

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

3  
4 September 21, 2010

5 Marc Mangel<sup>1</sup>, Jon Brodziak<sup>2</sup>, and Gerard DiNardo<sup>2</sup>

6 <sup>1</sup>Center for Stock Assessment Research and Department of Applied Mathematics and Statistics,  
7 University of California, Santa Cruz, CA 95064;<sup>2</sup>Pacific Islands Fisheries Science Center, Hon-  
8 olulu, HI

9  
10 Author for Correspondence: Marc Mangel (msmangel@ucsc.edu; 1 831 234 2970; FAX: 1 831  
11 459 4482)

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  $\alpha$  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  $\alpha_p$  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  $\alpha$  and  $\beta$  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  $\alpha_s$  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  $\alpha_s$  in the latter replacing  $\alpha_p$  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  $\delta$  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 Sella-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  $\alpha$  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  $\gamma$  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  $\alpha_p$  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  $\gamma$  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  $\alpha_s$ .

331 The two parameters that remain to be specified are  $\beta$  and  $B_c$ . In principle,  $\beta$  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  $\beta$  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  $\beta$  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  $\beta$  from Eqn 76. When  $\beta$  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 $\alpha_s$**

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),  $\alpha_s$  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  $\alpha_p$  can be computed by multiplying  $\alpha_s$  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 $\alpha_s$**

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  $\gamma$  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  $\gamma$  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  $\gamma$ . All of this remains to be done.

## 435 **References**

436 Bekkevold, D., Hansen, M.M., and V. loeschke. 2002. Male reproductive competition in spawn-  
437 ing aggregations of cod (*Gadus morhua* L.). *Molecular Ecology* 11:91-102

438 Chen, D.G., Irvine, J.R., and A.J. Cass. 2002. Incorporating Allee effects in fish-stock  
439 recruitment models and applications for determining reference points. *Canadian Journal of*  
440 *Fisheries and Aquatic Sciences*. 59:242-249

441 Courchamp, F., Berek, L. and J. Gascoigne. 2008. *Allee Effects in Ecology and Conservation*.  
442 Oxford University Press, Oxford, UK

443 Fowler, C.W. and J.D. Baker. 1991. A review of animal population dynamics at extremely  
444 reduction population levels. *Reports of the International Whaling Commission* 41:545-554

445 Gascoigne, J. and R. Lipcius. 2004 Allee effects in marine systems. *Marine Ecology Progress*  
446 *Series* 269:49-59

447 Gregory, S.D., Bradshaq, C.J., Brook, B.W., and F. Courchamp. 2010. Limited evidence  
448 for the demographic Allee effect from numerous species across taxa. *Ecology* 91:2151-2161

449 Iles, T.C. 1994. A review of stock-recruitment relationships with reference to flatfish popu-  
450 lations. *Netherlands Journal of Sea Research* 32:399-420

451 Lewin K. 1951. *Field theory in social science: Selected theoretical papers*. New York, NY:  
452 Harper & Row

453 Lierman, M. and R. Hilborn. Depensation: evidence, models and implications. *Fish and*  
454 *Fisheries* 2:33-58

455 Mangel, M., Brodziak, J.K.T., and G. DiNardo. 2010. Reproductive ecology and scientific  
456 inference of steepness: a fundamental metric of population dynamics and strategic fisheries  
457 management. *Fish and Fisheries* 11:89-104

458 McCoy, M.W. and J.F. Gillooly. 2008. Predicting natural mortality rates of plants and  
459 animals. *Ecology Letters* 11:710-716.

