

1 **Comparison of growth models for sequential hermaphrodites by considering multi-phasic**
2 **growth**

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10 **Abstract**

11 The von Bertalanffy (VB) growth model has been extensively used to describe fish growth.
12 However, it may not be the best predictor of lifetime growth patterns for fish with complex life
13 history (e.g., hermaphroditism). We sought to determine if growth models accounting for
14 maturity and sex change were more appropriate than the VB model at capturing the growth and
15 maturation patterns of Gag *Mycteroperca microlepis*, a protogynous hermaphrodite. To account
16 for changes in growth at maturity, we used the Lester et al. (2004) growth model (bi-phasic
17 Lester) and a modified Lester et al. (2004) model to account for an additional growth phase at
18 sex change (tri-phasic Lester). We also compared management reference points from each model
19 using a yield-per-recruit (YPR) framework. The tri-phasic Lester model described growth and
20 reproductive schedules better than the bi-phasic Lester or VB models, indicating separate growth
21 phases associated with maturation and sex change. Estimates of F_{MAX} from the YPR analysis
22 were lower when using the tri-phasic Lester model (0.21 yr^{-1}) compared to the VB model (0.33
23 yr^{-1}) when growth parameters were linked to natural mortality. Fishing mortality rates resulting

24 in 35% of unfished total and male-specific spawning stock biomasses-per-recruit were similar for
25 all models, but female-specific estimates were lower using the bi-phasic Lester model. Reference
26 points from the VB model were generally lower compared to either Lester model using natural
27 mortality rates that were not tied with the growth parameters. Our results support arguments that
28 a single growth curve is insufficient to capture lifetime growth of fish. However, growth curves
29 from the VB and tri-phasic Lester models were similar for all ages, especially less than age 12.
30 This suggests the VB model can be used to describe mean length-at-age when information on
31 reproductive status is not available, but may result in inappropriate management
32 recommendations.

33 **1. Introduction**

34 The von Bertalanffy growth model (hereafter referred to as VB; von Bertalanffy, 1938) has
35 been extensively used to describe growth of fish and other taxa that display indeterminate growth
36 (Ricker, 1975; Lester et al., 2004). One of the main advantages of the VB model is its strong
37 biological and empirical support (Beverton and Holt, 1957; Chen et al., 1992; Lester et al., 2004).
38 However, this model has been criticized because it seems unlikely that one growth curve should
39 be able to represent the complex physiological changes happening throughout the life of an
40 organism (Day and Taylor, 1997; Czarnolewski and Kozłowski, 1998; Lester et al., 2004). The
41 VB model is relatively inflexible as it considers only decreasing incremental growth throughout
42 the life of the organism, which may not hold true for very young fish (e.g., larval and early
43 juvenile growth phases; Beverton and Holt, 1957; Ricker, 1975; Walters and Martell, 2004).
44 More recently the model has been criticized because it does not account for changes in energy
45 allocation to reproduction after a fish reaches maturity (Charnov, 1993; Charnov et al., 2001;
46 Lester et al., 2004). This suggests that using the VB model can lead to misspecification of
47 management reference points and could result in over- or under-exploitation because the VB
48 model ignores potential changes in growth patterns before and after maturation.

49 Accurately estimating life history parameters, such as growth and reproductive schedules, are
50 crucial to management because these traits are often used to develop size-based regulations (e.g.,
51 size limits, harvest slots, etc.), to set harvest limits, and are major components in fisheries
52 assessment models (Ricker, 1975; Jennings et al., 2001; Radomski et al., 2001; Walters and
53 Martell, 2004). Commonly, fish growth is estimated independently of reproductive schedules
54 (e.g., length or age at maturation), where growth is assumed to follow the VB model and
55 estimates of age/length at maturation are obtained using a logistic regression. This process

56 assumes that age and length interact to influence the timing of maturation via: 1) the relationship
57 between age and length or 2) directly accounting for the growth variation by estimating both age
58 and length regression coefficients. This ignores any interaction between maturity and growth,
59 even though it has been shown that both the timing of maturation and the amount of energy
60 allocated towards reproduction may influence lifetime growth (Charnov, 1993; Charnov et al.,
61 2001; Lester et al., 2004). There are numerous examples of growth models that incorporate the
62 influence of maturity on growth (e.g., Brody, 1945; Lester et al., 2004) and assume that fish
63 grow according to multiple phases throughout their life. One such example, developed by Lester
64 et al. (2004), assumes a period(s) of linear growth prior to maturation (i.e. no reproductive
65 investment) and growth following the VB model after maturation. Because this and similar
66 models incorporate the age at maturation as a parameter, changes in the timing of or biased
67 estimates of maturity can have large impacts on the subsequent growth curves.

68 Thus, fish experiencing physiological or behavioral changes after maturity, such as sexual
69 transition, should experience an additional growth phase once individuals change sex. This is
70 because the energetic costs of producing eggs are markedly higher than those of producing sperm
71 (Asher et al., 2008). Therefore in protogynous hermaphrodites (individuals initially mature as
72 female), females that have transitioned to male will have additional energy resources to devote to
73 either growth or to mate acquisition (St. Mary, 1994; Chu and Lee, 2012; Cogalniceanu et al.,
74 2013). Additionally males often suffer from high energetic costs and increased mortality due to
75 increased levels of aggression and resource defense, reduced time foraging, or fasting during
76 mating season (e.g., Neuhaus and Pelletier, 2001; Hoffman et al., 2008; Georgiev et al., 2014).
77 However these changes associated with sex change are often ignored when estimating growth
78 because many authors use the VB model to describe growth rates (for examples see: Buxton,

79 1992; Garratt et al., 1993; Alonzo and Mangel, 2004; Alonzo et al., 2008; Cossington et al.,
80 2010; Linde et al., 2011; Fenberg and Roy, 2012).

81 It is important to consider models other than the VB to describe the complex changes
82 happening throughout the life of a sex-changing fish as a result of the physiological and
83 behavioral changes likely associated with sex change. Several authors have modified the VB
84 model to explain the sexual-size dimorphism observed in many sex-changing species (Garratt et
85 al., 1993; Adams and Williams, 2001; Munday et al., 2004; Linde et al., 2011), but have largely
86 ignored the physiological and behavioral changes also associated with changing sex. Garratt et al.
87 (1993) developed a bi-phasic VB model that described accelerated growth after transition (i.e. a
88 growth spurt). However this model did not incorporate changes associated with maturation.
89 Several authors back-calculated length-at-age estimates to compare the growth rates of fish that
90 had changed sex to those that were still the primary sex, but did not assess potential changes in
91 growth due to maturation or sex change (e.g., Adams and Williams, 2001; Munday et al., 2004;
92 Linde et al., 2011). We sought to expand on these studies by modifying the Lester et al. (2004)
93 growth model to account for an additional growth phase associated with sex change. Our primary
94 objective was to determine if accounting for just maturity (i.e. the bi-phasic model developed by
95 Lester et al. (2004) or accounting for growth transitions associated with maturity and sex change
96 (i.e. tri-phasic Lester) would more accurately describe the growth patterns of a protogynous
97 hermaphroditic fish than the standard VB model. Our second objective was to compare
98 management reference points from each model using a yield-per-recruit framework to determine
99 the implications of using each growth model.

