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1 A novel length-based empirical estimation method of spawning
2 potential ratio (SPR), and tests of its performance, for
3 small-scale, data-poor fisheries

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12 **Abstract**

13 The spawning potential ratio (SPR) is a well-established biological reference point, and esti-
14 mates of SPR for data-poor fisheries could be used to inform management decisions. Hordyk *et al.*
15 (this issue) demonstrated the link between the SPR and the life history ratios, the ratio of natural
16 mortality to the von Bertalanffy growth parameter ($\frac{M}{k}$) and the ratio of length at maturity to
17 asymptotic length ($\frac{L_m}{L_\infty}$), and highlighted the potential of this approach as a cost-effective stock
18 assessment tool for small-scale and data-poor fisheries. We carried out simulation studies to in-
19 vestigate the use of the length based model (LB-SPR) developed in Hordyk *et al.* (this issue) to
20 estimate the SPR of exploited fisheries directly from the size composition of the catch. The key pa-
21 rameters for the model are: $\frac{M}{k}$, L_∞ , and variation in length-at-age (CV_{L_∞}). The sensitivity of the

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22 estimated SPR to variation in these parameters, sample size of the length composition data, and
23 recruitment error, were investigated using Monte-Carlo simulations. The method uses maximum
24 likelihood methods to find the best values of relative fishing mortality ($\frac{F}{M}$) and selectivity-at-length
25 that minimises the difference between the observed and the expected length composition of the
26 catch, and calculates the resulting SPR. When parameterised with the correct input parameters,
27 the LB-SPR model returned accurate estimates of $\frac{F}{M}$ and SPR. Although the model performed
28 reasonably well with small sample sizes of length data ($n = 100$), variability in the estimates of SPR
29 were much reduced when sample sizes were based on $> 1,000$ individuals. With high variability in
30 annual recruitment the estimates of SPR became increasingly unreliable. However, as the median
31 error was centred on zero, this variability in the estimated SPR can likely be overcome by repeat-
32 ing the estimation procedure on an annual basis, and adjusting harvest strategies based on the
33 trends in estimated SPR. The results of this study suggest that the length-based SPR estimation
34 methodology is robust to equilibrium assumptions and uncertainty in the life history ratios, and
35 this method has potential to provide a tool for rapid, cost-effective, and conservative assessment
36 of data-poor fisheries.

37 **Keywords.** life history ratios, cost-effective, fish growth, size composition, Beverton-Holt invariants

38 Introduction

39 Measurements of the length composition of an exploited stock are relatively cheap and simple to collect,
40 and are one of the most common forms of data available to fisheries researchers (Quinn and Deriso,
41 1999). For small-scale and data-poor fisheries, where the collection of age data is often restricted by
42 lack of technical expertise and expense, length composition data is often the only form of information
43 available to researchers and managers. This is especially so for many tropical species, where the lack of
44 clearly defined annual growth rings in otoliths or other hard parts make the task of aging individuals
45 very difficult. As a result of the ready availability of length data for many stocks, a number of length-
46 based methods have been developed and applied to estimate biological parameters and to understand
47 the dynamics of fish populations (e.g., Basson *et al.*, 1988; Beverton and Holt, 1957; Gulland and
48 Rosenberg, 1992; Pauly and Morgan, 1987). Many of these size-based techniques were developed to
49 estimate the growth and mortality rates of fish without the need for expensive and difficult to obtain
50 age data (e.g., see many papers in Pauly and Morgan, 1987). Other length-based techniques aim to

51 use the length structure of the population to estimate the stock status and provide useful management
52 advice (e.g., Ault *et al.*, 2005; Gedamke and Hoenig, 2006; O’Farrell and Botsford, 2005, 2006).

53 Recent work has demonstrated that, assuming von Bertalanffy growth, constant natural mortality
54 for all age classes, no variability in length-at-age, and knife-edge selectivity, the standardised length
55 composition of two stocks with same ratio of natural mortality over the growth rate ($\frac{M}{k}$) and the
56 same ratio of fishing mortality to natural mortality ($\frac{F}{M}$) will be have the same length composition
57 (Hordyk *et al.*, this issue). The extension of this model to incorporate variability in length-at-age
58 and logistic selectivity, confirmed that the expected length composition of the catch of an exploited
59 stock is primarily determined by the ratios of $\frac{M}{k}$ and $\frac{F}{M}$. The analytical models developed in Hordyk
60 *et al.* (this issue) suggest that with knowledge of the von Bertalanffy asymptotic length L_∞ and the
61 coefficient of variation in L_∞ (CV_{L_∞}), the ratio of total mortality over the von Bertalanffy growth
62 coefficient ($\frac{Z}{k}$) for a particular stock can be estimated from a representative sample of the length
63 structure of the catch. If $\frac{M}{k}$ is also known (from meta-analysis, life history theory, expert judgment,
64 or biological studies of a stock), then the results of Hordyk *et al.* (this issue) suggest that it is possible
65 to estimate $\frac{F}{M}$ from the size composition of the catch. Given that M is assumed to be unknown, i.e.
66 only the ratio $\frac{M}{k}$ is known, it is not possible to estimate F using this method. However the ratio of
67 $\frac{F}{M}$ has often been used as a biological reference point, with $F_{MSY} = 0.87M$ considered as a reasonable
68 approximation for teleosts (Zhou *et al.*, 2012). However, the ratio of $\frac{F}{M}$ can be misleading if not
69 interpreted with care, as the selectivity of the fishery is also important. For example, it is possible that
70 a highly selective fishery could target only a few of the oldest year classes in a stock, which, even if $\frac{F}{M}$
71 is exceptionally high, is unlikely to affect the sustainability of the fishery, although the yield is likely
72 to be very low. Conversely, even a relatively low $\frac{F}{M}$ can reduce the spawning per recruit drastically if
73 the fishery catches a high proportion of immature individuals.

74 A persistent challenge for length-based methods has been to provide indicators of stock status that
75 can be compared against pre-defined biological reference points. The spawning potential ratio (SPR)
76 of a stock is defined as the proportion of the unfished reproductive potential left at any given level of
77 fishing pressure (Goodyear, 1993; Walters and Martell, 2004). By definition, the SPR equals 100% in
78 an unexploited stock, and zero in a stock with no spawning (e.g., all mature fish have been removed, or
79 all female fish have been caught). The SPR is commonly used to set target and limit reference points
80 for fisheries. For example, $F_{40\%}$, the fishing mortality rate that results in $SPR = 40\%$, is considered risk

81 adverse for many species (Clark, 2002), and suitable reference points can be derived from assumptions
82 about the steepness of the stock-recruit relationship (Brooks *et al.*, 2010). Hordyk *et al.* (this issue)
83 demonstrates that the SPR is determined by the ratios of $\frac{M}{k}$, $\frac{F}{M}$, $\frac{L_m}{L_\infty}$, and $\frac{L_c}{L_\infty}$, under the assumptions
84 of knife-edge selectivity-at-length at L_c , and knife-edge maturity at L_m .

85 The aims of this study were to evaluate the utility of the models developed in Hordyk *et al.* (this
86 issue) as a cost-effective methodology to assessing data-poor and small-scale stocks. The length-based
87 estimation model requires the following parameters: an estimate of the ratio $\frac{M}{k}$ (i.e. the individual
88 values of the M and k parameters are unknown), L_∞ or L_m , CV_{L_∞} , and knowledge of maturity-at-
89 size, and uses data on the length composition of the catch to estimate the SPR. A simulation model
90 was used to test the performance of the length-based SPR (LB-SPR) method for four species with a
91 diverse range of life histories. These life histories were chosen on the basis of the $\frac{M}{k}$ ratios, varying
92 from 0.3 for a species with a length composition dominated by large individuals, to 2.3, representing a
93 species with a length distribution dominated by smaller fish. In particular, the study investigated the
94 sensitivity of the LB-SPR model to error or misspecification of the input parameters, and to violations
95 of the equilibrium assumption of constant recruitment.

96 **Methods**

97 The LB-SPR method requires as input length composition data of the catch, as well as the three
98 parameters: $\frac{M}{k}$, L_∞ (or $\frac{L_m}{L_\infty}$), CV_{L_∞} . The model estimates the selectivity-at-length and the ratio $\frac{F}{M}$,
99 which in turn are used to calculate SPR. To test the utility and sensitivity of the estimation model
100 to a range of issues likely to be encountered in the real world an age-structured operating model
101 was developed to generate length composition data for a range of life-history types. All simulation
102 modelling was done using the open-source statistical software *R* (R Development Core Team, 2012).

103 **Operating model**

104 The population dynamics were modelled with a female-only, non-spatial, age-structured operating
105 model (OM), with the assumption that the population was closed with respect to immigration and
106 emigration. In general, the OM was modelled with annual time-steps. However, the OM was modelled
107 with monthly time-steps for short-lived species (i.e. species with life-span ≤ 10 years). The conversion

108 from annual to monthly time-steps was necessary to ensure the construction of smooth length com-
 109 positions for short-lived species, and was achieved by scaling the rate parameters appropriately. For
 110 example, an annual M is converted to a monthly rate by dividing by 12. For the short-lived species,
 111 recruitment was assumed to be continuous and occurred on the 1st day of every month.