460 McGurk, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: the role of  
461 spatial patchiness. *Marine Ecology Progress Series* 34:227-242

462 Morales-Bojorquez, E. and M.O. Nevarez-Martinez. 2005. Spawner-recruit patterns and  
463 investigation of Allee effect in Pacific sardine (*Sardinops Sagax*) in the Gulf of California, Mexico.  
464 *CalCOFI Reports* 46:161-174

465 Myers, R.A., Barrowman, N.J., Hutchings, J.A., and A.A. Rosenberg. 1995. Population  
466 dynamics of exploited fish stocks at low population levels. *Science* 269:1106-1108

467 Rothman, A.J. 2004. *International Journal of Behavioral Nutrition and Physical Activity*  
468 2004, 1:11 doi:10.1186/1479-5868-1-11

469 Rowe, S., Hutchings, J.A., Bekkevold, D., and A. Rakitin. 2004. Depensation, probability of  
470 fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.) *ICES Journal of Marine*  
471 *Science* 61:1144-1150

472 Shepherd, J.G. 1982. A versatile new stock-recruitment relationship for fisheries, and the



473 construction of sustainable yield curves. ICES Journal 40:67-75

474 Wiedenmann, J., Fujiwara, M., and M. Mangel. 2009 Transient population dynamics and  
475 viable stage or age distributions for effective conservation and recovery. Biological Conservation  
476 142:2990-2996

## 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  $\lambda$  and  $\mu$  have their usual interpretations for logistic growth ( $\lambda$  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  $\sigma_M$  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.

## 501 **References for the Appendix**

502 Costantino, R.F. and R.A. Desharnais. 1991. Population Dynamics and the *Tribolium* Model:  
 503 Genetics and Demography. Springer Verlag, New York.

504 Dennis, B. and R.F. Costantino. Analysis of steady-state populations with the gamma  
 505 abundance model: application to *Tribolium*. Ecology 69:1200-1213

506 Mangel, M. 1994. Barrier transitions driven by fluctuations, with applications to ecology  
 507 and evolution. Theoretical Population Biology. 45:16-40

508 Mangel, M. 2006. The Theoretical Biologist's Toolbox. Cambridge University Press, Cam-  
 509 bridge, UK

510 Schaefer, K.M., Fuller, D.W., and N. Miyabe. 2005. Reproductive biology of bigeye tuna  
 511 (*Thunnus obesus*) in the eastern and central Pacific Ocean. Inter-America Tropical Tuna Com-  
 512 mission Bulletin 23(1):3-31

513 Schaefer, K.M. and D.W. Fuller. 2006. Estimates of age and growth of bigeye tuna (*Thunnus*  
514 *obesus*) in the Eastern Pacific Ocean, based on otolith increments and tagging data. Inter-  
515 America Tropical Tuna Commission Bulletin 23(2):35-76

## 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

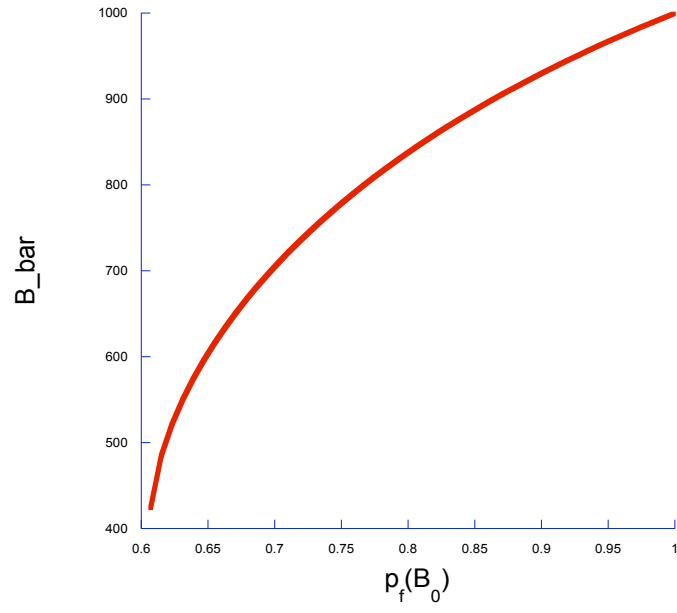
531 Figure 3 When there is an Allee effect, otherwise sustainable harvesting may become unusu-  
532 tainable. We show, as a function of the probability of fertilization when biomass is 1000,  $p_f(\bar{B}_0)$   
533 the biomass trajectory for fishing mortality  $F = M$  (panel a) or fixed catch  $C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

