273 This model assumes that the maturation rate for age 2 and age 3 fish is a non-separable
 274 function of age and cohort (the effect of age depends on the cohort), and that the natural
 275 mortality rate for juveniles and adults is a non-separable function of age-class and year (the
 276 effect of age-class depends on the year):

$$(13) \quad g(c_{ia}) = \eta_y + \lambda_a, \quad y = i + a$$

$$(14) \quad g(m_{ia}) = \begin{cases} \phi_{ia}, & a = 2, 3 \\ \psi, & a = 4 \end{cases}$$

$$(15) \quad g(d_{ia}) = \tau_{ya'}, \quad y = i + a,$$

277 with $\lambda_4 = \lambda_5 = 0$ so that η_y reflects the fully vulnerable fishing mortality rate in year y .

278 For the first cohort, the d_{11} , c_{12} , m_{12} , and d_{12} rates depend on four effects parameters
 279 (τ_{2J} , η_3 , ϕ_{12} , τ_{3A}) that are unique to those rates and are thus not identifiable given the
 280 dataset configuration. To make the SCR-1 model identifiable, for the first cohort we instead
 281 directly estimate the unconditional rates $\pi_{C_{12}}$, $\pi_{M_{12}}$, and S_{12} , on the complementary log-log
 282 scale, as single parameters rather than factoring them into their constituent vital rates with
 283 associated cohort and age, or year and age effects. Thus, the overall set of SCR-1 parameters
 284 to be estimated is

$$(16) \quad \boldsymbol{\theta}_1 = \{\{\eta_y\}, \{\lambda_a\}, \{\phi_{ia}\}, \psi, \{\tau_{ya'}\}, g(\pi_{C_{12}}), g(\pi_{M_{12}}), g(S_{12})\}.$$

285 SCR-2

286 This model is like SCR-1, but the maturation rate for age 2 and age 3 fish is a separable

287 function of cohort and age effects:

$$(17) \quad g(m_{ia}) = \begin{cases} \zeta_i + \delta_a, & a = 2, 3 \\ \psi, & a = 4, \end{cases}$$

288 with ζ_i defined as the cohort i effect relative to cohort 1 ($\zeta_1 = 0$), so that δ_a reflects the age a
 289 ($a = 2, 3$) maturation rate for cohort 1. The SCR-2 model is identifiable as defined, so that
 290 the overall set of parameters to be estimated is

$$(18) \quad \boldsymbol{\theta}_2 = \{\{\eta_y\}, \{\lambda_a\}, \{\zeta_i\}, \{\delta_a\}, \psi, \{\tau_{ya'}\}\}.$$

291 SCR-3

292 This model is like SCR-1, but the natural mortality rate for juvenile and adult fish is a
 293 separable function of year and age effects:

$$(19) \quad g(d_{ia}) = \xi_y + \gamma_{a'} \quad y = i + a,$$

294 with ξ_y defined as the year y effect relative to year 2 ($\xi_2 = 0$), so that $\gamma_{a'}$ reflects the age-
 295 class a' ($a' = J, A$) natural mortality rate for year 2. The SCR-3 model is identifiable as
 296 defined, so that the overall set of parameters to be estimated is

$$(20) \quad \boldsymbol{\theta}_3 = \{\{\eta_y\}, \{\lambda_a\}, \{\phi_{ia}\}, \psi, \{\xi_y\}, \{\gamma_{a'}\}\}.$$

297 SCR-4

298 This model assumes that the fishing mortality rate, maturation rate, and natural mor-

299 tality rate are all separable functions of year and age, or cohort and age effects:

$$(21) \quad g(c_{ia}) = \eta_y + \lambda_a, \quad y = i + a$$

$$(22) \quad g(m_{ia}) = \begin{cases} \zeta_i + \delta_a, & a = 2, 3 \\ \psi, & a = 4, \end{cases}$$

$$(23) \quad g(d_{ia}) = \xi_y + \gamma_{a'}, \quad y = i + a,$$

300 with the parameter baseline effects defined as for models SCR-1, SCR-2, and SCR-3. The
 301 SCR-4 model is identifiable as defined, so that the overall set of parameters to be estimated
 302 is

$$(24) \quad \boldsymbol{\theta}_4 = \{ \{ \eta_y \}, \{ \lambda_a \}, \{ \zeta_i \}, \{ \delta_a \}, \psi, \{ \xi_y \}, \{ \gamma_{a'} \} \}.$$

303 3.2.4 Maximum likelihood estimation

304 Maximum likelihood was used to estimate the SCR model parameters, $\boldsymbol{\theta}$, from which the
 305 $\{c_{ia}\}$, $\{m_{ia}\}$, and $\{d_{ia}\}$ rates were estimated by substitution of $\hat{\boldsymbol{\theta}}$ into equations (13)–(15),
 306 (17), (19), and (21)–(23), and applying the inverse of g . We took the likelihood to be the
 307 distribution specified by equation (10) when viewed as a function of the parameters $\{\pi_{C_{ia}}\}$
 308 and $\{\pi_{M_{ia}}\}$ given the estimates $\{\hat{C}_{ia}\}$, $\{\hat{M}_{ia}\}$. Therefore, the log-likelihood function, $\ell(\boldsymbol{\theta})$,
 309 ignoring the constants $\log(\hat{C}_{ia}!)$ and $\log(\hat{M}_{ia}!)$, was

$$(25) \quad \ell(\boldsymbol{\theta}) = \sum_i \sum_a \left\{ \hat{C}_{ia} \log(R_i \pi_{C_{ia}}) - R_i \pi_{C_{ia}} \right\} + \left\{ \hat{M}_{ia} \log(R_i \pi_{M_{ia}}) - R_i \pi_{M_{ia}} \right\},$$

310 where $\pi_{C_{ia}} = \pi_{C_{ia}}(\boldsymbol{\theta})$ and $\pi_{M_{ia}} = \pi_{M_{ia}}(\boldsymbol{\theta})$. We did not explicitly account for the sampling
 311 error of \hat{C}_{ia} and \hat{M}_{ia} as estimates of C_{ia} and M_{ia} in $\ell(\boldsymbol{\theta})$. This could be done by weighting
 312 the two curly-bracketed components of $\ell(\boldsymbol{\theta})$ by the inverse of the overall sampling fractions

313 associated with \hat{C}_{ia} and \hat{M}_{ia} , respectively. However, we did account for this sampling error
 314 when evaluating the estimation performance of the models (Sections 3.3 and 3.3.2).

315 A small penalty was subtracted from $\ell(\boldsymbol{\theta})$ whenever any of the $\{\pi_{C_{ia}}\}$ or $\{\pi_{M_{ia}}\}$ were
 316 near zero ($< 10^{-10}$) to prevent numerical instability when taking the log of a very small $R\pi$
 317 product. The penalty was equal to

$$(26) \quad 0.01 \sum_i \sum_a I_{C_{ia}} (10^{-10} - \pi_{C_{ia}})^2 + I_{M_{ia}} (10^{-10} - \pi_{M_{ia}})^2,$$

318 where I_z was 1 if $\pi_z < 10^{-10}$ and 0 otherwise.

319 We maximized $\ell(\boldsymbol{\theta})$ by minimizing $-\ell(\boldsymbol{\theta})$ via automatic differentiation using AD Model
 320 Builder (ADMB, Fournier et al., 2012), which requires starting values for all parameters.
 321 If $-\ell(\boldsymbol{\theta})$ has many local minima and the starting values are far from the global minimum,
 322 the resulting $\hat{\boldsymbol{\theta}}$ may be far from that which corresponds to the global minimum. In this
 323 case, the model may be sensitive to the initial conditions, making it necessary to start the
 324 minimization from multiple points to increase the chance of finding the global minimum.
 325 For an individual dataset, we attempted to fit each of the SCR models 100 times, each time
 326 generating starting values at random from *a priori* defined distributions (Supplementary
 327 Appendix A). For some attempts, ADMB stopped the minimization procedure prematurely
 328 and returned an error message, in which case model estimates were not produced. In other
 329 instances, estimates were returned but an error message indicated the corresponding Hessian
 330 may not be positive-definite or the corresponding maximum gradient component exceeded
 331 our convergence criterion (0.0001). We discarded such estimates but documented their fre-
 332 quency (Supplementary Appendix A). We note that these occurrences were mostly rare
 333 and were largely prevented by several techniques used to improve convergence, such as user
 334 defined boundaries and estimation phases (Supplementary Appendix A).

335 We defined a solution as unique if any estimated rate differed by at least 0.001 on the
 336 proportion scale. Within the parameter space searched, we confirmed the existence of a

337 single global solution (i.e., only one unique solution minimized $-\ell(\boldsymbol{\theta})$) and to illustrate the
338 complexity of the solution space we also documented the number of runs converging on local
339 minima (i.e., unique solutions corresponding to values of $-\ell(\boldsymbol{\theta})$ greater than the identified
340 minimum).

341 **3.3 Performance evaluation**

342 Performance of the CR and SCR estimation models was evaluated by simulating datasets us-
343 ing alternative sets of specified vital rates (“generating rates”), and then estimating the vital
344 rates from these simulated data using the estimation models. The adult natural mortality
345 generating rates evaluated included various constant and time varying scenarios. In all cases
346 a constant adult natural mortality rate of 0.2 was assumed in the CR estimation model. The
347 bias and accuracy of the CR and SCR model vital rate estimates were then assessed and
348 examined as a function of the adult natural mortality generating rate specifications.

349 **3.3.1 Simulation framework**

350 Demographic stochasticity was simulated in all datasets using the cohort sequential binomial
351 mortality model (equation (4)): catch followed by maturation followed by natural mortality.
352 To account for the additional variation introduced into the process through the use of $\{\hat{C}_{ia}\}$
353 and $\{\hat{M}_{ia}\}$ as estimates of the realized $\{C_{ia}\}$ and $\{M_{ia}\}$ (i.e., sampling error), the numbers
354 of fish sampled from ocean fisheries and escapement areas were then simulated as additional
355 binomial processes given the realized mortality model outcomes, assuming fixed sampling
356 rates of 0.2 (Nandor et al., 2010) and 0.34 (Winship et al., 2013) respectively, and then
357 expanded by the inverse of the respective sampling rate to simulate the $\{\hat{C}_{ia}\}$ and $\{\hat{M}_{ia}\}$
358 estimates used in the model estimation process. For each set of generating rates (described
359 below), 100 independent datasets were simulated and fit to allow for assessment of the bias
360 and accuracy (described in section 3.3.2) of the respective vital rate estimators.

361 Each set of generating rates consisted of values for the $\{c_{ia}\}$, $\{m_{ia}\}$, and $\{d_{i1}\}$ rates,

362 along with the adult natural mortality rates. A detailed description of each set of generating
 363 rates follows, but we note first that in all cases the values for the $\{c_{ia}\}$, $\{m_{ia}\}$, and $\{d_{i1}\}$
 364 rates were based on an actual set of estimates previously obtained for a series of 28 successive
 365 cohorts of Klamath River fall Chinook salmon yearlings released annually (one each year)
 366 from Iron Gate Hatchery (IGH) using the CR model assuming a constant adult natural
 367 mortality rate of 0.2. Because CR-derived estimates can be undefined when associated
 368 abundance estimates are zero, and can equal zero or one, we replaced in this set of estimates
 369 any undefined estimate with the corresponding mean rate, and any estimates equal to zero
 370 (one) with the next highest (lowest) estimated rate, and used linear interpolation to fill in
 371 rates for years with missing data. The resulting series of estimates (“IGH rates”) are shown
 372 in Fig. 1. The simulated datasets were the same length as the IGH dataset (one cohort
 373 released each year for 28 successive years), and the number of yearling fish released for each
 374 cohort was 70,000 (the approximate average for the IGH dataset).

375 For evaluations involving the CR estimation model only, the time series of IGH rates
 376 were used as is for the generating rates in combination with both constant and variable
 377 adult natural mortality rates. Evaluated constant adult natural mortality rates, $\{d_{ia} =$
 378 $d_A, a = 2, 3, 4\}$, included $d_A = 0.02, 0.04, \dots, 0.7$, resulting in 35 distinct sets of generating
 379 rates. To evaluate temporally variable (year-specific) adult natural mortality rates, $\{d_{ia} =$
 380 $d_{yA}, y = i + a, a = 2, 3, 4\}$, we considered two values for the mean rate, $\mu(d_{yA}) = 0.2, 0.4$,
 381 and coupled each with increasing coefficients of variation, $CV(d_{yA}) = 0, 0.1, 0.2, \dots, 0.5$. The
 382 d_{yA} generating rates were drawn at random from a beta distribution, $d_{yA} \sim \text{Beta}(\alpha, \beta)$, with
 383 $\alpha = (1 - \mu)CV^{-2} - \mu$ and $\beta = \alpha(\mu^{-1} - 1)$, where $\mu = \mu(d_{yA})$ and $CV = CV(d_{yA})$. For each
 384 of the twelve (μ, CV) combinations, 50 time series of year-specific adult natural mortality
 385 rates, $\{d_{yA}\}$, were drawn to improve the estimates of central tendency of the performance
 386 metrics described in Section 3.3.2. Together with the IGH rates, this resulted in a total of
 387 600 (12×50) distinct sets of generating rates.