112 The abundance, N , at age a at time t is given as:

$$N_{a,t} = \begin{cases} R_t & \text{if } a = 0 \\ N_{a-1,t-1}e^{Z_{a-1}} & \text{if } 0 \leq a \leq a_{\max} \end{cases} \quad (1)$$

113 where R_t is the number of recruits at time t , Z_a is instantaneous total mortality at age a , and a_{\max} is
 114 the maximum age. Total mortality at age a is given by:

$$Z_a = M + S_a F \quad (2)$$

115 where M is the annual instantaneous rate of natural mortality, S_a is selectivity at age a , and F is
 116 the annual instantaneous rate of fishing mortality. The catch-at-age (C_a) was calculated using the
 117 Baranov equation:

$$C_{a,t} = \frac{F_a}{Z_a} N_{a,t} (1 - e^{-Z_a}) \quad (3)$$

118 No plus-group was used, instead a_{\max} was determined as the first age class where the number of
 119 surviving individuals was $\leq 1\%$ of initial recruitment (Quinn and Deriso, 1999), so that:

$$a_{\max} = \frac{-\ln(0.01)}{M} \quad (4)$$

120 Natural mortality was assumed to be constant and independent of size or age, and fishing mortality was
 121 assumed to be constant for all t . Recruitment was related to the spawning biomass by the Beverton-
 122 Holt stock-recruit relationship with multiplicative log-normal error:

$$R_t = \frac{SB_{t-1}}{\delta + \rho SB_{t-1}} e^{\epsilon_t - \frac{\sigma_R^2}{2}} \quad (5)$$

123 where SB_t is the spawning stock biomass at time t , δ and ρ are parameters of the stock-recruit function,
 124 and ϵ_t is the recruitment residual at time t that is normally distributed by $N(0, \sigma_R^2)$, where σ_R is the

125 recruitment variability.

126 The δ and ρ parameters of the stock-recruit relationship were re-parameterised in terms of steepness
 127 (h), which is defined as the fraction of virgin recruitment (R_0) obtained when spawning biomass is 0.2
 128 of the unfished spawning biomass (i.e. $0.2SB_0$).

129 Growth was modelled with the 3 parameter von Bertalanffy function:

$$L_a = L_\infty \left(1 - e^{-k(a-t_0)}\right) \quad (6)$$

130 where L_∞ is asymptotic length, k is the growth coefficient, and t_0 the theoretical age when length
 131 is zero. Variation of length-at-age was assumed to be normally distributed, with variance increasing
 132 with increased mean length (Sainsbury, 1980):

$$\sigma_{L_a}^2 = \sigma_{L_\infty}^2 (1 - e^{-ka})^2 \quad (7)$$

133

$$\sigma_{L_\infty} = CV_{L_\infty} L_\infty \quad (8)$$

134 Maturity was assumed to be size-dependent, and was modelled with the two parameter logistic
 135 function:

$$\text{Mat}_l = \frac{1}{1 + e^{\frac{-\ln(19)(l-L_{50})}{L_{95}-L_{50}}}}$$

136 where Mat_l is maturity at length l , and L_{50} and L_{95} are lengths at 50% and 95% maturity respectively.

137 Maturity-at-length was converted to maturity-at-age (Mat_a):

$$\text{Mat}_a = \int_{l=0}^{l=\infty} \text{Mat}_l \frac{1}{\sqrt{2\pi}\sigma_{L_a}} e^{-\frac{(l-L_a)^2}{2\sigma_{L_a}^2}} \quad (9)$$

138 where $\sigma_{L_a}^2$ is the variance of length at age a . Spawning stock biomass was calculated at the end of
 139 each time-step as:

$$SB_t = \sum_a N_{a,t} \text{Mat}_a W_a \quad (10)$$

140 where W_a is weight at age a , which was calculated as:

$$W_a = \alpha L_a^\beta \quad (11)$$

141 where α and β are constants. Egg production at age a was assumed to be proportional to weight:

$$E_a \propto \text{Mat}_a W_a \quad (12)$$

142 Selectivity was assumed to be asymptotic and size dependent, and was modelled with a two parameter
143 logistic function:

$$S_l = \frac{1}{1 + e^{\frac{-\ln(19)(l-L_{S50})}{S_{L95}-L_{S50}}}} \quad (13)$$

144 where S_l is selectivity-at-length l , and L_{S50} and L_{S95} are the lengths at 50% and 95% selectivity
145 respectively. Selectivity-at-length was converted to selectivity-at-age (S_a) by:

$$S_a = \int_{l=0}^{l=\infty} S_l \frac{1}{\sqrt{2\pi}\sigma_{L_a}} e^{-\frac{(l-L_a)^2}{2\sigma_{L_a}^2}} \quad (14)$$

146 SPR was calculated following Goodyear (1993), by calculating the ratio of the average lifetime
147 production of eggs per recruit (EP) at equilibrium for the fished and unfished states, assuming no
148 density-dependant suppression of maturation or fecundity:

$$SPR = \frac{EP_{\text{Fished}}}{EP_{\text{Unfished}}} \quad (15)$$

149 where

$$EP_{\text{Fished}} = \sum_a \begin{cases} E_a e^{-Ma} & \text{for } a = 0 \\ E_{a-1} e^{-M+(FS_{a-1})} & \text{for } 0 < a \leq a_{\text{max}} \end{cases} \quad (16)$$

150 and

$$EP_{\text{Unfished}} = \sum_a E_a e^{-Ma}$$

151 An age-length transition matrix (Hilborn and Walters, 2001) was constructed from the assumptions
152 of mean length-at-age and variation of length-at-age, where the probability of an individual at age a

153 being in length class i is given by:

$$P_{i,a} = \begin{cases} \phi\left(\frac{l_{i+1}^{l_o} - L_a}{\sigma_{L_a}}\right) & \text{if } i = 1 \\ \phi\left(\frac{l_{i+1}^{l_o} - L_a}{\sigma_{L_a}}\right) - \left(\frac{l_i^{l_o} - L_a}{\sigma_{L_a}}\right) & \text{if } 1 < i \leq I \\ 1 - \left(\frac{l_i^{l_o} - L_a}{\sigma_{L_a}}\right) & \text{if } i = I \end{cases} \quad (17)$$

154 where ϕ is the standard normal cumulative distribution, $l_i^{l_o}$ is the upper bound of length class i , and I
 155 is the total number of length classes. The age-length probability matrix was modified for the expected
 156 age-length distribution of the catch (p) to account for the selectivity-at-length by multiplying the
 157 age-length transition matrix by the selectivity at length class i (S_i):

$$p_{i,a} = P_{i,a} S_i \quad (18)$$

158 The age-length transition matrix for the catch was standardised so that the probability of an individual
 159 in the catch at age a being in one of the I length classes was 1:

$$p_{i,a} = \frac{p_{i,a}}{\sum_a p_{i,a}} \quad (19)$$

160 The length composition of the catch (N_i) was then constructed by multiplying the vector of catch-at-
 161 age by the transpose of the matrix p :

$$N_i = C_a p^T \quad (20)$$

162 Estimation model

163 The estimation model was based on the analytical derivations developed in Hordyk *et al.* (this is-
 164 sue), but for completeness, it is fully described here. To ensure that there was no possibility of
 165 cross-contamination of parameter values between the operating model and the estimation model, the
 166 estimation model was coded separately in ADMB (Fournier *et al.*, 2012). Hordyk *et al.* (this issue)
 167 demonstrated that, once standardised (to L_∞ , or some other standardisation, e.g. L_{\max}), the expected
 168 length composition of the catch is determined by the interaction of selectivity and $\frac{Z}{k}$. If $\frac{M}{k}$ is known,
 169 from meta-analysis or some other method, then there is the potential to estimate $\frac{F}{M}$ and selectivity-

170 at-length from length frequency data of the catch. In turn, these estimated parameters can be used to
 171 calculate SPR which can be used for management of the fishery.

