

1 The Reproductive Biology of Steepness, A Fundamental Metric of  
2 Population Dynamics and Strategic Fisheries Management

3  
4 March 17, 2009

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11 **Abstract**

12 The relationship between the biomass of reproductively mature individuals (spawning stock) and  
13 the resulting offspring added to the population (recruitment), the stock recruitment relationship,  
14 is a fundamental and challenging problem in all of population biology. The steepness of this  
15 relationship is the fraction of unfished recruitment obtained when the spawning stock biomass  
16 is 20% of its unfished level. Since its introduction about 20 years ago, steepness has become  
17 widely used in fishery management, where it is usually treated as a statistical quantity. Here,  
18 we investigate the reproductive biology of steepness, using both unstructured (biomass) and  
19 age-structured models. We show that if one has sufficient information to construct a density  
20 independent population model (maximum per capita productivity and natural mortality for

21 the unstructured case or maximum per capita productivity, natural mortality and schedules of  
22 size and maturity at age for the structured model) then one can construct a point estimate for  
23 steepness. Thus, minimal information about the demography of a cohort leads to inferences  
24 about steepness, which cannot be chosen arbitrarily. If one assumes that individual survival  
25 fluctuates within populations, then it is possible to construct a prior distribution for steepness  
26 from this same minimal demographic information. We develop the ideas for both compensatory  
27 (Beverton-Holt) and over-compensatory (Ricker) stock-recruitment relationships. We illustrate  
28 our ideas with an example concerning bluefin tuna.

## 29 Introduction

30 Understanding the relationship between the biomass of reproductively mature individuals (spaw-  
31 ing stock) and the resulting offspring added to the population (recruitment), the stock recruit-  
32 ment relationship, is a fundamental and challenging problem in all of population biology. For  
33 example, strategic fisheries management requires estimates of biological reference points that  
34 often critically depend upon the nature of the stock-recruitment relationship (Brodziak 2002).  
35 The Beverton-Holt stock recruitment relationship (Beverton and Holt 1957/1993) is widely used  
36 in stock assessments of marine fishery resources and is an important feature of several modeling  
37 packages that are used for stock assessments. The recovery of threatened or endangered pop-  
38 ulations is in large part determined by the resilience of reproduction. In some assessments of  
39 Pacific tuna and billfish stocks, the available data are insufficient to directly estimate spawner  
40 recruitment relationship. In such cases (and others, e.g. Pacific rockfish *Sebastes* spp) it has  
41 become common practice to use the steepness of the stock recruitment relationship in lieu of the  
42 entire relationship.

43 Steepness was introduced by Mace and Doonan (1988), who defined it as the fraction of  
44 unfished recruitment ( $R_0$ ) when the spawning stock biomass is 20% of its unfished level ( $B_0$ ).  
45 They assumed that production follows a Beverton-Holt stock recruitment relationship so that  
46 when spawning biomass is  $B$  the resulting recruitment  $R(B)$  is

$$R(B) = \frac{B}{\alpha + \beta B} \quad (1)$$

47 where  $\alpha$  and  $\beta$  are parameters. In the form of Eqn 1 these parameters have clear, if somewhat  
48 unnatural interpretations. That is  $\frac{1}{\alpha}$  is the maximum per capita production of recruits (i.e., the  
49 limit of  $R(B)B$  for small  $B$ ) and  $R(B)$  approaches  $\frac{1}{\beta}$  as  $B$  increases.

50 If  $B_0$  and  $R_0$  denote the unfished spawning biomass and recruitment at that spawning  
51 biomass and  $h$  denotes steepness (Mace and Doonan (1988) use  $\Delta$ ) then

$$R_0 = \frac{B_0}{\alpha + \beta B_0} \quad (2)$$

$$hR_0 = \frac{0.2B_0}{\alpha + 0.2\beta B_0} \quad (3)$$

52 which can be used to relate  $\alpha$  and  $\beta$  to steepness

$$\alpha = \frac{B_0}{R_0} \frac{1-h}{4h} \quad (4)$$

$$\beta = \frac{5h-1}{4hR_0} \quad (5)$$

53 In the intervening years, a tradition has developed in which one estimates the parameters of  
 54 the unfished stock ( $B_0$  and  $R_0$ ) and specifies the steepness, after which the parameters in Eqn  
 55 1 can be determined from Eqns 4 and 5. In many cases, particularly data poor situations, it is  
 56 common to use plausible values of steepness in the absence of alternative information. This is  
 57 an implicit Bayesian approach, even if it is not acknowledged as such.

58 In other cases, when one assumes that recruitment is mainly determined by the environment,  
 59  $h$  is often set equal to 1. For example, Aires-da-Silva and Maunder (2007), who use a Beverton-  
 60 Holt stock recruitment relationship in the stock assessment of bigeye tuna, write “In practice,  
 61 it is often difficult to estimate steepness because of a lack of contrast in spawning biomass and  
 62 because there are other factors (e.g. environmental influences) that can cause recruitment to  
 63 be extremely variable. For the current assessment, recruitment is assumed to be independent  
 64 of stock size (steepness = 1). There is no evidence that recruitment is related to spawning  
 65 stock size for bigeye in the EPO [Eastern Pacific Ocean] and, if steepness is estimated as a free  
 66 parameter, it is estimated to be close to 1. We also present a sensitivity analysis with steepness=  
 67 0.5” (pg 111). Maunder (2007) makes the same assumption in the stock assessment for yellowfin  
 68 tuna (pg 9), conducts a sensitivity analysis when  $h = 0.75$ , and reports that best estimate when  
 69 treating steepness as a free parameter is  $h = 0.54$ . Clearly, there is a need to understand the  
 70 biology of steepness.

71 Determining the probable value of steepness for marine species is a very important research  
 72 topic. Stock-recruitment steepness is intrinsically related to the resilience of a species to harvest-  
 73 ing and effectively determines the average productivity of fishery resources within a stationary

74 environmental regime. The topic of estimating steepness has been addressed through meta-  
75 analyses of stockrecruitment data for several species and taxa (Myers et al. 1999). For example,  
76 Meyers et al (1999) estimated a family level median steepness for the scombrids (using data  
77 on Atlantic bluefin tuna, bigeye tuna, chub mackerel, Atlantic mackerel, southern bluefin tuna,  
78 and yellowfin tuna) at 0.52 with 20 and 80 percentiles 0.30 and 0.72 respectively; their median  
79 estimate for swordfish *Xiphias gladius* was 0.88. Although the Myers et al. paper was considered  
80 by many to be a breakthrough, the statistical approach was limited to commercially-exploited  
81 species for which there were sufficient data to conduct an assessment. Such species represent a  
82 modest fraction of the potential fishery resources worldwide. Thus, while Myers et al. (1999)  
83 provided a useful empirical basis for developing an informative prior belief about the steepness  
84 of some species for analyzing population dynamics, many other species were not considered and  
85 indeed could not be considered if the analyses were repeated today. Dorn (2002) developed a  
86 hierarchical Bayesian method for advice on harvest rates for west coast rockfish for which he  
87 constructed a prior for steepness and Munch et al (2005) show how to find a posterior distri-  
88 bution for steepness using Bayesian nonparametric methods. He et al (2006) use a stochastic  
89 simulation to construction a prior for steepness based on long-term persistence of the stock.