388 For evaluations involving both the CR and SCR models, four sets of generating rates were

389 used. The first set of rates, “Con.2” (Constant, 0.2 annual adult natural mortality rate), were
 390 constant across years, with $d_A = 0.2$ and the remaining rates equal to the age-specific means
 391 of the IGH rates, as shown in Fig. 1. For the three remaining generating rate sets, the adult
 392 natural mortality rate varied across years. The second set of rates, “Var.2” (Variable, 0.2),
 393 used the time series of IGH rates as is along with a random sequence of temporally variable
 394 $\{d_{yA}\}$ with $\mu(d_{yA}) = 0.2$ and $\text{CV}(d_{yA}) = 0.46$. The third set of rates, “Var.4” (Variable, 0.4),
 395 was identical to the second, except that $\mu(d_{yA}) = 0.4$ and $\text{CV}(d_{yA}) = 0.38$. The final set of
 396 generating rates, “Add.2” (Additive, 0.2), adhered to the SCR-4 additive model structure
 397 (equations (21)–(23)), which satisfies the assumptions of all of the SCR model variants. A
 398 time varying sequence for each vital rate on the complementary log-log scale was obtained
 399 by adding a random year or cohort effect (as appropriate) drawn from a uniform(-0.9,0.9)
 400 distribution to $g(p)$, with p being the age-specific mean of the respective IGH rate (except
 401 for the age 4 maturation rate which was time invariant), with the same year effect added to
 402 juvenile and adult natural mortality. The resulting set of generating rates is shown in Fig. 1,
 403 with $\mu(d_{yA}) = 0.22$ and $\text{CV}(d_{yA}) = 0.37$.

404 3.3.2 Performance metrics

405 To gauge the performance of the CR and SCR estimation models under the various simulation
 406 scenarios, we defined for each vital rate $p_{ia}, p = c, m, d$, the error in its estimated value for
 407 dataset k as $\hat{p}_{ia}(k) - p_{ia}(k)$, with $p_{ia}(k)$ being the actual, realized rate based on the binomial
 408 mortality model outcome for dataset k rather than the generating rate. For dataset k ,
 409 we defined the mean error (ME) and root mean square error (RMSE) for age a over the
 410 $i = 1, 2, \dots, I$ cohorts as

$$(27) \quad \text{ME}(\hat{p}_a; k) = \sum_i \left[\hat{p}_{ia}(k) - p_{ia}(k) \right] / I,$$

$$(28) \quad \text{RMSE}(\hat{p}_a; k) = \sqrt{\sum_i \left[\hat{p}_{ia}(k) - p_{ia}(k) \right]^2 / I}.$$

411 We then averaged each of these respective quantities over the replicate datasets to provide
 412 a measure of estimator bias ($\overline{\text{ME}}(\hat{p}_a)$) and accuracy ($\overline{\text{RMSE}}(\hat{p}_a)$), and regarded $|\overline{\text{ME}}(\hat{p}_a)| \leq$
 413 0.05 and $\overline{\text{RMSE}}(\hat{p}_a) \leq 0.05$ as acceptable levels of performance. Note that because the
 414 ME and RMSE metrics involve averages taken over cohorts, they reflect (on average) the
 415 estimation errors expected in cohort-specific estimates.

416 For the CR model we also evaluated the performance of cohort abundance estimation.
 417 Because abundance at age differs greatly in terms of scale, we used the percent error in
 418 its estimated value for dataset k as the base metric, $[\hat{N}_{ia}(k) - N_{ia}(k)] / N_{ia}(k)$, with $N_{ia}(k)$
 419 being the actual, realized abundance based on the binomial mortality model outcomes for
 420 dataset k rather than its expected value. For dataset k , we defined the mean percent error
 421 (MPE) and mean absolute percent error (MAPE) for age a over the $i = 1, 2, \dots, I$ cohorts
 422 as

$$(29) \quad \text{MPE}(\hat{N}_a; k) = \sum_i \left(\left[\hat{N}_{ia}(k) - N_{ia}(k) \right] / N_{ia}(k) \right) / I,$$

$$(30) \quad \text{MAPE}(\hat{N}_a; k) = \sum_i \left| \left[\hat{N}_{ia}(k) - N_{ia}(k) \right] / N_{ia}(k) \right| / I.$$

423 We then averaged $\text{MPE}(\hat{N}_a; k)$ and $\text{MAPE}(\hat{N}_a; k)$ over the replicate datasets to provide a
 424 measure of estimator bias ($\overline{\text{MPE}}(\hat{N}_a)$) and accuracy ($\overline{\text{MAPE}}(\hat{N}_a)$), and regarded $|\overline{\text{MPE}}(\hat{N}_a)|$
 425 ≤ 0.2 and $\overline{\text{MAPE}}(\hat{N}_a) \leq 0.2$ as acceptable levels of performance. Similarly, because the
 426 MPE and MAPE metrics involve averages taken over cohorts, they reflect (on average) the
 427 estimation errors expected in cohort-specific estimates.

428 Finally, for the CR model we also examined its ability to track temporal trends in the
 429 juvenile natural mortality rate, irrespective of whether the estimator itself is biased. For
 430 each dataset k we calculated Pearson's product-moment correlation coefficient between the
 431 estimated and the actual, realized set of juvenile natural mortality rates, $\rho(\hat{d}_1; k)$, averaged
 432 this over the replicate datasets to provide a measure of tracking ability ($\bar{\rho}(\hat{d}_1)$), and regarded
 433 $\bar{\rho}(\hat{d}_1) \geq 0.75$ as an acceptable level of performance.

434 Although all of these criteria for acceptable performance are somewhat arbitrary, we
 435 deemed them reasonable based on our experience participating in the management process
 436 for Pacific salmon fisheries. We note also that interpreting errors in values close to either
 437 0.0 (i.e., maturation and exploitation rates for the youngest age classes) or 1.0 (i.e., juvenile
 438 natural mortality rate) can be problematic. For juvenile natural mortality, this problem
 439 can largely be alleviated by looking instead at percent error in reconstructed abundance
 440 at age, which is typically of more interest to managers due to its use in forecast models
 441 (e.g., Winship et al., 2015). Managers typically already regard estimates of maturation and
 442 exploitation rates for the youngest age classes with caution due to the small numbers of tag
 443 recoveries driving these estimates, and for exploitation rates there is additional uncertainty
 444 introduced by the large expansion factors and uncertain mortality rates needed to account
 445 for the discarding of sublegal-sized fish (e.g., Satterthwaite et al., 2013).

446 4 Results

447 4.1 CR model performance

448 With a constant adult natural mortality rate, estimated age 2 exploitation rates have ac-
 449 ceptable bias and accuracy over the full range of d_A considered (owing in part to the small
 450 scale of these rates), and bias in exploitation rates for older ages remains acceptable in all
 451 cases considered except for age 3 if $d_A > 0.6$, while the accuracy is acceptable in all cases
 452 except for ages 3 and 4 if $d_A > 0.4$ (Fig. 2a). Variation in ME and RMSE over replicate
 453 datasets is greatest for age 3 and age 4, and this variation increases as d_A increases.

454 Although estimates of maturation rates at age 2 and age 4 are generally robust (Fig. 2b),
 455 age 3 rates are sensitive to misspecification of the adult natural mortality rate with $\overline{\text{ME}}(\hat{m}_3) >$
 456 0.05 for $d_A > 0.4$ and $\overline{\text{ME}}(\hat{m}_3) > 0.15$ for $d_A > 0.6$. Acceptable levels of $\overline{\text{RMSE}}(\hat{m}_3)$ occur for
 457 $d_A \leq 0.3$. Variation in ME over replicate datasets is minimal for all ages, whereas variation
 458 in RMSE is apparent for ages 3 and 4 and increases somewhat as d_A increases.

459 Juvenile natural mortality rates are estimated well by the CR model over the full range of
 460 d_A considered (Fig. 2c), although small errors in this rate can reflect large relative errors in
 461 (small) juvenile survival rates. Thus it is instructive to also consider errors in reconstructed
 462 abundance at age (Fig. 2d), especially for age 2 as this equals the estimated juvenile survival
 463 rate multiplied by the release group size. For age 2 abundance, the bias and accuracy
 464 are unacceptable unless $0.1 \leq d_A \leq 0.3$. Sensitivity of reconstructed abundance-at-age to
 465 misspecification of d_A is lower for older age classes, with both bias and accuracy acceptable
 466 for $d_A < 0.5$ for age 3 and over the full range of d_A considered for age 4. Little variation in
 467 the juvenile natural mortality rate and abundance-at-age bias and accuracy measures over
 468 replicate datasets was evident, except for age 4 with $d_A > 0.5$.

469 Vital rate estimation is less sensitive to variability in the adult natural mortality rate.
 470 When $\mu(d_{yA})$ matched the value assumed (0.2) in the CR model, all estimators meet the
 471 accuracy performance criteria over the full range of $CV(d_{yA})$ explored (Fig. 3, left column),
 472 and display little sensitivity to the amount of variability (all curves are nearly horizontal
 473 lines). Accuracy is lowest for the age 4 exploitation rate (due in part to the reduced abun-
 474 dance at age 4, and to the relatively low magnitude of the rate in contrast to the relatively
 475 high magnitude of the age 4 maturation rate).

476 When the adult natural mortality rate varies around a mean (0.4) which differs from
 477 the assumed value (Fig. 3, right column), sensitivity to variability increases (curvature is
 478 more apparent in the plots). Accuracy for age 3 exploitation rates is unacceptable for
 479 $CV(d_{yA}) > 0.4$, but for all other rates performance is either acceptable (\hat{c}_2 , \hat{m}_2 , \hat{m}_4 , \hat{d}_1 ,
 480 \hat{N}_3 , \hat{N}_4) or unacceptable (\hat{c}_4 , \hat{m}_3 , \hat{N}_2) over the full range of variability considered, with
 481 the \hat{m}_3 performance noticeably degrading as $CV(d_{yA})$ increases. Variation in the respective
 482 RMSE values over replicate datasets also increased, and in most cases increased further with
 483 increases in $CV(d_{yA})$.

484 Despite the difficulty in estimating age 2 abundance accurately when $\mu(d_{yA}) = 0.4$
 485 (Fig. 3d, right column), estimates of the juvenile natural mortality rate did tend to track the

486 simulated variation across years under several different combinations of $\mu(d_{yA})$ and $CV(d_{yA})$
 487 values (Fig. 4). The mean correlation, $\bar{\rho}(\hat{d}_1)$, over the range of $CV(d_{yA})$ examined is very
 488 high when $\mu(d_{yA})$ is correctly specified (0.2), and remains above 0.9 even when $\mu(d_{yA})$ is 0.4
 489 versus the specified 0.2, but falls below 0.75 when d_{yA} is both badly misspecified ($\mu(d_{yA}) =$
 490 0.6) and variable ($CV(d_{yA}) > 0.35$).

491 4.2 SCR model performance

492 The performance of the SCR-1 and SCR-2 models (jointly referred to below as SCR-1-2)
 493 was very similar overall, both in terms of bias (Fig. 5) and accuracy (Fig. 6). Likewise, the
 494 performance of the SCR-3 and SCR-4 models (jointly referred to below as SCR-3-4) was
 495 very similar overall (Figs. 5 and 6). And, in general, the SCR-3-4 models outperformed the
 496 SCR-1-2 models.

497 SCR-1-2 generally underestimated exploitation rates, maturation rates, and the juvenile
 498 natural mortality rate, and overestimated the adult natural mortality rate. The bias and
 499 accuracy of \hat{m}_3 , \hat{d}_J , and \hat{d}_A , in particular, were unacceptable for most of the generating rate
 500 sets examined, and accuracy for the remaining estimated rates (\hat{c}_3 , \hat{c}_4 , \hat{m}_4) was unacceptable
 501 for Var.2 and Var.4. We therefore focus our attention below on the SCR-3-4 and CR model
 502 results.