100 **2. Methods**

101 We used the Gulf of Mexico Gag *Mycteroperca microlepis* as a case study for this analysis.
102 Gag is a long-lived (maximum observed age 31 years) protogynous hermaphrodite. Gag are
103 targeted in both commercial and recreational fisheries. Gag length (fork length in mm), age, and
104 histology data were obtained from fisheries-dependent and -independent samples between 1979-
105 2012 from the National Marine Fisheries Service (NMFS) used in the 2013 Gag stock
106 assessment (SEDAR, 2014). Gag length-, maturity-, and sex change-at-age data were fit using a
107 Bayesian hierarchical framework to predict growth using VB, bi- and tri-phasic Lester models,
108 and timing of maturation and sex change assuming logistic functions. Growth models were run
109 in program R version 3.1.3 using runjags version 3.3.0 (Denwood, 2013; R Development Core
110 Team, 2013) and yield-per-recruit models were run in program R version 3.1.3 (R Development
111 Core Team, 2013). All equations for the growth models and yield-per-recruit equations are
112 presented in Tables 1 and 2 respectively.

113 The data came from multiple fishery-dependent sources (~31,700) and fishery-independent
114 surveys (~1,500). Because of the selectivity of the fishery-dependent sources, growth was
115 modeled in the recent Gag assessment using a truncated normal distribution with a constant
116 standard deviation to account for minimum length limits in commercial and recreational fisheries
117 (developed by McGarvey and Fowler, 2002; SEDAR, 2014). Additionally, they used a modified
118 VB model that assumed a period of linear growth from age-0 (fixed at 10 cm) to age-1 (SEDAR,
119 2014). We chose to use the traditional formulation of the VB model incorporating an age-
120 specific standard deviation in order to reduce model complexity and avoid the assumption of a
121 constant standard deviation. Because there were samples of small, young fish from fishery
122 independent surveys (~1,750 less than 500 mm and almost 300 less than age-1), data were
123 aggregated without any consideration for sample sizes within each gear type following the

124 recommendations of Wilson et al. (2015). As shown in Wilson et al. (2015), when there are
125 samples of small, young fish, this method helps account for some of the effects of gear
126 selectivity on growth parameter estimation.

127 2.1. Growth Models

128 Mean length-at-age from the VB model was estimated using the standard formulation of the
129 von Bertalanffy growth equation; where L_{∞} is the average maximum attainable length, k is the
130 Brody growth coefficient scaling size to catabolism, and t_0 is the theoretical length-at-age 0 if the
131 fish always grew according to the VB model (Eq. 1; Table 1). For the bi-phasic Lester model,
132 mean length-at-age was estimated using the growth model developed by Lester et al. (2004);
133 where h is the pre-reproductive growth rate, t_1 is the age intercept for the pre-reproductive
134 growth phase, and T is age at maturity (Eq. 2; Table 1). The Lester et al. (2004) formulation also
135 estimates reproductive investment (g), which is used to estimate k and L_{∞} in the post-maturation
136 growth phase (Eq. 2; Table 1). The tri-phasic Lester model is identical to the bi-phasic Lester,
137 except there is an additional growth phase after transition to male at age τ and sex-specific
138 estimates of g_s , k_s , and $L_{\infty,s}$ (Eq. 3; Table 1). We assumed length-at-age was normally distributed
139 with a constant coefficient of variation (Eq. 4; Table 1).

140 Age-based maturity $m_{a,i}$ and sex change $D_{a,i}$ for individual i was described using
141 Bernoulli trials with age-specific probabilities of being mature or male (Eqs. 7 and 8; Table 1).
142 Age-specific probabilities of being mature or male were estimated with a logistic function where
143 T and τ are the age at which 50% of the of individuals are mature or male and the sigma terms
144 (σ_T and σ_{τ}) represent the slope of the logistic function for being mature (i.e. female) or male,
145 respectively (Eqs. 5 and 6; Table 1). These equations were the same for all growth models.

146 The VB, bi- and tri-phasic Lester model fits were compared using deviance information
147 criterion (DIC; Spiegelhalter et al., 2002) where $p(y|\bar{\theta})$ is the value of the likelihood at the mean
148 parameter values, $p(y|\theta_n)$ is the value of the likelihood function for draw n of the joint posterior
149 distribution, and N is the number of samples in the posterior distribution (Eqs. 9 and 10; Table 1).
150 Bayesian models were run using seven chains, each generating 1,500 samples of the posterior
151 distribution using a thinning rate of 100. Convergence was verified using Gelman and Rubin
152 diagnostics (Gelman and Rubin, 1992; Brooks and Gelman, 1998). All estimated parameters
153 from the growth models and logistic regressions had uninformative priors.

154 2.2. Yield-Per-Recruit Models

155 We used age-structured yield-per-recruit models to calculate the fishing mortality rates that
156 would result in maximum yield-per-recruit (F_{MAX}) and spawning stock biomass being 35% of
157 unfished condition using total biomass (F_{35T}) and sex-specific biomasses (F_{35F} , F_{35M} for female
158 and male respectively). The models incorporated age-specific growth in length and weight, and
159 survival schedules. Growth equations used, described in the previous section, were the VB, bi-
160 phasic Lester and tri-phasic Lester (Eqs. 1-3; Table 1). For this model we chose to make the
161 simplifying assumption that the timing of both maturation and sex change remained constant
162 over exploitation rates, similar to many assessment models (including Gag; SEDAR, 2014; see
163 Provost and Jensen, 2015) and Alonzo and Mangel (2004) and Brooks et al. (2008).

164 Survivorship schedules (l_a) were used to calculate the probability of a recruit surviving to
165 each age using Lorenzen (2000) size-based natural mortality (M_a), fishing mortality (F) and age-
166 specific vulnerability to harvest (V_a ; Eq. 1; Table 2). Unfished conditions were determined by
167 setting F to zero when calculating the survivorship schedule (Eq. 1; Table 2). Uncertainty in
168 overall natural mortality rate (M_{base}) was assessed using two methods; 1) M_{base} was assumed to

169 be equal to the k estimated from the appropriate growth model (Walters and Martell, 2004); and
170 2) M_{base} was held constant over all growth models and set to 0.1342 yr^{-1} , the estimate of natural
171 mortality used in the 2013 stock assessment (Eqs. 2 and 3; Table 2; SEDAR, 2014). These two
172 scenarios represent likely scenarios for assessment models, where an estimate of natural
173 mortality is obtained using surrogate information obtained from the growth model (Charnov,
174 1993; Jensen, 1996; Walters and Martell, 2004), and when there is an independent estimate of
175 natural mortality (i.e. via methods developed by Hoenig, 1983; SEDAR, 2014). When M_{base} was
176 set equal to k , we further assumed two scenarios for the tri-phasic Lester model where; 1) M_{base}
177 was sex-specific and changed with sexual transition and 2) M_{base} was constant post maturation
178 and was set to the female estimate of k (Eq. 3; Table 1). Juvenile mortality rates were held
179 constant and set to equal the female estimate for k from the appropriate growth model. Age-
180 specific vulnerability was simulated using a logistic model where L_{lim} is the minimum length
181 limit in the Gulf of Mexico recreational fishery (56 cm; Eq. 4; Table 2).