534

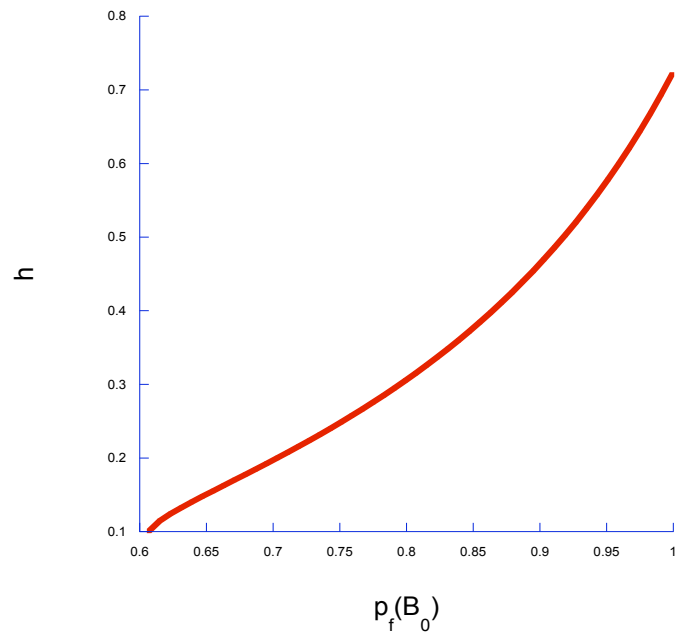
535 Figure 4 A probability distribution for natural mortality (panel a; here the gamma density  
536 used by Mangel *et al* (2010)) induces a probability distribution for steepness for Ricker density  
537 dependence and algebraic probability of fertilization (panel b) or Beverton-Holt density depen-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

539

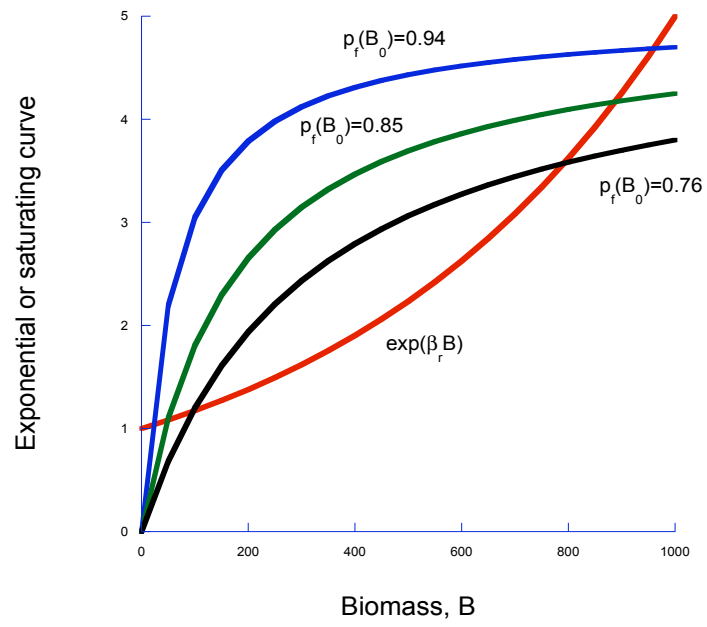
540 Figure 5 The point estimate of steepness for bigeye tuna as a function of the probability that  
541 an egg is fertilized when the population is in the stable age distribution.