172 To make the problem numerically tractable, the estimation model was constructed from a modified
 173 age-structured model, with “age” defined in arbitrary units. Let X be the number of discrete “age”
 174 classes in the estimation model, where X is a fixed parameter of the estimation model. The vector x
 175 is then defined as a sequence of “ages” in an arbitrary temporal scale from 0 to $X-1$ (i.e maximum
 176 “age” = $X - 1$), and \tilde{x} is a vector of relative “ages” defined between 0 and 1:

$$\tilde{x} = \frac{x}{X} \quad (21)$$

177 It is important to remember that the units of x are undefined, and that any ages in the estimation
 178 model are only meaningful in relative terms. Mean standardised length (\tilde{l}) at age x can then be given
 179 in terms of $\frac{M}{k}$ (Hordyk *et al.*, this issue):

$$\tilde{l}_x = 1 - 0.01^{\tilde{x} \frac{1}{M/k}} \quad (22)$$

180 Assuming that length-at-age is normally distributed with constant CV, the standard deviation of \tilde{l}_x is
 181 (Hordyk *et al.*, this issue):

$$\sigma_{\tilde{l}_x} = \text{CV} \left(1 - 0.01^{\tilde{x} \frac{1}{M/k}} \right) \quad (23)$$

182 If there are I length classes in the observed length composition of the catch, and the length composition
 183 is standardised to L_∞ , then the probability of an individual at age x being in length class i can be
 184 given as a $I \times X$ age-length transition matrix:

$$\tilde{P}_{i,x} \begin{cases} \phi \left(\frac{l_{i+1}^{\text{lo}} - \tilde{l}_x}{\sigma_{\tilde{l}_x}} \right) & \text{if } i = 1 \\ \phi \left(\frac{l_{i+1}^{\text{lo}} - \tilde{l}_x}{\sigma_{\tilde{l}_x}} \right) - \phi \left(\frac{l_i^{\text{lo}} - \tilde{l}_x}{\sigma_{\tilde{l}_x}} \right) & \text{if } 1 < i < I \\ 1 - \phi \left(\frac{l_i^{\text{lo}} - \tilde{l}_x}{\sigma_{\tilde{l}_x}} \right) & \text{if } i = I \end{cases} \quad (24)$$

185 where l_i^{lo} is the lower bound of length class i , and ϕ is the standard normal cumulative density function.

186 Assuming a logistic selectivity pattern, selectivity at standardised length \tilde{l} can be modelled as:

$$\tilde{S}_{\tilde{l}} = \frac{1}{1 + e^{\frac{-\ln(19)(\tilde{l}-l_{S50})}{l_{S95}-l_{S50}}}} \quad (25)$$

187 where l_{S50} and l_{S95} are the standardised lengths at 50% and 95% selectivity respectively. The matrix
 188 \tilde{P} can be modified to account for the selectivity-at-length, to give the probability that an individual
 189 in the catch at age x is in size class i :

$$\tilde{C}_{i,x} = \tilde{P}_{i,x} \tilde{S}_i \quad (26)$$

190 where \tilde{S}_i is the selectivity for length class i , calculated by substituting \tilde{l} in Equation 25 with \tilde{l}_i , which
 191 is the mid-point of length class i . The matrix \tilde{C} must be standardised so that there is a probability of
 192 1 that an individual in the catch at age x is in one of the I length classes:

$$\tilde{C}_{i,x} = \frac{\tilde{C}_{i,x}}{\sum_x \tilde{C}_{i,x}} \quad (27)$$

193 Hordyk *et al.* (this issue) demonstrates that it is difficult to calculate the number of individuals
 194 at age x in terms of $\frac{M}{k}$ and $\frac{F}{M}$ with logistic selectivity and variability in length-at-age. However,
 195 the age-structured estimation model allows the calculation of the number of individuals at age x
 196 by taking advantage of the assumed relationship between longevity and natural mortality. If X is
 197 the number of discrete age classes, then the corresponding M can be calculated from Equation 4:
 198 $M = \frac{-\ln(0.01)}{t_{\max}} = \frac{-\ln(0.01)}{X-1}$. The unit of time relating to t_{\max} (and therefore M) is not known, so let
 199 this M be referred to as M^{gen} to identify it as a generic parameter with unknown time scale. A vector
 200 of total mortality at age x can then be given as:

$$Z_x^{\text{gen}} = M^{\text{gen}} + M^{\text{gen}} \frac{F}{M} \tilde{S}_x \quad (28)$$

201 where \tilde{S}_x is the selectivity at age x (in unknown units of time) determined by multiplying the matrix
 202 \tilde{P} by the vector \tilde{S}_i :

$$\tilde{S}_x = \tilde{S}_i \tilde{P} \quad (29)$$

203 The relative number of individuals at age x can then be calculated using the traditional fisheries model:

$$\tilde{N}_x = \begin{cases} 1 & \text{if } x = 0 \\ \tilde{N}_{x-1} e^{-Z_{x-1}^{\text{gen}}} & \text{if } 0 < x \leq X \end{cases} \quad (30)$$

204 The expected proportion of individuals in the catch in length class i is then:

$$\tilde{P}_i^{\text{Catch}} = \frac{(\tilde{N}_x \tilde{S}_x) \tilde{C}^T}{\sum_i (\tilde{N}_x \tilde{S}_x) \tilde{C}^T} \quad (31)$$

205 With the assumptions of constant CV in variance of length-at-age, logistic selectivity, and constant
 206 natural mortality, the above algorithm gives the predicted proportion of the catch in length class
 207 i in terms of $\frac{M}{k}$, $\frac{F}{M}$ and selectivity at relative length (l_{S50} and l_{S95}). When the observed length
 208 composition of the catch is standardised to L_∞ then the two selectivity parameters are equal to $\frac{L_{S50}}{L_\infty}$
 209 and $\frac{L_{S95}}{L_\infty}$ respectively. Given knowledge of $\frac{M}{k}$, the parameters $\frac{F}{M}$, $\frac{L_{S50}}{L_\infty}$ and $\frac{L_{S95}}{L_\infty}$ can be estimated from
 210 the standardised length composition of the catch by minimising the following multinomial negative
 211 log-likelihood function (NLL):

$$NLL = \arg \min_{\frac{F}{M}, \frac{L_{S50}}{L_\infty}, \frac{L_{S95}}{L_\infty}} \sum_i O_i \ln \frac{\tilde{P}_i^{\text{Catch}}}{O_i^P} \quad (32)$$

212 where O_i and O_i^P are the observed number and proportion of the catch respectively in length class i .

213 Hordyk *et al.* (this issue) demonstrated that, with the simplifying assumptions of no variation
 214 of length-at-age, and knife-edge selectivity, SPR is invariant with respect to the ratios $\frac{M}{k}$ and $\frac{F}{M}$.
 215 Extending the model further to account for more realistic assumptions also showed the relationship
 216 between SPR and $\frac{M}{k}$ and $\frac{F}{M}$ holds with logistic selectivity and variable length-at-age. Using the generic
 217 age-structure of the estimation model, and given estimates of maturity-at-age and the size-fecundity
 218 relationship, SPR can be calculated from the estimated parameters. Assuming that maturity is a
 219 logistic function of length, then maturity at relative length \tilde{l} can be given by:

$$\text{Mat}_{\tilde{l}} = \frac{1}{1 + e^{\frac{-\ln(19)(\tilde{l}-l_{50})}{l_{95}-l_{50}}}} \quad (33)$$

220 where \tilde{l}_{50} and \tilde{l}_{95} are the relative lengths at 50% and 95% maturity respectively, and defined as:

$$\tilde{l}_{50} = \frac{L_{50}}{L_{\infty}} \quad (34)$$

$$\tilde{l}_{95} = \frac{L_{95}}{L_{\infty}} \quad (35)$$

221 where L_{50} and L_{95} are the lengths at 50% and 95% maturity respectively. Similarly to selectivity-at-
 222 length, maturity-at-length can be converted to maturity at age x by multiplying the vector $\text{Mat}_{\tilde{l}}$ by
 223 the age-length transition matrix \tilde{P} :

$$\text{Mat}_x = \text{Mat}_i \tilde{P} \quad (36)$$

224 where Mat_i is the probability that an individual in length class i is mature, calculated by substituting
 225 \tilde{l} in Equation 33 with \tilde{l}_i , which is the mid-point of length class i . Assuming that fecundity is linearly
 226 related to weight, which is a cubic function of length, the relative egg production (\tilde{E}) at relative age
 227 x is:

$$\tilde{E}_x = \text{Mat}_x \tilde{l}_x^3 \quad (37)$$

228 Total relative egg production ($\tilde{\text{EP}}_{\text{Fished}}$) for the fished state is then:

$$\tilde{\text{EP}}_{\text{Fished}} = \sum_x \begin{cases} \tilde{E}_x e^{-M} & \text{if } x = 0 \\ \tilde{E}_{x-1} e^{-Z_{x-1}} & \text{if } 0 < x \leq X \end{cases} \quad (38)$$

229 and for the unfished state:

$$\tilde{\text{EP}}_{\text{Unfished}} = \sum_x \begin{cases} \tilde{E}_x e^{-M} & \text{if } x = 0 \\ \tilde{E}_{x-1} e^{-M} & \text{if } 0 < x \leq X \end{cases} \quad (39)$$

230 SPR can then be calculated as:

$$SPR = \frac{\tilde{\text{EP}}_{\text{Fished}}}{\tilde{\text{EP}}_{\text{Unfished}}} \quad (40)$$

Table 1: The biological and selectivity parameters for the 4 test species used in the robustness tests of the LB-SPR model

Parameter	Species				Definition
	I	II	III	IV	
L_∞ (mm)	376	170	530	342	Asymptotic size
CV_{L_∞}	0.1	0.1	0.1	0.1	Coefficient of variation of L_∞
M	0.42	0.44	0.63	1.25	Natural mortality
k	0.79	0.535	0.41	0.41	Growth coefficient
t_0	0	0	0	0	Theoretical age at zero length
$\frac{M}{k}$	0.53	0.82	1.54	3.05	$\frac{M}{k}$ ratio
L_{50} (mm)	290	121	259	194	Length at 50% maturity
L_{95} (mm)	320	170	344	204	Length at 95% maturity
L_{S50} (mm)	240	94	220	130	Length at 50% selectivity
L_{S95} (mm)	260	108	260	145	Length at 95% selectivity

Table 2: Description of the 10 tests to understand the robustness and sensitivity of the LB-SPR model to a range of parameter misspecification and assumption violations.