90 At the end of the day, however, steepness itself must be firmly rooted in the evolutionary  
91 ecology of the species and reproductive biology of a stock must surely be important for its  
92 management (Morgan 2008). More problematic, however, was the lack of an explanatory theory  
93 to predict steepness based on the evolutionary ecology and associated life history parameters  
94 of a species, information which is more readily available and less expensive to generate than  
95 assessment data (there are other concerns with the meta-analyses, lack of representativeness of  
96 the selected stocks, bias towards temperate fishes, lack of independence of stock response to  
97 the impact of environmental variation on recruitment). This paper provides a new look at the  
98 evolutionary ecology of steepness and its theoretical basis. A practical framework for estimating  
99 the probable value of steepness is developed based on life history parameters.

100 We use scombrids to illustrate the framework for estimating the probable value of steepness  
101 because they are commercially-valuable, highly productive, and intensively-exploited fishery  
102 resources for which steepness is often assumed to be unity in stock assessments. This assumption  
103 implies an ecologically optimistic compensatory response in the stock-recruitment dynamics at  
104 low fish stock sizes and can lead to unrealistic expectations about stock resilience at high harvest  
105 rates.

106 In the next section, we begin with the production model, for which one is required to know  
107 maximum per capita productivity and natural mortality to be able to construct steepness. We  
108 then consider the age-structured model, for which one additionally needs to know the schedule of  
109 size and maturity as a function of age. We show the conditions under which the age-structured  
110 result collapses to the production model. We then discuss sources of stochasticity and uncer-  
111 tainty, focussing on variation in mortality rates. We use a Monte Carlo simulation to estimate  
112 maximum productivity from early life history (egg to recruited) stages. We illustrate our analy-  
113 sis using data on bluefin tuna and, in the On-Line Appendix provide data on a variety of other  
114 scombrids. We construct priors for steepness based on reproductive biology and then fit these  
115 to transformed beta-densities. Finally, we discuss extensions of the method.

## 116 **Methods**

117 Although biomass production models are currently out of favor among many fisheries scientists,  
118 we begin with such a model and then introduce the more commonly used age structured model  
119 and show how steepness in the two models is related.

### 120 **The Production Model**

121 We work with a biomass production model, very much in the spirit of MacCall (2002). We let  
122  $B(t)$  denote the total biomass at time  $t$  and assume that the fraction of males at birth is  $r$ ,  
123 so that spawning (i.e. female) biomass at any time is  $(1 - r)B(t)$ . If  $M$  is the rate of natural

124 mortality and  $F$  is the rate of fishing mortality then the dynamics of biomass are

$$\frac{dB}{dt} = \frac{\alpha_p(1-r)B}{1+\beta(1-r)B} - (M+F)B \quad (6)$$

125 where  $\alpha_p$  is subscripted to note *production* and has units of new biomass per existing spawning  
 126 biomass per time, so that it is a rate, comparable to the rate of natural mortality  $M$  or of fishing  
 127 mortality  $F$ . Clearly, if we were just interested in statistical estimation of parameters, rather than  
 128 a more complete biological interpretation,  $1-r$  could be folded into  $\alpha_p$  and  $\beta$ . However, by keeping  
 129  $1-r$  out of the parameters, we are explicitly able to connect total biomass with spawning  
 130 (female) biomass.

131 The steady state biomass at fishing mortality rate  $F$  is

$$\bar{B}(F) = \frac{1}{\beta(1-r)} \left( \frac{\alpha_p(1-r)}{M+F} - 1 \right) \quad (7)$$

132 so that

$$B_0 = \frac{1}{\beta(1-r)} \left( \frac{\alpha_p(1-r)}{M} - 1 \right) \quad (8)$$

133 We thus see that existence of a steady state requires that the dimensionless variable  $\frac{\alpha_p(1-r)}{M} > 1$   
 134 and that density dependence scales the overall size of the steady state. Thus, this parametriza-  
 135 tion in some sense separates the roles of  $\alpha$  and  $\beta$  in determining  $B_0$ . The separation becomes  
 136 even clearer when we consider steepness.

137 According to its definition, steepness is

$$h = \frac{\frac{0.2\alpha_p(1-r)B_0}{1+0.2\beta(1-r)B_0}}{\frac{\alpha_p(1-r)B_0}{1+\beta(1-r)B_0}} \quad (9)$$

138 from which we obtain

$$h = 0.2 \cdot \frac{1 + \beta(1-r)B_0}{1 + 0.2\beta(1-r)B_0} \quad (10)$$

139 However, in light of Eqn 8

$$\beta(1-r)B_0 = \left[ \frac{\alpha_p(1-r)}{M} - 1 \right] \quad (11)$$

140 so that we find

$$h = \frac{\alpha_p(1-r)}{4M + \alpha_p(1-r)} \quad (12)$$

141 which can also be rewritten as

$$h = \frac{\frac{\alpha_p(1-r)}{M}}{4 + \frac{\alpha_p(1-r)}{M}} \quad (13)$$

142 Note that as  $\alpha_p \rightarrow \infty$ ,  $h \uparrow 1$  and as  $\alpha_p(1-r) \downarrow M$ ,  $h \downarrow 0.2$ , as they must. This equation was  
 143 derived by Myers et al (1999) using a discrete-time Ricker model and without considering sex  
 144 ratio. As will be seen, the continuous time production and discrete time age structured models  
 145 are deeply interconnected.

## 146 The Age Structured Model

147 In a standard age-structured model with Beverton-Holt recruitment,  $N(a, t)$  denotes the number  
 148 of individuals of age  $a$  alive at time  $t$ . For the recruited class

$$N(0, t) = \frac{\alpha_s B_s(t)}{1 + \beta B_s(t)} \quad (14)$$

149 where  $B_s(t)$  is the spawning biomass at time  $t$  and  $\alpha_s$  has units of *new individuals/spawning*  
 150 *biomass* and is subscripted with  $s$  to denote that this is a structured model. The spawning  
 151 biomass is

$$B_s(t) = (1-r) \sum_{a=1}^{a_{max}} N(a, t) W_f(a) p_{f,m}(a) \quad (15)$$

152 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  
 153 mature and  $a_{max}$  is the maximum age that an individual can attain (with suitable modification  
 154 of the dynamics of the last age class, we can incorporate a ‘plus’ group into this formulation).

155 For ages  $a > 0$  we have

$$N(a, t) = N(a-1, t-1) e^{-Z(a-1)} \quad (16)$$

156 where  $Z(a-1)$  is the total mortality at age  $a-1$ , given by the sum of natural mortality  $M(a-1)$   
 157 and fishing mortality  $F(a-1)$  at age. Since neither of the mortality rates depend upon time  
 158 the population will reach a steady state and a stable age distribution.



