

1 Accounting for Variation in Mortality and Allee Effects When
2 Computing Steepness for Strategic Fisheries Management

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12
13 **Abstract**

14 We update recent work on the scientific inference and reproductive biology of steepness in three
15 directions. First, we show how variation in natural mortality can be included in the formula
16 for steepness, for both a biomass dynamics and age-structure models. We do this using the
17 delta-method, so that only the mean and covariance of natural mortality rates appear in the
18 characterization of steepness. Second, we show how to generalize the previous methods for cases
19 in which the stock recruitment relationship is depensatory or has an Allee effect: as spawning
20 population falls below a certain level, per capita reproduction starts to fall, rather than approach

21 a constant. We generally assume that the mechanism of depensation is imperfect fertilization
22 (and thus develop a two-sex generalization of our previous work) and determine steepness in
23 this case for both a biomass production model and an age-structured model and explore the
24 implications of such depensatory reproduction on the response of stocks to harvesting. We
25 briefly discuss how an increase in mortality as population size declines (as has been suggested
26 for penguins) could also be a mechanism for depensation. Third, we describe an improved
27 method for computing the maximum per capita reproduction in the age-structured model, and
28 show how the equivalent for the biomass dynamics model is computed.

29 **Introduction**

30 Mangel *et al* (2010) developed methods for the computation of steepness of a Beverton-Holt
31 (BH) or Ricker (R) stock recruitment relationship (SRR) from first biological principles. In this
32 paper, we extend their work in two directions. First, Mangel *et al* (2010) show that steepness
33 can be expressed in terms of natural mortality rates and maximum per capita productivity (see
34 below for a summary). They also show that maximum per capita productivity can be estimated
35 using a stochastic simulation in which the rate of natural mortality fluctuates, drawn from a
36 known probability distribution. To improve the self-consistency of the methods, we show how
37 the probabilistic properties of natural mortality can be included, succinctly approximately, in the
38 expression for steepness.

39 Mangel *et al* (2010) also assumed that as the size of the spawning population declined the
40 maximum per capita reproduction approached a positive constant, for example in the way that
41 $\frac{1-\exp(-\alpha S)}{S}$ approaches α as $S \rightarrow 0$. A population exhibits an Allee effect or a depensatory SRR
42 if per capita reproduction declines as the size of the population falls below a certain level (Fowler
43 and Baker 1991; Courchamp *et al* 2008, Gregory *et al* 2010). In fishery science, these effects are
44 commonly called depensation (see Iles 1994, Liermann and Hilborn 2001, Gascoigne and Lipcius
45 2004 for review). Since many fish, seabird, and marine mammal populations may in principle

46 exhibit a compensatory SRR, we show how the methods of Mangel *et al* (2010) can be extended
47 for those kinds of SRRs. In doing so, we learn a variety of interesting qualitative properties of
48 such systems when stressed by fishing mortality (or incidental mortality for seabirds or marine
49 mammals). To do this , we develop an explicit two sex model for the case of a structured
50 population. Finally, we describe an improved version of the stochastic simulation used by Mangel
51 *et al* (2010) to compute maximum per capita reproduction.

52 **Review of The Approach**

53 In order to make this paper self-contained, we review the approach used in Mangel *et al.* (2010).
54 We first consider a production or biomass dynamic model and then generalize the age-structured
55 model to two sexes.

56 *The Production Model*

57 In this case, we let $B(t)$ denote the total biomass at time t and assume that the fraction of males
58 at birth is r , so that spawning (i.e. female) biomass at any time is $(1 - r)B(t)$. If M is the rate
59 of natural mortality, then in the absence of fishing the dynamics of biomass are

$$\frac{dB}{dt} = \frac{\alpha_p(1 - r)B}{1 + \beta B} - M \cdot B \quad (1)$$

60 where α_p is subscripted to note *production* and has units of new biomass per existing spawning
61 (female) biomass per time, so that it is a rate, comparable to the rate of natural mortality M .
62 The steady state biomass is

$$B_0 = \frac{1}{\beta} \left(\frac{\alpha_p(1 - r)}{M} - 1 \right) \quad (2)$$

63 We thus see that existence of a steady state requires that the Beverton number (*sensu* Mangel
64 2005) $\frac{\alpha_p(1-r)}{M} > 1$ and that density dependence scales the overall size of the steady state. Thus,
65 the parametrization in Equation 1 separates the roles of α and β in shape and scale when
66 determining B_0 . The separation becomes even clearer when we consider steepness.

67 According to its definition, steepness is

$$h = \frac{\frac{0.2\alpha_p(1-r)B_0}{1+0.2\beta B_0}}{\frac{\alpha_p(1-r)B_0}{1+\beta B_0}} \quad (3)$$

68 from which we obtain

$$h = 0.2 \cdot \frac{1 + \beta B_0}{1 + 0.2\beta B_0} \quad (4)$$

69 However, in light of Equation 2

$$\beta B_0 = \left[\frac{\alpha_p(1-r)}{M} - 1 \right] \quad (5)$$

70 so that we find

$$h = \frac{\alpha_p(1-r)}{4M + \alpha_p(1-r)} \quad (6)$$

71 which can also be rewritten as

$$h = \frac{\frac{\alpha_p(1-r)}{M}}{4 + \frac{\alpha_p(1-r)}{M}} \quad (7)$$

72 If the Beverton-Holt production term in Eqn 1 is replaced by the Ricker form, $\alpha_p(1-r)Be^{-\beta B}$
 73 then Eqn 7 is replaced by (see the Appendix of Mangel *et al* (2010))

$$h = 0.2 \left(\frac{\alpha}{M} \right)^{0.8} \quad (8)$$

74 *The Age-Structured Model*

75 To generalize the age-structured model of Mangel *et al* (2010) to two sexes, we let $N_m(a, t)$ and
 76 $N_f(a, t)$ denote the number of males and females of age a at time t respectively. The spawning
 77 stock biomass at time t is

$$B_s(t) = \sum_{a=1}^{a_{max}} N_f(a, t) W_f(a) p_{f,m}(a) \quad (9)$$

78 where $W_f(a)$ is the mass of a female at age a and $p_{f,m}$ is the probability that a female of age a is
 79 mature and a_{max} is the maximum age that an individual can attain (with suitable modification
 80 of the dynamics of the last age class, we can incorporate a ‘plus’ group into this formulation).

81 If we assume that egg production is proportional to biomass then the recruited class numbers
 82 are

$$N_f(0, t) = \frac{\alpha_s(1-r)B_s(t)}{1 + \beta B_s(t)} \quad (10)$$

$$N_m(0, t) = \frac{\alpha_s r B_s(t)}{1 + \beta B_s(t)} \quad (11)$$

83 where α_s has units of *new individuals/spawning biomass* and is subscripted with s to denote
 84 that this is a structured model. The sum of Eqns 10 and 11 gives the total recruitment. As will
 85 be seen, it does not matter whether we use spawning biomass or total biomass to characterize
 86 the density dependence.

87 For ages $a > 0$, in the absence of fishing mortality we have

$$N_f(a, t) = N_f(a-1, t-1)e^{-M_f(a-1)} \quad (12)$$

$$N_m(a, t) = N_m(a-1, t-1)e^{-M_m(a-1)} \quad (13)$$

88 where $M_f(a-1)$ and $M_m(a-1)$ are the natural mortality rates of females and males at age
 89 $a-1$. Typically, mortality rates of males are higher than those of females. Since neither of
 90 the mortality rates depend upon time, the population will reach a steady state and a stable age
 91 distribution.

92 We denote the steady state female biomass by \bar{B}_s . This biomass produces a steady state
 93 female recruitment

$$\bar{N}_f(0) = \frac{\alpha_s(1-r)\bar{B}_s}{1 + \beta\bar{B}_s} \quad (14)$$

94 The steady state female biomass is

$$\bar{B}_s = \sum_{a=1}^{a_{max}} \bar{N}_f(a)W_f(a)p_{f,m}(a) = \sum_{a=1}^{a_{max}} \bar{N}_f(0)S_f(a)W_f(a)p_{f,m}(a) \quad (15)$$

95 where $S_f(a)$ is survival from age 0 to age a , i.e. $S_f(a) = \prod_{i=0}^{a-1} e^{-M_f(i)}$. We factor $\bar{N}_f(0)$ from
 96 the last expression in Eqn 15, define $\bar{W}_f = \sum_{a=1}^{a_{max}} S_f(a)W_f(a)p_{f,m}(a)$ and thus write

$$\bar{B}_s = \bar{N}_f(0)\bar{W}_f \quad (16)$$

97 We now rewrite Eqn 14 as

$$\bar{N}_f(0) = \frac{\alpha_s(1-r)\bar{N}_f(0)\bar{W}_f}{1+\beta\bar{B}_s} \quad (17)$$

98 from which we conclude

$$1 + \beta\bar{B}_s = (1-r)\alpha_s\bar{W}_f \quad (18)$$

99 Since reproduction is assessed counting both males and females, steepness is given by

$$h = \frac{0.2\alpha_s\bar{B}_s}{1+0.2\beta\bar{B}_s} \cdot \frac{1+\beta\bar{B}_s}{\alpha_s\bar{B}_s} = \frac{0.2(1+\beta\bar{B}_s)}{1+0.2\beta\bar{B}_s} \quad (19)$$

100 We now use Eqn 18 in the last expression in Eqn 19 and simplify to obtain

$$h = \frac{(1-r)\alpha_s\bar{W}_f}{4+(1-r)\alpha_s\bar{W}_f} \quad (20)$$

101 For the case of Ricker density dependence, Eqns 12 and 13 are replaced by

$$N_f(0, t) = \alpha_s(1-r)B_s(t)e^{-\beta B_s(t)} \quad (21)$$

$$N_m(0, t) = \alpha_s r B_s(t)e^{-\beta B_s(t)} \quad (22)$$

102 Following the steps above leads to

$$h = 0.2 \left((1-r)\alpha_s\bar{W}_f \right)^{0.8} \quad (23)$$

103 Comparing Eqns 7 and 8 with Eqns 20 and 23 we see that the functional form is the same
 104 and that with the exception of α_s in the latter replacing α_p in the former we can make them
 105 “identical” by setting $\bar{W}_f = \frac{1}{M}$. Mangel *et al.* (2010) explicitly show the conditions under which
 106 the result for the age-structured model becomes the result for the production model.