Test	Description
1	assumed $\frac{M}{k}$ parameter ranging $\pm 25\%$ of true value
2	assumed L_∞ parameter ranging $\pm 25\%$ from true value
3	assumed CV_{L_∞} parameter ranging $\pm 25\%$ from true value
4	X (the length of vector x in the estimation model) ranging from 10–208
5	Sample size reduced to 100, 500, 1,000, 5,000 & 10,000 individuals
6	Length-at-birth (L_0) ranging 0–0.25 L_∞
7	True $\frac{F}{M}$ ranging 0.01–5
8	Population disequilibria with $\sigma_R = 0.1, 0.3, 0.6$ & 0.9
9	Same as Test 8, with auto-correlated recruitment error
10	Same as Test 8, with episodic recruitment failure

231 Simulation and evaluation

232 The utility of the LB-SPR method was evaluated by using the operating model to generate length data,
 233 and comparing the estimates of $\frac{F}{M}$, selectivity-at-length, and SPR from the estimation model with the
 234 true values of the OM. Biological parameters for the simulated data were based on four species with
 235 a range of life-histories: I) sand sole (*Psettiichthys melanostictus*), II) Puget Sound rockfish (*Sebastes*
 236 *emphaeus*), III) yellowtail flathead (*Platycephalus endrachtensis*) and IV) Pacific saury (*Cololabis*
 237 *saira*) (hereafter referred to as Species I, II, III, & IV) (Hughes, 1974; Watanabe *et al.*, 1988; Beckmann
 238 *et al.*, 1998; Pearson and McNally, 2005; Coulson *et al.*, 2007). The selectivity-at-length parameters
 239 were arbitrarily set lower than maturity-at-length for each species, and CV_{L_∞} was set at 0.1, and t_0
 240 was assumed to be 0 for all species (1). Steepness was set to 0.7 for all cases.

241 A number of robustness tests were conducted to assess the utility of the LB-SPR model, and to

242 understand the sensitivity of the model to various assumptions, input parameters and life-histories
243 (2). The assessment model was parametrised with the “true” value of the $\frac{M}{k}$, L_∞ , CV_{L_∞} parameters,
244 except in the cases where sensitivity to those parameters was being tested (i.e. Tests 1-3). Similarly,
245 the sampling of the catch was assumed to be 100% except in the case of Test 5. Fishing mortality
246 was set equal to natural mortality for all cases except Test 7. For Test 1-7, σ_R was set to 0 (i.e.
247 no variability in recruitment), and the operating model was projected forward until the stock was at
248 fished equilibrium. The X parameter of the estimation model was set at 100 for all cases except Test
249 4.

250 Tests 1-3 examined the sensitivity of the estimation model to misspecification of the $\frac{M}{k}$, L_∞ ,
251 and CV_{L_∞} parameters respectively. For each test, the estimation model was run 100 times with the
252 assumed value of the relevant parameter ranging from -25% to $+25\%$ of the true value. Results for
253 these tests were summarised by determining the bias in the estimated parameters as a function of the
254 error in the assumed parameters.

255 Test 4 determined the sensitivity of the estimation model to X , the temporal resolution of the
256 estimation model. For this test, the estimation model was repeatedly run 100 times with X in Equation
257 21 ranging from 10 to 208. The results of this tests were summarised as bias in the estimated parameters
258 as a function of X .

259 Although samples of the length composition of the catch are relatively cheap and simple to obtain,
260 it is unreasonable to expect that the entire catch will be sampled. Test 5 examined the impact of sample
261 size on the effectiveness of the LB-SPR method. Five levels of sampling coverage were examined, with
262 sample sizes of 100, 500, 1,000, 5,000, and 10,000 individuals respectively. For each case and test
263 species, length compositions were generated from 200 Monte Carlo simulations by randomly sampling
264 with replacement from the age composition of the catch, with the probability proportional to that
265 in the true age composition of the catch. The estimation model was run on each generated length
266 composition, and results summarised as boxplots of bias in the estimated parameters for each sample
267 size.

268 The estimation model assumes that length at birth (L_0) is 0 mm (Equation 22). In many of species
269 of fish this assumption is likely to be a reasonable assumption. However, in some species, for example
270 live-bearing teleosts and many sharks, L_0 is considerably larger. When modelling fish growth with
271 the von Bertalanffy function, this is accounted for with the inclusion of the t_0 parameter, which is

272 the theoretical age at which the length of the animal would be 0. In most cases the t_0 is ≤ 0 , which
 273 indicates that $L_0 \geq 0$. In cases where $t_0 > 0$, L_0 is < 0 which is biologically impossible, and the von
 274 Bertalanffy growth function may not be the most appropriate model to use in these situations. The
 275 effect of alternative growth models has not been examined in this study. However, the sensitivity of
 276 the estimation model to $L_0 > 0$ was examined in Test 6. For this test, the length compositions were
 277 generated with L_0 ranging from 0 to $0.25L_\infty$ for each species. To generate the length compositions,
 278 the appropriate t_0 parameter was calculated in the operating model by manipulating Equation 6:

$$t_0 = \frac{\ln\left(1 - \frac{L_0}{L_\infty}\right)}{k} \quad (41)$$

279 Test 7 investigated the sensitivity of the assessment model to the true $\frac{F}{M}$. For this test, length
 280 compositions were generated from 100 Monte Carlo simulations with the true $\frac{F}{M}$ ranging from 0.01 to
 281 5, and the resulting estimated $\frac{F}{M}$ was compared against the true value.

282 Like many length-based methods, the LB-SPR technique is an equilibrium-based method, which
 283 compares the observed length composition of the catch with the expected length composition in equi-
 284 librium conditions. In reality an exploited stock is rarely at equilibrium. Even if exploitation rates
 285 are held constant for some time, a stock is still likely to be at disequilibrium due to variability in
 286 recruitment. The last 3 tests examined the sensitivity of the estimation model to population dise-
 287 quilibrium by generating length compositions from stocks with variable recruitment. For Test 8, 200
 288 Monte Carlo simulations of the operating model were projected forward under 4 levels of log-normally
 289 distributed recruitment variability, with σ_R set at 0.1, 0.3, 0.6 and 0.9 respectively. For each of the
 290 Monte Carlo simulations, a length composition of the catch was generated from the last year. Test
 291 9 repeated a similar test to Test 8, but with the addition of auto-correlated recruitment error, with
 292 a lag of 1 year and an auto-correlation coefficient of 0.6. Test 10 further extended the examination
 293 of recruitment variability by investigating the impact of episodic recruitment failure. For this test
 294 there was a 15% chance in any given time-step (usually yearly, but monthly for short-lived species)
 295 of recruitment failure. 200 Monte Carlo simulations were conducted for each of the 4 species for the
 296 same range of recruitment variability as Tests 8 & 9.

Results

The sensitivity tests revealed that, for all 4 species, there is a direct relationship between the accuracy of the estimated $\frac{F}{M}$ and the assumed values of the parameters for the LB-SPR method (Figures 1a, b & c). When the 3 parameters of the LB-SPR model were set equal to the true values, the estimation model returned estimates of $\frac{F}{M}$, the selectivity parameters, and SPR that were very close to the true values (Figures 1a, b & c). The model had similar behaviour for all 4 species when $\frac{M}{k}$ was misspecified (Test 1), with $\frac{F}{M}$ over-estimated by about 70% when $\frac{M}{k}$ was assumed to be 25% lower than the true value, and under-estimated by about 40% when $\frac{M}{k}$ was assumed to be 25% higher than the true value (Figure 1a). The selectivity parameters L_{S50} and L_{S95} were insensitive to the assumed $\frac{M}{k}$. The exact relationship between $\frac{F}{M}$ and SPR depends on the selectivity pattern; however, in general SPR decreases as $\frac{F}{M}$ increases. As expected, the relationship between estimated SPR and the degree of misspecification in the assumed $\frac{M}{k}$ parameter is the reverse to the pattern observed between the estimated $\frac{F}{M}$ and assumed $\frac{M}{k}$, with SPR being increasingly over-estimated as the $\frac{M}{k}$ parameter is assumed to be higher than the true value (Figure 1a).