159 We let  $B_0$  and  $R_0$  the values of spawning biomass and associated recruitment in this steady  
 160 state and in the absence of fishing and  $\bar{N}(a)$  the number of individuals of age  $a$  in this steady  
 161 state so that

$$\bar{N}(a) = S(a) \cdot R_0 \quad (17)$$

162 where  $S(a)$  is survival from age 0 to age  $a$ , i.e.  $S(a) = \prod_{i=0}^{a-1} e^{-M(i)}$ . In the steady state, Eqn  
 163 14 becomes

$$R_0 = \frac{\alpha_s B_0}{1 + \beta B_0} \quad (18)$$

164 and where

$$B_0 = (1 - r) \sum_{a=1}^{a_{max}} \bar{N}(a) W_f(a) p_{f,m}(a) \quad (19)$$

165 We now define

$$\bar{W}_f = \sum_{a=1}^{a_{max}} S(a) W_f(a) p_{f,m}(a) \quad (20)$$

166 which has the interpretation of the expected surviving mature biomass per recruit. Since  $\bar{N}(a) =$   
 167  $S(a)R_0$  and  $B_0 = (1 - r)R_0\bar{W}_f$  we have

$$R_0 = \frac{\alpha_s \cdot (1 - r)R_0\bar{W}_f}{1 + \beta \cdot R_0\bar{W}_f} \quad (21)$$

168 which can be seen as an equation for  $R_0$ . In particular, we have

$$\beta(1 - r)R_0\bar{W}_f = \alpha_s(1 - r)\bar{W}_f - 1. \quad (22)$$

169 When spawning stock biomass is 20% of  $B_0$  the recruitment is

$$R = \frac{\alpha_s(1 - r) \cdot 0.2R_0\bar{W}_f}{1 + \beta(1 - r) \cdot 0.2R_0\bar{W}_f} \quad (23)$$

170 and in analogy to Eqns 12, 13 steepness is

$$h = \frac{\frac{\alpha_s \cdot 0.2(1-r)R_0\bar{W}_f}{1 + \beta \cdot 0.2(1-r)R_0\bar{W}_f}}{R_0} \quad (24)$$

171 so that

$$h = \frac{0.2\alpha_s(1 - r)\bar{W}_f}{1 + 0.2\beta(1 - r)R_0\bar{W}_f} \quad (25)$$

172 and in light of Eqn 22

$$h = \frac{0.2\alpha_s(1-r)\bar{W}_f}{1 + 0.2[\alpha_s(1-r)\bar{W}_f - 1]} = \frac{\alpha_s(1-r)\bar{W}_f}{4 + \alpha_s(1-r)\bar{W}_f} \quad (26)$$

173 This equation generalizes Eqn 5 and following of Myers et al (1999).

174 To connect Eqns 13 and 26 note that the production model requires that  $M(a)$  is a constant  
175 ( $M$ ). Then

$$S(a) = e^{-Ma} \quad (27)$$

176 In addition, the production model cannot have age structure, let us assume that we can  
177 replace  $W_f(a)p_{f,m}(a)$  in Eqn 20 by a constant, say  $\bar{W}_{f,m}$ , interpreted as the average biomass of  
178 a spawning female. With this assumption we can rewrite Eqn 20 as

$$\bar{W}_f = \sum_{a=1}^{a_{max}} e^{-Ma}\bar{W}_{f,m} = \bar{W}_{f,m} \frac{1 - e^{-Ma_{max}}}{1 - e^{-M}} \quad (28)$$

179 If  $a_{max}$  is sufficiently large then the numerator in the last expression in Eqn 28 is approximately  
180 1. If  $M$  is not too large, then we can Taylor expand the denominator as  $1 - e^{-M} \approx M$ . Thus  
181  $\bar{W}_f \approx \frac{\bar{W}_{f,m}}{M}$  and Eqn 26 becomes

$$h = \frac{\alpha_s(1-r)\frac{\bar{W}_{f,m}}{M}}{4 + \alpha_s(1-r)\frac{\bar{W}_{f,m}}{M}} \quad (29)$$

182 By defining  $\alpha_p = \alpha_s\bar{W}_{f,m}$  Eqns 13 and 29 are the same.

183 For completeness, in the Appendix we derive the analogue of Eqn 26 for the case of an  
184 over-compensatory recruitment function.

## 185 Accounting for Uncertainty and Stochasticity

186 Eqns 13 and 26 involve the quantities  $\alpha_p, M, r, \alpha_s$  and  $\bar{W}_f$ . We assume that  $W(a)$  is the result  
187 of a model based on von Bertalanffy growth in length so that  $W(a) = c_1 \cdot L(a)^{c_2}$  where  $c_1$  and  
188  $c_2$  are constants and where

$$L(a) = L_\infty(1 - e^{-k(a-a_0)}) \quad (30)$$

189 where  $L_\infty$  is asymptotic size,  $k$  is the growth rate, and  $a_0$  is the (theoretical) age at which size is  
 190 0 or is a parameter that allows us to account for the initial condition  $L(0) = l_0$ . It is possible to  
 191 associate probability distributions with both asymptotic size and growth rate (e.g. Siegfried and  
 192 Sanso 2006) from single set of data or to conduct a meta-analysis on published growth curves  
 193 (see the On-line Appendix for examples of those).

194 Uncertainty in  $M$  for the production model or  $M(a)$  for the age structured model will lead  
 195 to stochasticity in survival trajectories and we focus on such uncertainty here, postponing for  
 196 the future including distributions on life history parameters.

197 First consider the production model. If  $M$  were known with certainty then survival to age  $a$   
 198 is given by Eqn 27. To characterize variation in the rate of natural mortality, we use the gamma  
 199 density (Mangel 2006) so that

$$Pr[m \leq M \leq m + dm] = f(m)dm + o(dm) = \frac{\lambda^\nu}{\Gamma(\nu)} e^{-\lambda m} m^{\nu-1} dm + o(dm) \quad (31)$$

200 where  $o(dm)$  denotes terms that are higher order powers of  $dm$  (ie  $dm^2$  etc). In this formulation  
 201 the expected value of  $M$  is  $E(M) = \bar{M} = \frac{\nu}{\lambda}$  and the coefficient of variation is  $CV(M) = \frac{1}{\sqrt{\nu}}$ .

202 Given that  $M$  has a probability distribution, imagine drawing a sequence  $m_0, m_1, , m_2, m_3, \dots, m_{a-1}$   
 203 from the gamma density given by Eqn 31. From those, we can construct a random variable  $\tilde{S}(a)$   
 204 for survival to age  $a$  according to

$$\tilde{S}(a) = \prod_{i=0}^{a-1} e^{-m_i} \quad (32)$$

205 In this way we can generate a family of survival trajectories that account for the uncertainty in  
 206 natural mortality, and also allow for individuals experiencing differences in natural mortality at  
 207 age.