107 Imperfect Fertilization as a Mechanism for Depensation

108 Both the Ricker SRR

$$R = \alpha S e^{-\beta S}$$

109 and the Beverton-Holt SRR

$$R = \frac{\alpha S}{1 + \beta S}$$

110 have the property that as $S \rightarrow 0$, $R \rightarrow \alpha S$. A depensatory SRR will arise if for small S
111 recruitment becomes sublinear. For example, Myers *et al* (1995) modify the Beverton-Holt SRR
112 to

$$R = \frac{\alpha S^\delta}{1 + \beta S^\delta}$$

113 and treat δ as a parameter to be estimated, understanding that $\delta > 1$ corresponds to de-
114 pensation. Morales-Bojorquez and Nevarez-Martinez (2005) modify the Shepherd (1982) SRR
115 (itself a modification of the Beverton-Holt) to explicitly consider a threshold level below which
116 recruitment fails

$$R = \max\left[0, \frac{\alpha(S - S_c)}{1 + \beta(S - S_c)^\delta}\right]$$

117 where S_c is the critical level at which recruitment drops to 0 (also see Chen *et al* 2002).

118 Similarly, modifying the Ricker SRR to

$$R = \alpha S^\delta e^{-\beta S}$$

119 produces the Salla-Lorda SRR (Iles 1994) and gives a depensatory relationship whenever $\delta > 1$.

120 These are *ad hoc* modifications of the SRR, which is fine if one wants to study the problem
121 are purely a statistical one. However, if one approaches this as a problem in reproductive
122 biology of fish, then the actual mechanism for depensation becomes important. For most of the
123 analysis, we assume that the mechanism of depensation is imperfect fertilization as population
124 size declines, but also discuss increased mortality as a mechanism for depensation. Imperfect
125 fertilization could be caused by at least two factors. First, at low population sizes individuals
126 simply may not be able to find each other. Second, even in species that form very tight mating
127 aggregations, an individual male cannot fertilize an unlimited number of females due to sperm
128 limitation. Thus, in some sense all populations must experience Allee effects and the question
129 is at what level of population size the effects become important.

130 In order to make further progress, we must select a mechanism for the Allee effect. In
131 this paper, we consider imperfect fertilization— that some eggs remain unfertilized – as the

132 mechanism. We let

$$p_f(B) = \Pr[\text{an egg is fertilized given that the biomass of the population is } B] \quad (24)$$

133 and consider two forms the probability of fertilization. When the biomass of the population is
 134 B the biomass of males is rB ; for the algebraic representation of probability of fertilization we
 135 write

$$p_f(B) = \frac{rB}{rB_c + rB} = \frac{B}{B_c + B} \quad (25)$$

136 where rB_c is the male biomass at which the probability of fertilization drops to 50%.

137 The second functional form is motivated by the re-analysis by Rowe *et al.* (2004) of the
 138 data of Bekkevold *et al.* (2002). Rowe *et al.* (2004) conclude that the exponential asymptotic
 139 function that best describes the fertilization rate is $0.97 \cdot (1 - e^{-2.02 \cdot N_m})$ where N_m is the number
 140 of males. We let p_0 denote the probability that a focal egg is not fertilized when a single male
 141 is present. If W_m denotes the mass of a male, then the number of males in the population when
 142 biomass is B is $\frac{rB}{W_m}$ so that

$$p_f(B) = 1 - p_0^{\frac{rB}{W_m}} = 1 - \exp\left[\frac{rB}{W_m} \cdot \log(p_0)\right] = 1 - e^{-\gamma \cdot B} \quad (26)$$

143 where $\gamma = r|\log(p_0)|/W_m$. Note that $B_c \rightarrow 0$ or $\gamma \rightarrow \infty$ correspond to Allee effects becoming
 144 weaker and weaker.

145 To account for Allee effect in the production model, we replace Eqn 1 by

$$\frac{dB}{dt} = \frac{\alpha_p(1-r) \cdot p_f(B) \cdot B}{1 + \beta B} - M \cdot B \quad (27)$$

146 with a similar modification for a Ricker SRR and for the age-structured model (Eqns 10,11).

147 In summary, there are four cases: 1) Beverton-Holt density dependence of recruitment and
 148 algebraic probability of fertilization; 2) Ricker density-dependence of recruitment and algebraic
 149 probability of fertilization; 3) Beverton-Holt density dependence of recruitment and exponential
 150 probability of fertilization; and 4) Ricker density-dependence of recruitment and exponential
 151 probability of fertilization. Each of these cases may apply for the biomass dynamics model or
 152 the age-structured model.

153 **Including Variation in Natural Mortality in the Equations for**
 154 **Steepness**

155 We now show how variation in natural mortality can be incorporated into the formula for
 156 steepness. We begin with Eqn 7 written as

$$h = \frac{\alpha}{4M + \alpha} \equiv f(M) \quad (28)$$

157 When natural mortality M fluctuates, as is assumed in the stochastic simulation used to estimate
 158 maximum per capita reproduction, $f(M)$ is itself a random variable. To incorporate the variation
 159 in M into steepness, we use the delta method (Mangel 2006) to compute the expected value of
 160 $f(M)$. That is if \bar{M} and $Var(M)$ denote the expected value and variance of M and $E_M[\cdot]$ the
 161 expectation over M we have

$$E_M[f(M)] = E_M[f(\bar{M}) + f'(\bar{M})(M - \bar{M}) + \frac{1}{2}f''(\bar{M})(M - \bar{M})^2] \quad (29)$$

162 In light of Eqn 28

$$f'(M) = -\frac{4\alpha}{(4M + \alpha)^2} \quad (30)$$

$$f''(M) = \frac{32\alpha}{(4M + \alpha)^3} \quad (31)$$

163 We thus conclude

$$E_M[h] = \frac{\alpha}{4\bar{M} + \alpha} + \frac{16\alpha}{(4\bar{M} + \alpha)^3}Var(M) \quad (32)$$

164 which allows us to incorporate the stochastic variation of M into the formula for steepness.

165 We now turn to the age-structured case, for which we rewrite Eqn 20 as

$$h = \frac{\alpha\bar{W}_f}{4 + \alpha\bar{W}_f} \quad (33)$$

166 where $\bar{W}_f = \sum_{a=1}^{a_{max}} S_f(a)W_f(a)p_{f,m}(a)$, more explicitly written as

$$\bar{W}_f = \sum_{a=1}^{a_{max}} \exp\left(\sum_{a'=1}^{a-1} -M(a')\right)W_f(a)p_{f,m}(a) \quad (34)$$

167 We recognize that each of the $M(a')$ in this equation may have its own probability distribution.
 168 (Mathematically speaking, \bar{W}_f is a functional, since it takes a vector of mortality rates and
 169 returns a scalar. There is a large literature on functional derivatives, but we can do all that is
 170 needed here using elementary calculus). For simplicity, we use the notation $M_1 = M(1), M_2 =$
 171 $M(2)$ etc to denote the rate of mortality at age, $\bar{M}_a, Var(M_a)$ and $Cov(M_a, M_{a'})$ to denote the
 172 mean, variance, and covariance of the mortality rates and $\langle \bar{W}_f \rangle$ to denote the value of \bar{W}_f
 173 obtained when the means of the rates of mortality are used. The analogue of Eqn 31 is now

$$E_M[h] = \langle \bar{W}_f \rangle + \frac{1}{2} \sum_a \frac{\partial^2 h}{\partial^2 M_a} Var(M_a) + \sum_a \sum_{a' \neq a} \frac{\partial^2 h}{\partial M_a \partial M_{a'}} Cov(M_a, M_{a'}) \quad (35)$$