182 These models produced yield-per-recruit and spawning stock biomass-per-recruit. Because
183 Gag are sequential hermaphrodites, we chose to assess the impacts of fishing mortality rate for
184 each sex separately and for combined sexes. Generally assessment models are concerned with
185 either female biomass or total biomass (Brooks et al., 2008). However this ignores male
186 reproductive contribution. Therefore we assessed male spawning stock biomass in order to
187 highlight the sex-specific impacts of exploitation on the male-phase because overharvest of
188 males could result in sperm limitation if male biomass falls too low (Coleman et al., 1996;
189 Alonzo and Mangel, 2004).

190 Weight-at-age was calculated using the length-weight equation (Eq. 5; Table 2) and was used
191 to calculate adult female and male spawning stock biomass per recruit ($SSB_{F/R}$ and $SSB_{M/R}$

192 respectively; Eqs. 6 and 7; Table 2). Parameter values for the length-weight equation were
193 obtained from SEDAR (2014). Total spawning stock biomass ($SSB_{T/R}$) was calculated as the
194 sum of $SSB_{F/R}$ and $SSB_{M/R}$ for a given fishing mortality rate. The probabilities associated with
195 being a female ($P_{fem,a}$) or male ($P_{male,a}$) at age were modeled using a double logistic for females
196 (i.e. the probability of being mature minus the probability of being male) and a single logistic for
197 males (Eqs. 8 and 9; Table 2). Yield-per-recruit (Y) was summed over all ages for each fishing
198 mortality rate (Eq. 10; Table 2). For each growth model, the yield-per-recruit model was repeated
199 $N=10,500$ times and parameter values for the growth models and probabilities of being female or
200 male were drawn from the joint posterior distributions.

201 **3. Results**

202 The tri-phasic Lester model performed the best, using DIC, when describing the length-at-
203 age and reproductive schedules of Gag. Additionally, both the bi- and tri-phasic Lester models
204 performed better than the VB model (Δ DIC values of 110, 0, and 722 respectively). However, all
205 of the models predicted similar growth patterns up to the age at transition, about age 12 (Fig. 1A).
206 All models overestimated the length-at-age of individuals between the ages of 1 and 2,
207 presumably due to selectivity, but appeared to fit the samples less than age-1 and greater than
208 age 2 (Fig. 2). After about age 12, the models diverged, with the bi-phasic Lester model slightly
209 overestimating and the VB model slightly underestimating the length of the oldest fish relative to
210 the tri-phasic model (Figs. 1A and 2). Comparing the age-based maturity estimates, the VB
211 model (i.e. growth and reproductive schedules estimated independently) had a higher estimate of
212 age-at-50% maturity than the other models ($T=3.5$ vs. 2.6 and 2.7 years for the bi- and tri-phasic
213 Lester models respectively; Table 3; Fig. 1). For the timing of sex change, all models produced

214 similar estimates and fits, with the age-at-50% sex change around 12.6 or 12.7 years; Table 3;
215 Fig. 1).

216 The tri-phasic Lester growth model had the lowest Δ DIC, indicating that growth decreases
217 after females transition to males. This model suggests that fish allocated more resources to
218 reproduction after sex change than before ($g_{s=f}=0.28 \text{ yr}^{-1}$ (0.27-0.29) vs. $g_{s=m}=0.32 \text{ yr}^{-1}$ (0.31-
219 0.33)). Further, estimates from the tri-phasic Lester model indicated higher metabolic rates (k)
220 and lower L_{∞} for males compared with females (Table 4). This model also appeared to perform
221 best at estimating the length of the oldest fish given the available data (ages 20-30; Figs. 1A and
222 2).

223 Assuming metabolic rates are proportional to the base natural mortality, the F_{MAX} estimates
224 for each model ranged from 0.21-0.33 yr^{-1} , with the estimates using the tri-phasic Lester model
225 resulting in the lowest and the VB being the highest values (Table 4; Fig. 3). Fishing mortality
226 rates resulting in total spawning stock biomasses (F_{35T}) were quite variable, ranging from 0.15 to
227 0.18 yr^{-1} , with the VB model resulting in the highest estimate and both tri-phasic Lester models
228 being the lowest (Table 4; Fig. 3). Female specific SSB/R , F_{35F} estimates from the bi-phasic
229 Lester model were lowest ($F_{35F}=0.23 \text{ yr}^{-1}$) and estimates from the VB and both tri-phasic Lester
230 were similar ($F_{35F}=0.34 \text{ yr}^{-1}$; Table 4; Fig. 3). Fishing mortality rates resulting in the male
231 spawning stock biomasses of 0.35 of unfished were similar between all models ($F_{35M}=0.07$ - 0.08
232 yr^{-1} ; Table 4, Fig. 3).

233 With equal values for the base mortality rate ($M_{base}=0.1342 \text{ yr}^{-1}$), the F_{MAX} estimates for each
234 model ranged from 0.30 to 0.40 yr^{-1} , with the estimates using the bi-phasic Lester model
235 resulting in the highest and the VB being the lowest values (Table 5; Fig. 4). Fishing mortality
236 rates resulting in total spawning stock biomasses were the lowest for the VB model ($F_{35T}=0.18$

237 yr⁻¹) and were the highest for the bi-phasic Lester model ($F_{35T}=0.26$ yr⁻¹; Table 5; Fig. 4). Female
238 specific SSB/R , F_{35F} estimates from the bi-phasic Lester model were lowest ($F_{35F}=0.32$ yr⁻¹) and
239 highest from the tri-phasic Lester model ($F_{35F}=0.44$ yr⁻¹; Table 4; Fig. 4). Estimates of fishing
240 mortality rates resulting in the male spawning stock biomasses of 0.35 of unfished were similar
241 between all models ($F_{35M}=0.08$ yr⁻¹; Table 4; Fig. 4).