208 Although the assumption of a constant rate of natural mortality is commonly used in stock  
 209 assessments, it cannot apply across the range of a fish's life – where individuals may be prey  
 210 when young and predators when older. When such data are available, they should be used. For  
 211 example, for yellowfin and bigeye tuna Hampton (2000) shows classical trajectories of mortality  
 212 as a function of age: a rapid decline from the youngest age class a leveling out of mortality and

213 then an increase of mortality with increasing age (also see Chen and Watanabe 1989). This  
214 suggests that we replace constant natural mortality by a function of size and age, as in

$$M(l, a) = m_0 + \frac{m_1}{l} + m_2 \cdot a \quad (33)$$

215 where  $L(a) = l$  is length at age  $a$  and the parameters  $m_0$ ,  $m_1$  and  $m_2$  are to be determined. Such  
216 data, in which age and length are treated separately, do not exist to our knowledge. However,  
217 if length is a known function of age, then  $M(l, a) = M(l(a), a) = M(a)$  only. We take these as  
218 the means for the probability density Eqn 31 and assume that the same value of  $\nu$  applies to  
219 the case of constant mortality or age dependent mortality.

220 Given the distribution of age-dependent mortality, we follow a prescription similar to the  
221 one leading to Eqn 32 to develop survival to age functions that take size dependent natural  
222 mortality into account and these can be used in the age structured model.

## 223 **The Early Life History**

224 In almost all fishery population dynamics models, the early life history of the fish is treated  
225 separately from the later ages (the notion being that the von Bertalanffy parameter  $a_0$  captures  
226 the early life history). However, a biological interpretation of steepness requires that we consider  
227 the early life history in more detail. Suppose that a fish is recruited to the population dynamics  
228 model at mass  $W(0)$  after a juvenile period of  $d_l$  days. We let  $w_l(d)$  denote the wet mass of the  
229 larvae on day  $d$ .

230 Assuming exponential growth during this phase (Kaji et al 1996, Shoji et al 2005) we have

$$w_l(d) = w_l(0) \cdot \exp(k_l \cdot d) \quad (34)$$

231 where  $k_l$  is determined so that the individual grows from  $w_l(0)$  to  $W(0)$  in  $d_l$  days.

232 To compute the expected mass that an egg contributes to future biomass, we need to find  
233 the survival during the period before being recruited to the population dynamics model. We  
234 use McGurk (1986) to characterize mortality. In particular, we let  $M_l(w_d)$  denote the daily

235 mortality rate of an individual of dry mass  $w_d$ . McGurk (1986, Eqn 7) reports that if  $w_d$  is  
 236 less than  $w_c = 0.00504$  g then

$$M_l(w_d) = 2.2 \cdot 10^{-4} \cdot w_d^{-.85} \quad (35)$$

237 and otherwise (McGurk 1986, Eqn 2)

$$M_l(w_d) = 5.26 \cdot 10^{-3} \cdot w_d^{-.25} \quad (36)$$

238 Eqn 35 applies to fish eggs and larvae and Eqn 36 to juvenile fish (McGurk 1986, Figure 1). Fish  
 239 eggs and larvae typically have a different hydration factor than juveniles. We use the general  
 240 values reported by Kamler (1992) of a 65% hydration factor for eggs and larvae and 85% for  
 241 juveniles and convert the crossing value of dry weight,  $w_c$  to a wet weight value by assuming the  
 242 weight wet crossing is  $4.76 \cdot w_c$  (obtained by averaging the wet weights based on 65% or 85%  
 243 hydration).

244 Larval survival to day  $d$ ,  $S_l(d)$  (with  $S_l(0) = 1$ ) is

$$S_l(d) = S_l(d-1) \cdot \exp(-M_l(w_d)) \quad (37)$$

245 Because survival may be a very small number, it is also useful to consider the accumulated  
 246 mortality  $M_a(d)$  to day  $d$ . We have  $M_a(0) = 0$  and

$$M_a(d) = M_a(d-1) + M_l(w_d) \quad (38)$$

247 Thus, we compute dry weight from  $w_l(d-1)$  and then use Eqn 35 or 36 as appropriate.

## 248 **Interpreting $\alpha_p$ and $\alpha_s$**

249 We are now provide an interpretation of  $\alpha_p$  and  $\alpha_s$ . First consider  $\alpha_p$ . Note that

$$\frac{\alpha_p(1-r)B}{1+\beta(1-r)B} = \alpha_p(1-r)B \cdot \frac{1}{1+\beta(1-r)B} \quad (39)$$

250 Thus  $\alpha_p B$  is the maximum rate at which biomass is added before density dependence acts and

251  $\frac{1}{1+\beta(1-r)B}$  is the fraction of that biomass which survives to increase the population.

252 To find  $\alpha_p$ , consider a female fish of age  $a$ , with mass  $W(a)$ , length  $L(a)$ , and probability of  
 253 being mature  $p_{f,m}(a)$ . Suppose that  $\mathcal{E}(W(a))$  is the batch fecundity of this individual and  $s_f$  is  
 254 the spawning frequency. Each egg contributes  $W(0) \cdot S_l(d_l)$  to new biomass so that

$$\alpha_p = \frac{\mathcal{E}(W(a)) \cdot W(0) \cdot S_l(d_l) \cdot s_f}{W(a)} \quad (40)$$

255 (In practice, since  $\mathcal{E}(w)$  will be a typically large number and  $S_l(d_l)$  a small number, it is wiser  
 256 to compute their product as  $\mathcal{E}(w) \cdot S_l(d_l) = \exp(\log(\mathcal{E}(w) - M_a(d_l)))$ ).

257 In order to implement Eqn 40, we employ a simulation algorithm. Imagine  $K$  populations of  
 258 simulated fish, with  $N$  female fish in each population. We denote the age of the  $n^{th}$  fish in the  
 259  $k^{th}$  population by  $a_{n,k}$ . It is found by choosing a uniformly distributed random variable  $\tilde{U}_{nk}$  and  
 260 then setting  $\tilde{S}(a_{n,k}) = \tilde{U}_{nk}$ . For the case of constant mortality  $M$ , this equation is easily solved  
 261 and we find  $a_{n,k} = -\frac{1}{M} \log(\tilde{U}_{nk})$ . For the case of age-dependent natural mortality we first find  
 262 the age  $j$  that makes  $\sum_{a=0}^j M(a) < \log(\tilde{U}_{nk}) < \sum_{a=0}^{j+1} M(a)$ ;  $a_{n,k}$  is then this age plus a linearly  
 263 interpolated increment between the two years. When employing these algorithms, for the case of  
 264 constant natural mortality, each population  $k$  experienced a different value of  $m$ , drawn from the  
 265 gamma density in Eqn 31; for the case of age dependent mortality, each population experienced  
 266 a series of values of  $m_0, m_1, \dots, m_{a-1}$ , drawn from age-specific gamma densities.