The estimation model was most sensitive to the assumed L_∞ , with considerable over-estimation in $\frac{F}{M}$ when the assumed L_∞ was specified to be higher than the true value (Test 2; Figure 1b). Sensitivity to the assumed L_∞ increased with decreasing $\frac{M}{k}$, with Species I the most sensitive to misspecification of L_∞ ($\frac{F}{M}$ over-estimated by about 400% when L_∞ assumed to be 25% higher than true value) and Species IV the least ($\frac{F}{M}$ over-estimated by about 100% when L_∞ assumed to be 25% higher than true value). The model under-estimated $\frac{F}{M}$ when L_∞ was assumed to be lower than the true value, with $\frac{F}{M}$ estimated to be 0 (i.e. $F=0$) when the assumed L_∞ was specified to be 10-20% lower than the true value. As with Test 1, the selectivity-at-length parameters were well estimated and were not sensitive to the misspecification of the assumed L_∞ parameter. However, SPR showed the same sensitivity as $\frac{F}{M}$, with the estimated SPR rapidly increasing as the assumed L_∞ was decreased below the true value, and rapidly decreasing when the assumed L_∞ was increased above the true value (Figure 1b).

The estimation model was relatively insensitive to the assumed CV_{L_∞} for all 4 life-history types, although species with low $\frac{M}{k}$ appeared the most sensitive to this parameter (Figure 1). The model was also completely insensitive to the temporal scale of the estimation model when X was above about 50 (Figure 1d). Below this value, the model behaved somewhat chaotically and often did not fit the data

326 well.

327 As expected, there was greater variability in the estimates of $\frac{F}{M}$, selectivity-at-length and SPR
328 when sampling coverage was reduced. In particular, a sample size of 100 individuals often resulted in
329 bias estimates of the selectivity-at-length parameters and $\frac{F}{M}$. However, even with the bias in these
330 parameters, SPR was still estimated quite well for small sample sizes. The median bias in $\frac{F}{M}$ was close
331 to 0 for all sample sizes, and SPR was well estimated, particularly for sample sizes of 1000 individuals
332 or greater (Figure 2).

333 Species with higher $\frac{M}{k}$ appear to be the most sensitive to the assumption that $L_0 = 0$ (i.e. $t_0 = 0$),
334 however the estimation model was relatively insensitive to $L_0 > 0$, with $\frac{F}{M}$ being over-estimated by
335 5-10% when $L_0 = 0.25L_\infty$ (Test 6; Figure 3a). The estimation model was also not sensitive to the true
336 $\frac{F}{M}$ of the operating model and returned accurate estimates for the entire range of $\frac{F}{M}$ (Test 7; Figure
337 3b).

338 There was relatively low bias in the estimated selectivity parameters when the assumption of a stock
339 at equilibrium was violated (Test 8; Figure 4). Not unexpectedly, bias in the selectivity parameters
340 increased with increasing recruitment error, however in most cases the selectivity parameters were
341 estimated within 10% of the true values. A similar pattern was observed in the estimated $\frac{F}{M}$ for all
342 4 species, with variance increasing with increased recruitment error (Figure 4). However, the median
343 bias in the estimated $\frac{F}{M}$ for all 4 life history types was centred around 0, indicating that on average
344 the method was successful in correctly estimating the parameters. The variance in the estimates of
345 $\frac{F}{M}$ and the selectivity parameters directly translates through to the estimates of SPR; however SPR
346 appeared to be well estimated for all 4 life-history types and 4 levels of recruitment error (Figure 4).

347 The inclusion of auto-correlated recruitment error resulted in increased variance in the 3 estimated
348 parameters, particularly when σ_R was 0.6 or 0.9 (Test 9; Figure 5). The estimates of the selectivity
349 parameters were reasonable, however the bias in $\frac{F}{M}$ was often quite large. While the median bias
350 in $\frac{F}{M}$ was centred around 0, $\frac{F}{M}$ was sometimes considerably over-estimated, which resulted in SPR
351 being considerably under-estimated. In addition, $\frac{F}{M}$ was also occasionally under-estimated by close to
352 100%, resulting in SPR being greatly over-estimated. There appeared to be little extra impact from the
353 inclusion of episodic recruitment variability, with the estimation model appearing to behave in a similar
354 manner to Test 8 (Test 10; Figure 6). As with the other tests involving stock disequilibria, the bias
355 in the estimated parameters increased with increasing recruitment error, with $\frac{F}{M}$ being occasionally

356 over-estimated and under-estimated by up to 100% when $\sigma_R = 0.9$.

357 Discussion

358 The length-based technique developed in this study offers an alternative method to estimate $\frac{F}{M}$,
359 selectivity-at-length and the spawning potential ratio (SPR) for an exploited stock based only on
360 length frequency data. Length frequency data are one of the easiest and most affordable metrics to
361 collect, and for many small-scale, data-poor fisheries, may be the only data that are available. Our
362 technique provides a means of estimating the biological reference points, $\frac{F}{M}$ and SPR, which previously
363 required expensive and technically challenging catch-at-age analyses.

364 In this study, we simulated length data from four species with diverse life histories, spanning
365 the range of $\frac{M}{k}$ in the meta-analysis of Prince *et al.* (this issue). The results from the simulations
366 showed that the length based SPR (LB-SPR) method appeared to work well, especially for species
367 with $\frac{M}{k} > 0.53$. However, it is likely that the model will be increasingly biased for species with $\frac{M}{k} < 0.53$,
368 as the method relies on detecting the signal of fishing mortality in the right-hand side of the length
369 composition. Species with low $\frac{M}{k}$ are expected to have an unfished length composition very strongly
370 skewed to the left and as a consequence, fishing would not be expected to have a big impact on the
371 size structure of the stock, as the length composition consists of adults of widely varying age, but at
372 a similar size.

373 As modelled here, the LB-SPR method assumes that length-at-age is normally distributed with a
374 constant coefficient of variation (CV), an assumption that does not always appear to hold (Bowker,
375 1995; Erzini, 1994). Detailed costly ageing studies are required to test this assumption, research
376 that is not feasible for small-scale, data-poor fisheries. However, meta-analyses of existing length-at-
377 age studies are likely to provide a cost-effective way to determine whether the assumption of normally
378 distributed length-at-age is commonly violated, or if there are predictable violations of this assumption
379 amongst some species. The impact of violating the assumption of normally distributed length-at-age
380 has not been investigated in this study but knowledge of the distribution of length-at-age could be
381 incorporated into the LB-SPR method for specific species.

382 Influence of variation in parameters on estimating SPR

383 The accuracy of the estimated SPR at from the LB-SPR method depends on the precision of the
384 $\frac{M}{k}$ ratio and the CV_{L_∞} and L_∞ parameters that are assumed for the stock. The research required
385 to estimate these three individual parameters directly from the stock is time-consuming, somewhat
386 complex, and expensive; precisely the factors that limit age-based population modelling from being
387 applied to data-poor and small-scale fisheries. Without relatively expensive ageing studies, it is difficult
388 to obtain reliable estimates of the individual parameters M and k . A number of length-based methods
389 exist which aim to estimate k from size-frequency or tagging studies (e.g., Pauly and Morgan, 1987;
390 Siegfried and Sansó, 2006; Smith *et al.*, 1998). Estimating M is often more difficult, especially for
391 stocks with a long history of exploitation. However, the ratio of $\frac{M}{k}$ is known to be often less variable
392 between species than either of the individual parameters in the ratio (Beverton, 1992). Numerous
393 rules-of-thumb have been developed to estimate L_∞ in data-poor stocks. For example, Taylor (1958)
394 suggested that the life-span of a fish species could be estimated as the age at which fish reach 95%
395 of their asymptotic length; i.e. the mean length of the cohort is $0.95L_\infty$ at a_{\max} . Assuming that a
396 cohort is at its mean maximum length (L_{\max}) at a_{\max} , this suggests that L_∞ could be estimated by:
397 $L_\infty = \frac{L_{\max}}{0.95}$ (Pauly, 1984). If a stock is only relatively lightly exploited, it would be reasonable to
398 assume that L_{\max} could be approximated by the maximum observed length. However, as demonstrated
399 by Hordyk *et al.* (this issue, their Figure 1), the assumption that fish are $0.95L_\infty$ at a_{\max} does not
400 hold for species where $\frac{M}{k}$ diverges away from the Beverton Holt Life History Invariant value of 1.5. For
401 example, a species with a $\frac{M}{k}$ ratio of 0.7 (i.e., species where individuals reach maximum size relatively
402 early in life) would be expected to reach L_∞ at about $0.7 a_{\max}$ (i.e. $L_{\max} = L_\infty$), while a species with a
403 $\frac{M}{k}$ ratio of 2.3, i.e. a species that has indeterminate growth, would be expected to only reach $0.8L_\infty$ at
404 the end of its life (i.e., $L_{\max} = 0.8L_\infty$) (see Figure 1 in Hordyk *et al.*, this issue). If an estimate of the
405 ratio $\frac{M}{k}$ is known, then the equations derived in Hordyk *et al.* (this issue) could be used to estimate
406 L_∞ from L_{\max} and $\frac{M}{k}$, which could be used to as an estimate to parametrise L_∞ for the LB-SPR
407 model developed in the current study.