174 The partial derivatives of steepness with respect to the mortality rates are

$$\frac{\partial h}{\partial M_a} = \frac{\partial h}{\partial \bar{W}_f} \cdot \frac{\partial \bar{W}_f}{\partial M_a} \quad (36)$$

$$\frac{\partial^2 h}{\partial M_a \partial M_{a'}} = \left[\frac{\partial^2 h}{\partial \bar{W}_f^2} \cdot \frac{\partial \bar{W}_f}{\partial M_a} \cdot \frac{\partial \bar{W}_f}{\partial M_{a'}} + \frac{\partial h}{\partial \bar{W}_f} \cdot \frac{\partial^2 \bar{W}_f}{\partial M_a \partial M_{a'}} \right] \quad (37)$$

175 The easiest part in the next step is to show that

$$\frac{\partial h}{\partial \bar{W}_f} = \frac{4\alpha}{(4 + \alpha \bar{W}_f)^2} \quad (38)$$

$$\frac{\partial^2 h}{\partial \bar{W}_f^2} = \frac{-8\alpha^2}{(4 + \alpha \bar{W}_f)^3} \quad (39)$$

176 We now evaluate the derivatives of \bar{W}_f by first rewriting Eqn 34 as

$$\bar{W}_f = e^{-M_1} W_f(1) p_{f,m}(1) + e^{-M_1 - M_2} W_f(2) p_{f,m}(2) + e^{-M_1 - M_2 - M_3} W_f(3) p_{f,m}(3) + \dots \quad (40)$$

177 from which we can see the pattern of first derivatives

$$\frac{\partial \bar{W}_f}{\partial M_1} = -\bar{W}_f \quad (41)$$

$$\frac{\partial \bar{W}_f}{\partial M_2} = -\bar{W}_f + e^{-M_1} W_1 p_{f,m}(1) \quad (42)$$

$$\frac{\partial \bar{W}_f}{\partial M_3} = -\bar{W}_f + e^{-M_1} W_1 + e^{-M_1 - M_2} W_2 p_{f,m}(2) \quad (43)$$

$$\vdots \quad (44)$$

178 Similarly, the pattern of second derivatives is

$$\frac{\partial^2 \bar{W}_f}{\partial M_1^2} = -\frac{\partial \bar{W}_f}{\partial M_1} = \bar{W}_f \quad (45)$$

$$\frac{\partial^2 \bar{W}_f}{\partial M_1 \partial M_2} = \bar{W}_f - e^{-M_1} W_1 p_{f,m}(1) \quad (46)$$

$$\frac{\partial^2 \bar{W}_f}{\partial M_2^2} = \bar{W}_f \quad (47)$$

$$\frac{\partial^2 \bar{W}_f}{\partial M_1 \partial M_3} = \bar{W}_f - e^{-M_1} W_1 p_{f,m}(1) - e^{-M_1 - M_2} W_2 p_{f,m}(2) \quad (48)$$

$$\vdots \quad (49)$$

179 It is then possible to implement Eqns 32 or 35ff in the code determining steepness. We now turn
180 to depensation.

181 Steepness for a Production Model with Depensatory SRR

182 For each of the cases, we can find steepness by repeating the process outlined in Eqns 1-9. Since
183 it is straightforward but somewhat tedious algebra, we simply give the results.

184 Beverton-Holt density dependence and algebraic probability of fertilization

185 In this case, the steady state biomass satisfies the algebraic equation

$$\frac{\alpha_p \cdot (1-r) \cdot \bar{B}}{(\bar{B} + B_c)(1 + \beta \cdot \bar{B})} = M \quad (50)$$

186 which can easily be solved using the quadratic formula. Steepness is given by

$$h = \frac{0.2 \frac{\alpha_p(1-r)}{M} \cdot \bar{B}}{(B_c + 0.2\bar{B})(4 + \frac{\alpha_p(1-r)\bar{B}}{M(B_c + \bar{B})})} \quad (51)$$

187 As $B_c \rightarrow 0$, this equation becomes Eqn 7, as it must. Note the important differences,
188 however, between Eqns 7 and 51: the former only involves α and M whereas the latter includes
189 B_c and \bar{B} .

190 Ricker density-dependence and algebraic probability of fertilization

191 In this case the steady state biomass \bar{B} satisfies

$$\frac{\alpha_p(1-r)}{M} \cdot \frac{\bar{B}}{B_c + \bar{B}} = e^{\beta \cdot \bar{B}} \quad (52)$$

192 Although this equation does not have an analytical solution, \bar{B} can easily be found using New-
 193 ton's method (Mangel 2006). Steepness is given by

$$h = \frac{0.04(B_c + \bar{B})}{B_c + 0.2\bar{B}} \left(\frac{\alpha_p(1-r)}{M} \cdot \frac{\bar{B}}{B_c + \bar{B}} \right)^{0.8} \quad (53)$$

194 As $B_c \rightarrow 0$, this equation becomes Eqn 8, as it must. Once again, note the important differences
 195 between Eqns 8 and 53, since the latter involves both B_c and \bar{B} .

196 Beverton-Holt density dependence and exponential probability of fertilization

197 In this case the steady state biomass satisfies

$$\beta \cdot \bar{B} = \frac{\alpha_p(1-r)}{M} (1 - e^{-\gamma \bar{B}}) - 1 \quad (54)$$

198 which again requires numerical solution to find \bar{B} . Steepness is given by

$$h = \frac{\frac{\alpha_p(1-r)}{M} (1 - e^{-0.2\gamma \bar{B}})}{4 + \frac{\alpha_p(1-r)}{M} (1 - e^{-0.2\gamma \bar{B}})} \quad (55)$$

199 which clearly approaches steepness in Eqn 7 as $\gamma \rightarrow \infty$.

200 Ricker density-dependence and exponential probability of fertilization In this case, \bar{B} satisfies

$$\frac{\alpha_p(1-r)}{M} (1 - e^{-\gamma \bar{B}}) = e^{\beta \bar{B}} \quad (56)$$

201 and steepness is given by

$$h = 0.2 \left[\frac{1 - e^{-0.2\gamma \bar{B}}}{1 - e^{-\gamma \bar{B}}} \right] \left(\frac{\alpha_p(1-r)}{M} \cdot (1 - e^{-\gamma \bar{B}}) \right)^{0.8} \quad (57)$$

202 Numerical Results When Maximum Productivity is Known

203 To illustrate the above results, we assume that maximum productivity is known and fixed, sex
 204 ratio at birth is 0.5, the mean of natural mortality is 0.2 and that in the absence of an Allee
 205 effect the steady state biomass is $\bar{B}_0=1000$. For these parameters $h = 0.725$ for Ricker den-
 206 sity dependence and $h = 0.556$ for Beverton-Holt density dependence. For simplicity, we only
 207 present results for cases involving algebraic probability of fertilization We then determine B_c or
 208 γ by specifying $p_f(B_0)$ and solving Eqn 25 for B_c .

210 Ricker density-dependence and algebraic probability of fertilization

211 The solution of Eqn 52 rapidly converged with Newton's method. In Figure 1a, we show \bar{B} as a
 212 function of the as a function of $p_f(B_0)$ as this probability ranges from about 0.6 to 0.999 (note
 213 that if $p_f(B_0) = 1$, then B_c must be 0). In Figure 1b we show steepness, given by Eqn 52.

214 We illustrate the Allee effect by plotting the saturating function (left hand side) and exponential
 215 function (right hand side) of Eqn 52 and considering their intersection point (Figure 1c). As long
 216 as the probability of fertilization is less than 1, there will be an Allee value of population size,
 217 which is larger for smaller values of probability of fertilization. Populations will decline if their
 218 size is smaller than this Allee value.

219 Since steepness is typically computed at 20% of the unfished biomass, we compute the per
 220 capita growth rate at 20% of $\bar{B}(p_f(B_0))$ as a function of the probability of fertilization were the
 221 population at B_0 (Figure 1d). Note that it is only for relatively low values of the probability of
 222 fertilization that per capita growth rate at $0.2\bar{B}$ falls below 0. But, as will be explained below,
 223 the Allee effect is important even if per capita growth rate is positive.

224

225 Beverton-Holt density dependence and algebraic probability of fertilization

226

227 We found the solution of Eqn 50 by using the quadratic formula (and advantage of Beverton-Holt
 228 density dependence and algebraic probability of fertilization). In Figures 2a-c we show steepness
 229 as a function of the probability of fertilization, the graphical determination of the Allee level
 230 (based on rewriting Eqn 50 as $\frac{\alpha_p(1-r)\bar{B}}{\bar{B}+B_c} = (1 + \beta \cdot \bar{B})M$), and the per capita growth rate at 20%
 231 of \bar{B} , the analogue of Figure 1. Although the numerical values differ, the qualitative results for
 232 the two forms of density dependence are very similar, so we focus the rest of this section on
 233 Ricker density dependence and algebraic probability of fertilization.

234 **The Unstable Steady State is the Wrong Focus of Attention for Population**
235 **Dynamics with Harvesting**

236 It is common in the discussion of Allee effects to focus on the unstable steady state, because if
237 the population size is below this level, the population will decline even in the absence of human-
238 induced take. However, when a population is harvested things can go wildly wrong long before
239 the Allee level is reached, as the following analysis suggests.