503 For models SCR-3-4, unlike SCR-1-2, the adult natural mortality rate was not consis-
 504 tently positively biased across the generating rate sets but, as for SCR-1-2, when \hat{d}_A was
 505 positively biased, the remaining estimated rates were negatively biased, and vice-versa. For
 506 Add.2 and Var.2, models SCR-3-4 were essentially unbiased for all rates (borderline for \hat{d}_A),
 507 and the accuracy was also mostly acceptable for Add.2 (nearly so for \hat{d}_A), but for Var.2 it was
 508 unacceptable for \hat{c}_4 , \hat{m}_3 , and \hat{d}_A . For Con.2 and Var.4, the \hat{d}_A bias was unacceptable, and for
 509 Var.4 this was also the case for \hat{m}_3 . For Con.2 and Var.4, the accuracy was unacceptable for
 510 \hat{m}_3 and \hat{d}_A , and for Var.4 this was also the case for \hat{c}_3 and \hat{c}_4 . Variation in ME and RMSE
 511 over replicate datasets was greater for all rates with Con.2, and greatest for \hat{m}_3 and \hat{d}_A .

512 Considering the SCR-3-4 rates individually, the estimated exploitation rates had an ac-
 513 ceptable bias, but the accuracy for \hat{c}_3 was unacceptable for Var.4, and for \hat{c}_4 the accuracy was
 514 unacceptable for Var.2 and Var.4. Estimated maturation rates had an acceptable bias except
 515 for \hat{m}_3 with Var.4, and an acceptable accuracy except for \hat{m}_3 with Con.2, Var.2, and Var.4.
 516 Variation in ME and RMSE over replicate datasets for \hat{m}_3 was relatively high for Con.2.
 517 The estimated juvenile mortality rate bias and accuracy was acceptable across all generating
 518 rate sets. For the estimated adult natural mortality rate, the bias was clearly unacceptable
 519 for Con.2 (biased high) and Var.4 (biased low), and the accuracy was unacceptable for all
 520 but the Add.2 generating rate set. And for \hat{d}_A , as for \hat{m}_3 , variation in ME and RMSE over
 521 replicate datasets was relatively high for Con.2.

522 By comparison, the CR model was essentially unbiased (Fig. 5) for those generating rate
 523 sets in which d_A or $\mu(d_{yA})$ was equal to, or approximately equal to, the assumed constant
 524 value of 0.2 (Con.2, Add.2, Var.2), and its accuracy was also acceptable (Fig. 6), except
 525 in the case of \hat{c}_4 for Add.2. For the $\mu(d_{yA}) = 0.4$ generating rate set (Var.4), some bias
 526 was evident, most notably in the age 3 estimated rates. The pattern of this bias across
 527 the various rates was similar to that of the SCR-3-4 models for Var.4, with unacceptable
 528 performance (bias and accuracy) for \hat{m}_3 , and borderline unacceptable accuracy for \hat{c}_3 and
 529 \hat{c}_4 . Variation alone in d_A about the assumed constant value of 0.2 (Add.2 and Var.2 versus
 530 Con.2) had relatively little impact on estimator performance. The doubling of $\mu(d_{yA})$ to
 531 0.4 versus the assumed constant value of 0.2 (Var.4 versus Con.2) resulted in acceptable
 532 performance except for \hat{m}_3 (accuracy of exploitation rates was borderline unacceptable).

533 Overall, the CR model performed as well as, or better than, the SCR-3-4 models. How-
 534 ever, in the case of the Add.2 generating rate set, where the performance was mostly similar
 535 for the non- d_A estimated rates, the SCR-3-4 models were additionally able to estimate d_A
 536 reasonably well (the CR model assumes that d_A is known) and provided slightly better
 537 accuracy for some vital rates.

5 Discussion

5.1 CR model performance

Our evaluation of the performance of cohort reconstruction techniques across a wide range of plausible scenarios for salmon populations can serve to generally increase confidence in management applications of CR, and ecological inference using CR to estimate vital rates other than adult natural mortality, unless the adult natural mortality rate is at least twice as high as commonly assumed. Although the true adult natural mortality rate is unknown and surely varies (to an unknown extent), our results suggest only small consequences from assuming a known, constant adult natural mortality rate of 0.2 unless the true value exceeds approximately 0.4, or variability around an appropriately specified mean value substantially exceeds a CV of 0.5.

CR estimates of the age 2 abundance and age 3 maturation rate display the highest sensitivity to the misspecification of adult natural mortality rates, while juvenile natural mortality rates were well estimated over the entire range of adult natural mortality rates considered. However, it is important to realize that juvenile mortality rates are high and so juvenile survival, which is correspondingly small, may be estimated with more substantial relative error. Nevertheless, relative error in juvenile survival rates, like that of age 2 abundance, should be acceptably small (≤ 0.2) given adult natural mortality rates between 0.1 and 0.3. High correlation (≥ 0.75) between estimated and realized juvenile natural mortality rates suggest that, despite any bias introduced through misspecification of the mean adult natural mortality rate, and the difficulty of estimating the age 2 abundance accurately, temporal trends in the juvenile survival rate should be reliably detected unless adult natural mortality rates are very high (≥ 0.6) and highly variable ($CV > 0.35$).

The results of our performance evaluation of the CR model are mostly consistent with the conclusions reached by Hankin and Logan (2010) in an analysis of juvenile survival for salmon and for all vital rates in similar studies applied to long-lived iteroparous species.

564 Agger et al. (1973) and Ulltang (1977) found that when natural mortality is lower than
565 assumed, fishing mortality is generally underestimated, and vice versa. For our analysis, this
566 is most evident for the age 3 estimated exploitation rate. Agger et al. (1973) calculated that
567 underspecification of the instantaneous natural mortality rate by 0.1 yr^{-1} results in a mean
568 percent error of approximately 0.2 in the age 3 instantaneous fishing mortality rate, whereas
569 we found an average percent error of 0.08 in this rate (after converting our exploitation and
570 natural mortality rates to the instantaneous scale and assuming $d_A = 0.2$ versus an actual
571 value of $d_A = 0.28$). Ulltang (1977) concluded that errors in fishing mortality and abundance
572 estimates are likely to be small when the natural mortality rate fluctuates randomly around
573 a correctly specified mean, similar to our results. We note however that our specific findings
574 may not be broadly applicable outside the range of scenarios considered. For instance,
575 Sims (1984) and Sampson (1988) found that the misspecification of natural mortality rates
576 creates higher percent errors in estimates of abundance for lightly fished stocks. Indeed,
577 when generating exploitation rates were halved in our analysis (not presented), the percent
578 error of abundance estimates increased. Similarly, we would expect an increase (decrease)
579 in accuracy with an increase (decrease) in the number of tagged fish released as juveniles.

580 Our estimation model performance metrics are defined relative to the realized demo-
581 graphic model outcomes and rates, and in this sense are conditional metrics. Thus, variation
582 in the CR model estimates over replicate datasets, for example, was due primarily to sampling
583 error (the use of sample-expanded estimates of catch and escapement) rather than demo-
584 graphic stochasticity. Alternative definitions for these performance metrics are of course
585 possible. In particular, unconditional metrics could be defined relative to the demographic
586 model expectations and generating rates. However, given that the focus of this paper is
587 on the reconstruction of realized cohort outcomes and estimation of the associated rates,
588 conditional performance metrics seem most appropriate. In addition, our simulated datasets
589 were necessarily simplified compared to complications expected in real-world stock dynamics.
590 For example, environmental conditions and their effects on vital rates are likely temporally

591 autocorrelated, exploitation rates vary as a function of abundance forecasts which likely cor-
592 relate with juvenile survival (e.g., Winship et al., 2015), and changes in fishery minimum
593 size limits would be expected to change age effects on fishing mortality rates by changing
594 the proportion of fish of legal size at each age. Increases in the number of tagged fish in each
595 release group and/or sampling rates would be expected to reduce sensitivity to sampling
596 and process error in the data and thereby improve the performance of CR models somewhat,
597 but no increase in sample sizes can compensate for biases introduced by unmet assumptions.
598 Implications of release group sizes and sampling rates for CR were discussed extensively by
599 the PSC CWTWG (2008), so we did not explore sample sizes in further detail here.

600 **5.2 SCR model performance**

601 The ability to estimate time-varying natural mortality, maturation and exploitation rates
602 simultaneously is expected to improve salmon assessments performed using cohort recon-
603 struction methods. With increasing emphasis on determining relationships between envi-
604 ronmental drivers and vital rates as well as synchrony in vital rates across release groups
605 and populations (e.g., Sharma et al., 2013; Kilduff et al., 2014, 2015), there is also strong
606 scientific motivation to ensure that the vital rates entering into these analyses are generated
607 in the most rigorous way possible. Most applications of other salmon assessment models such
608 as statistical catch-at-age models typically also require the assumption of known, constant
609 adult natural mortality rates (e.g., Brenden et al., 2012), so the ability to quantify temporal
610 variation in adult survival would have wide-ranging benefits.

611 That said, the SCR estimation models explored here all exhibited instances of unaccept-
612 able performance in at least some simulated scenarios, and would be ill suited for application
613 to empirical datasets with no tag recoveries in particular age/stage categories. In addition,
614 we have not (and could not have) rigorously tested all possible scenarios in which the model
615 assumption of additive effects of year and age on vital rates might break down. Thus model
616 results need to be interpreted with caution. Confidence in SCR model results when applied

617 to an existing (real) dataset might be increased if multiple simulated datasets were gener-
618 ated based on the fitted vital rates, and the model did consistently well at estimating these
619 generating vital rates across datasets.

620 Our results imply that the additive structure assumed for the maturation rates by models
621 SCR-2 and SCR-4 did not lead to improved overall estimation performance versus SCR-1
622 and SCR-3, respectively. This may in part stem from the fact that the age 4 maturation
623 rate was assumed to be constant for all SCR models. Thus although we considered an
624 alternative SCR model formulation with constant maturation rates for each age, we expected
625 this might do relatively little to improve model performance, and of course it would sacrifice
626 the ability to estimate year-specific maturation rates. Our results also imply that the additive
627 structure assumed for the natural mortality rates by model SCR-3 did lead to improved
628 overall estimation performance versus SCR-1, regardless of whether the underlying rates
629 were additive or not. In this case, since the juvenile mortality rates were well estimated
630 under all scenarios (and thereby the year effects), the additive linkage presumably helped to
631 resolve the overall adult age effect, scaling mean adult mortality relative to mean juvenile
632 mortality but not necessarily tracking annual variation in adult natural mortality.

633 The performance of the SCR-3-4 estimation models when the adult natural mortality
634 rate was a constant equal to 0.2 (Con.2), or was relatively high with a mean value of 0.4
635 (Var.4), was unacceptable for several rates. However, the performance was acceptable for all
636 rates when the underlying natural mortality rates were variable with a mean of 0.2 and all
637 vital rates were additive on the complementary log-log scale. Estimates were also essentially
638 unbiased (in terms of the mean across cohorts/years) for all rates when the adult natural
639 mortality rates were independently variable with a mean of 0.2 but the accuracy for several
640 parameters, including the adult natural mortality rate, was unacceptable.

641 Overall, the alternative SCR models for estimating adult natural mortality rates directly
642 did not clearly outperform the CR model in any of the scenarios we examined and proved
643 sensitive to violations of functional assumptions and/or sampling variation. Although in

644 some scenarios most parameter estimates from models SCR-3-4 were relatively robust to
645 sampling variation, both models assume covariation between juvenile and adult natural
646 mortality rates, and tracked juvenile natural mortality rates closely. Therefore even if they
647 can unbiasedly estimate the mean adult natural mortality rate by fitting an appropriate age
648 effect, the annual variation in adult natural mortality rate estimates will likely be driven
649 by variation in juvenile natural mortality rates and thus may not provide real insight into
650 true variation in adult natural mortality rates. As with the CR model, increases in the
651 number of tagged fish in each release group and/or sampling rates would be expected to
652 reduce sensitivity to sampling and process error in the data, but could not compensate
653 for violation of model assumptions. Temporally autocorrelated environmental drivers likely
654 lead to temporal autocorrelation in vital rates, with unknown implications for partitioning
655 variation into year- versus age-effects. Future research could explore the implications of
656 temporal autocorrelation, and the degree of correlation between juvenile and adult mortality,
657 for the performance of the SCR approach described here. SCR model performance might be
658 improved through approaches that incorporate autocorrelation into the estimation process
659 (e.g., Johnson et al., 2016), or by developing a hierarchical approach to share information
660 across release groups or stocks sharing a common ocean environment (e.g., Thorson et al.,
661 2013).