267 Once we know the age of the fish, we know its length, weight, and probability of being  
 268 mature. It is then possible to compute  $\alpha_p(n, k)$  from Eqn 40. The total biomass in population  
 269  $k$  is  $\sum_{n=1}^N W(a_{n,k})$  and the total reproduction is  $W(0) \cdot S_l(d_l) \cdot s_f \sum_{n=1}^N \mathcal{E}(W(a_{n,k}))$ . Thus the  
 270 estimate for  $\alpha_p$  in this population is

$$\tilde{\alpha}_p(k) = W(0) \cdot S_l(d_l) \cdot s_f \frac{\sum_{n=1}^N \mathcal{E}(W(a_{n,k}))}{\sum_{n=1}^N W(a_{n,k})} \quad (41)$$

271 which is a random variable because  $a_{n,k}$  is a random variable. Note that the units of  $\alpha_p$  are *new*  
 272 *biomass per spawning biomass* while those of  $\alpha_s$  are *new individuals per spawning biomass*. Thus  
 273 with  $W(0)$  removed, Eqn 40 gives us an estimate  $\alpha_s$  and with  $W(0)$  removed, Eqn 41 provides  
 274 an estimate of  $\tilde{\alpha}_s(k)$ . Note that the sex ratio would appear in both numerator and denominator  
 275 of Eqn 41, thus cancelling, so that we can think of the simulation as drawing only female fish.

Eqns 13 and 43 (or Eqn 26 and the modification of Eqn 43 for the age structured model) allow us to generate a frequency distribution for steepness based on the  $K$  populations (we use  $K = 200$  for computation) of  $N$  fish (we also use  $N = 200$  for computations). To create the frequency distribution, we discretize values of steepness between 0.2 and 1.0 in increments of 0.013. Repeating the process summarized in Eqns 13 or 26, and 41 multiple times allows us to obtain multiple versions of the frequency distribution for steepness. Since steepness ranges between 0.2 and 1, it is natural to fit the frequency distribution of steepness to a transformed beta density (Mangel 2006). To do this, we introduce the variable  $y = 1.25 \cdot h - 0.25$  which ranges from 0 to 1 as steepness ranges from 0.2 to 1.0. Thinking of steepness now as a random variable,  $\tilde{h}$ , the transformed variable also becomes one  $\tilde{y}$  and

$$E[\tilde{y}] = 1.25 \cdot E[\tilde{h}] - 0.25 \quad (42)$$

$$Var[\tilde{y}] = 1.5625 \cdot Var[\tilde{h}] \quad (43)$$

If  $\tilde{y}$  follows a beta density with parameters  $a_\beta, b_\beta$ , so that its probability density is

$f_\beta(y) = \frac{\Gamma(a_\beta + b_\beta)}{\Gamma(a_\beta)\Gamma(b_\beta)} y^{a_\beta - 1} (1 - y)^{b_\beta - 1}$ , and if we introduce the parametrizations (Dorazio and Royle 2003)  $\mu_\beta = \frac{a_\beta}{a_\beta + b_\beta}$  and  $\tau_\beta = a_\beta + b_\beta$  then

$$E[\tilde{y}] = \mu_\beta \quad (44)$$

$$Var[\tilde{y}] = \frac{\mu_\beta \cdot (1 - \mu_\beta)}{\tau_\beta + 1} \quad (45)$$

We thus obtain numerical values for  $\mu_\beta$  and  $\tau_\beta$  from Eqns 42-45 and then determine the values of the beta density from  $a_\beta = \tau_\beta \cdot \mu_\beta$  and  $b_\beta = \tau_\beta \cdot (1 - \mu_\beta)$ .

## An Example With Bluefin Tuna

To illustrate our ideas, we use the parameters reported in Bayliff (1994) for northern bluefin tuna. Bayliff (1994) estimates natural mortality to have mean value  $\overline{M} = 0.276$  and that the 90% confidence interval for mortality is [0.16,0.471]. Anonymous (2008) give age dependent mortality

295  $M(a)$  for bluefin tuna:  $M(0) = 1.6$ ,  $M(1) = 0.46$ ,  $M(2) = 0.27$ ,  $M(3) = 0.2$  and  $M(a) = 0.12$  for  
296  $a \geq 4$ .

297 We use von Bertalanffy growth (Eqn 30) with the parameters that Bayliff (1994) cites from  
298 Yukinawa and Yabuta (1967):  $L_\infty = 320.5 \text{ cm}$ ,  $k = .1035 \text{ yr}^{-1}$ , and  $a_0 = -0.7034 \text{ yr}$ . We assume  
299 the length weight allometry  $W(a) = .001 L(a)^{2.4}$ . These values produce a fish that is about 215  
300  $\text{cm}$  and 400  $\text{kg}$  at age 10 (see results for more details). We assume that the probability that a  
301 fish is mature at age  $a$  is

$$p_m(a) = \frac{e^{\frac{a-a_{50}}{\sigma_m}}}{1 + e^{\frac{a-a_{50}}{\sigma_m}}} \quad (46)$$

302 where  $a_{50}$  is the age at which 50 percent of a cohort is mature. We choose  $a_{50}=5$ .

303 For the early life history, we use an initial egg wet mass of 0.00035  $g$ , which corresponds to  
304 an egg radius of about 0.5  $\text{mm}$  and assumes neutral buoyancy at  $25^\circ \text{C}$  and assume 256 days  
305 [corresponding to the value of  $a_0$ ] to  $W(0)=1.76 \text{ kg}$ . For spawning information, we use Chen et  
306 al (2006). Batch fecundity at length  $L$  is

$$\mathcal{E}(L(a)) = 3.24 \cdot 10^5 \cdot L - 5.21 \cdot 10^7 \quad (47)$$

307 Spawning frequency is every 3.3 days during the spawning season, which is 6 weeks from late  
308 April to mid-June.

## 309 Results

310 Using Bayliff's (1994) data, we find that  $\nu = 9.7$  for the probability density in Eqn 31. The  
311 resulting probability density (Figure 1a) is peaked close to the mean and relatively symmetric,  
312 although there is a somewhat wider right hand tail. There is noticeable variation in survival  
313 determined by Eqn 32 (Figure 1b) and especially at the oldest ages where we expect fish to be  
314 the biggest and most productive (Figure 1c). When we do the same assuming age dependent  
315 mortality, we generate a series of probability densities for mortality rate (Figure 1d) which then



316 show more variation in survival (Figures 1e,f). For the von Bertalanffy growth parameters given  
317 above, length at age is nearly a linear function as Bayliff (1994) noted, and the inflection point  
318 in mass at age occurs very early in the life of a tuna. The probability that an individual is  
319 mature ranges from about 20% at age 4 to nearly 100% at age 8.

320 In Figure 2, we show the probability distributions obtained for 200 replicate runs of our  
321 method using the production model (panel a) or the age structured model (panel b). The  
322 production model shows a relatively tight distribution and an excellent fitted beta density, with  
323 a peak around  $h = 0.85$  and all of the probability in about  $0.8 \leq h \leq 0.92$ . The situation changes  
324 noticeably when the age-structured model is used. Now, nearly the entire range of steepness is  
325 possible and the fitted beta density, while generally doing well, misses the peak.