242 **4. Discussion**

243 Growth models incorporating changes in growth rates at maturation and sex change were
244 found to be statistically better at describing Gag growth than the VB model. Following the
245 growth models through a simple YPR analysis revealed very different estimates of F_{MAX} and
246 fishing mortality rates that resulted in the spawning stock biomasses falling below 35% of the
247 unfished conditions. Along with the work of Charnov, Lester, and associates (Charnov, 1993;
248 Charnov et al., 2001; Lester et al., 2004), this analysis showed that it is important to consider
249 multi-phasic growth models for species with complex life history traits such as sex change when
250 predicting growth patterns and developing management strategies.

251 Our study supports the arguments of Charnov (1993), Day and Taylor (1997), Czarnolewski
252 and Kozłowski (1998), Charnov et al. (2001) and Lester et al. (2004) that a single growth curve
253 is not suited to describe the lifetime growth of fish. However, it is important to note that the
254 predicted length-at-age for fish below approximately age 12-13 were almost visually identical
255 between all of the models. It was also striking how similar the VB and the tri-phasic Lester
256 model predictions were for all ages, even for the oldest ages (20-30 years). This suggests the VB
257 model can be used to predict the growth of sex changing fish when reproductive status is not
258 available. However, it is important to avoid using the VB model without consideration of other
259 models if life history traits are linked to growth characteristics.

260 The tri-phasic model predicted higher energy allocation towards reproduction in the male
261 phase than the female phase. However this does not imply that males are allocating energy
262 towards increasing gonad tissue growth. This increase in reproductive investment is likely
263 associated with increased aggression and changes in behavior because more aggressive males
264 will have a greater chance at defending mating opportunities, mating sites, and territories (Tecot
265 et al., 2013; Georgiev et al., 2014). However, this usually comes at the cost of riskier behaviors,
266 higher metabolic rates (k) and increased mortality from decreased foraging time or direct male-
267 male conflict (e.g., Neuhaus and Pelletier, 2001; Hoffman et al., 2008; Georgiev et al., 2014).
268 This increase in mortality after transitioning to males is also supported by the empirical
269 relationship between natural mortality and k (e.g. $M=1.65*k$, $M=1.5*k$ or $M=k$; Charnov, 1993;
270 Jensen, 1996; Walters and Martell, 2004), as well as the invariant relationship between
271 reproductive effort and M derived using the VB model (Charnov, 2008). However, further work
272 is still needed to determine if there are differences in sex-specific natural mortality rates for Gag.

273 Currently, models used to predict the growth of sex changing fish ignore gender by using the
274 VB model or estimate separate growth curves for fish that changed sex and those that had not
275 (e.g., Garratt et al., 1993; Adams and Williams, 2001; Munday et al., 2004; Linde et al., 2011).
276 Often maturation or gender data are not available so using a single model to describe fish growth
277 may be unavoidable. Using models such as those developed by Garratt et al. (1993), Adams and
278 Williams (2001), Munday et al. (2004) or Linde et al. (2011) would exclude age-length pairs
279 where there is no information on the reproductive state. In the case of Gag, this would result in
280 the loss of over 97% of the total data. By excluding this much data, we would be introducing
281 additional parameter uncertainty and potential biases if reproductive state information were not
282 missing at random. Using growth models such as the tri-phasic Lester model would avoid some

283 of these issues and unlike the VB models, provide a way to describe sex-specific changes in
284 growth when at least some gender and maturity data exist.

285 Other studies assessing changes in growth associated with sex change have found that males
286 experience a growth spurt surrounding the timing of transition (e.g., Garratt et al., 1993; Walker
287 and McCormick, 2004, 2009; Walker et al., 2007; Munday et al., 2009; McCormick et al., 2010).
288 These studies mainly used daily otolith increment analysis to measure the otolith growth rates
289 before and after sex change for small, short-lived sex changing species (e.g. Walker and
290 McCormick, 2004, 2009; Walker et al., 2007; Munday et al., 2009; McCormick et al., 2010). It is
291 expected that this growth spurt allows newly transitioned males to gain an additional size
292 advantage over large females within the harem and further allows them to suppress the growth of
293 the largest females (McCormick et al., 2010). Garratt et al. (1993) fit a sex-specific bi-phasic VB
294 growth model to a protogynous hermaphrodite *Chrysoblephus puniceus* to describe the male-
295 biased sexual size dimorphism by assuming a male growth spurt. This model assumed females
296 followed the typical VB model and fish that transitioned to male were fit with the bi-phasic VB
297 model. Unlike the aforementioned studies, Adams and Williams (2001), Munday et al. (2004),
298 and Linde et al. (2011) examined the growth of protogynous hermaphrodites Coral Trout
299 *Plectropomus maculatus* and Rainbow Wrasse *Coris julis* and did not find a growth spurt at sex
300 change for either of these species. Similar to these studies, the tri-phasic Lester model does not
301 provide evidence for a transitional growth spurt in Gag because the estimates of the age-at-sex
302 change were almost identical for all models and because the predicted growth curves were very
303 similar. Additionally, it is believed that the Gag mating system is not harem, suggesting that a
304 lack of a male growth spurt could provide evidence against harem mating systems. However,

305 this study did not directly test for transitional growth spurt and further work is needed to address
306 the possibility of a growth spurt in Gag.

307 Management of fish populations often relies on estimates of growth and reproductive
308 schedules to set harvest regulations. Age- and length-structured population models are often
309 constructed using information from the VB model, and surrogate information on age-specific
310 fecundity, vulnerability, and natural mortality that are dependent on the VB model (e.g., using
311 the relationships by Jensen, 1996; Lorenzen, 1996, 2000; Gwinn et al., 2010). When we assumed
312 $M_{base}=k$, the VB models generally produced the highest estimates for each reference point.
313 Conversely, when using an estimate of natural mortality that was not based on information from
314 the growth model, the VB model generally produced the lowest reference point estimates.
315 Because of the differences in reference points based on our assumptions, obtaining accurate
316 estimates of both growth and natural mortality are necessary to inform management decisions
317 and perform stock assessments, especially when natural mortality is based on information from
318 the growth model.

319 The major focus to improve growth estimates has been to assess ways to improve the VB fit
320 to account for non-representative sampling (see Gwinn et al., 2010; Wilson et al., 2015). These
321 studies have focused on the effects of sampling bias on parameter estimates, not on the impacts
322 of using models other than the VB. By using models other than the VB, our results showed that
323 common management reference points (F_{MAX} , F_{35T} , F_{35F} , and F_{35M}) were highly dependent on the
324 assumptions of how fish grow throughout their lives. Further, using the incorrect growth model
325 will affect biological reference points associated with spawning stock biomass or spawning
326 potential ratio. In this study, we assessed the sensitivity of equilibrium reference points to

327 different growth models. Further research will be needed to assess the impacts of switching from
328 the VB to tri-phasic Lester models when using more advanced assessment models.