240 We assume that in addition to the natural dynamics, which we assume to be Ricker density
241 dependence, the population experiences fishery induced mortality, written either as a fishing
242 mortality rate (F) or as a catch (C)

$$\frac{dB}{dt} = \alpha_p(1-r) \cdot p_f(B) \cdot B \cdot e^{-\beta B} - (F + M) \cdot B \quad (58)$$

$$\frac{dB}{dt} = \alpha_p(1-r) \cdot p_f(B) \cdot B \cdot e^{-\beta B} - M \cdot B - C \quad (59)$$

243 and use two commonly suggested management strategies $F = M$ for Eqn 58 or $C = 0.5M \cdot \bar{B}$
244 for Eqn 59. We implemented these equations as difference equations, ensuring that B never fell
245 below zero.

246 The results are shown in Figure 3a for harvest proportional to biomass and Figure 3b for
247 fixed harvest. Perhaps the most important message here is that the Allee effect is hidden but
248 has clear consequences. For example, for probability of fertilization of about 0.74, the per capita
249 growth rate at 20 % of unfished biomass is positive (Figure 1d) but a fishing mortality rate
250 of $F = M$ drives the population to extinction. For a fixed harvest, the result is even more
251 dramatic: even a fertilization probability of almost 90% is insufficient to prevent extinction.

252 **The Probability Density for Steepness**

253 As described in Mangel *et al* (2010) in detail, uncertainty in M itself can induce a probability
254 distribution on steepness. That is, all of the equations characterizing steepness are conditioned
255 on a particular value of M . Then if $f_m(m)$ denotes the probability density for M , since the

256 relationship between steepness and rate of mortality is unique, we are easily able to compute
 257 the probability density for steepness, $f_h(h)$. All of this can be done for the production model
 258 without simulation if α_p is treated as a constant.

259 For example, we assume that the rate of mortality follows a gamma density with mean
 260 0.2 and coefficient of variation $\frac{1}{3}$. This frequency distribution is shown in Figure 4a and the
 261 resulting frequency distributions for steepness in Figure 4b for Ricker density dependence and
 262 Figure 4c for Beverton-Holt density dependence when the probability of fertilization at \bar{B}_0 is
 263 0.887. We note two observations about these figures. First, that for Ricker density dependence,
 264 steepness can be arbitrarily large but in this particular case there is little probability of it being
 265 larger than about 2.0. Second, although in the absence of Allee effects, steepness for Beverton
 266 Holt density dependence cannot fall below 0.2, when there are Allee effects steepness can be less
 267 than 0.2.

268 Steepness for the Age-Structured, Two Sex Model with Depen- 269 satory SRR

270 We now turn to the age-structured model. Age structure introduces the biological complexity
 271 that the same biomass may be represented by very different age structures, and thus a given
 272 biomass does not imply a unique recruitment unless the population is in a deterministic Stable
 273 Age Distribution (most likely never; see Wiedenmann *et al* (2009)).

274 In an age-structured population, we may expect that the probability of successful fertilization
 275 depends upon either numbers of biomasses of mature individuals. We will focus on biomass
 276 and let B_f and B_m denote the biomass of mature females and males, suppressing the index on
 277 time. They are given by

$$B_f = \sum_{a=1}^{a_{max}} N_f(a, t) W_f(a) p_{f,m}(a) \quad (60)$$

$$B_m = \sum_{a=1}^{a_{max}} N_m(a, t) W_m(a) p_{m,m}(a) \quad (61)$$

278 where the terms in the latter equation have the obvious interpretations based on the case without
 279 depensation. We assume that the probability of fertilization depends upon the relative mature
 280 biomasses. Thus, the analogue of Eqn 25 is

$$p_f(B_f, B_m) = \frac{B_m/B_f}{B_c/B_f + B_m/B_f} = \frac{B_m}{B_c + B_m} \quad (62)$$

281 where B_c has exactly the same interpretation as in the production model. The analogue of Eqn
 282 26, for the exponential probability of fertilization is

$$p_f(B_f, B_m) = 1 - p_0^{\frac{B_m}{B_f}} = 1 - \exp\left[-\frac{B_m}{B_f}|\log(p_0)|\right] = 1 - \exp\left[-\gamma\frac{B_m}{B_f}\right] \quad (63)$$

283 so that γ has exactly the same interpretation as before. Readers who would prefer to think of
 284 probability of fertilization in terms of mature numbers rather than mature biomass are encour-
 285 aged to reproduce the calculations that follow using mature numbers.

286 A subtlety now arises. Steepness is defined by spawning biomass reduced from its unfished
 287 level to 20% of that level. For the production model, this can happen in only one way. However,
 288 for the age-structured model there is an infinite number of ways of reducing mature male and
 289 female biomasses so that the total is 20% of the unfished level. For example, if we interpret
 290 20% of the unfished level to mean that mature male biomass is 20% of its unfished level and
 291 mature female biomass is 20% of its unfished level. Then according to Eqn 62 the probability of
 292 successful fertilization will decline. However, according to Eqn 63 it will remain the same, which
 293 might occur for species in very tight spawning aggregations and highly fecund males. Overall,
 294 however, it seems that the algebraic probability of fertilization may capture the effects that we
 295 seek to explore more effectively, so we shall use it.

296 **Beverton-Holt Density Dependence and Algebraic Probability of Fertilization**

297 We begin with Beverton-Holt density dependence and algebraic probability of fertilization for
 298 two reasons. First, the calculations are the simplest ones possible – there are no transcendal
 299 equations and all quantities can be determined using no more than the quadratic formula.

300 Second, in the absence of Allee effects, steepness for this case ranges between 0.2 and 1, so
 301 results are more easily interpreted than for Ricker density dependence.

302 If density dependence is caused by the entire biomass (not just spawning biomass) the
 303 production of young of the year females and males in the steady state is

$$\bar{N}_f(0) = (1 - r)\alpha_s \bar{B}_f \cdot \frac{1}{1 + \beta \bar{B}} \cdot \frac{\bar{B}_m}{B_c + \bar{B}_m} \quad (64)$$

$$\bar{N}_m(0) = r\alpha_s \bar{B}_f \cdot \frac{1}{1 + \beta \bar{B}} \cdot \frac{\bar{B}_m}{B_c + \bar{B}_m} \quad (65)$$

304 and in analogy with Eqn 16 we have

$$\bar{B}_f = \bar{N}_f(0) \bar{W}_f \quad (66)$$

$$\bar{B}_m = \bar{N}_m(0) \bar{W}_m \quad (67)$$

$$\bar{B} = \bar{N}_f(0) \langle W_f \rangle + \bar{N}_m(0) \langle W_m \rangle \quad (68)$$

305 where $\langle W_f \rangle = \sum_{a=1}^{a_{max}} S_f(a) W_f(a)$ and $\langle W_m \rangle = \sum_{a=1}^{a_{max}} S_m(a) W_m(a)$ are the average masses
 306 females and male fish, regardless of the maturation status.

307 Note from Eqns 64 and 65 that

$$\frac{\bar{N}_m(0)}{\bar{N}_f(0)} = \frac{r}{1 - r} \quad (69)$$

308 so that it is helpful to define $\rho_r = \frac{r}{1-r}$ and compactly write $\bar{N}_m(0) = \rho_r \bar{N}_f(0)$.

309 We now use Eqns 65, 67 and 68 to rewrite Eqn 64 as a single equation for $\bar{N}_f(0)$

$$\bar{N}_f(0) = (1 - r)\alpha_s \bar{N}_f(0) \bar{W}_f \cdot \frac{1}{1 + \beta \bar{N}_f(0) (\langle W_f \rangle + \rho_r \langle W_m \rangle)} \cdot \frac{\rho_r \bar{N}_f(0) \bar{W}_m}{B_c + \rho_r \bar{N}_f(0) \bar{W}_m} \quad (70)$$

310 which can be re-arranged to give

$$1 + \beta \bar{N}_f(0) [\langle W_f \rangle + \rho_r \langle W_m \rangle] = \frac{(1 - r)\alpha_s \bar{W}_f \rho_r \bar{N}_f(0) \bar{W}_m}{B_c + \rho_r \bar{N}_f(0) \bar{W}_m} \quad (71)$$

311 and cross-multiplying by the denominator on the right hand side, we see that Eqn 71 – as
 312 complicated as it looks — is simply a quadratic equation for the single unknown $\bar{N}_f(0)$. Once
 313 we find that, we know all the other steady state population numbers and biomasses from Eqns
 314 65-68.