## 326 Discussion

327 In this paper, we have shown how to formulate steepness for a production model (Eqn 13) such  
328 as might be used in the management of data-poor fisheries and for an age-structured model  
329 (Eqn 26) for a fishery that is richer in data. We have also shown (Eqns 27-29) how the two  
330 formulations are connected by making simplifying assumptions about the age structure. For data  
331 poor fisheries, in the absence of an empirical estimate of the natural mortality rate, the value  
332 for the mean of natural mortality rate for could be obtained estimated from basic life history  
333 information like the age of maturity ( $a_m$ ) and the growth coefficient ( $k$ ) assuming Beverton-Holt  
334 life history invariants (Jensen 1996, Mangel 2006, Mangel et al 2007).

335 By assuming that annual mortality is a random variable with a gamma density, we have  
336 been able to derive our main result – a prior for steepness that can be fit with a transformed  
337 beta density (Figure 2). Clearly fluctuations in annual mortality is only one source of variation.  
338 Our results are conditioned, on asymptotic size  $L_\infty$ , growth rate  $k$ , and the mortality rate in  
339 the early life history. A fuller analysis would construct prior distributions on each of these,  
340 using the kind of data described in the On-Line Appendix, to thus construct an even fuller

341 probability distribution for steepness. He et al (2006) used an evolutionary persistence principle  
 342 for a production model as a means of constructing a prior for steepness and showed that low  
 343 values of steepness are unlikely because of the low probability that a population with such low  
 344 values can persistence in the face of recruitment fluctuations. Our result for the production  
 345 model could be combined with that of He et al (2006), which requires an assumption about the  
 346 rate of natural mortality, but only in a qualitative way since He et al (2006) did not assume  
 347 fluctuations in the rate of natural mortality.

348 Perhaps most importantly, Eqns 20 and 26 (and 53) show that as soon as we are able to  
 349 develop a demographic model for the survival and reproduction of a cohort (Eqn 20) we are  
 350 able to obtain a point estimate for steepness (Eqn 26 or 53). That is, an important message  
 351 is that steepness is endogenous to the demography of the stock; it cannot be chosen arbitrarily  
 352 This point is buried in other work on steepness, but needs to be made explicit: demographic  
 353 information about the fate of a cohort also tells us about the reproductive resilience of the  
 354 population.

355 This is of more than academic or theoretical interest. Many fish stocks are managed on the  
 356 basis of reduction in Spawning Per Recruit (*SPR*). That is, if we define Lifetime Egg Production  
 357 when fishing mortality is  $F$  as  $LPR(F)$  then

$$SPR(F) = \frac{LEP(F)}{LEP(0)} = \frac{\sum_{a=0}^{a_{max}} e^{-\sum_{a'=0}^{a-1} (M(a)+F(a))} W_f(a) p_{f,m}(a)}{\sum_{a=0}^{a_{max}} e^{-\sum_{a'=0}^{a-1} M(a)} W_f(a) p_{f,m}(a)} \quad (48)$$

358 where  $F(a)$  is the product of  $F$  and a measure of selectivity of the fishery for individuals of age  
 359  $a$ . The typical management strategy is to choose  $F_{x\%}$  so that  $SPR(F_{x\%}) = x/100$  but such  
 360 management has often had to be readjusted to be more conservative (ie to increase  $x$  because  
 361 of declines of stocks). Note that Eqn 48 includes all of the information needed to obtain a point  
 362 estimate for steepness, so we are thus able to ask if the *SPR* chosen for management is consistent  
 363 with the reproductive resilience implied by the steepness. Most importantly, assuming steepness  
 364  $h = 1$  to assess intensively exploited resources is not a good idea and cannot be consistent  
 365 with the demographic information. Using yield-based biological reference points that implicitly

366 assume a steepness of  $h = 1$ , e.g.,  $F_{MAX}$  or  $F_{0.1}$  is also a bad idea.

367 The structured model can clearly be extended to species that change sex, e.g., protogynous  
368 hermaphrodites such as the Hawaiian grouper Hapuùpuù (*Epinephelus quernus*), California  
369 sheephead (*Semicossyphus pulcher* (Ayres, 1854)), black sea bass (*Centropristis striata* (Lin-  
370 naeus, 1758)), gag grouper (*Mycteroperca microlepis* (Goode and Bean, 1879)), or red grouper  
371 (*Epinephelus morio* (Valenciennes, 1828)) by adjustment of the population dynamics and ma-  
372 turity schedule (Alonzo and Mangel 2004, 2005; Alonzo et al 2008). Both the production and  
373 structured model can be extended to account for changes in steepness due to fluctuating environ-  
374 mental regimes, such as the California Current System – and Eqns 13 and 26 provide direction  
375 on what variables should be measured. As described in the Appendix, our approach immedi-  
376 ately extends to species that may exhibit overcompensatory stock-recruitment dynamics, such  
377 as Dungeness crab (*Cancer magister*).

378 For the example of bluefin tuna that we considered, the results are consistent with the  
379 expectation that steepness is relatively high for this stock and that environmental forcing is  
380 an important determinant of recruitment strength. Such environmental forcing can be built  
381 into the early life history through fluctuations in mortality rate and into productivity through  
382 fluctuations in egg production. There is much more to be done by taking a biological rather  
383 than statistical view of steepness.

## 384 **Acknowledgments**

385 This work was mainly supported by the Pacific Islands Fishery Science Center through grant  
386 XX to MRAG Americas. The final stages were supported by the Center for Stock Assessment  
387 Research, a partnership between the Southwest Fisheries Science Center Santa Cruz Labora-  
388 tory and the University of California Santa Cruz. For comments on previous versions of the  
389 manuscript we thank...

## 390 Appendix: The Over-compensatory Recruitment Function

391 In this Appendix, we derive the analogue of Eqn 26 for the case of an over-compensatory  
 392 recruitment function. That is, we replace Eqn 14 by

$$N(0, t) = \alpha_s B_s(t) e^{-\beta B_s(t)} \quad (49)$$

393 where  $B_s(t)$  is still given by Eqn 15 and the age dependent dynamics in Eqn 16 apply. Note  
 394 that we could generalize even further (but will not do so) by writing

$$N(0, t) = \alpha_s B_s(t) f_d(B_s(t), \beta) \quad (50)$$

395 where  $f_d(z, \beta)$  characterizes the nature of the density dependence and is a decreasing function  
 396 of  $z$  and  $\beta$ .