662 **5.3 Conclusions and recommendations**

663 Taken together, our results suggest that CR methods are fairly robust in their applications to
664 Pacific salmon unless common assumptions about adult natural mortality rates are seriously
665 wrong. Because separable models SCR-3-4 were able to unbiasedly estimate the mean adult
666 natural mortality rate under multiple sets of conditions conducive to CR, confidence in CR
667 results might be increased if application of a model similar to SCR-3-4 yielded a mean adult
668 natural mortality rate similar to that assumed in the CR, and that estimate might be used as
669 the assumed natural mortality rate in a subsequent CR for the same or similar stocks. Given

670 the apparent negative bias in adult natural mortality rate estimates from models SCR-3-4
671 when adult natural mortality rates are high and do not covary with juvenile natural mortality
672 rates (Var.4), an acceptably low adult natural mortality rate estimate does not assure that
673 CR results are reliable, but a high adult natural mortality rate estimate would be a definite
674 cause for concern (although it should be noted that SCR-3-4 overestimated the adult natural
675 mortality rate in the constant scenario, Con.2). Due to the limited accuracy of the SCR-3-4
676 models when the additivity assumptions are not met, these models may be less informative
677 on whether adult natural mortality rates are unacceptably variable, unless there is strong
678 reason to believe juvenile and adult natural mortality rates should covary.

679 In cases where SCR adult natural mortality rate estimates suggest application of typical
680 CR may be problematic, managers and scientists would be wise to evaluate the sensitivity
681 of key results and metrics to higher adult natural mortality rates and/or variable rates,
682 as appropriate. It would also be advisable to consider all possible alternative sources of
683 information on the adult natural mortality rate and the extent to which it might covary
684 with the juvenile natural mortality rate (e.g., due to similarities or differences in feeding
685 ecologies and spatial locations). Unless there is reason to believe the adult natural mortality
686 rate has increased as a result of recent changes in the environment, one might also consider
687 whether high estimates of adult natural mortality rates are consistent with expectations
688 from life history theory if accompanied by low maturation rates (Mangel and Satterthwaite,
689 2008).

690 Direct estimation of adult natural mortality rates for salmon through other means has not
691 received substantial attention in the published literature, but according to Hankin and Healey
692 (1986), two empirical studies estimated an annual adult natural mortality rate of around 0.35
693 for Chinook salmon although maturation and mortality were confounded, suggesting actual
694 mortality rates may have been lower. Thus, confidence in CR results could be improved
695 in the future by field studies directly estimating adult natural mortality such as through
696 adult tagging studies (Walters and Martell, 2004) which, if repeated over multiple years,

697 could also yield insight into the degree of temporal variability in adult natural mortality and
698 possibly insights into drivers of this variation. Such studies would be costly and logistically
699 challenging, but the resulting insights could be highly worthwhile.

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706 **References**

- 707 [Agger, P., Boëtius, I., Lassen, H., 1973. Error in the Virtual Population Analysis: the effect](#)
708 [of uncertainties in the natural mortality coefficient. J. Cons. Int. Explor. Mer 35 \(1\), 93.](#)
- 709 Brenden, T.O., Bence, J.R., Szalai, E.B., 2012. An age-structured integrated assessment of
710 Chinook salmon population dynamics in Lake Huron's main basin since 1968. *Trans. Am.*
711 *Fish. Soc.* 141 (4), 919–933.
- 712 [Brodziak, J., Ianelli, J., Lorenzen, K., Methot Jr, R.D., 2011. Estimating natural mortal-](#)
713 [ity in stock assessment applications. U.S. Department of Commerce, NOAA Technical](#)
714 [Memorandum NMFS-F/SPO-119.](#)
- 715 [Brownie, C., Anderson, D.R., Burnham, K.P., Robson, D.S., 1985. Statistical inference from](#)
716 [band recovery data: a handbook, second edition. U.S. Department of the Interior, Fish](#)
717 [and Wildlife Service, Resource publication 156.](#)

- 718 Choquet, R., Cole, D.J., 2012. A hybrid symbolic-numerical method for determining model
719 structure. *Math. Biosci.* 236 (2), 117–125.
- 720 Cole, D.J., Morgan, B.J.T., 2010. A note on determining parameter redundancy in age-
721 dependent tag return models for estimating fishing mortality, natural mortality and selec-
722 tivity. *J. Agric. Biol. Environ. Stat.* 15 (4), 431–434.
- 723 Cole, D.J., Morgan, B.J.T., Catchpole, E.A., Hubbard, B.A., 2012. Parameter redundancy
724 in mark-recovery models. *Biom. J.* 54 (4), 507–523.
- 725 Cole, D.J., Morgan, B.J.T., Titterton, D.M., 2010. Determining the parametric structure
726 of models. *Math. Biosci.* 228 (1), 16–30.
- 727 Deroba, J.J., Schueller, A.M., 2013. Performance of stock assessments with misspecified age-
728 and time-varying natural mortality. *Fish. Res.* 146, 27–40.
- 729 Doubleday, W.G., 1976. A least squares approach to analyzing catch-at-age data. *ICNAF*
730 *Res. Bull.* 12, 69–81.
- 731 Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen,
732 A., Sibert, J., 2012. AD Model Builder: using automatic differentiation for statistical
733 inference of highly parameterized complex nonlinear models. *Optim. Method. Softw.* 27 (2),
734 233–249.
- 735 Francis, R.I.C.C., 2012. The reliability of estimates of natural mortality from stock assess-
736 ment models. *Fish. Res.* 119–120, 133–134.
- 737 Fry, F.E.J., 1949. Statistics of a lake trout fishery. *Biometrics* 5 (1), 27–67.
- 738 Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: founda-
739 tion and current use. In: Smith, S.J., Hunt, J.J., Rivard, D. (Eds.), *Risk evaluation and*
740 *biological reference points for fisheries management*. No. 120. Canadian Special Publica-
741 *tion of Fisheries and Aquatic Science*, pp. 67–81.

- 742 Hankin, D.G., Healey, M.C., 1986. Dependence of exploitation rates for maximum yield and
743 stock collapse on age and sex structure of chinook salmon (*Oncorhynchus tshawytscha*)
744 stocks. Can. J. Fish. Aquat. Sci. 43 (9), 1746–1759.
- 745 Hankin, D.G., Logan, E., 2010. A preliminary analysis of Chinook salmon coded-wire tag
746 recovery data from Iron Gate, Trinity River and Cole Rivers Hatcheries, brood years 1978–
747 2004. Prepared for The Hoopa Valley Tribal Council and the Arcata Office, U.S. Fish and
748 Wildlife Service. Available from [https://www.fws.gov/arcata/fisheries/reports/technical/
749 IGHTRH.CWTanalysis2009%20Hankin%20Rpt.pdf](https://www.fws.gov/arcata/fisheries/reports/technical/IGHTRH.CWTanalysis2009%20Hankin%20Rpt.pdf).
- 750 Hankin, D.G., Mohr, M.S., 1993. New methods for analysis of coded-wire tag recovery data:
751 final report. Prepared for Trinity River Basin Field Office, U.S. Fish and Wildlife Ser-
752 vice, Weaverville, California. Available from D.G. Hankin, Humboldt State University,
753 Department of Fisheries Biology, Arcata, CA 95521.
- 754 Hankin, D.G., Morishima, G.S., Clark, J.H., Riddell, B.E., Deriso, R.B., Schwarz, C., Garza,
755 J.C., Scott, J.B., 2005. Report of the expert panel on the future of the coded wire tag
756 recovery program for Pacific salmon. Pacific Salmon Commission, Technical Report No.
757 18. Available from <https://swfsc.noaa.gov/publications/FED/00791.pdf>.
- 758 Hilborn, R., Cox, S.P., Gulland, F. M.D., Hankin, D.G., Hobbs, N.T., Schindler, D.E.,
759 Trites, A.W., 2012. The effects of salmon fisheries on southern resident killer whales: final
760 report of the independent science panel. Prepared with the assistance of D.R. Marmorek
761 and A.W. Hall, ESSA Technologies Ltd., Vancouver, B.C. for National Marine Fisheries
762 Service (Seattle, WA) and Fisheries and Oceans Canada (Vancouver, BC). Available from
763 [http://www.westcoast.fisheries.noaa.gov/publications/protected_species/marine_mammals/
764 killer_whales/esa_status/reflections1.pdf](http://www.westcoast.fisheries.noaa.gov/publications/protected_species/marine_mammals/killer_whales/esa_status/reflections1.pdf).
- 765 Hilborn, R., Walters, C.J., 1992. Quantitative fisheries stock assessment: choice, dynamics
766 and uncertainty. Chapman and Hall, New York.

- 767 Hollowed, A.B., Ianelli, J.N., Livingston, P.A., 2000. Including predation mortality in stock
768 assessments: a case study for Gulf of Alaska walleye pollock. *ICES J. Mar. Sci.* 57, 279–293.
- 769 Johnson, K.F., Councill, E., Thorson, J.T., Brooks, E., Methot, R.D., Punt, A.E., 2016. Can
770 autocorrelated recruitment be estimated using integrated assessment models and how does
771 it affect population forecasts? *Fish. Res.* 183, 222–232.
- 772 Kilduff, D.P., Botsford, L.W., Teo, S.L.H., 2014. Spatial and temporal covariability in early
773 ocean survival of Chinook salmon (*Oncorhynchus tshawytscha*) along the west coast of
774 North America. *ICES J. Mar. Sci.* 71 (7), 1671–1682.
- 775 Kilduff, D.P., Di Lorenzo, E., Botsford, L.W., Teo, S.L.H., 2015. Changing central Pacific
776 El Niños reduce stability of North American salmon survival rates. *Proc. Natl. Acad. Sci.*
777 U. S. A. 112 (35), 10962–10966.
- 778 Kope, R.G., 1987. Separable virtual population analysis of Pacific salmon with application
779 to marked Chinook salmon, *Oncorhynchus tshawytscha*, from California’s Central Valley.
780 *Can. J. Fish. Aquat. Sci.* 44 (6), 1213–1220.
- 781 Lee, H.-H., Maunder, M.N., Piner, K.R., Methot, R.D., 2011. Estimating natural mortality
782 within a fisheries stock assessment model: an evaluation using simulation analysis based
783 on twelve stock assessments. *Fish. Res.* 109, 89–94.
- 784 Mangel, M., Satterthwaite, W.H., 2008. Combining proximate and ultimate approaches to
785 understand life history variation in salmonids with application to fisheries, conservation,
786 and aquaculture. *Bull. Mar. Sci.* 83 (1), 107–130.
- 787 Maunder, M.N., Wong, R.A., 2011. Approaches for estimating natural mortality: application
788 to summer flounder (*Paralichthys dentatus*) in the U.S. mid-Atlantic. *Fish. Res.* 111, 92–
789 99.

- 790 McCullagh, P., Nelder, J.A., 1989. Generalized linear models, second edition. Chapman and
791 Hall, New York.
- 792 McDonald, D.R., 1980. On the Poisson approximation to the multinomial distribution. Can.
793 J. Stat. 8 (1), 115–118.
- 794 Megrey, B.A., 1989. Review and comparison of age-structured stock assessment models from
795 theoretical and applied points of view. In: Edwards, E.F., Megrey, B.A. (Eds.), Math-
796 ematical analysis of fish stock dynamics. Symposium 6. American Fisheries Society, pp.
797 8–48.
- 798 Mohr, M.S., 2006. The cohort reconstruction model for Klamath River fall Chinook salmon.
799 Available from M.S. Mohr, National Marine Fisheries Service, 110 Shaffer Road, Santa
800 Cruz, California 95060, USA.
- 801 Nandor, G.F., Longwill, J.R., Webb, D.L., 2010. Overview of the coded wire tag
802 program in the greater Pacific region of North America. In: Wolf, K.S., O’Neal,
803 J.S. (Eds.), PNAMP Special Publication: Tagging, telemetry and marking mea-
804 sures for monitoring fish populations—A compendium of new and recent science
805 for use in informing technique and decision modalities. Pacific Northwest Aquatic
806 Monitoring Partnership Special Publication 2010-002, pp. 5–46. Available from
807 http://www.pnamp.org/sites/default/files/PNAMP_2010_002_TTMfirst.pdf
- 808 O’Farrell, M.R., Mohr, M.S., Grover, A.M., Satterthwaite, W.H., 2012. Sacramento River
809 winter Chinook cohort reconstruction: analysis of ocean fishery impacts. U.S. Department
810 of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-491.
- 811 Pope, J.G., 1972. An investigation of the accuracy of virtual population analysis using cohort
812 analysis. ICNAF Res. Bull. 9, 65–74.
- 813 Pope, J.G., 1974. A possible alternative method to virtual population analysis for
814 the calculation of fishing mortality from catch at age data. ICNAF Annual Meet-

- 815 ing, June 1974, Research Document 74/20, Serial Number 3166. Available from
816 <http://icnaf.nafo.int/docs/1974/res-20.pdf>.
- 817 PSC CTC (Pacific Salmon Commission Chinook Technical Committee), 2014. 2013 exploita-
818 tion rate analysis and model calibration, volume 1. Pacific Salmon Commission, TCCHI-
819 NOOK (14)-1 V.1. Available from [http://www.psc.org/pubs/TCCHINOOK\(14\)-1_V1.pdf](http://www.psc.org/pubs/TCCHINOOK(14)-1_V1.pdf).
- 820 PSC CWTWG (Pacific Salmon Commission Coded Wire Tag Workgroup), 2008.
821 An action plan in response to coded wire tag (CWT) expert panel recommen-
822 dations. Pacific Salmon Commission, Technical Report No. 25. Available from
823 <http://www.psc.org/pubs/psctr25.pdf>.
- 824 Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish popula-
825 tions. Fisheries Research Board of Canada, Bulletin 191.
- 826 Sampson, D.B., 1988. The stability of Virtual Population Analysis cohort size estimates. J.
827 Cons. Int. Explor. Mer 44 (2), 135–142.
- 828 Satterthwaite, W.H., Mohr, M.S., O’Farrell, M.R., Wells, B.K., 2013. A comparison of tem-
829 poral patterns in the ocean spatial distribution of California’s Central Valley Chinook
830 salmon runs. Can. J. Fish. Aquat. Sci. 70, 574–584.
- 831 Seber, G.A.F., 1970. Estimating time-specific survival and reporting rates for adult birds
832 from band returns. Biometrika 57 (2), 313–318.
- 833 Sharma, R., Vélez-Espino, L.A., Wertheimer, A.C., Mantua, N., Francis, R.C., 2013. Re-
834 lating spatial and temporal scales of climate and ocean variability to survival of Pacific
835 Northwest Chinook salmon (*Oncorhynchus tshawytscha*). Fish. Oceanogr. 22 (1), 14–31.
- 836 Sims, S.E., 1984. An analysis of the effect of errors in the natural mortality rate on stock-size
837 estimates using Virtual Population Analysis (Cohort Analysis). J. Cons. Int. Explor. Mer
838 41 (2), 149–153.