315 Assuming that 20% of unfished biomass is understood as equivalent reductions in female and
 316 male populations, steepness is computed from

$$h = \frac{0.2\alpha_s \bar{B}_f \frac{1}{0.2\beta \bar{B}} \frac{0.2\bar{B}_m}{B_c + 0.2\bar{B}_m}}{\alpha_s \bar{B}_f \frac{1}{\beta \bar{B}} \frac{0.2\bar{B}_m}{B_c + \bar{B}_m}} \quad (72)$$

317 which simplifies to

$$h = 0.04 \left[\frac{1 + \beta \bar{B}}{1 + 0.2\beta \bar{B}} \left[\frac{B_c + \bar{B}_m}{B_c + 0.2\bar{B}_m} \right] \right] \quad (73)$$

318 Note that the left hand side of Eqn 71 is exactly $1 + \beta \bar{B}$, so we solve that equation for $\beta \bar{B}$
 319 and substitute into Eqn 73 to obtain the final result for steepness with Beverton-Holt density
 320 dependence and

$$h = 0.2 \left[\frac{(1-r)\alpha_s \bar{W}_f \frac{\rho_r \bar{N}_f(0) \bar{W}_m}{B_c + \rho_r \bar{N}_f(0) \bar{W}_m}}{4 + (1-r)\alpha_s \bar{W}_f \frac{\rho_r \bar{N}_f(0) \bar{W}_m}{B_c + \rho_r \bar{N}_f(0) \bar{W}_m}} \right] \left[\frac{B_c + \rho_r \bar{N}_f(0) \bar{W}_m}{B_c + 0.2\rho_r \bar{N}_f(0) \bar{W}_m} \right] \quad (74)$$

321 Note that if we set $B_c = 0$ then we recover Eqn 20 as must happen.

322 **The Deterministic Estimate of Steepness of Bigeye Tuna *Thun-*** 323 ***nus obesus***

324 For this example, we used the same parameters as in Mangel *et al* (2010) and assumed that the
 325 rate of mortality, $M_f(a)$ (Eqn 12), for females could be determined from the allometry for fish
 326 given by McCoy and Gillooly (2008) assuming a dry mass of 55% of wet mass, and that the rate
 327 of mortality for males is given by

$$M_m(a) = \frac{k_m}{k_f} M_f(a) \quad (75)$$

328 where k_m and k_f are respectively the von Bertalanffy growth rates for males and females re-
 329 spectively. We used exactly deterministic version of the procedure, based on the allometry in
 330 McGurk (1986), in Mangel *et al.* (2010) for determining α_s .

331 The two parameters that remain to be specified are β and B_c . In principle, β can be
 332 computed from the dynamics underlying the Beverton-Holt recruitment function, in which per

333 capita larval mortality is a linear function of larval numbers (Mangel 2006, pg 213) but for
 334 illustration here we proceed differently. Note from Eqn 71 that in the absence of Allee effects
 335 we have

$$1 + \beta \bar{N}_f(0) [\langle W_f \rangle + \rho_r \langle W_m \rangle] = (1 - r) \alpha_s \bar{W}_f \quad (76)$$

336 The the term in [] on the left-hand side and the right-hand side of Eqn 76 is known once the
 337 life history parameters are known. Thus (as observed by many authors), the parametrization
 338 of the Beverton-Holt stock-recruitment relationship that we have used means β scales the size
 339 of $\bar{N}_f(0)$ and that if we specify one of them the other is fixed by the life history parameters.
 340 Consequently, one can imagine that both β and $\bar{N}_f(0)$ are measured in some appropriate volume
 341 of ocean. For the computations here, we assume that in the absence of Allee effects, $\bar{N}_f(0)$ would
 342 be 500 individuals. We then determine β from Eqn 76. When β is determined in this manner,
 343 the only unknown in Eqn 53 is the value of $\bar{N}_f(0)$ in the presence of Allee effects; we find this
 344 using the quadratic formula.

345 Steepness is then computed from Eqn 74. Clearly steepness depends upon B_c , however as
 346 with the production model it is difficult to interpret results in terms of B_c , so we plot steepness
 347 as a function of the probability of fertilization, given by

$$p_f = \frac{\rho_r \bar{N}_f(0) \bar{W}_m}{B_c + \rho_r \bar{N}_f(0) \bar{W}_m} \quad (77)$$

348 We find that the probability of fertilization is 1 (i.e. $B_c = 0$) steepness is close to 1, but not
 349 equal to 1 (Figure 5). However the relationship is highly nonlinear. If $p_f = .976$, then $h = 0.908$
 350 and but if $p_f = 0.9$ of the eggs are fertilized, steepness is about 70%. Note that as with the
 351 production model it is possible for steepness to fall below 0.2 if Allee effects are considered.

352 **An Improved Approach for Estimating α_s**

353 The stochastic simulation used in Mangel *et al* (2010) is not appropriate for case in which the
 354 mechanism of depensation is reduced probability of fertilization, because we must track the

355 size of both male and female populations. In this section, we introduce an improved stochastic
356 simulation, which can be used for either the depensatory case or the non-depensatory case.

357 As noted in Mangel *et al* (2010), α_s can be interpreted as the maximum number of new
358 individuals added to the population per unit of spawning biomass before density dependence
359 acts on the recruited class (and α_p can be computed by multiplying α_s by the biomass of a
360 recruit. In the previous paper we used an artifice of ‘populations’ but here we return to the
361 more common approach based on cohort analysis.

362 **The Cohort Based Computation of α_s**

363 We implement the calculations described below in a stochastic simulation over survival tra-
364 jectories, but for simplicity ignore the index on the iterate of the simulation in the following
365 description. Imagine a cohort of N_0 individuals in which individuals are indexed by i . We begin
366 by drawing a random variable U_s which we compare with the sex ratio at birth to determine
367 whether the i^{th} fish is a female ($s(i) = 1$) or a male ($s(i)=2$). In this manner we determine the
368 number of female and male fish, $N_f(0)$ and $N_m(0)$, in the cohort.

369 Next we compute the number of females and males of age a using the survival functions, so
370 that $N_f(a) = N_f(0) \cdot S_f(a)$ and $N_m(a) = N_m(0) \cdot S_m(a)$ where $S_f(a)$ and $S_m(a)$ are respectively
371 the probabilities that a female or male survives to age a . In this way we uniquely identify the
372 age $a(i)$ of the i^{th} fish, in which there are a total of $N_T(a) = N_f(a) + N_m(a)$ fish of age a .

373 Once the age of the i^{th} fish is known we are able to compute the probability that it is mature,
374 $p_m(i)$, from the schedule of maturity. This is a binary variable, with $p_m(i) = 0$ corresponding
375 to an immature fish and $p_m(i) = 1$ corresponding to a mature fish.

376 In order to account for fertilization based depensation, we must specify the size of the mating
377 group, G . We let B_m and B_f respectively denote the biomass of males and females in the
378 currently simulated mating group and E_T denote the number of eggs that survive to recruit to
379 the population produced by females in the currently simulated mating group. One can imagine

380 a variety of means of assembling the mating group. For example, mature individuals may join
381 mating groups randomly (the pseudocode for this situation is given below) or they may join
382 through size association (so that larger fish are paired with larger fish; smaller fish are paired
383 with smaller fish).

384 If mating groups involve random association of mature fish, the following pseudocode can be
385 followed:

386 Step 1. Set the size of the current group to 0, and set $B_m = B_f = 0$.

387 Step 2. Draw a test value, i_{test} that is uniformly distributed across the total number of fish.
388 If $p_m(a(i_{test})) = 0$, so that the fish is immature, return to Step 1. If $p_m(a(i_{test})) = 1$, so that
389 the fish is mature, proceed to Step 3.

390 Step 3. Increment the current size of the mating group by 1 individual.

391 Step 4. If $s(i_{test}) = 2$, so that the test individual is a male, increment B_m by $W_m(a(i_{test}))$.

392 Step 5. If $s(i_{test}) = 1$, so that the test individual is a female, increment B_f by $W_f(a(i_{test}))$,
393 compute the number of surviving eggs (using the same, but corrected and improved, algorithm
394 as in Mangel *et al* (2010)) and increment total eggs E_T by this amount.

395 Step 6. If the current group size is less than G return to Step 2. Otherwise, continue to Step
396 7a or Step 7b.

397 At this point another decision must be made. If one wished to use Eqn 56, in which a mean
398 probability of fertilization is applied, then

399 Step 7. Compute $\alpha_s = \frac{E_T}{B_f}$.

400 Step 8. Compute $p_f(B_f, B_m)$ using either Eqn 44 or 45. In this way one obtains the effective
401 maximum production of the test fish.

402 Step 9. If current group size is less than G return to Step 2.

403 **Increased Mortality as the Depensatory Mechanism**

404 An alternative depensatory mechanism is that mortality rate increases as population size declines
405 (George Watters, personal communication). For example, we might modify the production
406 model as

$$\frac{dB}{dt} = \alpha_p(1-r)Bg(B) - M_0\left(\frac{B+B_2}{B}\right) \quad (78)$$

407 where $g(B)$ denotes the density dependent component of reproduction, M_0 the rate of natural
408 mortality when biomass is large, and B_2 the value of biomass at which the rate of natural
409 mortality is twice M_0 . For the case of Beverton-Holt density dependence, the steady state
410 biomass satisfies

$$\frac{\alpha_p(1-r)}{M_0} = 1 + \frac{B_2}{\bar{B}} + \beta\bar{B} + \beta B_2 \quad (79)$$

411 which is once again a quadratic equation for \bar{B} .