329 Management reference points often rely solely on mature female biomass for dioecious
330 species and are focused either on total mature biomass or just female biomass for hermaphroditic
331 species (Brooks et al., 2008). Similar to Alonzo et al. (2008), our results show that relatively low
332 fishing mortality rates decreased male spawning stock biomass to 35% of the unfished condition,
333 and therefore can become severely depleted at fishing mortality rates associated with F_{MAX} , F_{35T}
334 and F_{35F} . However, the extent and implications of severely reduced male biomass depends on
335 fertilization rates, which are often unknown for many species (Brooks et al., 2008), and plasticity
336 in the timing of sex change. Brooks et al. (2008) suggested using female-specific reference
337 points if fertilization rates are high, but at low fertilization rates, male reference points performed
338 better when the timing of sex change is static. Because we used a per-recruit framework and did
339 not incorporate stock-recruitment relationships, egg fertilization, or variation in the timing of sex
340 change, we did not assess the implications of using sex-specific or total spawning stock biomass
341 reference points and further work is still needed to determine the appropriate reference points for
342 sex changing fish.

343 In addition to differences in management and biological reference points between the VB and
344 tri-phasic Lester models, the assumptions being made about the interactions between growth and
345 maturity can have large impacts on management outcomes. It is well supported that life history
346 traits, such as growth and reproductive traits can change due to size selective fishing mortality
347 (Jørgensen, 1990; Rijnsdorp, 1993; Grift et al., 2003; Olsen et al., 2004, 2005; Sattar et al., 2008).
348 Because the VB model does not explicitly account for reproduction, changes in the timing of
349 maturation and/or sex change must be accounted for by assuming changes in one or more

350 parameters (e.g. k or L_{∞}). Unlike the VB model, changes in growth can solely be accounted for
351 by assuming changes in the timing of maturity or sex change when using the tri-phasic Lester
352 model. For instance, a decrease in the age at maturity will also decrease the mean size-at-age of
353 mature fish because they spend less time as a juvenile experiencing high growth rates. This will
354 also influence the timing of sex change due to the decreased size-at-age and interactions between
355 fertility, mortality and the population structure (Iwasa, 1991; Munday et al., 2006; Warner, 1988).
356 Therefore, in populations that have experienced changes in the timing of maturation or sex
357 change, it is even more important to consider models other than the VB to account for the
358 impacts of reproduction on fish growth.

359

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519 Table Captions:

520 Table 1. List of equations used in describing length- and maturity-at-age for Gag.

521 Table 2. List of equations used in the yield-per-recruit analysis for Gag.

522 Table 3. Mean parameter estimates and 95% credible intervals (in parentheses) from each of
523 the growth models. The tri-phasic Lester estimates of g , L_∞ and k are broken into female-specific
524 (within the tri-phasic Lester column) and male-specific estimates (in the male estimates column).
525 Note that L_∞ and k from the bi- and tri-phasic Lester growth models were derived from the
526 estimates of h and g .

527 Table 4. Fishing mortality rates resulting in maximum yield per recruit (F_{MAX}) and spawning
528 stock biomasses of 0.35 of unfished for combined sexes (F_{35T}), females only (F_{35F}) and males
529 only (F_{35M}). The 95% credible intervals for each estimate are in parentheses. The von Bertalanffy
530 and bi-phasic Lester models assume size-based, sex-independent natural mortality rates equal to
531 the Brody growth coefficient (k). The tri-phasic Lester model with variable M assumes size-
532 based natural mortality changes after sex change and equals the sex-specific k whereas the tri-
533 phasic Lester model with constant M assumes natural mortality is equal to the female-specific
534 estimate of k for all ages.

535 Table 5. Fishing mortality rates resulting in maximum yield-per-recruit (F_{MAX}) and spawning
536 stock biomasses of 0.35 of unfished for combined sexes (F_{35T}), females only (F_{35F}) and males
537 only (F_{35M}). The 95% credible intervals for each estimate are in parentheses. All models assume
538 a size-based natural mortality rate, with natural mortality constant across all growth models (i.e.,
539 $M=0.1342 \text{ yr}^{-1}$).

540

541

542

543 Figure Captions:

544 Figure 1. Observed (dots) and predicted length-at-age (A), maturity-at-age (B, D, F) and sex
545 change-at-age (C, E, G) of Gag using the von Bertalanffy model with reproductive schedules
546 estimated separately (solid line; A-C), bi-phasic Lester (long-dashed line; A, D, E) and tri-phasic
547 Lester (short-dashed line; A, F, G) models. Maturity- and sex change-at-age were estimated
548 using logistic regression concurrently with the growth models.

549 Figure 2. Residual plots of the predicted length-at-age for each of the growth models. The
550 solid line represents a Lowess smoother and the dotted line is set at zero.

551 Figure 3. Yield-per-recruit (YPR ; A), total spawning stock biomass-per-recruit (SSB_T/R ; B)
552 and sex-specific SSB/R for females (SSB_F/R ; C) and males (SSB_M/R ; D) over a range of
553 instantaneous fishing mortality rates (F) and growth models, assuming a size-based natural
554 mortality rate. The von Bertalanffy and bi-phasic Lester models (solid and dotted black lines
555 respectively) assume a sex-independent natural mortality rate equal to the Brody growth
556 coefficient (k). The tri-phasic Lester model with variable M (dashed black line) assumes natural
557 mortality rate changes after sex change and equals the sex-specific k whereas the tri-phasic
558 Lester with constant M (dashed grey line) assumes natural mortality is equal to the female-
559 specific estimate of k for the entire life. The vertical lines highlight the growth-model specific
560 estimates of F_{MAX} (A) and where the spawning stock biomasses drop below 35% of unfished (B-
561 D). It is important to note that in panel C, both of the tri-phasic Lester estimates are the same.

562 Figure 4. Yield-per-recruit (YPR ; A), total spawning stock biomass-per-recruit (SSB_T/R ; B)
563 and sex-specific SSB/R for females (SSB_F/R ; C) and males (SSB_M/R ; D) over a range of
564 instantaneous fishing mortality rates (F) and growth models. All models assume a size-based

565 natural mortality rate with a natural mortality constant across all growth models (i.e. $M=0.1342$
566 yr^{-1}). The vertical lines highlight the growth-model specific estimates of F_{MAX} (A) and where the
567 spawning stock biomasses drop below 35% of unfished condition (B-D).

Table 1

Description	Equation	Components and Priors
<i>Growth Models</i>		
1 von Bertalanffy predicted length (mm) at age a	L	—
2 bi-phasic Lester predicted length (mm) at age a		—
3 tri-phasic Lester predicted length (mm) at age a		—
4 Likelihood of observed length L at age a for individual i		
<i>Reproductive Models</i>		
5 Probability of being mature at age a		
6 Probability of being male at age a		
7 Likelihood of age a individual i being		

8 mature
Likelihood of age a
individual i being male $D_{a,i} \sim \text{Bernoulli}(P_{d,a})$

Model Comparison

9 Deviance Information
Criterion $DIC = 2\bar{D} - 2 \ln(p(y|\bar{\theta}))$

10 Posterior mean of the
deviance $\bar{D} = \sum_{n=1}^N -\frac{2 \ln(p(y|\theta_n))}{N}$

Table 2. List of equations used in equilibrium yield per recruit analysis for Gag.