- 839 Thorson, J.T., Stewart, I.J., Taylor, I.G., Punt, A.E., 2013. Using a recruitment-linked
840 multispecies stock assessment model to estimate common trends in recruitment for US
841 West Coast groundfishes. *Mar. Ecol. Prog. Ser.* 483, 245–256.
- 842 Ulltang, Ø., 1977. Sources of errors in and limitations of Virtual Population Analysis (Cohort
843 Analysis). *J. Cons. Int. Explor. Mer* 37 (3), 249–260.
- 844 Viallefont, A., Lebreton, J.-D., Reboulet, A.-M., Gory, G., 1998. Parameter identifiability
845 and model selection in capture-recapture models: a numerical approach. *Biom. J.* 40 (3),
846 313–325.
- 847 Walters, C.J., Martell, S.J.D., 2004. *Fisheries ecology and management*. Princeton University
848 Press, New Jersey.
- 849 Winship, A.J., O’Farrell, M.R., Mohr, M.S., 2013. Management strategy evaluation applied
850 to the conservation of an endangered population subject to incidental take. *Biol. Cons.*
851 158, 155–166.
- 852 Winship, A.J., O’Farrell, M.R., Satterthwaite, W.H., Wells, B.K., Mohr, M.S., 2015. Ex-
853 pected future performance of salmon abundance forecast models with varying complexity.
854 *Can. J. Fish. Aquat. Sci.* 72, 557–569.
- 855 Xiao, Y., Wang, Y.-G., 2007. A revisit to Pope’s cohort analysis. *Fish. Res.* 86 (2), 153–158.
- 856 Zippin, C., 1956. An evaluation of the removal method of estimating animal populations.
857 *Biometrics* 12 (2), 163–189.

Table 1 Abbreviations used and their definition.

Abbreviation	Definition
IGH	Iron Gate Hatchery
ME	Mean error
RMSE	Root mean square error
MPE	Mean percent error
MAPE	Mean absolute percent error
CR	Cohort reconstruction
SCR	Separable cohort reconstruction
SCR-1	SCR model variant 1: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation non-separable (age * cohort) for age 2 and 3, constant for age 4; natural mortality non-separable (age-class * year).
SCR-2	SCR model variant 2: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation separable (age + cohort) for age 2 and 3, constant for age 4; natural mortality non-separable (age-class * year).
SCR-3	SCR model variant 3: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation non-separable (age * cohort) for age 2 and 3, constant for age 4; natural mortality separable (age-class + year).
SCR-4	SCR model variant 4: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation separable (age + cohort) for age 2 and 3, constant for age 4; natural mortality separable (age-class + year).
Con.2	Constant generating rates with an adult natural mortality rate of 0.2.
Var.2	Time varying generating rates with an adult natural mortality rate mean value of 0.2.
Var.4	Time varying generating rates with an adult natural mortality rate mean value of 0.4.
Add.2	Time varying generating rates with additive year and age or cohort and age effects on the complementary log-log scale and an adult natural mortality rate mean value of 0.22.

Table 2 Symbols used and their definition.

Symbol	Definition
$\hat{}$	Estimated quantity (overscript)
$\tilde{}$	Assumed quantity (overscript)
$\bar{}$	Average quantity (overscript)
i	Cohort (brood year), $i = 1, 2, \dots, I$
a	Age, $a = 1, 2, \dots, 5$
a'	Age class: J ($a = 1$) or A ($a = 2, 3, 4$)
y	Calendar year, $y = i + a$
k	Simulated dataset index, $k = 1, 2, \dots$
R	Number of tagged fish released
N	Abundance
C	Ocean catch
M	River escapement
D	Natural mortality (deaths)
c	Exploitation rate
m	Maturation rate
d	Natural mortality rate
p	Conditional mortality rate (c , m , or d)
π	Unconditional mortality rate
S	Survival rate (from release)
$g()$	Complementary log-log function
$l()$	Log-likelihood function
θ	Parameter set (SCR models)
η	$g(c)$ year effect
λ	$g(c)$ age effect
ϕ	$g(m)$ cohort-age effect
ζ	$g(m)$ cohort effect
δ	$g(m)$ age effect ($a = 2, 3$)
ψ	$g(m)$ age effect ($a = 4$)
τ	$g(d)$ year-age-class effect
ξ	$g(d)$ year effect
γ	$g(d)$ age-class effect
μ	Mean value
ρ	Correlation coefficient
CV	Coefficient of variation

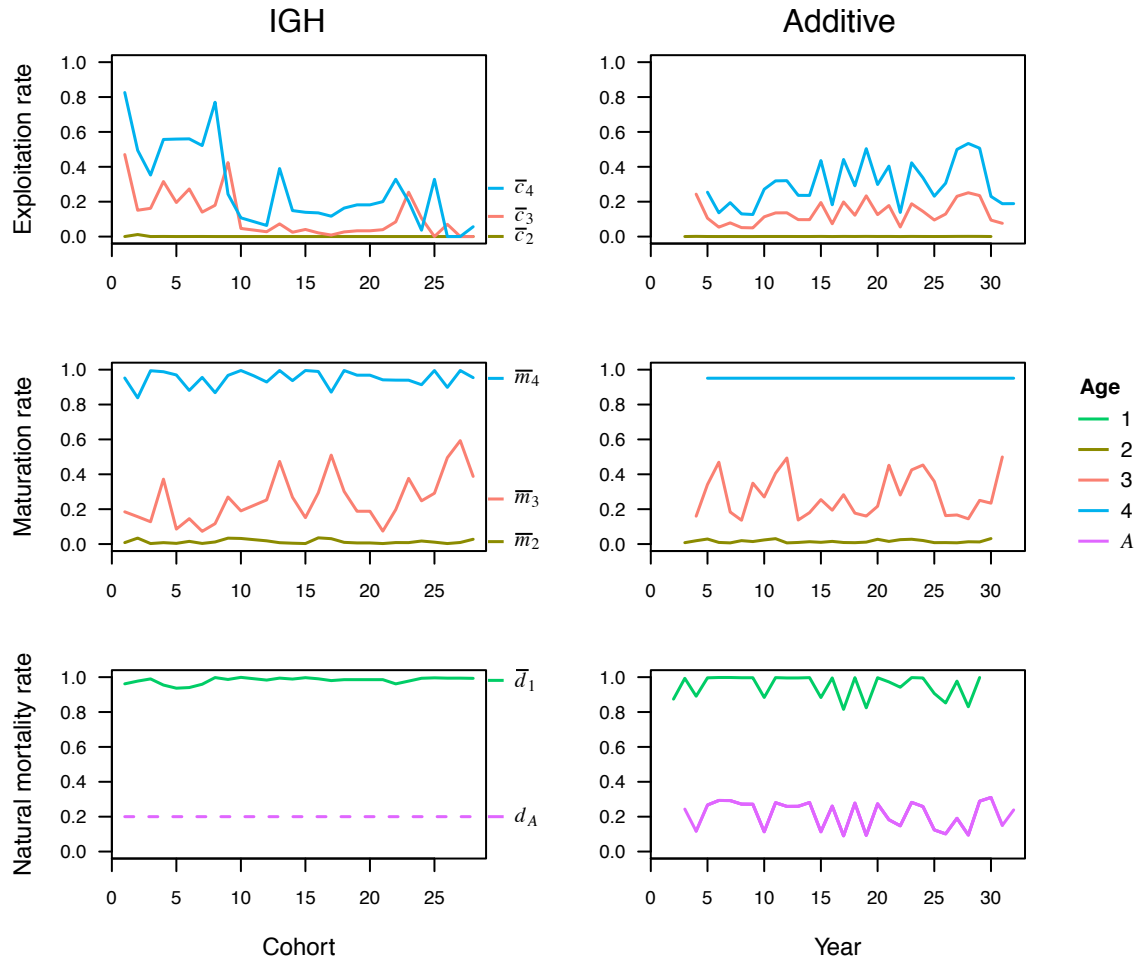


Fig. 1. Generating rates used for performance evaluation. Left column: IGH rates with mean values indicated on right vertical axis. Right column: additive (on complementary log-log scale) rates derived from IGH mean rates assuming SCR-4 model structure. Adult natural mortality is assumed fixed at 0.2 for the IGH rates (dashed line). The additive scenario is parameterized to yield mean and variability in vital rates comparable to IGH but with independently drawn random effects of years/cohorts.

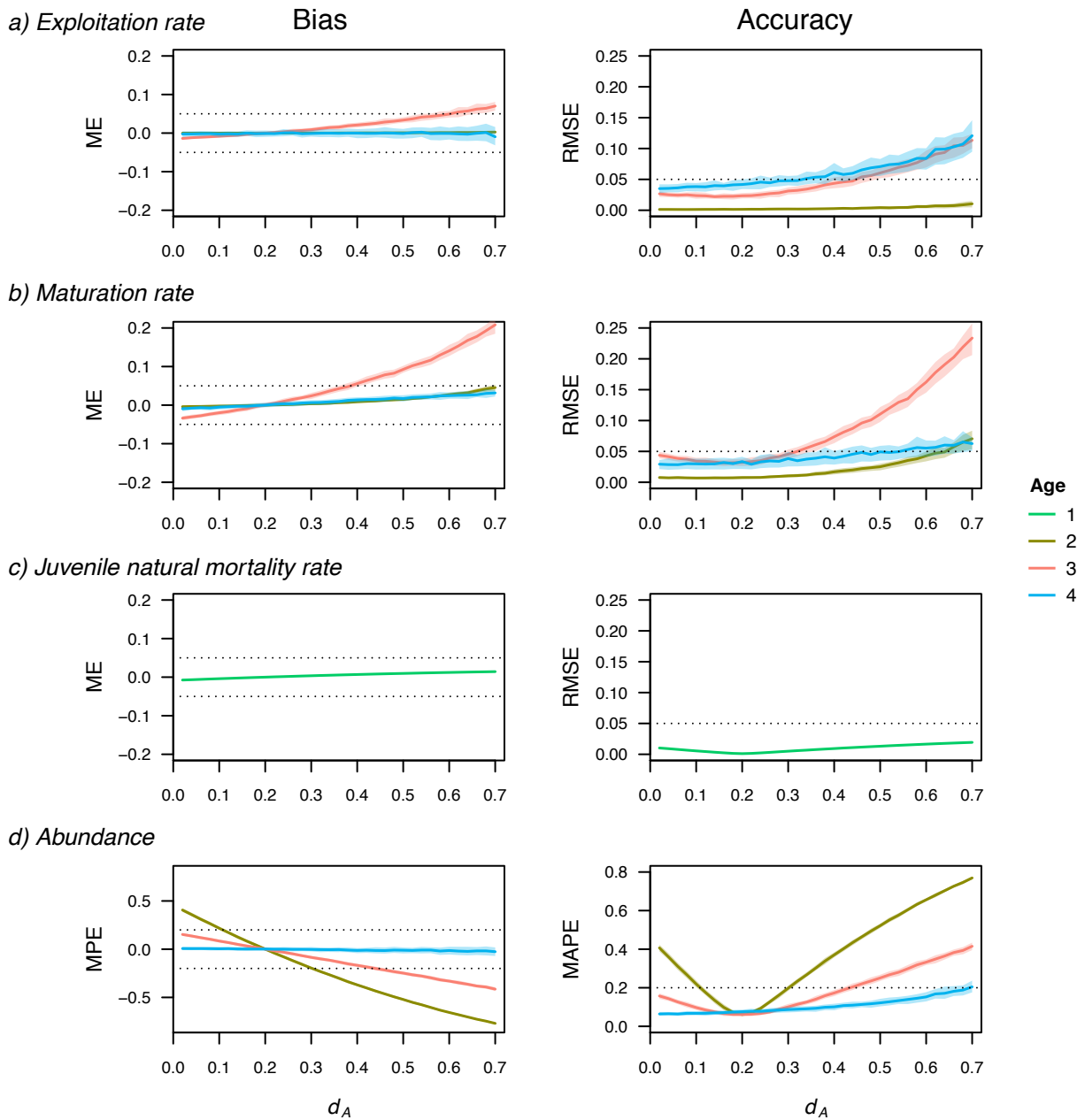


Fig. 2. CR estimation model performance when the underlying adult natural mortality rate is constant (d_A), but misspecified (assumed equal to 0.2). Solid lines indicate bias (left column) and accuracy (right column) as a function of the actual d_A value. Shaded regions about lines depict central 68% quantiles of respective metrics over replicate datasets. Dotted lines reference acceptable performance levels. Note scale of y-axis differs for abundance panels.