412 **Empirical Assessment for the Depensatory Mechanism**

413 The social psychologist Kurt Lewin is reknowned for his comment that ‘there is nothing as
414 practical as a good theory’ (Lewin 1951, pg 169). Rothman (2004) revisited Lewin and noted
415 ‘Although Lewin may have been right that there is “nothing more practical than a good theory”
416 (p.169; [24]), his dictum rests on the assumption that good theories are available to address
417 practical problems. The development of “good” theories that is, theories that are both accurate
418 and applicable has been hindered by a breakdown in the on-going collaboration between basic
419 and applied behavioral scientists.’ (pg 6).

420 As emphasized in Mangel *et al.* (2010), steepness is a derived quantity – related to things
421 that can be measured, but itself never measured. For the theory of steepness developed here to
422 be practicable, it is necessary to find a way to measure the effect of depensation, captured in
423 either Eqn 25 or 26.

424 Some very simple statistical methods can be applied to estimate B_c in Eqn 25 or γ in Eqn
425 26. Inverting Eqn 25 and simplifying shows that (suppressing the dependence of the probability

426 of fertilization on biomass)

$$\frac{1}{p_f} - 1 = B_c \cdot \frac{1}{B} \quad (80)$$

427 so that B_c can be estimated as the slope of the plot of $\frac{1}{p_f} - 1$ vs. $1/B$. (This is similar to
428 methods for estimating the rate constant in Michaelis-Menten enzyme kinetics). Similarly, Eqn
429 26 can be simply manipulated to give

$$\log(1 - p_f) = \gamma \cdot B \quad (81)$$

430 so that γ can be estimated as the slope of the plot of $\log(1 - p_f)$ vs B .

431 Alternatively, Eqns 25 and 26 can be viewed as the foundation of nonlinear statistical models,
432 particularly when converted to a logit-form.

433 Finally, it is natural to consider Bayesian methods by introducing appropriate priors for
434 either B_c or γ . All of this remains to be done.

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477 **Appendix: The Production Model as a System of Stochastic Dif-** 478 **ferential Equations**

479 The gamma density that we use to characterize natural mortality can be viewed as the steady
480 state frequency distribution for the following stochastic differential equation (Dennis and Costantino
481 1988, Costantino and Desharnais 1991)

$$dM = M[\lambda - \mu \cdot M]dt + \sigma_M M dW_1 \quad (\text{A1})$$

482 where λ and μ have their usual interpretations for logistic growth (λ is maximum per capita
483 growth rate and carrying capacity is $\frac{\lambda}{\mu}$), dW_1 is an increment of standard Brownian motion
484 (Mangel 2006) and σ_M is the standard deviation of fluctuations in mortality. Eqn A1 can be
485 interpreted as follows: given that $M(t) = m$, then $dM = M(t+dt) - M(t)$ is normally distributed
486 with mean

$$E[dM] = m(\lambda - \mu m)dt + o(dt) \quad (\text{A2})$$

487 and variance

$$Var[dM] = \sigma_M^2 m^2 dt + o(dt) \quad (\text{A3})$$

488 and variance, where $o(dt)$ represents terms that are higher order than dt .

489 This observation suggests that we can interpret Eqn 1 or the equivalent using Ricker den-
490 sity dependence and the probability density for gamma in the context of stochastic differential
491 equations. If we let $g(B)$ denote the density dependence, then if the source of stochasticity for

492 changes in biomass is a birth and death process, the stochastic version of either equation is
 493 (Mangel 1994, 2006)

$$dB = [\alpha_p(1-r)Bg(B)p_f(B) - M \cdot B]dt + \sqrt{\alpha_p(1-r)Bg(B)p_f(B) + M \cdot B} \cdot dW_2 \quad (\text{A4})$$

494 where dW_2 is another increment in standard Brownian motion. The interpretation for the
 495 distribution, mean, and variance of $dB = B(t+dt) - B(t)$ condition on $B(t) = b$ is similar to
 496 the one given above for dM .

497 If $f(m, b)$ is the stationary probability density for M and B , then under the assumptions in
 498 Eqns A1-A4, it will satisfy the equation

$$\begin{aligned} & \frac{1}{2} \left[\sigma_M^2 m^2 \frac{\partial^2 f}{\partial m^2} + (\alpha_p(1-r)bg(b)p_f(b) + m \cdot b) \frac{\partial^2 f}{\partial b^2} \right] \\ & - [m(\lambda - \mu m) \frac{\partial f}{\partial m}] - [(\alpha_p(1-r)bg(b)p_f(b) - m \cdot b) \frac{\partial f}{\partial b}] = 0 \end{aligned} \quad (\text{A5})$$

500 Whether or not this proves to be useful remains to be seen.

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516 Captions for Figures

517 Figure 1. Results for the production model with illustrative parameters. a) The steady state
518 biomass in the presence of an Allee effect as a function of the probability of fertilization $p_f(\bar{B}_0)$
519 when biomass is $\bar{B}_0 = 1000$; b) Steepness for the production model with Ricker density depen-
520 dence and algebraic probability of fertilization as a function of the probability of fertilization
521 $p_f(\bar{B}_0)$; c) Graphical determination of the unstable steady state biomass as the solution of the
522 associated transcendental equation. d) Per capita growth rate at 20% of steady state biomass
523 as a function of of the probability of fertilization $p_f(\bar{B}_0)$.

524

525 Figure 2. Similar calculations for Beverton Holt density dependence and algebraic probabili-
526 ty of fertilization. a) Steepness as a function of the probability of fertilization when biomass
527 is 1000, $p_f(\bar{B}_0)$; b) Illustration of graphical determination of the unstable steady state. c) Per
528 capita growth rate at 20% of steady state biomass as a function of of the probability of fertil-
529 ization when biomass is 1000, $p_f(\bar{B}_0)$.

530

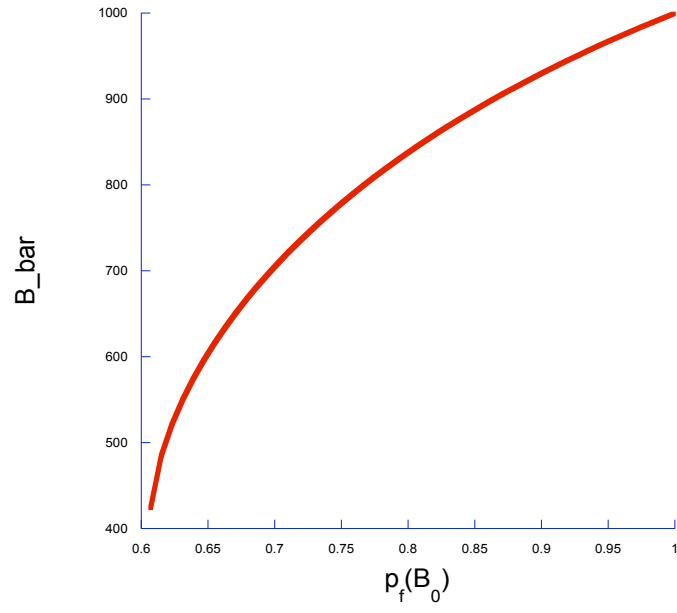
531 Figure 3 When there is an Allee effect, otherwise sustainable harvesting may become unusu-
532 tainable. We show, as a function of the probability of fertilization when biomass is 1000, $p_f(\bar{B}_0)$
533 the biomass trajectory for fishing mortality $F = M$ (panel a) or fixed catch $C = 0.5M\bar{B}$ (panel b)

534

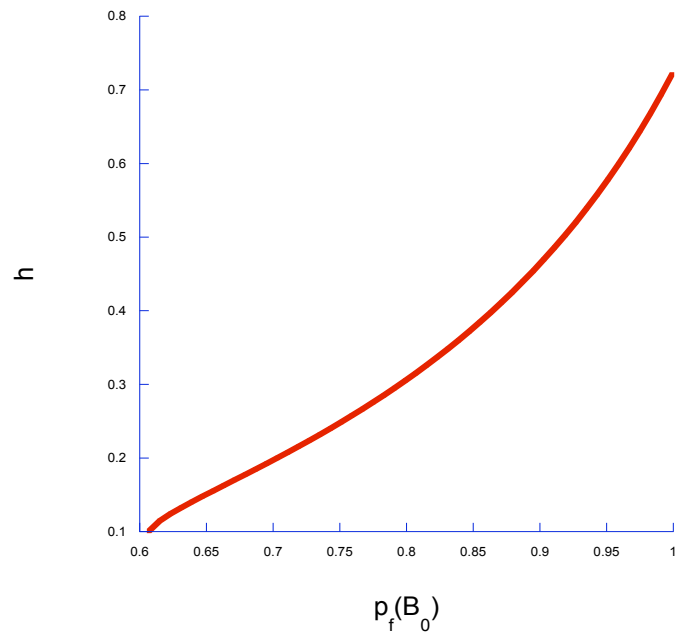
535 Figure 4 A probability distribution for natural mortality (panel a; here the gamma density
536 used by Mangel *et al* (2010)) induces a probability distribution for steepness for Ricker density
537 dependence and algebraic probability of fertilization (panel b) or Beverton-Holt density depen-
538 dence and algebraic probability of fertilization (panel c).