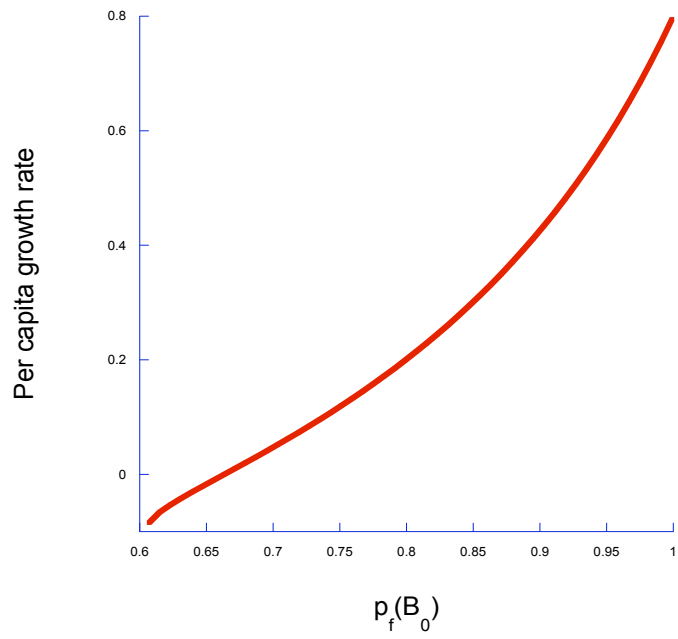
543 Figure 1a.pdf



544 Figure 1b.pdf



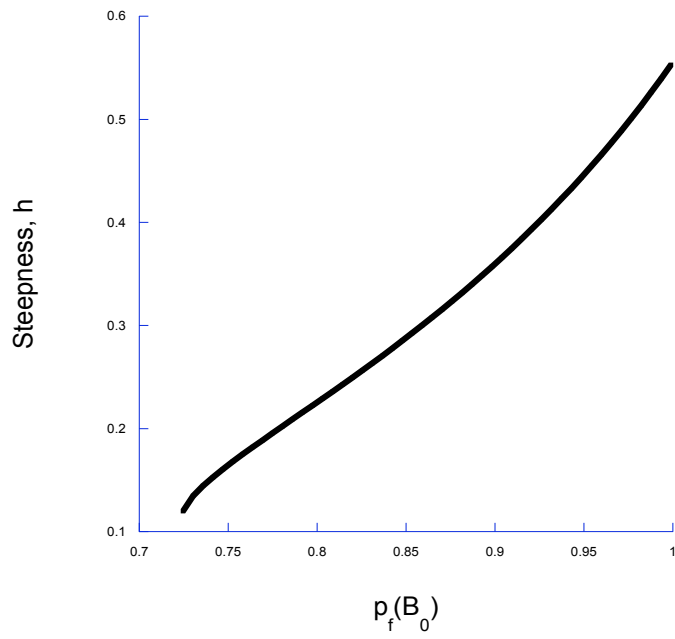
545 Figure 1c.pdf



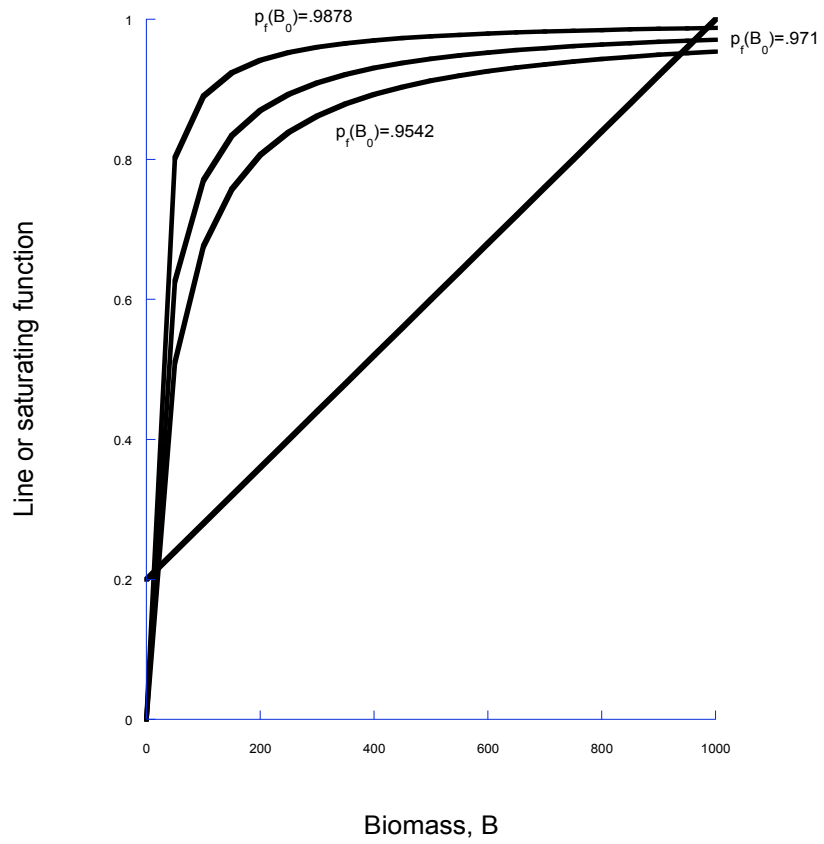