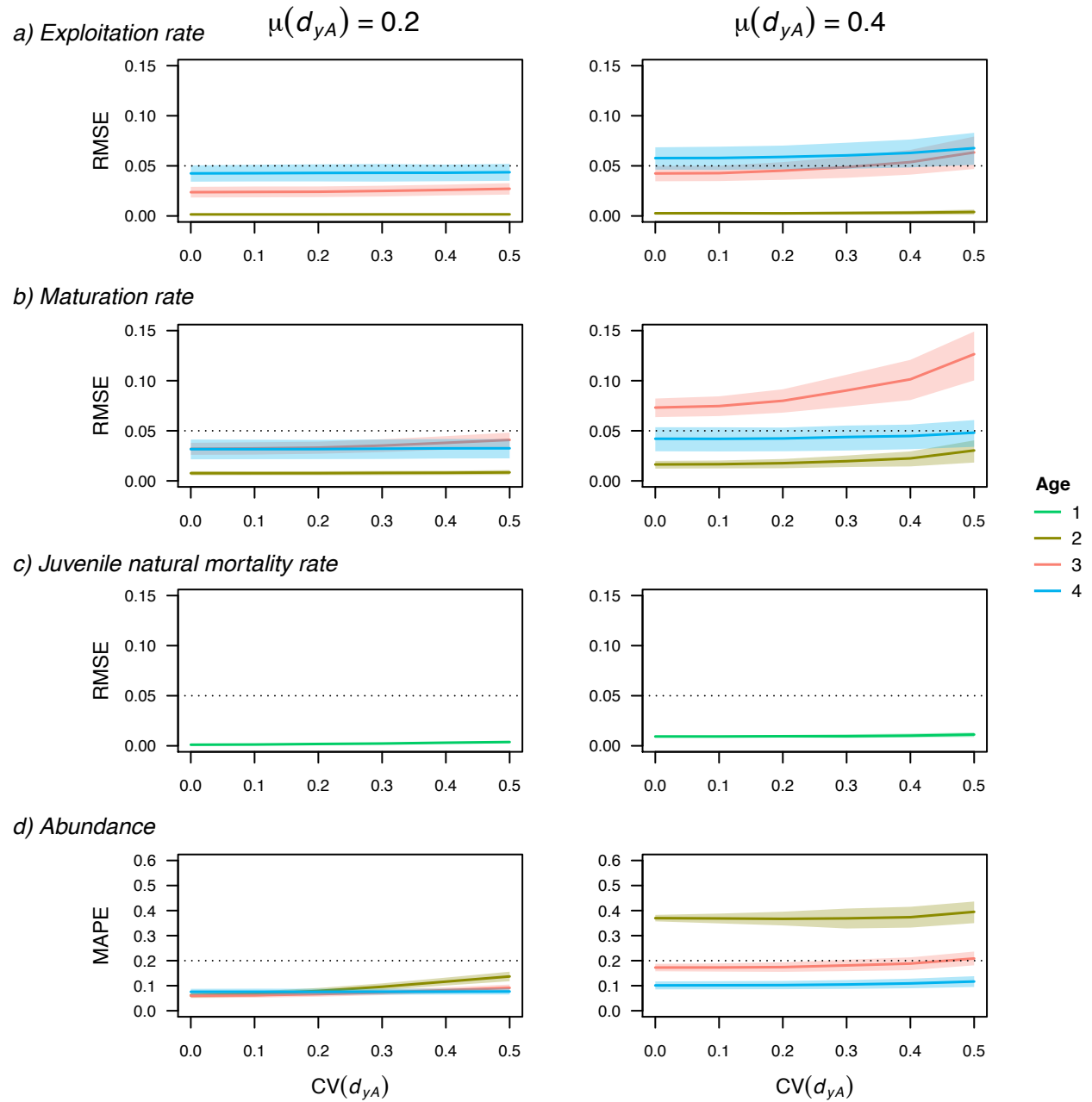


Fig. 3. CR estimation model accuracy measures when the underlying adult natural mortality rate is variable ($\{d_{yA}\}$), but assumed constant (equal to 0.2). Solid lines indicate accuracy as a function of the coefficient of variation when the mean rate is equal to the assumed constant (left column), and twice that of the assumed constant (right column). Shaded regions about lines depict central 68% quantiles of respective metrics over replicated datasets. Dotted lines reference acceptable performance levels. Note scale of y-axis differs for abundance panels.

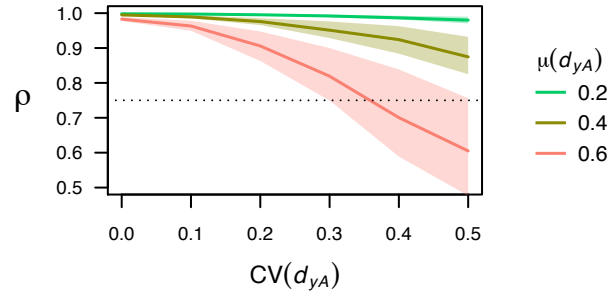


Fig. 4. CR estimation model ability to track temporal trends in the juvenile natural mortality rate when the underlying adult natural mortality rate is variable ($\{d_{yA}\}$), but assumed constant (equal to 0.2). Correlation (ρ) between the estimated and realized set of juvenile natural mortality rates as a function of the coefficient of variation when the mean rate is equal to, twice, or three times that of the assumed constant. Solid lines indicate mean correlation. Shaded regions about lines depict central 68% quantiles of ρ over replicated datasets. Dotted line references acceptable performance level.

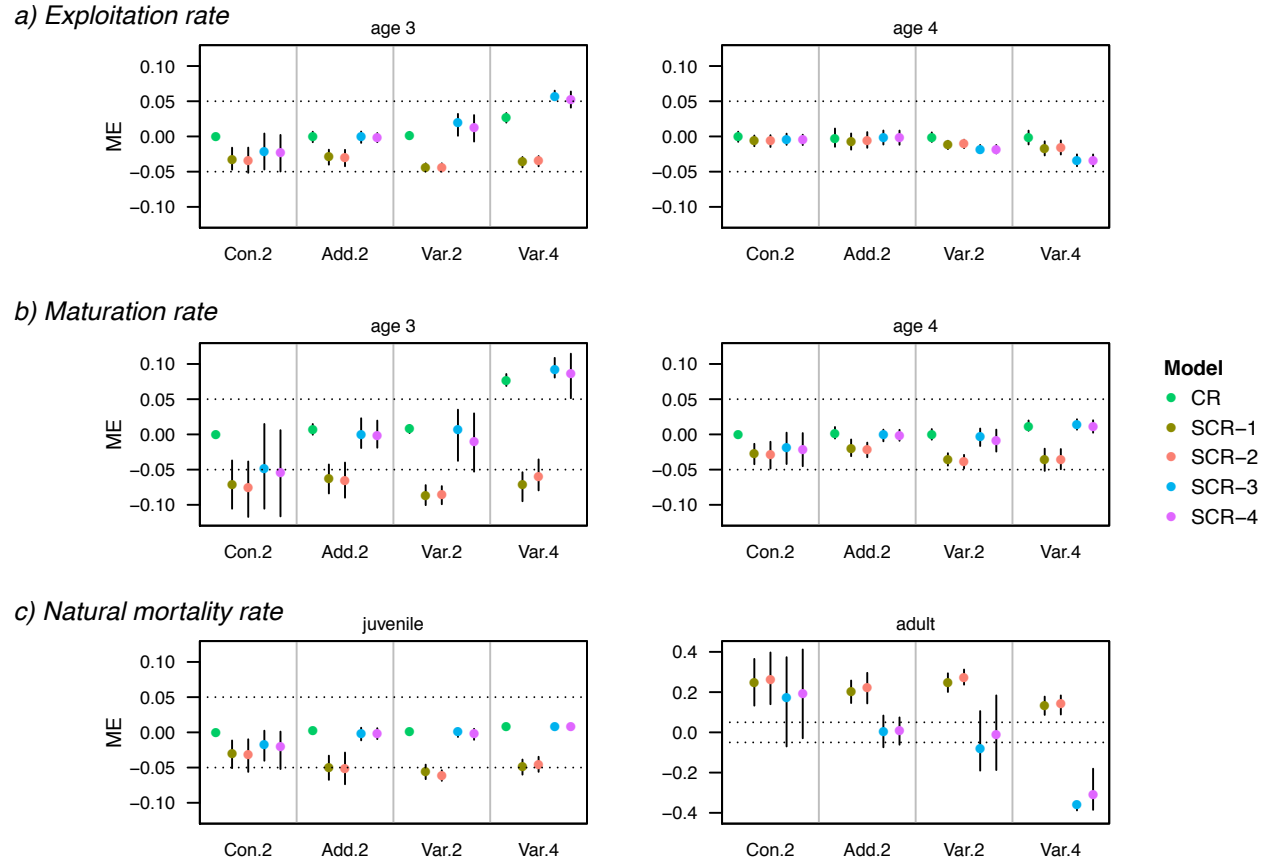


Fig. 5. SCR and CR estimation model bias for one constant (Con.2) and three variable (Add.2, Var.2, Var.4) generating rate scenarios (Figure 1): Con.2 rates are the IGH mean values with $d_A = 0.2$; Add.2 rates are additive on the complementary log-log scale with $\mu(d_{yA}) = 0.22$; Var.2 rates are the IGH rates with $\mu(d_{yA}) = 0.2$; Var.4 rates are the IGH rates with $\mu(d_{yA}) = 0.4$. In all cases, the CR model assumes the adult natural mortality rate is a constant equal to 0.2. Dots indicate bias, and vertical bars depict central 68% quantiles of the ME metric over replicate datasets. Dotted lines reference acceptable performance level. Note scale of y-axis differs for adult natural mortality rate panel.