408 Beverton (1992) demonstrated that a relationship between $\frac{M}{k}$ and the ratio of size at maturity to
409 asymptotic size $\left(\frac{L_m}{L_\infty}\right)$ can be derived analytically for teleosts. Hordyk *et al.* (this issue) and Prince
410 *et al.* (this issue) confirm this relationship from an empirical analytical approach with a meta-analysis

411 of these ratios for 123 species in the literature, and suggest that the co-varying ratios can be predicted
412 for species on the basis of taxonomic relationships and a species' life history strategy. Meta-analysis
413 and life-history theory appear to offer a way of estimating these parameters for small-scale and data-
414 poor stocks (Prince *et al.*, this issue). Assuming that other closely related species, or nearby stocks,
415 have a similar life-history and are well studied, the ratio $\frac{L_m}{L_\infty}$ from these stocks could be used as a
416 starting estimate for the data-poor stock of interest (Prince *et al.*, this issue).

417 **Influence of sample size on estimating SPR**

418 Hilborn and Walters (2001) warn against using length-based methods, and note that length compo-
419 sitions are often not representative of the whole stock. Unrepresentative length samples would cause
420 bias in any stock assessment method, and the resulting evaluation of the condition of the stock. Con-
421 sequently, ensuring high quality, representative length data are collected for the stock should be an
422 important research priority and emphasises the importance of designing rigorous sampling programs
423 to collect length data. Since the LB-SPR method assumes that any large fish that are missing from
424 the data have been removed by fishing, if the large fish are under-represented in the length sample for
425 any reason, the LB-SPR method will over-estimate $\frac{F}{M}$ and under-estimate the SPR.

426 The precision of the estimated SPR the data on length composition can be increased by simply
427 increasing the sample size of the length measurements. Gerritsen and McGrath (2006) recommend
428 a rule-of-thumb where the minimum sample size is 10 times the number of length classes in the
429 sample. Other simulation work suggests that sample sizes of 1,000 length measurements are required
430 to sufficiently capture the features of a length composition Erzini (1990). This conclusion is supported
431 by the simulation studies from our study which showed that the variation in the estimated SPR was
432 reduced greatly when $\geq 1,000$ measurements were taken (Figure 2). In addition to measuring an
433 adequate number of fish to increase the precision of the estimated SPR, the sampling design should
434 consider the temporal and spatial distribution of the fished stocks to ensure that the true length
435 composition of the stock is estimated in the sample (Gerritsen and McGrath, 2006).

436 **Dynamic effects on estimating SPR**

437 The model developed in this study assumes that the stock is in equilibrium which means that the
438 current size composition of the stock is assessed against the expected size composition if the stock had

439 experiences a constant level of fishing pressure and constant recruitment. The assumption of constant
 440 fishing effort may hold for a number of years for the small-scale fisheries that are the focus of this
 441 methodology. The second assumption of constant recruitment, however, is unlikely to hold for many
 442 stocks (e.g., Myers, 2001). The simulation of variation in recruitment examined in this study ranged
 443 from low, where the standard deviation of recruitment = 0.1 (i.e., $\sigma_R = 0.1$); and the difference between
 444 the strongest and weakest year classes is $\approx 1.5:1$, to reasonably high, where $\sigma_R = 0.9$ and the difference
 445 in magnitude between the strongest and weakest year classes is $\approx 30:1$. Not unexpectedly, the results
 446 of the LB-SPR model are most variable when the annual recruitment error is high. The results from
 447 our simulations showed that high recruitment variability is likely to cause considerable bias in the
 448 LB-SPR method, especially when σ_R is ≥ 0.6 . At low levels of recruitment variability ($\sigma_R = 0.1$)
 449 and constant F , the stock is essentially at equilibrium, and $\frac{F}{M}$, the selectivity parameters, and the
 450 SPRs are estimated with minimal error (Figures 4, 5 & 6). However, as the recruitment variation
 451 was increased ($\sigma_R = 0.6$ and 0.9), the estimated $\frac{F}{M}$ in any given year could be under-estimated by
 452 close to 100% ($\frac{F}{M} = 0, \text{SPR} = 1$), or over-estimated by over 100% (Figures 4, 5 & 6). The bias
 453 in the estimated parameters in the simulations with recruitment error, however, was centred on 0,
 454 and SPR was estimated reasonably well, i.e. within 30% of the real value, in most of the Monte
 455 Carlo simulations for all four modelled species. Occasionally, particularly for high recruitment error
 456 ($\sigma_R = 0.9$), the estimates of $\frac{F}{M}$ and the selectivity parameters were very biased, resulting in large over-
 457 or under-estimates of SPR.

458 As the LB-SPR model is an equilibrium based method, and assumes constant recruitment, it cannot
 459 fit multi-modal length compositions well. Modes in length compositions often occur from a disparity
 460 in year class strength, and following the progression of these modes through time is the foundation of
 461 many length-based techniques used to estimate growth and mortality (Pauly and Morgan, 1987). If
 462 the length frequency of a population is highly multi-modal, the LB-SPR model will not fit the data
 463 well, and any estimates of $\frac{F}{M}$, selectivity and SPR are likely to be unrealistic. While a good fit of the
 464 LB-SPR model does not necessarily imply that the estimates are accurate (the model can potentially
 465 fit the data very well even if $\frac{M}{k}$ or L_∞ are mis-specified), a poor fit of the model to multi-modal length
 466 data indicates that the results are likely to be untrustworthy. If the year-classes are clearly identified as
 467 modes in the length data, the LB-SPR method may not be the most suitable technique for estimating
 468 the condition of the stock and other more traditional length-based methods may be more applicable.

469 Alternatively, collecting data at a higher temporal resolution (e.g. monthly for short lived species)
470 and then aggregating the data over a year, may provide a means of constructing a length composition
471 more representative of the equilibrium size composition. .

472 The management strategy evaluation (MSE) modelling conducted by Wayte and Klaer (2010) and
473 Prince *et al.* (2011) on harvest control rules based on equilibrium based Catch-at-Age and SPR-based
474 size targets, shows that while individual assessments of size composition may be imprecise due to the
475 transitory dynamics of a population's size structure, smoothed trends estimated over several years
476 provided an accurate basis for harvest control rules. Our observations support their finding, in that
477 some of the transitory size dynamics we simulated gave LB-SPR estimates that were quite biased, but
478 the mean bias across estimates was zero. We have incorporated the LB-SPR into a harvest control rule
479 and our own limited MSE modelling suggests that it will be able to respond to transitory dynamics
480 similarly to those modelled by Wayte and Klaer (2010) and Prince *et al.* (2011) and provide an accurate
481 basis for harvest control rules. This will be a topic of further research.

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574 **Figure Captions**

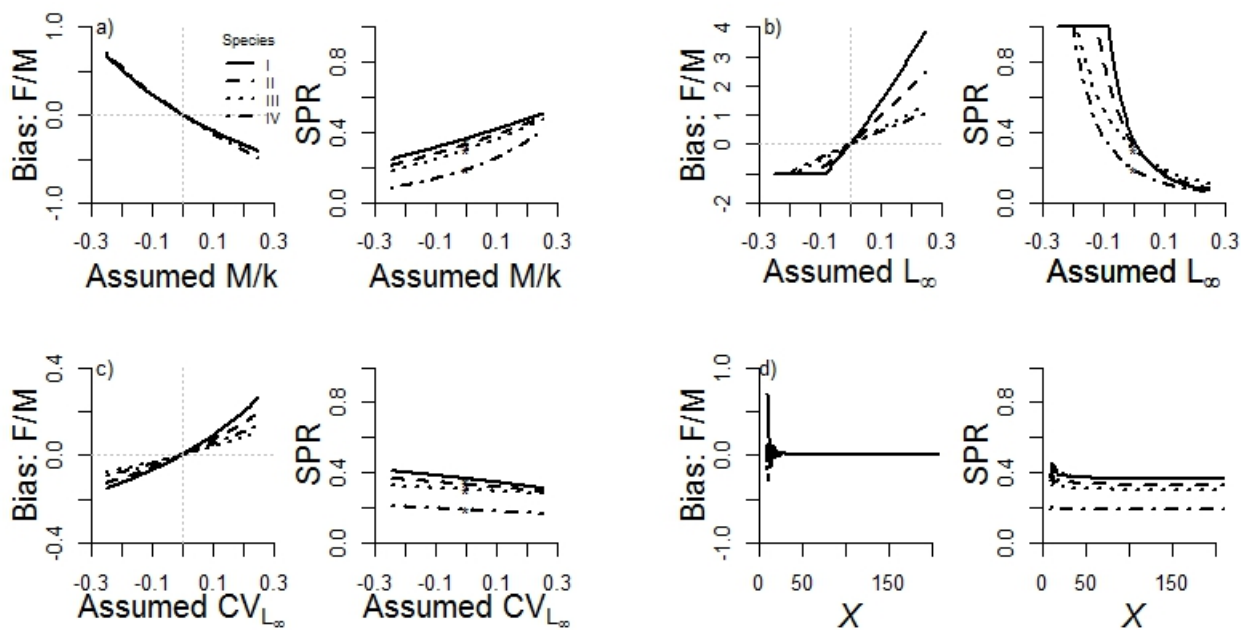


Figure 1: Bias in the estimated $\frac{F}{M}$ and resulting estimate of SPR for the 4 simulated species for a) Test 1: misspecification of $\frac{M}{k}$, b) Test 2: misspecification of L_∞ , c) Test 3: misspecification of CV_{L_∞} , and d) value of the X parameter. Asterisks in the SPR panels of a), b) & c) indicate the “true” SPR for each species.