539

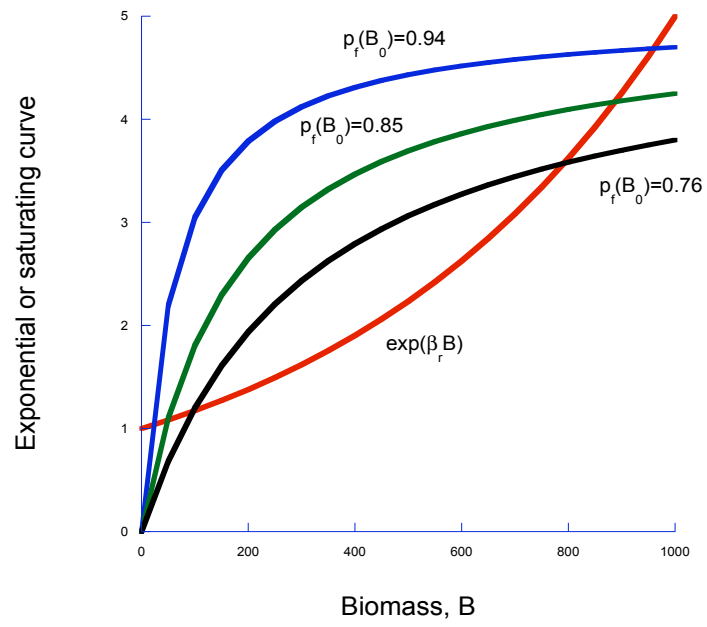
540 Figure 5 The point estimate of steepness for bigeye tuna as a function of the probability that
541 an egg is fertilized when the population is in the stable age distribution.



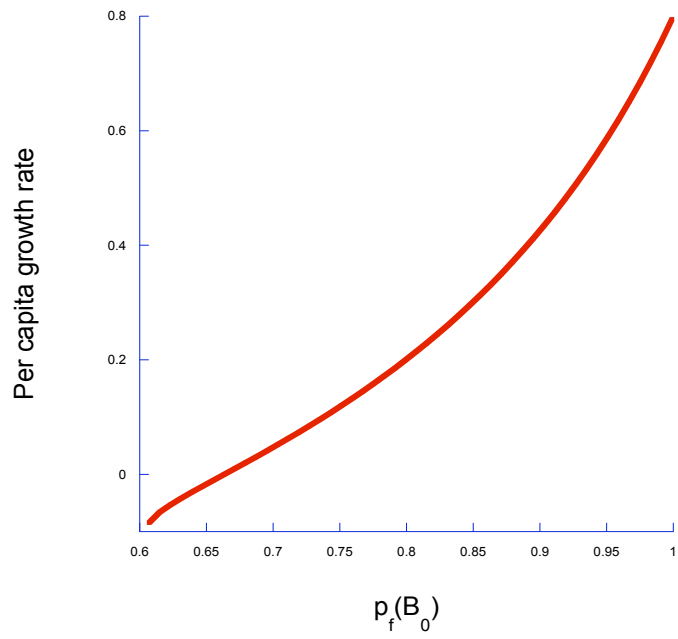
543 Figure 1a.pdf



544 Figure 1b.pdf

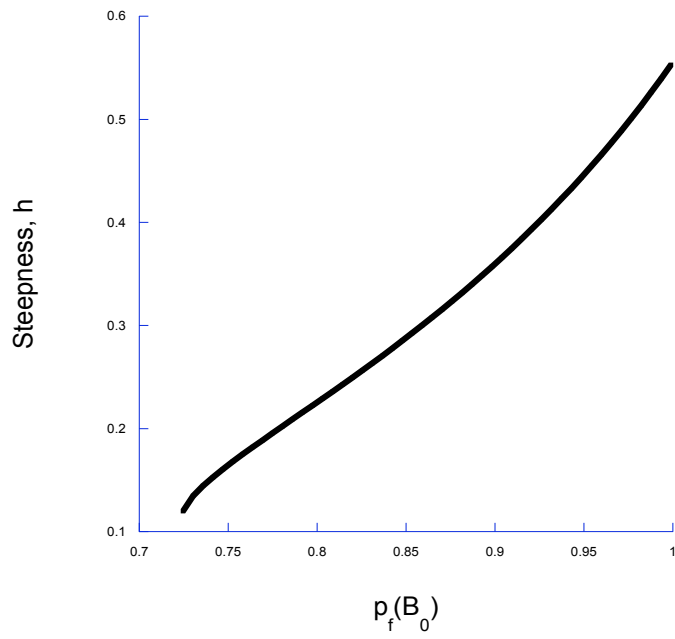


545 Figure 1c.pdf

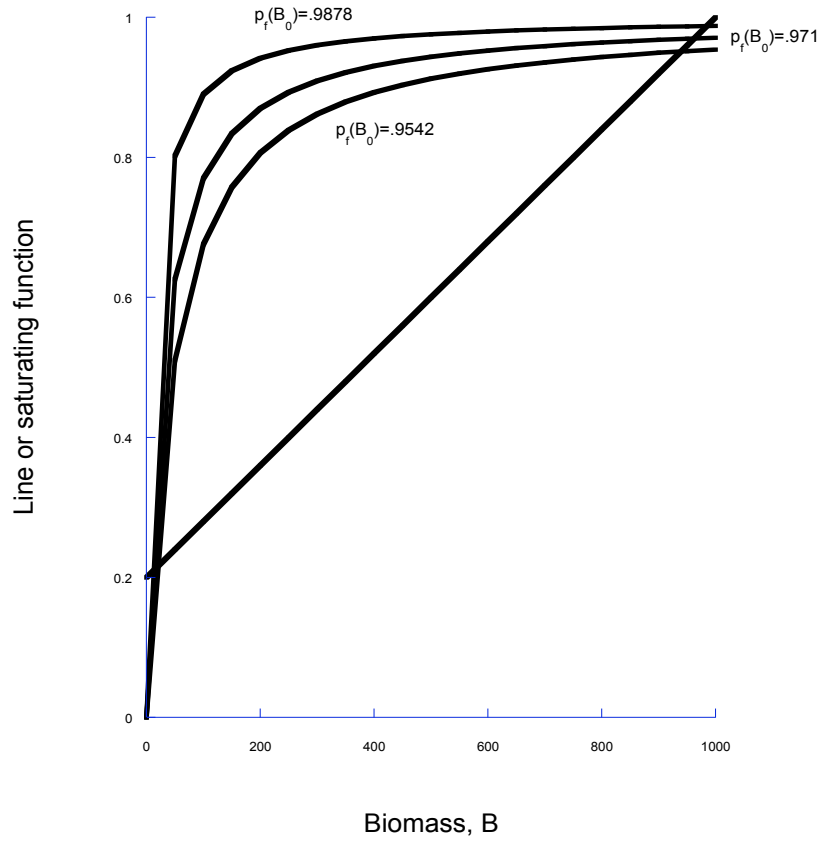


546 Figure 1d.pdf

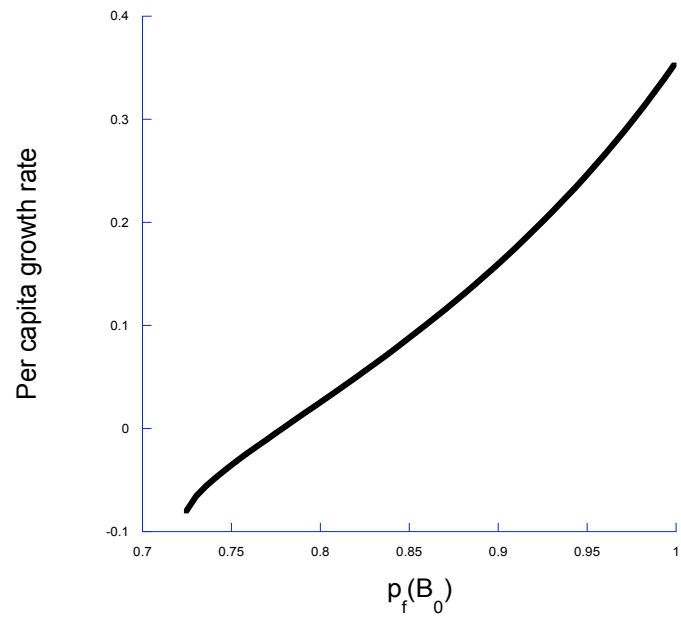
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548 Figure 2a.pdf