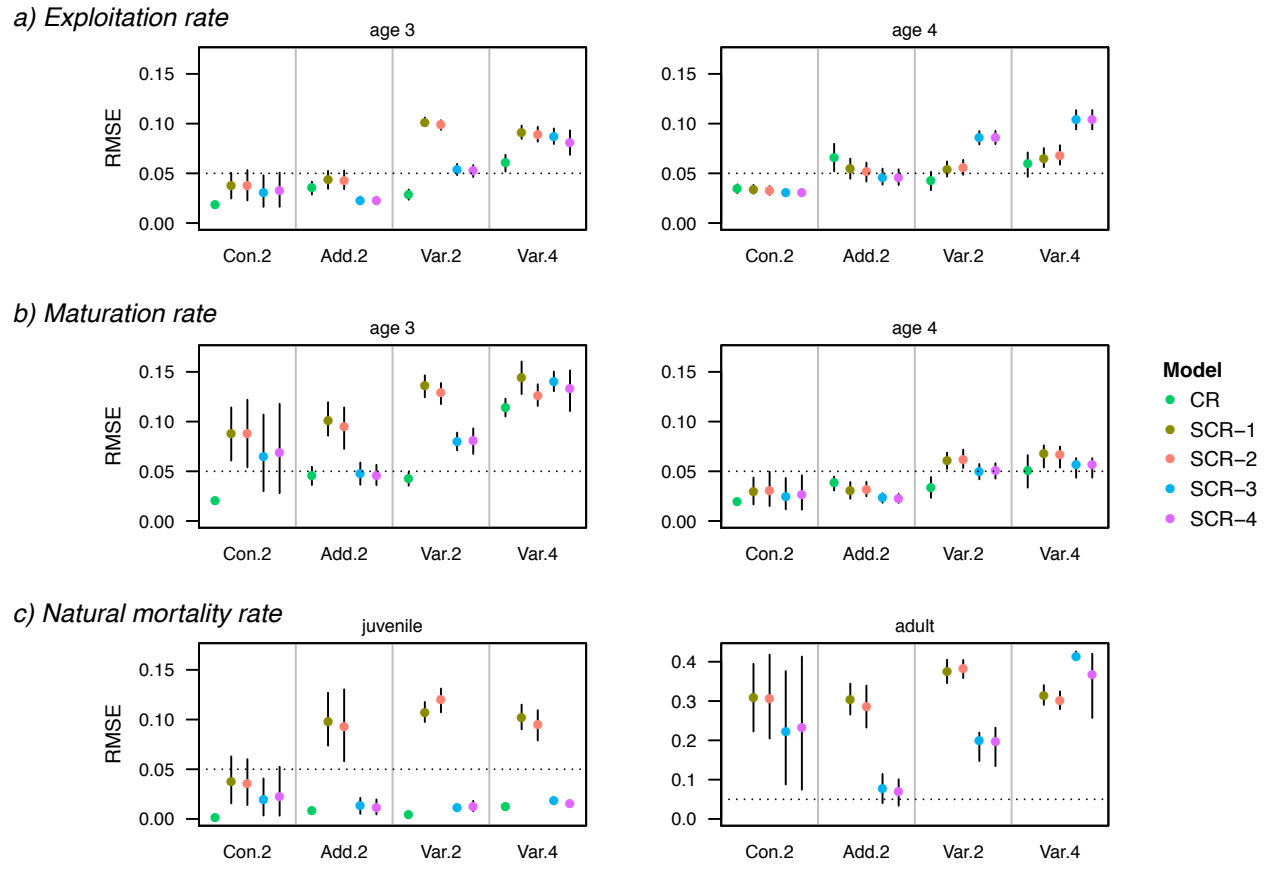


Fig. 6. SCR and CR estimation model accuracy for one constant (Con.2) and three variable (Add.2, Var.2, Var.4) generating rate scenarios (Figure 1): Con.2 rates are the IGH mean values with $d_A = 0.2$; Add.2 rates are additive on the complementary log-log scale with $\mu(d_{yA}) = 0.22$; Var.2 rates are the IGH rates with $\mu(d_{yA}) = 0.2$; Var.4 rates are the IGH rates with $\mu(d_{yA}) = 0.4$. In all cases, the CR model assumes the adult natural mortality rate is a constant equal to 0.2. Dots indicate accuracy, and vertical lines depict central 68% quantiles of the RMSE metric over replicate datasets. Dotted line references acceptable performance level. Note scale of y-axis differs for adult natural mortality rate panel.

858 **Appendix A SCR model fitting and optimization**

859 **Starting values**

860 ADMB, like many other nonlinear optimization routines, cannot exit from local minima,
861 making it necessary to repeatedly fit the models starting from a wide range of initial values
862 as opposed to only one set of values. We chose distributions of starting values with the goal
863 of encompassing a wide, yet biologically plausible range. These ranges were either set to the
864 parameter estimation boundary constraints (see below), or were narrowed slightly to increase
865 the potential for convergence. Starting values for parameters on the complementary log-log
866 scale were time invariant and drawn from normal distributions centered on the generating
867 rates (averaged over years), but had relatively large variances. Randomly drawn values
868 outside of the specified permissible range were truncated to the nearest range endpoint, and
869 adjusted if necessary to satisfy any additional specified constraints among the parameters.
870 Starting value distribution means and coefficients of variation, as well as the permissible
871 ranges and additional specified constraints, are presented in Tables A.1, A.2, A.3, and A.4,
872 for the SCR-1, SCR-2, SCR-3, and SCR-4 model variants, respectively. For reference, we also
873 include in these tables the translation of these specifications to the vital rate (proportion)
874 scale.

875 **Boundaries and phase estimation**

876 To increase the potential for convergence, we specified boundary constraints and the phase of
877 estimation for each of the parameters to be estimated (Tables A.1, A.2, A.3, A.4). Bound-
878 ary constraints ensured that the estimated parameters fell within a reasonable range and
879 restricted the solution space. Phase estimation allowed us to specify when to initiate opti-
880 mization for a given parameter within the overall search. This enabled difficult parameters
881 to be estimated after other, less difficult to estimate parameters were at or near their opti-
882 mal values. In each phase, the parameters activated in the current or previous phase were

883 optimized using their estimated values in the previous phase as initial values.

884 **Convergence performance**

885 For each attempted fitting of an SCR model to a dataset using a randomly drawn set of start-
886 ing values, we documented whether ADMB (a) failed to produce an estimate because the
887 minimization procedure was terminated prematurely (“failed”), (b) produced an estimate
888 but reported that the Hessian may not be positive-definite (“non-positive-definite Hessian”),
889 (c) produced an estimate with a positive-definite Hessian, but the maximum gradient com-
890 ponent exceeded our convergence criterion of 0.0001 (“convergence criterion not met”), or
891 (d) produced an estimate with a positive-definite Hessian, and the maximum gradient com-
892 ponent was less than or equal to our convergence criterion of 0.0001 (“convergence criterion
893 met”). Over the 100 attempted fittings to the dataset, where the convergence criterion was
894 met, we determined which estimate minimized the negative of the log-likelihood function
895 (the maximum likelihood estimate), and also recorded the number of local minima (unique
896 solutions in which at least one estimated vital rate differed by at least 0.001 from the maxi-
897 mum likelihood estimate). The frequency of the above outcomes for each of the SCR models
898 and generating rate sets is shown in Table A.5, where the frequencies are over the 100 fitting
899 attempts (averaged across the 100 independent datasets).

900 Overall, starting values leading to failure or non-positive-definite Hessian matrices oc-
901 curred less than 1.6% of the time. And, other than for the SCR-4 model and Add.2 gener-
902 ating rate set, greater than 97.3% of the starting value sets led to the convergence criterion
903 being met. For the Add.2 generating set, the convergence success rate was much lower:
904 43.9–77.7%. However, based on limited testing, we suspect that a slight increase in our
905 convergence criterion (e.g., from 0.0001 to 0.001) would have resulted in a much higher con-
906 vergence success rate for the Add.2 generating set, and few additional local minima. While
907 the convergence rate for the SCR-4 model in particular was only 43.9% for this generating
908 rate set, the SCR-4 convergence rate was 88.5–95.2% for the other generating rate sets. Note

909 that in these cases of a lower convergence success rate, it was not primarily due to failure
910 or a non-positive-definite Hessian, and multiple minima occurred less than 0.2% of the time.
911 We also note that, anecdotally, in many instances in which the convergence criterion was
912 not met, the estimate was in fact very close to the maximum likelihood estimate, but the
913 minimization routine was terminated “early” relative to our criterion because it met one of
914 the other ADMB built-in convergence criteria (Fournier, 2015). In general, the SCR models
915 were not particularly difficult to fit once the user defined boundaries and estimation phases
916 were appropriately set up, and we suspect that in an application consisting of a single, real
917 dataset, the boundaries, phases, and convergence criterion could be fine-tuned to yield a
918 high convergence success rate.

919 **References**

920 Fournier, D., 2015. AUTODIF: A C++ array language extension with automatic differen-
921 tiation for use in nonlinear modeling and statistics, version 11.4. ADMB Foundation,
922 Honolulu, available from <http://admb-project.org/documentation/manuals>.

Table A.1 Model SCR-1 parameter starting values and estimation specifications (upper portion), and translation of specifications to vital rate scale (lower portion).

Parameter	Starting Value			Estimation		
	Mean	CV	Range	Additional constraints	Bounds	Phase
η_y	$g(\bar{c}_4)$	0.4	[-7.0, 0.5]	$\eta_4 = \eta_5 = \dots = \eta_{I+5} = \eta^*$	[-7.0, 0.5]	1
λ_2	$g(\bar{c}_2) - \eta^*$	0.4	[-6.5, -2.2]	$\lambda_2 \geq -9 - \eta^*$	[-7.5, -2.0]	1
λ_3	$g(\bar{c}_3) - \eta^*$	0.4	[-6.5, -0.4]	$\lambda_3 \geq -8 - \eta^*$, $\lambda_3 \geq \lambda_2$	[-7.5, -0.1]	2
ϕ_{i2}	$g(\bar{m}_2)$	0.4	[-7.9, -1.2]	$\phi_{22} = \phi_{32} = \dots = \phi_{I2} = \phi_2^*$	[-8.0, -1.0]	3
ϕ_{i3}	$g(\bar{m}_3)$	0.4	[-7.8, 1.9]	$\phi_{13} = \phi_{23} = \dots = \phi_{I3} = \phi_3^*$, $\phi_3^* \geq \phi_2^*$	[-7.8, 2.0]	3
ψ	$g(\bar{m}_4)$	0.4	[0.0, 1.9]	$\psi \geq \phi_3^*$	[0.0, 2.0]	1
τ_{yJ}	$g(\bar{d}_J)$	0.4	[-0.3, 1.8]	$\tau_{3J} = \tau_{4J} = \dots = \tau_{I+1 J} = \tau_J^*$	[-0.4, 2.0]	3
τ_{yA}	$g(\bar{d}_A)$	0.5	[-3.7, 0.1]	$\tau_{4A} = \tau_{5A} = \dots = \tau_{I+4 A} = \tau_A^*$, $\tau_A^* \leq \tau_J^*$	[-5.4, 1.0]	3
$g(\pi_{C_{12}})$	$g(C_{12}/R_1)$	0.0	[-7.2, -0.6]		[-8.0, -0.5]	4
$g(\pi_{M_{12}})$	$g(M_{12}/R_1)$	0.0	[-7.2, -0.6]		[-8.0, -0.5]	4
$g(S_{12})$	$g(\frac{C_{13}/\bar{c}_3}{R_1})$	0.0	[-7.2, -0.6]		[-8.0, -0.5]	4
c_{i2}			(0.00, 0.17]	$c_{22} = c_{32} = \dots = c_{I2} = c_2^*$	(0.00, 0.20]	
c_{i3}			(0.00, 0.67]	$c_{13} = c_{23} = \dots = c_{I3} = c_3^*$, $c_3^* \geq c_2^*$	(0.00, 0.76]	
c_{i4}			(0.00, 0.81]	$c_{14} = c_{24} = \dots = c_{I4} = c_4^*$	(0.00, 0.81]	
c_{i5}			(0.00, 0.81]	$c_{15} = c_{25} = \dots = c_{I5} = c_4^*$	(0.00, 0.81]	
m_{i2}			(0.00, 0.26]	$m_{22} = m_{32} = \dots = m_{I2} = m_2^*$	(0.00, 0.31]	
m_{i3}			(0.00, 1.00)	$m_{13} = m_{23} = \dots = m_{I3} = m_3^*$, $m_3^* \geq m_2^*$	(0.00, 1.00)	
m_{i4}			[0.63, 1.00)	$m_{14} = m_{24} = \dots = m_{I4} = m_4^*$, $m_4^* \geq m_3^*$	[0.63, 1.00)	
d_{i1}			[0.52, 1.00)	$d_{21} = d_{31} = \dots = d_{I1} = d_J^*$	[0.50, 1.00)	
d_{i2}			[0.03, 0.65]	$d_{22} = d_{32} = \dots = d_{I2} = d_A^*$, $d_A^* \leq d_J^*$	[0.01, 0.93]	
$d_{ia}, a \geq 3$			[0.03, 0.65]	$d_{1a} = d_{2a} = \dots = d_{Ia} = d_A^*$	[0.01, 0.93]	
$\pi_{C_{12}}$			(0.00, 0.42]		(0.00, 0.46]	
$\pi_{M_{12}}$			(0.00, 0.42]		(0.00, 0.46]	
S_{12}			(0.00, 0.42]		(0.00, 0.46]	

Table A.2 Model SCR-2 parameter starting values and estimation specifications (upper portion), and translation of specifications to vital rate scale (lower portion).