Description	Equation	Components
1 Survivorship at age a	l	= Fishing Mortality Rate
2 Lorenzen mortality at age a	$\frac{\infty}{\quad}$	= Base Natural Mortality Rate
3 Lorenzen mortality at age a	$\frac{\infty, s}{\quad}$	= Sex-specific Base Natural Mortality Rate
4 Vulnerability to harvest at age a		= Length Limit
5 Weight at age a		
6 Female spawning stock biomass		
7 Male spawning stock biomass		
8 Probability of being female at age a		
9 Probability of being male at age a		
10 Yield (Y) for a given F		

Table 3

Parameter	von Bertalanffy	Bi-phasic Lester	Tri-phasic Lester	Male Est.
h (mm)		139.3 (137.7, 141.0)	134.2 (131.6, 136.4)	
g (yr ⁻¹)		0.30 (0.30, 0.31)	0.28 (0.27, 0.29)	0.32 (0.31, 0.33)
L_{∞} (mm)	1210 (1200, 1219)	1381 (1367, 1395)	1449 (1427, 1474)	1264 (1238, 1289)
k (yr ⁻¹)	0.14 (0.14, 0.14)	0.10 (0.09, 0.10)	0.09 (0.09, 0.09)	0.10 (0.10, 0.10)
t_0 or t_1 (yr)	-1.05 (-1.08, -1.02)	-1.08 (-1.12, -1.05)	-1.17 (-1.22, -1.13)	
cv	0.11 (0.11, 0.11)	0.11 (0.10, 0.11)	0.11 (0.10, 0.11)	
T (yr)	3.45 (3.20, 3.65)	2.60 (2.54, 2.66)	2.70 (2.62, 2.82)	
τ (yr)	12.60 (12.00, 13.31)	12.61 (12.01, 13.32)	12.70 (12.10, 13.43)	
σ_T	0.53 (0.44, 0.66)	0.86 (0.75, 0.99)	0.81 (0.70, 0.94)	
σ_{τ}	1.84 (1.58, 2.15)	1.84 (1.59, 2.14)	1.86 (1.61, 2.18)	

Table 4

Metric	von Bertalanffy	Bi-phasic Lester	Tri-phasic Lester (Variable M)	Tri-phasic Lester (Constant M)
F_{MAX} (yr ⁻¹)	0.326 (0.318, 0.333)	0.245 (0.237, 0.253)	0.206 (0.200, 0.211)	0.206 (0.200, 0.211)
F_{35T} (yr ⁻¹)	0.184 (0.181, 0.188)	0.176 (0.170, 0.182)	0.145 (0.142, 0.148)	0.145 (0.142, 0.148)
F_{35F} (yr ⁻¹)	0.336 (0.309, 0.354)	0.231 (0.218, 0.243)	0.337 (0.301, 0.344)	0.337 (0.301, 0.344)
F_{35M} (yr ⁻¹)	0.076 (0.071, 0.078)	0.076 (0.071, 0.081)	0.071 (0.067, 0.071)	0.071 (0.067, 0.071)

Table 5

Metric	von Bertalanffy	Bi-phasic Lester	Tri-phasic Lester
$F_{MAX}(\text{yr}^{-1})$	0.303 (0.302, 0.304)	0.389 (0.381, 0.394)	0.394 (0.385, 0.410)
$F_{35T}(\text{yr}^{-1})$	0.175 (0.174, 0.175)	0.256 (0.248, 0.264)	0.223 (0.220, 0.227)
$F_{35F}(\text{yr}^{-1})$	0.329 (0.302, 347)	0.323 (0.305, 0.342)	0.442 (0.399, 0.454)
$F_{35M}(\text{yr}^{-1})$	0.075 (0.071, 0.078)	0.081 (0.075, 0.087)	0.075 (0.072, 0.078)