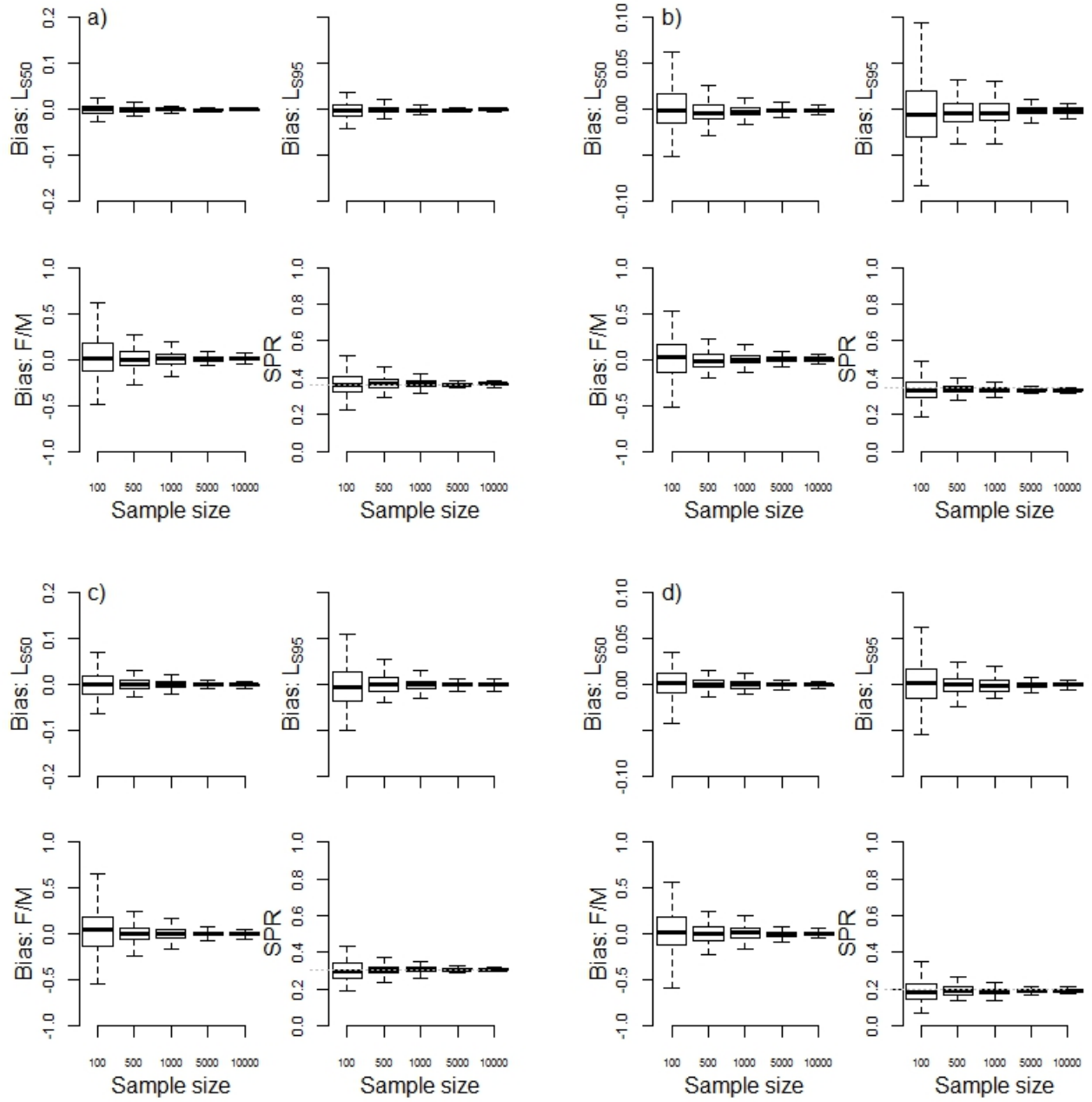


Figure 2: Bias in the estimated $\frac{F}{M}$, L_{S50} , L_{S95} and resulting estimate of SPR for a range of sample sizes for a) Species I, b) Species II, c) Species III, and d) Species IV.

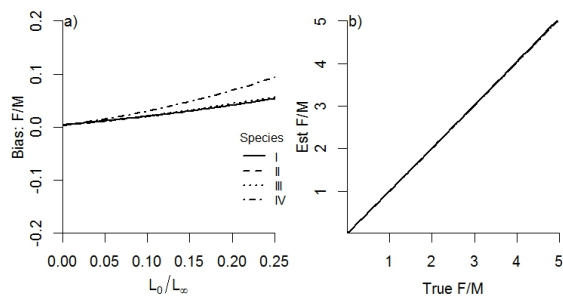


Figure 3: Results of a) Test 6, showing the bias is estimated $\frac{F}{M}$ for the 4 species for L_0 ranging $0-0.25L_\infty$, and b) comparison of true $\frac{F}{M}$ to estimated $\frac{F}{M}$ for the 4 species.

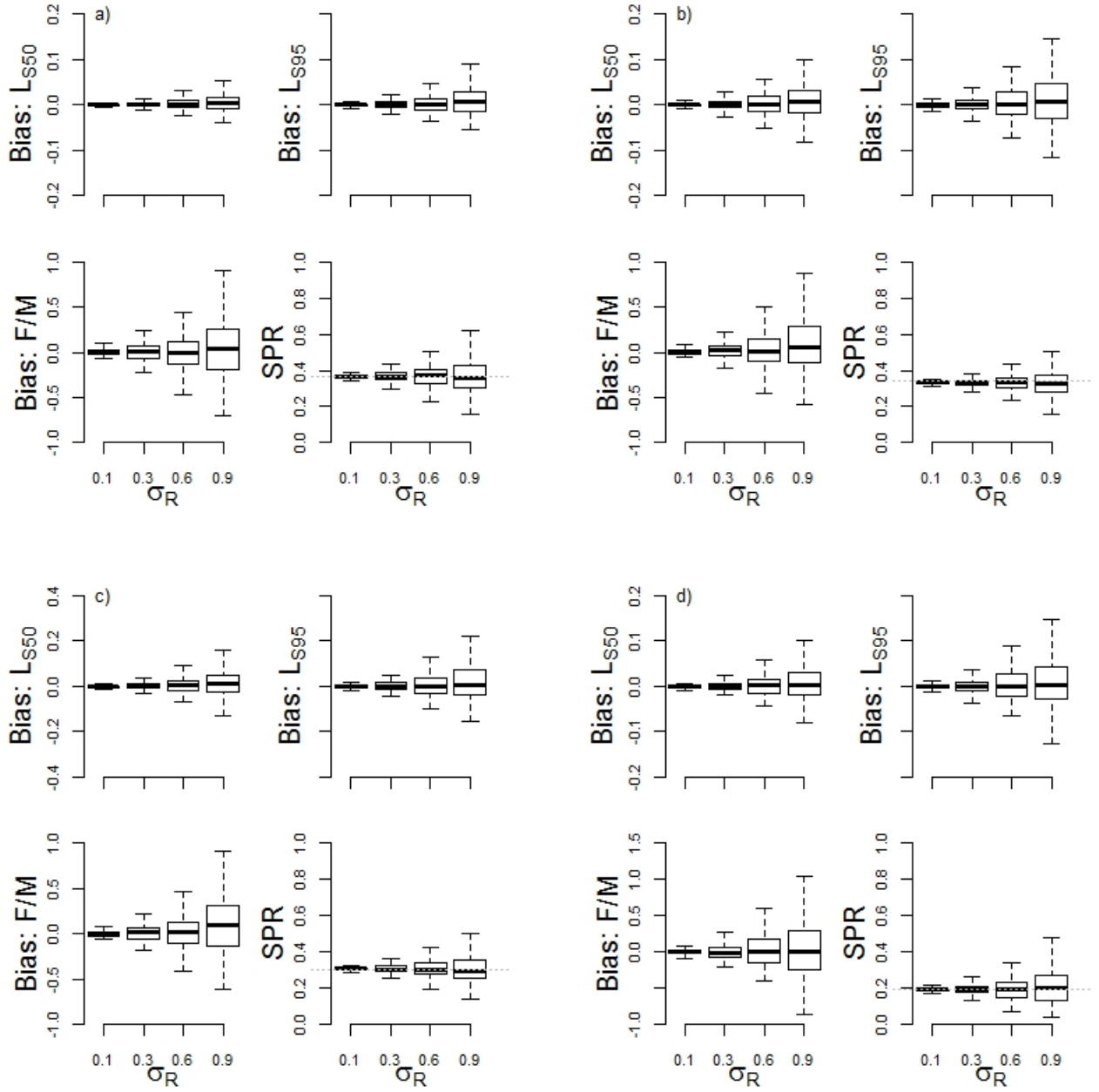


Figure 4: Bias in estimated $\frac{F}{M}$, L_{S50} , L_{S95} and the resulting estimate of SPR with recruitment error for a) Species I, b) Species II, c) Species III, and d) Species IV.