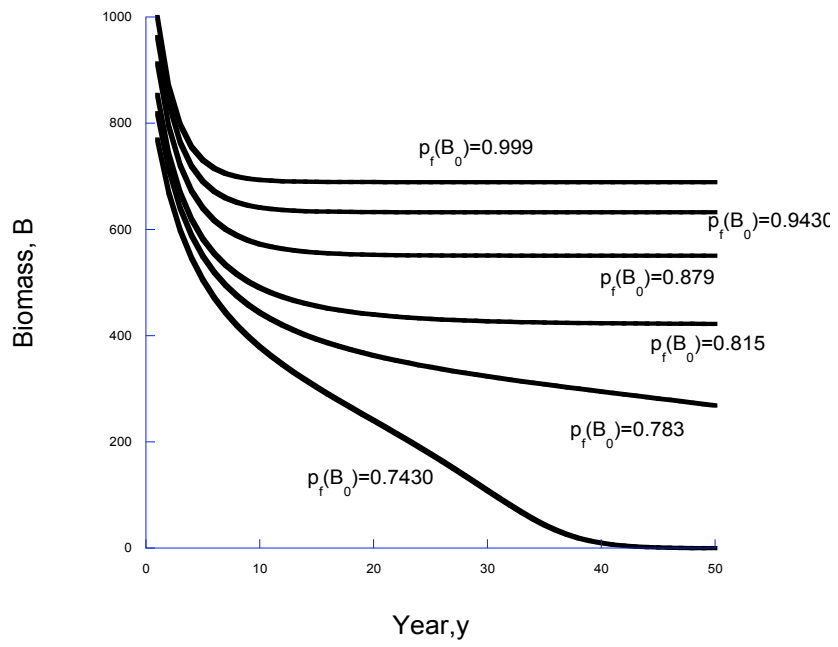


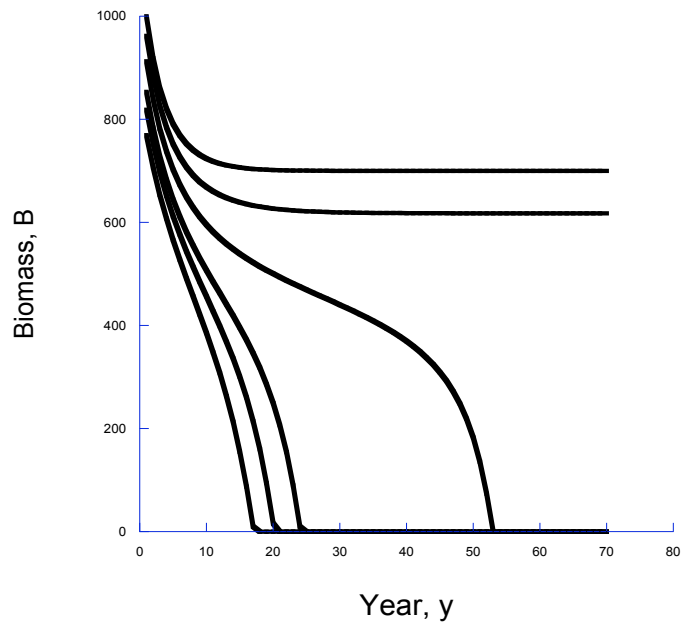
549 Figure 2b.pdf



550 Figure 2c.pdf

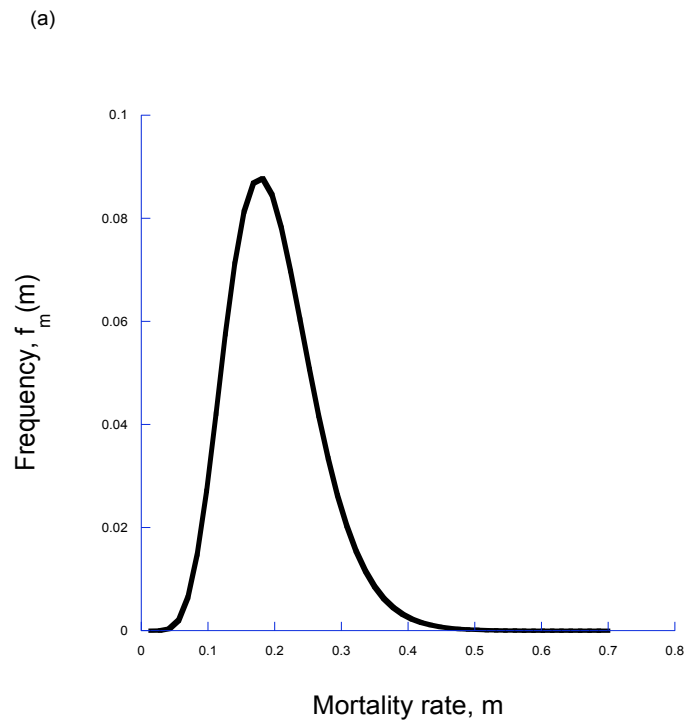
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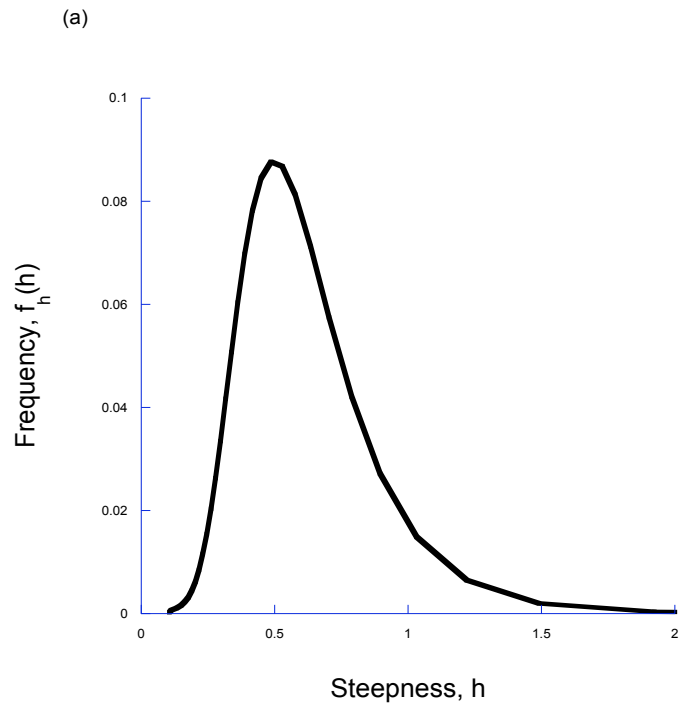


553 Figure 3b.pdf

554



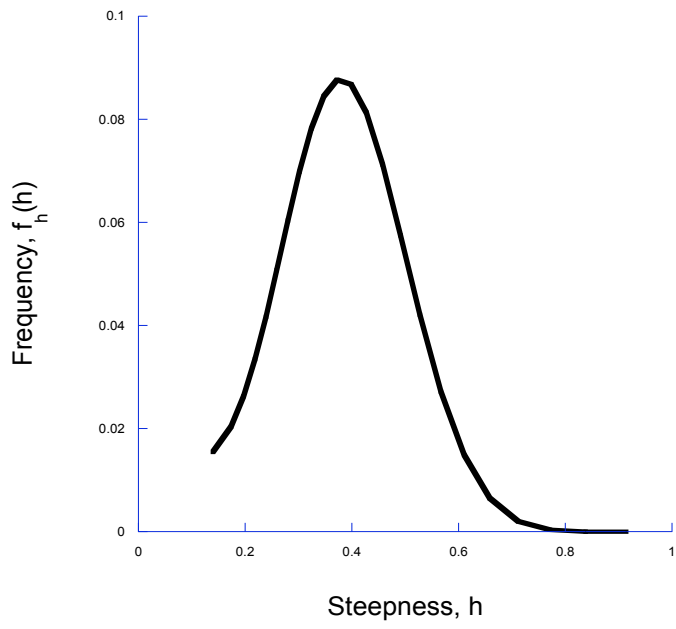
555 Figure 4a.pdf



556 Figure 4b.pdf

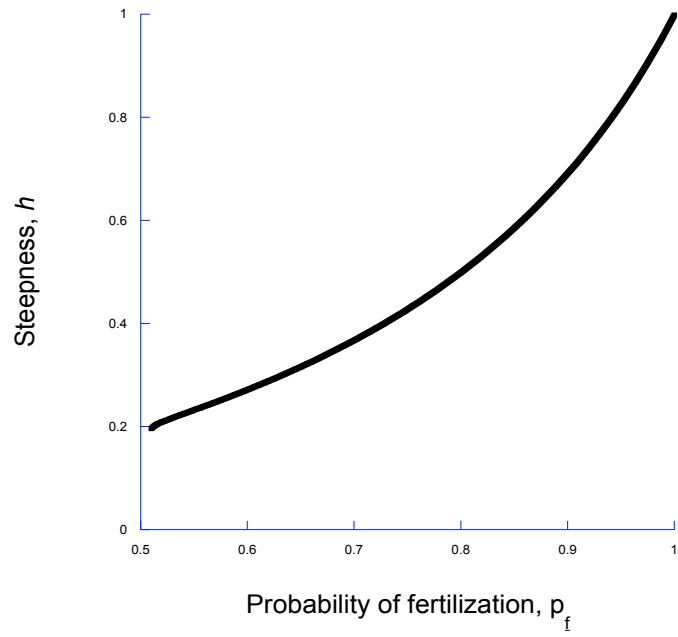
Figure 4c.pdf

(b)



557

558



559 Figure 5.pdf

560 Figure 5. The point estimate of steepness for the age structured model.