Figure 1

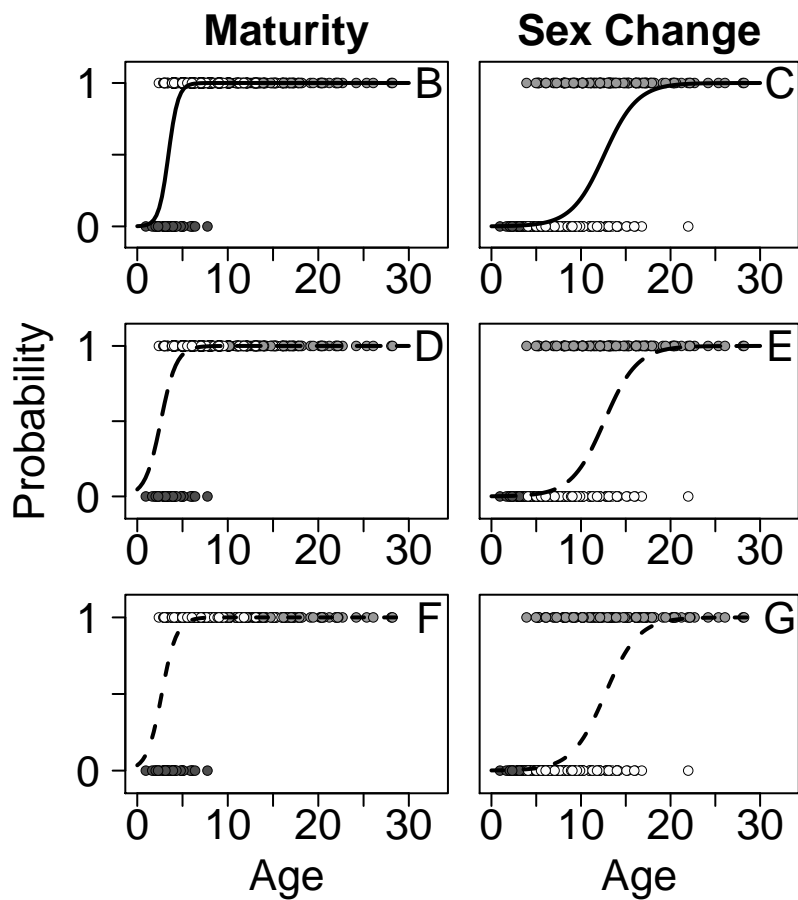
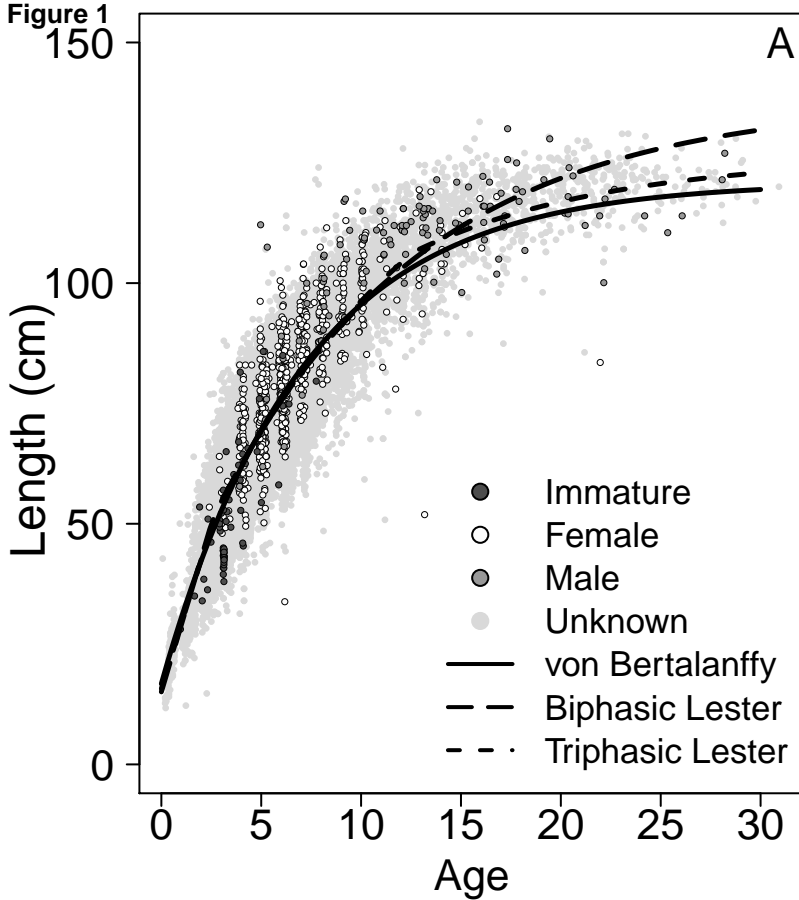
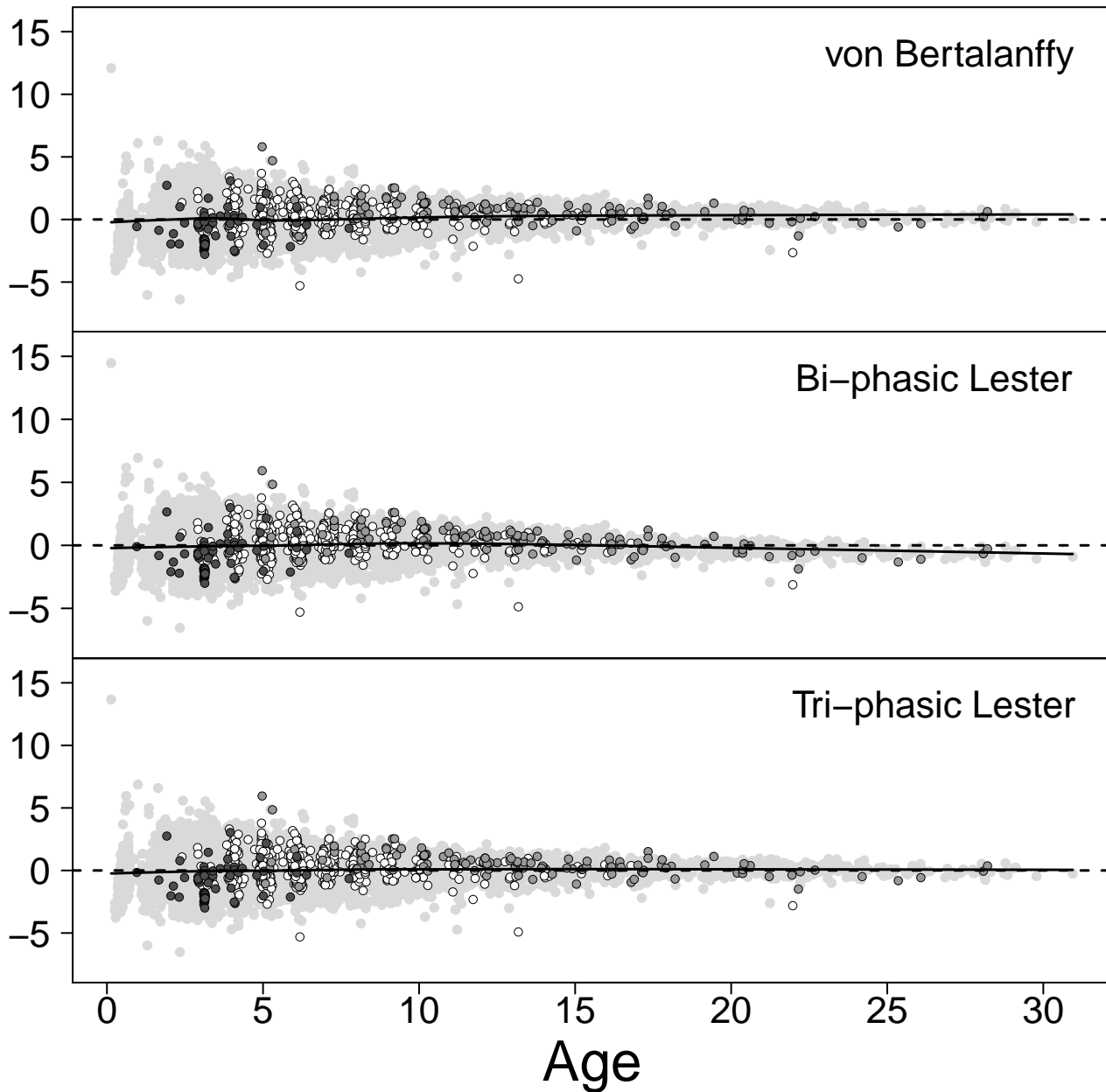