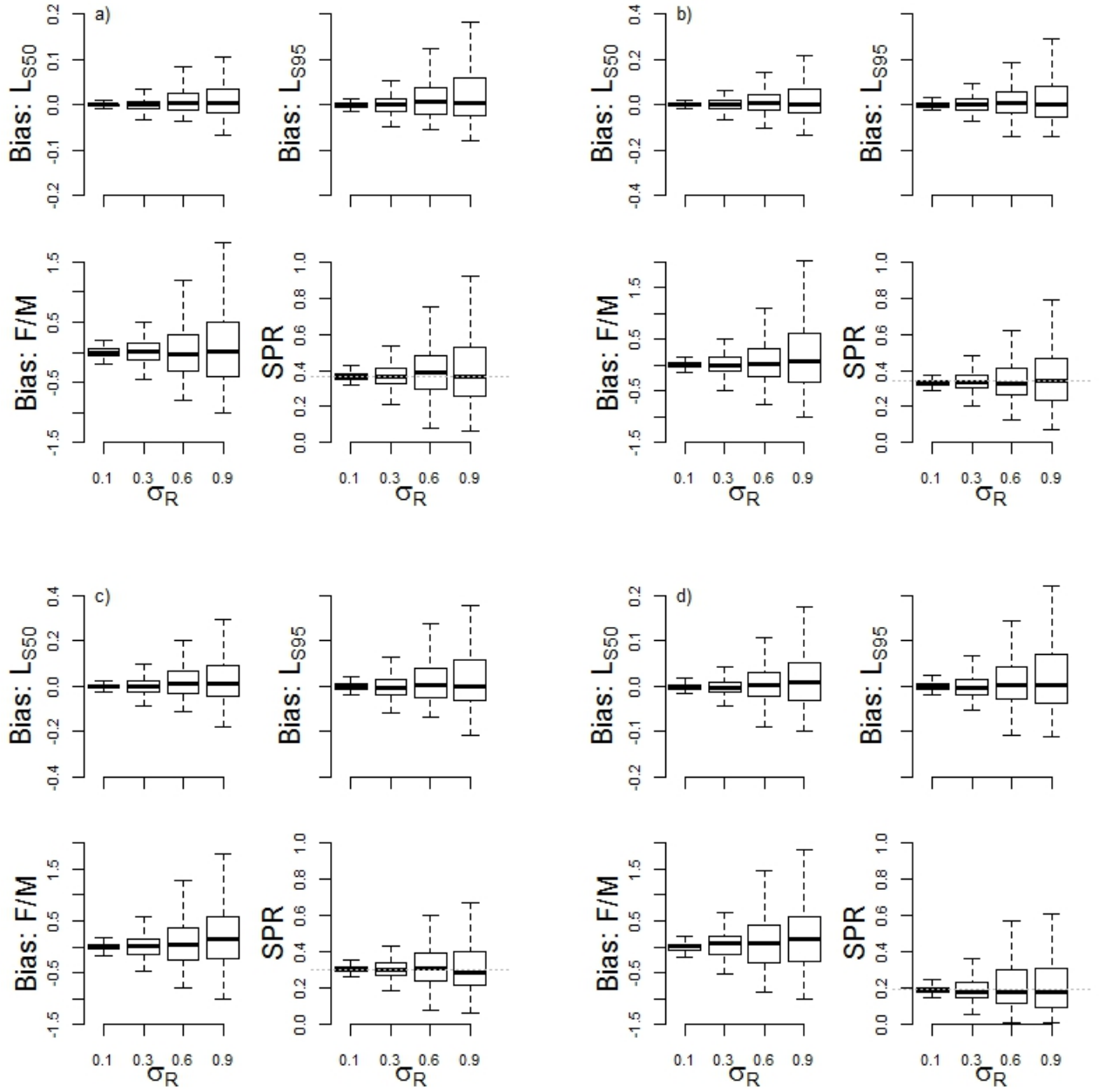


Figure 5: Bias in estimated $\frac{F}{M}$, L_{S50} , L_{S95} and the resulting estimate of SPR with auto-correlated recruitment error for a) Species I, b) Species II, c) Species III, and d) Species IV

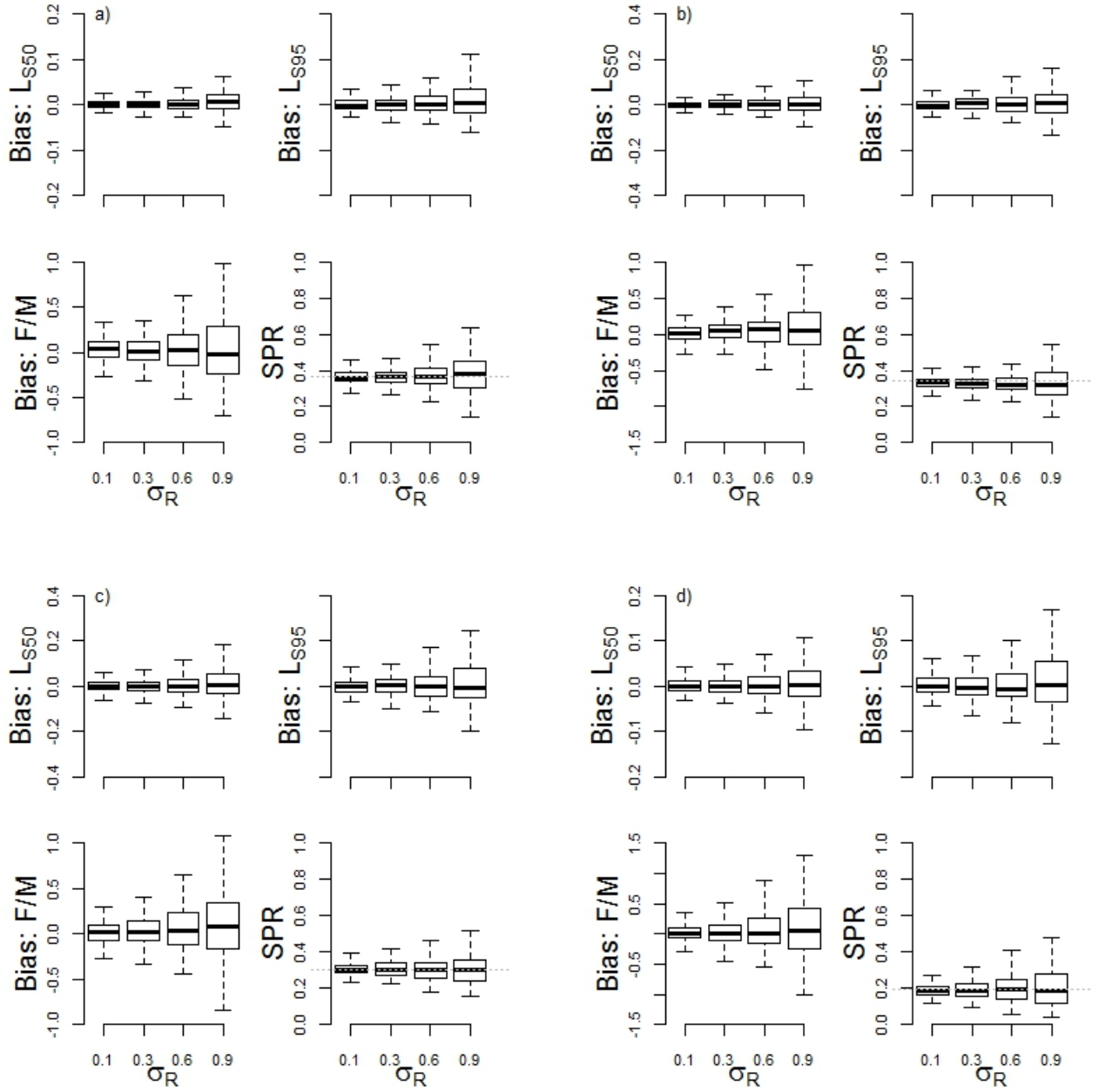


Figure 6: Bias in estimated $\frac{F}{M}$, L_{S50} , L_{S95} and the resulting estimate of SPR with recruitment error and episodic recruitment failure for a) Species I, b) Species II, c) Species III, and d) Species IV