546 Figure 1d.pdf

547

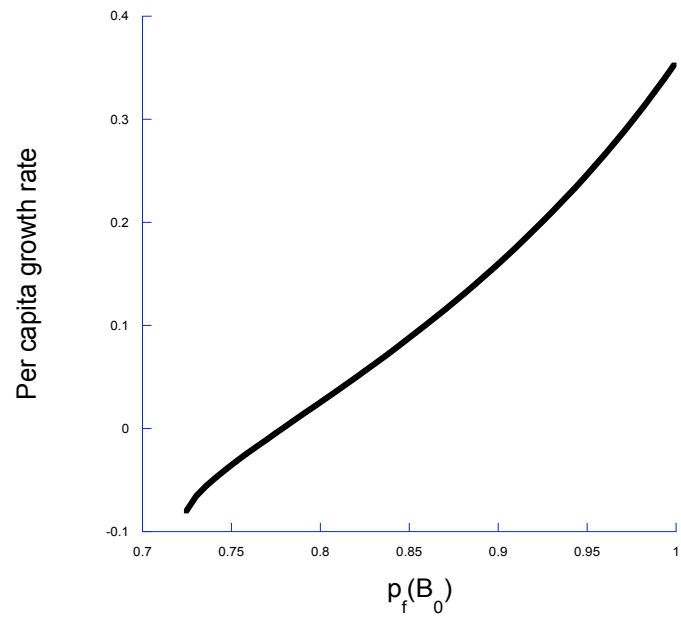




548 Figure 2a.pdf

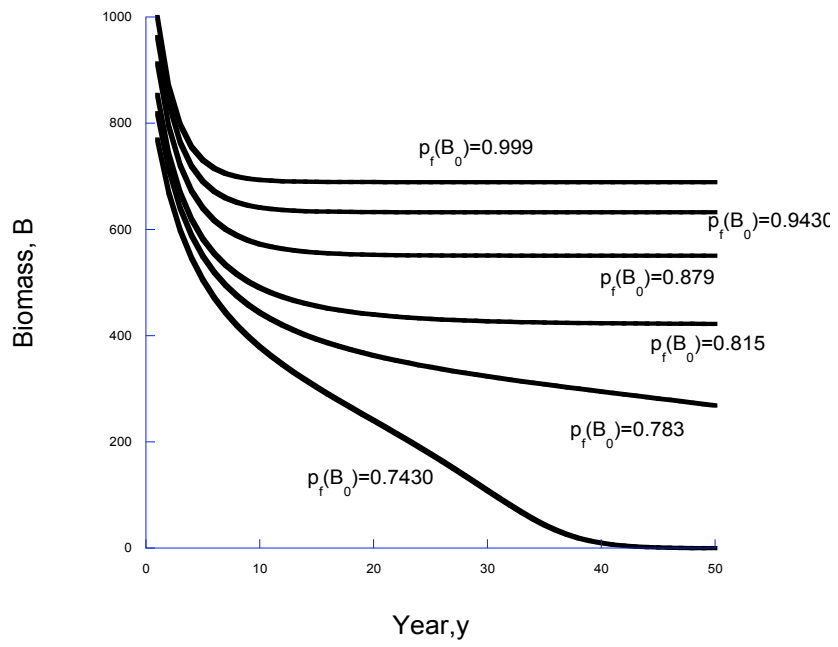


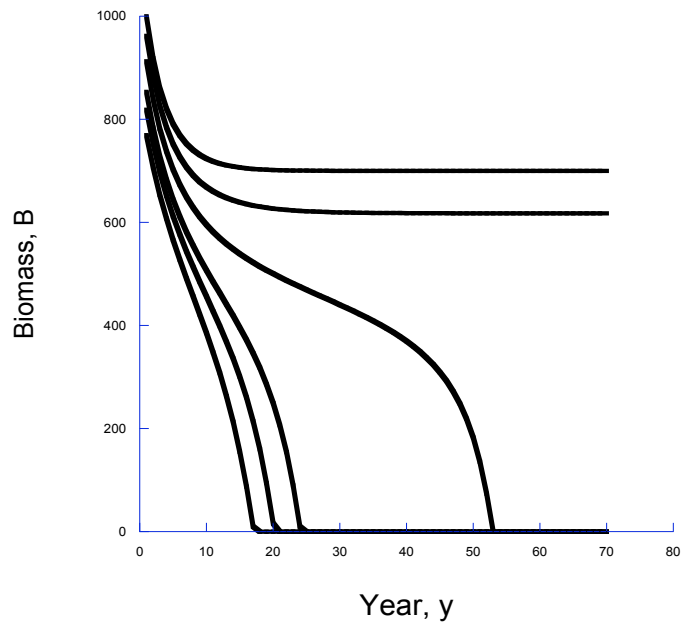
549 Figure 2b.pdf