397 In the steady state, we have

$$R_0 = \alpha_s B_0 e^{-\beta B_0} \quad (51)$$

398 and where  $B_0$  is still given by Eqn 19. We solve Eqn 51 for  $\beta B_0$ ; noting that  $B_0 = (1 - r) R_0 \bar{W}_f$   
 399 allows us to cancel  $R_0$  from both sides and obtain

$$\beta B_0 = \log(\alpha_s (1 - r) \bar{W}_f) \quad (52)$$

400 Steepness is now

$$h = \frac{\alpha_s (1 - r) 0.2 B_0^{-0.2 \beta B_0}}{\alpha_s (1 - r) B_0 e^{-\beta B_0}} = 0.2 e^{0.8 \beta B_0} \quad (53)$$

401 Substituting Eqn 52 into the final term on the right hand side of Eqn 53 we obtain

$$h = 0.2 (\alpha_s (1 - r) \bar{W}_f)^{0.8} \quad (54)$$

402 Note that now steepness no longer ranges from 0.2 to 1, but rather from 0.2 to  $\infty$ ; which was  
 403 noted by Steve Munch in conversation with one of us (MM) many years ago. This can be  
 404 understood as follows. The function  $b e^{-\beta b}$  is maximized at  $b^* = \frac{1}{\beta}$ , so that for values of  $B_0 > b^*$ ,  
 405  $R_0$  declines. A large value of  $B_0$  may thus imply a small value of recruitment, and reducing the

406 stock to 20% of that value may increase recruitment by many multiples of the value at  $B_0$ . This  
407 is a small, but perhaps under-appreciated point.

408 For the more theoretically inclined reader, we note that if we use Eqn 50, then steepness is

$$h = 0.2\alpha_s(1-r)\bar{W}_f f\left(0.2f^{-1}\left(\frac{1}{\alpha_s(1-r)\bar{W}_f}\right)\right) \quad (55)$$

409 where  $f^{-1}$  is the inverse function of the density dependent term on the right hand side of Eqn  
410 50, ie  $f(f^{-1}(x)) = f^{-1}(f(x)) = x$ .

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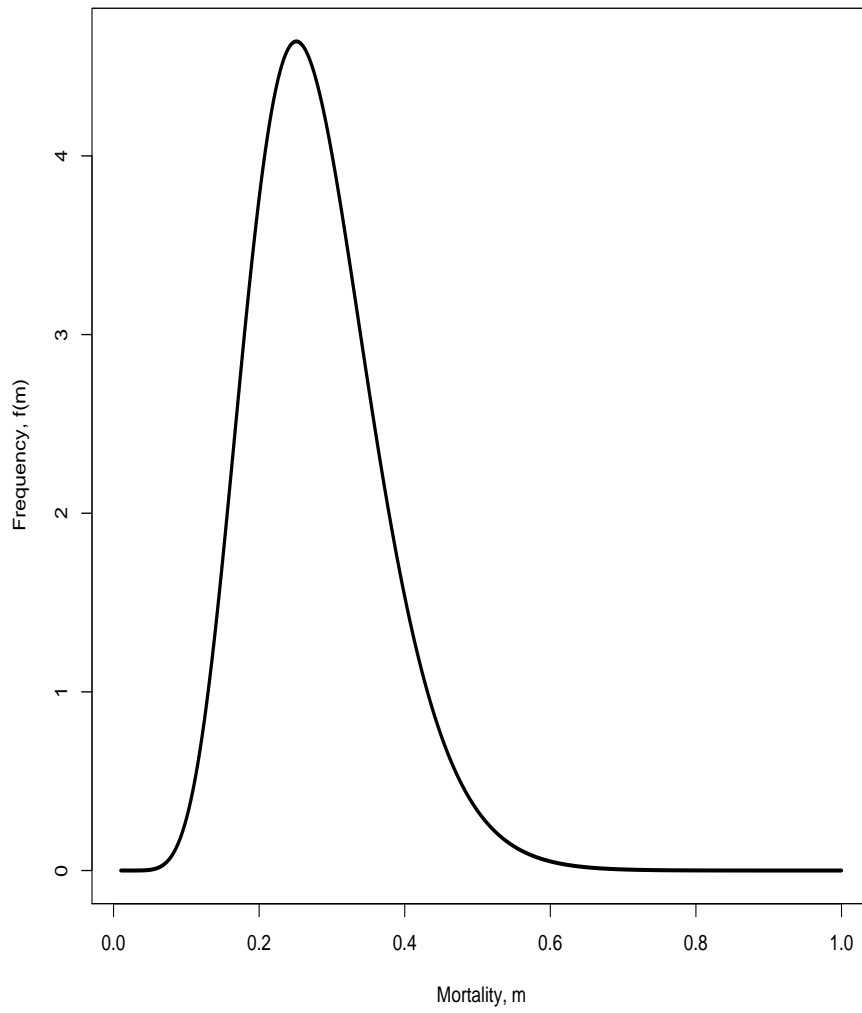
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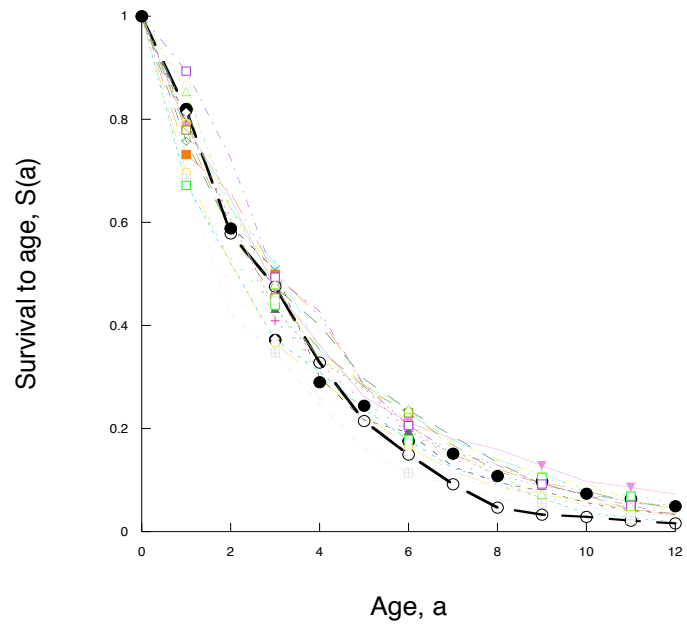
504 **Captions for Figures**

505 Figure 1 a) The gamma frequency distribution  $f(m)$  for constant natural mortality estimated  
506 from Eqn XXX and b,c) sample survival trajectories created by assuming annual mortality is  
507 drawn from that distribution on a yearly basis. d) If we assume age dependent mortality with  
508 the same coefficient of variation as that used in panel a), then there is a family of probability dis-  
509 tributions for the rate of mortality, depending upon age  $a$  and this introduces more variability in  
510 survival to age (panels e,f). Regardless of whether we use constant or age dependent mortalities,  
511 the consequence is variation in survival, which will then feed into variation in steepness.

512 Figure 2. We used Eqn 41 to simulate 200 times, 200 populations, each with 200 fish. From  
513 that we can construct an empirical frequency distribution, for which we show the mean (solid  
514 line) and standard deviation (error bars) and then estimate the parameters for a beta density  
515 (Eqns 42-45). In panel a) we show the results for the production model and in panel b) the  
516 results for the age-structured model.