Figure 2

● Unknown ● Immature ○ Female ● Male

Standardized Residuals



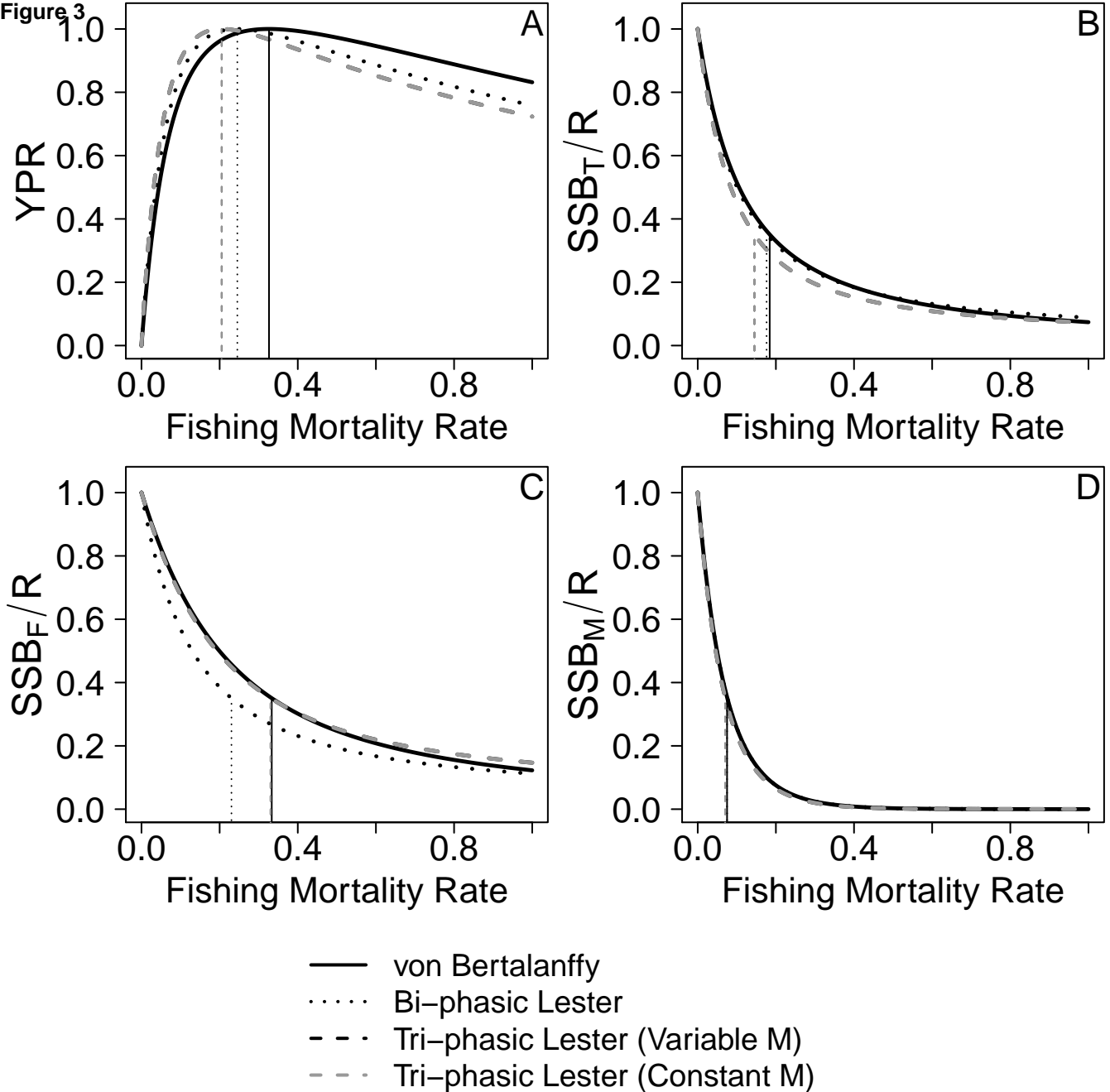
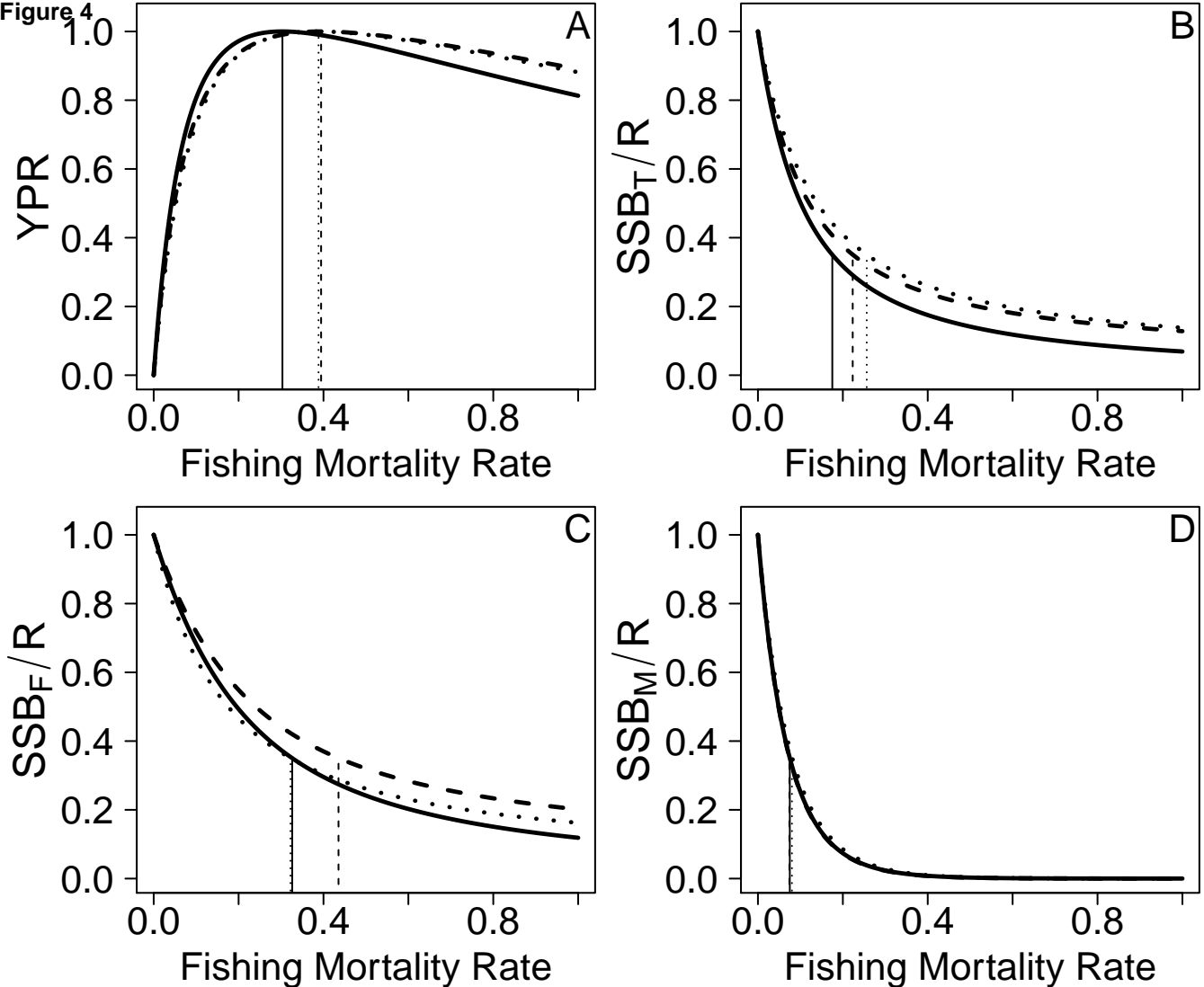


Figure 4



— von Bertalanffy
..... Bi-phasic Lester
- - - Tri-phasic Lester