550 Figure 2c.pdf

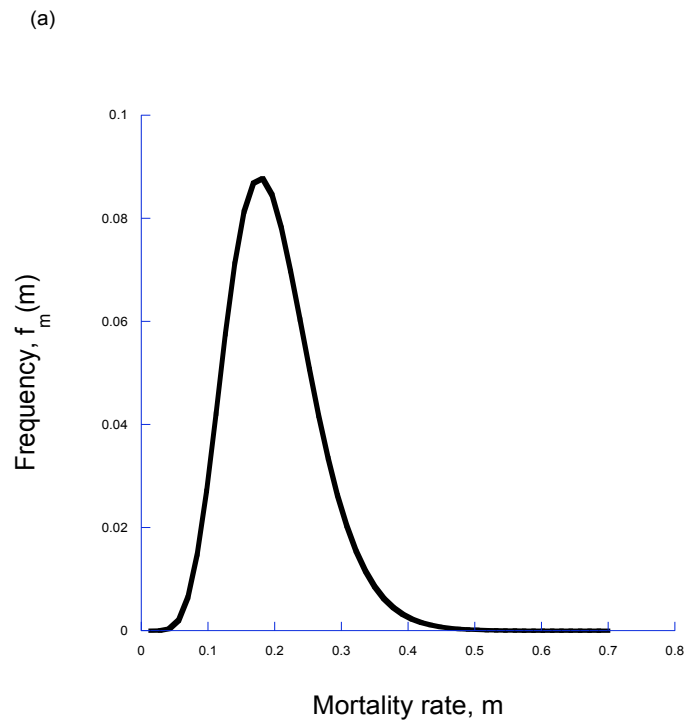
551



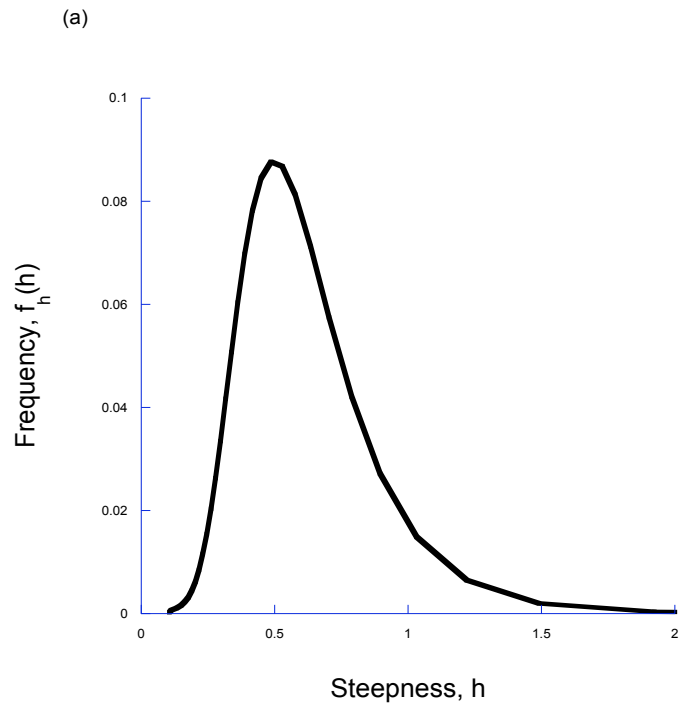


553 Figure 3b.pdf

554



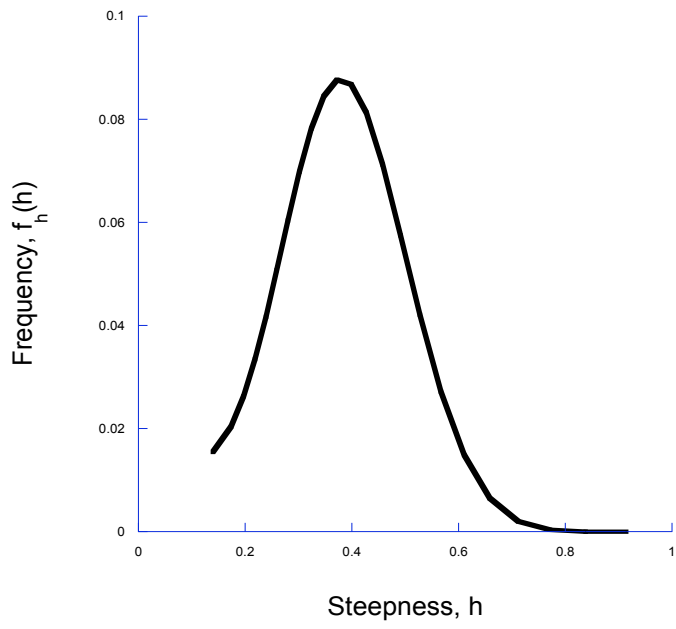