Parameter	Starting Value				Estimation	
	Mean	CV	Range	Additional constraints	Bounds	Phase
η_y	$g(\bar{c}_4)$	0.4	[-7.0, 0.5]	$\eta_3 = \eta_4 = \dots = \eta_{I+5} = \eta^*$	[-7.0, 0.5]	1
λ_2	$g(\bar{c}_2) - \eta^*$	0.4	[-6.4, -2.8]	$\lambda_2 \geq -9 - \eta^*$	[-7.5, -2.0]	1
λ_3	$g(\bar{c}_3) - \eta^*$	0.4	[-6.4, -0.5]	$\lambda_3 \geq -8 - \eta^*$, $\lambda_3 \geq \lambda_2$	[-7.5, -0.1]	2
ζ_i	0	0.0	[0.0, 0.0]		[-7.0, 7.0]	3
δ_2	$g(\bar{m}_2)$	0.4	[-7.9, -1.5]		[-8.0, -1.0]	3
δ_3	$g(\bar{m}_3) - \delta_2$	0.4	[0.7, 9.0]	$\delta_3 \leq 2 - \delta_2$	[0.2, 9.0]	3
ψ	$g(\bar{m}_4)$	0.4	[0.0, 1.7]	$\psi \geq \delta_2 + \delta_3$	[0.0, 2.0]	1
τ_{yJ}	$g(\bar{d}_J)$	0.4	[-0.3, 1.8]	$\tau_{2J} = \tau_{3J} = \dots = \tau_{I+1 J} = \tau_J^*$	[-0.4, 2.0]	3
τ_{yA}	$g(\bar{d}_A)$	0.5	[-3.7, 0.1]	$\tau_{3A} = \tau_{4A} = \dots = \tau_{I+4 A} = \tau_A^*$, $\tau_A^* \leq \tau_J^*$	[-5.4, 1.0]	3
c_{i2}			(0.00, 0.10]	$c_{12} = c_{22} = \dots = c_{I2} = c_2^*$	(0.00, 0.20]	
c_{i3}			(0.00, 0.63]	$c_{13} = c_{23} = \dots = c_{I3} = c_3^*$, $c_3^* \geq c_2^*$	(0.00, 0.76]	
c_{i4}			(0.00, 0.81]	$c_{14} = c_{24} = \dots = c_{I4} = c_4^*$	(0.00, 0.81]	
c_{i5}			(0.00, 0.81]	$c_{15} = c_{25} = \dots = c_{I5} = c_4^*$	(0.00, 0.81]	
m_{12}			(0.00, 0.20]	$m_{12} = m_2^*$	(0.00, 0.31]	
$m_{i2}, i \geq 2$			(0.00, 0.20]	$m_{22} = m_{32} = \dots = m_{I2} = m_2^*$	(0.00, 1.00)	
m_{13}			(0.00, 1.00)	$m_{13} = m_3^*$	(0.00, 1.00)	
$m_{i3}, i \geq 2$			(0.00, 1.00)	$m_{23} = m_{33} = \dots = m_{I3} = m_3^*$	(0.00, 1.00)	
m_{i4}			[0.63, 1.00)	$m_{14} = m_{24} = \dots = m_{I4} = m_4^*$, $m_4^* \geq m_3^*$	[0.63, 1.00)	
d_{i1}			[0.52, 1.00)	$d_{11} = d_{21} = \dots = d_{I1} = d_J^*$	[0.50, 1.00)	
$d_{ia}, a \geq 2$			[0.03, 0.65]	$d_{1a} = d_{2a} = \dots = d_{Ia} = d_A^*$, $d_A^* \leq d_J^*$	[0.01, 0.93]	

Table A.3 Model SCR-3 parameter starting values and estimation specifications (upper portion), and translation of specifications to vital rate scale (lower portion).

Parameter	Starting Value				Estimation	
	Mean	CV	Range	Additional constraints	Bounds	Phase
η_y	$g(\bar{c}_4)$	0.4	[-7.0, 0.5]	$\eta_3 = \eta_4 = \dots = \eta_{I+5} = \eta^*$	[-7.0, 0.5]	1
λ_2	$g(\bar{c}_2) - \eta^*$	0.4	[-7.0, -2.6]	$\lambda_2 \geq -9 - \eta^*$	[-7.5, -2.0]	1
λ_3	$g(\bar{c}_3) - \eta^*$	0.4	[-7.0, -0.4]	$\lambda_3 \geq -8 - \eta^*, \lambda_3 \geq \lambda_2$	[-7.5, -0.1]	1
ϕ_{i2}	$g(\bar{m}_2)$	0.4	[-7.9, -1.3]	$\phi_{12} = \phi_{22} = \dots = \phi_{I2} = \phi_2^*$	[-8.0, -1.0]	2
ϕ_{i3}	$g(\bar{m}_3)$	0.4	[-7.8, 1.6]	$\phi_{13} = \phi_{23} = \dots = \phi_{I3} = \phi_3^*, \phi_3^* \geq \phi_2^*$	[-7.8, 2.0]	2
ψ	$g(\bar{m}_4)$	0.4	[0.0, 1.6]	$\psi \geq \phi_3^*$	[0.0, 2.0]	1
$\xi_y, y \leq I+3$	0	0.0	[0.0, 0.0]		[-5.0, 5.0]	2
ξ_{I+4}	0	0.0	[0.0, 0.0]		[-2.0, 2.0]	2
γ_J	$g(\bar{d}_J)$	0.4	[-0.3, 1.7]		[-0.4, 2.0]	2
γ_A	$g(\bar{d}_A) - \gamma_J$	0.5	[-4.9, -1.5]	$-3.7 - \gamma_J \leq \gamma_A \leq 0.1 - \gamma_J$	[-5.0, -1.0]	2
c_{i2}			(0.00, 0.12]	$c_{12} = c_{22} = \dots = c_{I2} = c_2^*$	(0.00, 0.20]	
c_{i3}			(0.00, 0.67]	$c_{13} = c_{23} = \dots = c_{I3} = c_3^*, c_3^* \geq c_2^*$	(0.00, 0.76]	
c_{i4}			(0.00, 0.81]	$c_{14} = c_{24} = \dots = c_{I4} = c_4^*$	(0.00, 0.81]	
c_{i5}			(0.00, 0.81]	$c_{15} = c_{25} = \dots = c_{I5} = c_4^*$	(0.00, 0.81]	
m_{i2}			(0.00, 0.24]	$m_{12} = m_{22} = \dots = m_{I2} = m_2^*$	(0.00, 0.31]	
m_{i3}			(0.00, 0.99]	$m_{13} = m_{23} = \dots = m_{I3} = m_3^*, m_3^* \geq m_2^*$	(0.00, 1.00)	
m_{i4}			[0.63, 0.99]	$m_{14} = m_{24} = \dots = m_{I4} = m_4^*, m_4^* \geq m_3^*$	[0.63, 1.00)	
d_{11}			[0.52, 1.00)	$d_{11} = d_J^*$	[0.50, 1.00)	
$d_{i1}, i \geq 2$			[0.52, 1.00)	$d_{21} = d_{31} = \dots = d_{I1} = d_J^*$	[0.01, 1.00)	
$d_{1a}, a \geq 2$			[0.03, 0.65]	$d_{1a} = d_A^*$	[0.01, 0.93]	
$d_{ia}, i \geq 2, a \geq 2$			[0.03, 0.65]	$d_{2a} = d_{3a} = \dots = d_{Ia} = d_A^*$	(0.00, 1.00)	

Table A.4 Model SCR-4 parameter starting values and estimation specifications (upper portion), and translation of specifications to vital rate scale (lower portion).

Parameter	Starting Value			Estimation	
	Mean	CV	Range	Additional constraints	Bounds Phase
η_y	$g(\bar{c}_4)$	0.4	[-7.0, 0.5]	$\eta_3 = \eta_4 = \dots = \eta_{I+5} = \eta^*$	[-7.0, 0.5] 1
λ_2	$g(\bar{c}_2) - \eta^*$	0.4	[-6.7, -2.2]	$\lambda_2 \geq -9 - \eta^*$	[-7.5, -2.0] 1
λ_3	$g(\bar{c}_3) - \eta^*$	0.4	[-6.7, -0.4]	$\lambda_3 \geq -8 - \eta^*, \lambda_3 \geq \lambda_2$	[-7.5, -0.1] 1
ζ_i	0	0.0	[0.0, 0.0]		[-7.0, 7.0] 2
δ_2	$g(\bar{m}_2)$	0.4	[-7.9, -1.4]		[-8.0, -1.0] 2
δ_3	$g(\bar{m}_3) - \delta_2$	0.4	[0.5, 9.0]	$\delta_3 \leq 2 - \delta_2$	[0.2, 9.0] 2
ψ	$g(\bar{m}_4)$	0.4	[0.0, 1.6]	$\psi \geq \delta_2 + \delta_3$	[0.0, 2.0] 1
$\xi_{y, y \leq I+3}$	0	0.0	[0.0, 0.0]		[-5.0, 5.0] 4
ξ_{I+4}	0	0.0	[0.0, 0.0]		[-2.0, 2.0] 4
γ_J	$g(\bar{d}_J)$	0.4	[-0.3, 1.9]		[-0.4, 2.0] 3
γ_A	$g(\bar{d}_A) - \gamma_J$	0.5	[-4.9, -1.1]	$-3.7 - \gamma_J \leq \gamma_A \leq 0.1 - \gamma_J$	[-5.0, -1.0] 3
c_{i2}			(0.00, 0.17]	$c_{12} = c_{22} = \dots = c_{I2} = c_2^*$	(0.00, 0.20]
c_{i3}			(0.00, 0.67]	$c_{13} = c_{23} = \dots = c_{I3} = c_3^*, c_3^* \geq c_2^*$	(0.00, 0.76]
c_{i4}			(0.00, 0.81]	$c_{14} = c_{24} = \dots = c_{I4} = c_4^*$	(0.00, 0.81]
c_{i5}			(0.00, 0.81]	$c_{15} = c_{25} = \dots = c_{I5} = c_4^*$	(0.00, 0.81]
m_{12}			(0.00, 0.22]	$m_{12} = m_2^*$	(0.00, 0.31]
$m_{i2, i \geq 2}$			(0.00, 0.22]	$m_{22} = m_{32} = \dots = m_{I2} = m_2^*$	(0.00, 1.00)
m_{13}			(0.00, 1.00)	$m_{13} = m_3^*$	(0.00, 1.00)
$m_{i3, i \geq 2}$			(0.00, 1.00)	$m_{23} = m_{33} = \dots = m_{I3} = m_3^*$	(0.00, 1.00)
m_{i4}			[0.63, 1.00)	$m_{14} = m_{24} = \dots = m_{I4} = m_4^*, m_4^* \geq m_3^*$	[0.63, 1.00)
d_{11}			[0.52, 1.00)	$d_{11} = d_J^*$	[0.50, 1.00)
$d_{i1, i \geq 2}$			[0.52, 1.00)	$d_{21} = d_{31} = \dots = d_{I1} = d_J^*$	[0.01, 1.00)
$d_{1a, a \geq 2}$			[0.03, 0.65]	$d_{1a} = d_A^*$	[0.01, 0.93]
$d_{ia, i \geq 2, a \geq 2}$			[0.03, 0.65]	$d_{2a} = d_{3a} = \dots = d_{Ia} = d_A^*$	(0.00, 1.00)

Table A.5 Convergence performance of SCR models. For each model and generating rate set, the frequency of outcomes over the 100 attempted fittings to a dataset (averaged across the 100 independent datasets) is listed. “Convergence criterion met” outcome includes both global and local minima. For further definition of outcomes see text.

Model	Outcome	Generating rate set			
		Con.2	Add.2	Var.2	Var.4
SCR-1	Failed	0.00	0.05	0.01	0.00
	Non-positive-definite Hessian	0.02	0.00	0.00	0.00
	Convergence criterion not met	1.12	24.48	1.38	0.64
	Convergence criterion met	98.86	75.47	98.61	99.36
	Local minima	0.03	0.00	0.00	0.00
SCR-2	Failed	0.00	0.20	0.04	0.08
	Non-positive-definite Hessian	0.01	0.09	0.14	0.01
	Convergence criterion not met	2.45	35.49	2.47	1.67
	Convergence criterion met	97.54	64.22	97.35	98.24
	Local minima	0.01	0.01	0.00	0.01
SCR-3	Failed	0.06	0.12	0.35	0.39
	Non-positive-definite Hessian	0.05	0.03	0.01	0.00
	Convergence criterion not met	0.53	22.11	1.27	0.29
	Convergence criterion met	99.36	77.74	98.37	99.32
	Local minima	0.20	0.15	0.39	0.38
SCR-4	Failed	0.00	0.00	0.12	0.67
	Non-positive-definite Hessian	0.00	0.00	0.00	0.92
	Convergence criterion not met	4.82	56.13	11.38	3.73
	Convergence criterion met	95.18	43.87	88.50	94.68
	Local minima	0.01	0.00	0.01	0.04