555 Figure 4a.pdf



556 Figure 4b.pdf

Figure 4c.pdf

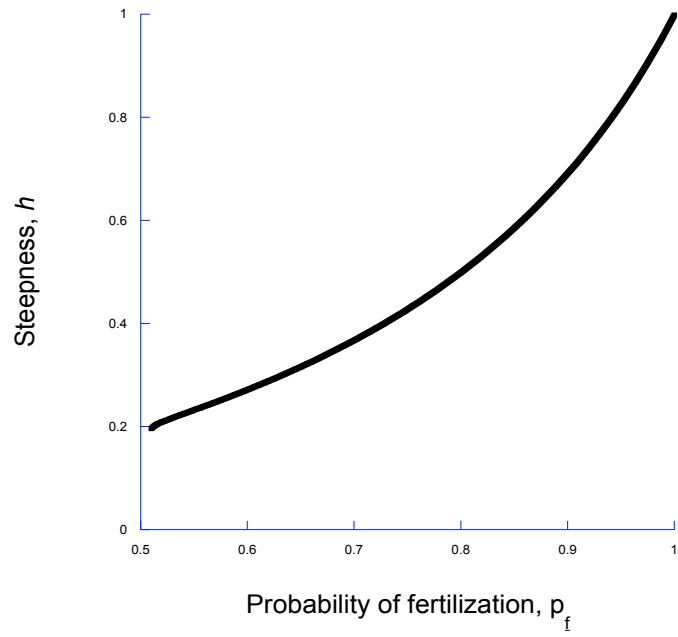
(b)



557

558





559 Figure 5.pdf

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