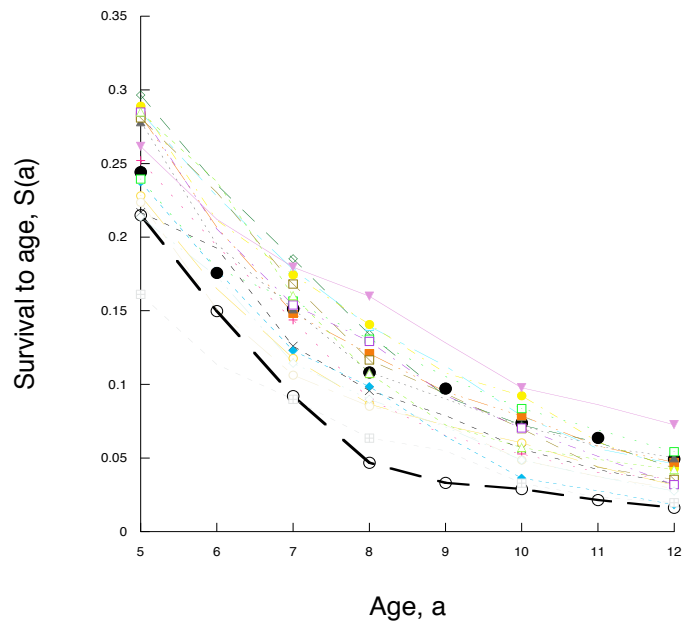


517 Figure 1a.pdf

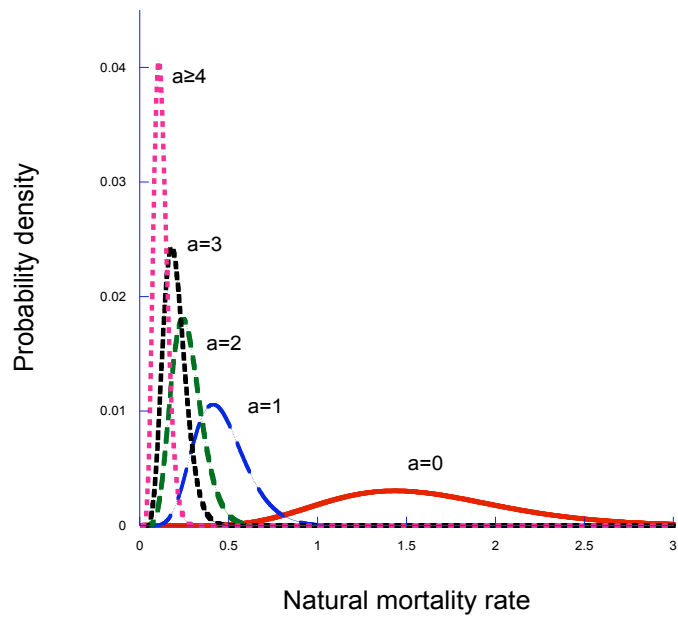


518 Figure 1b.pdf

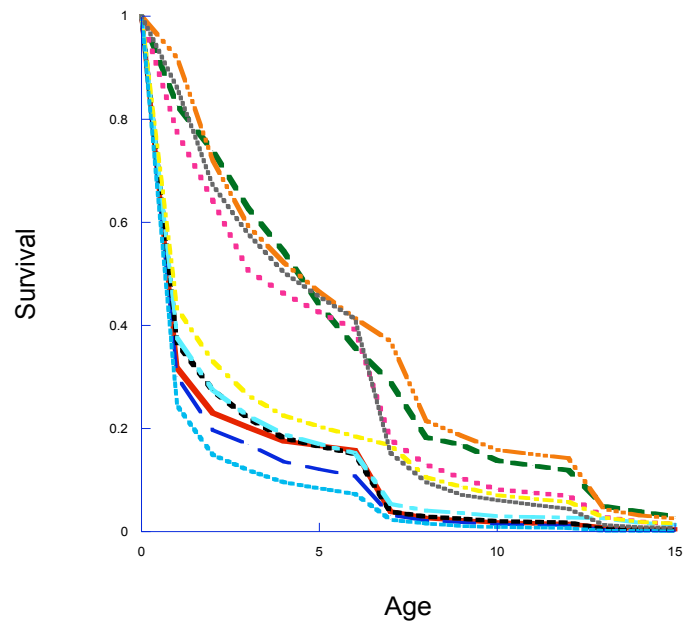
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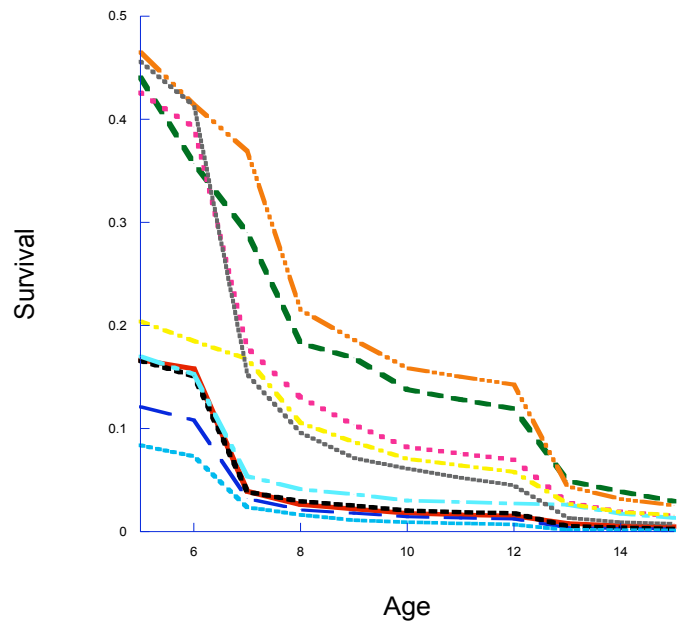
520 Figure 1c.pdf



521 Figure 1d.pdf

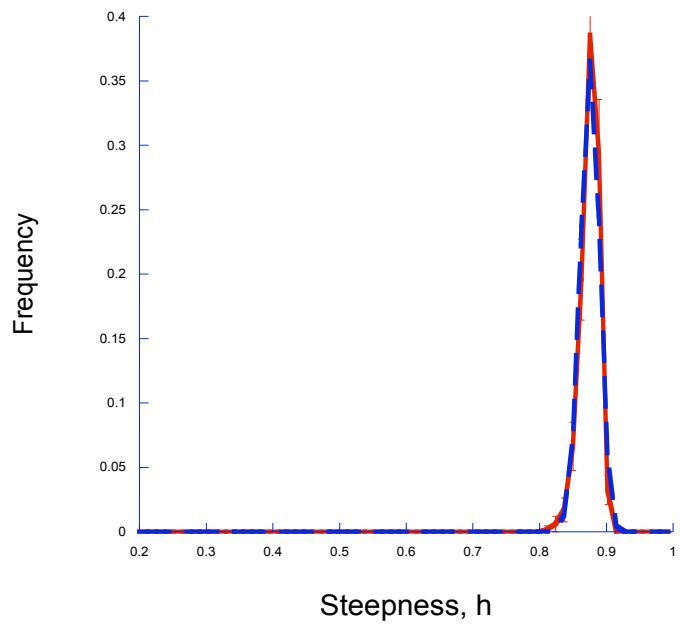


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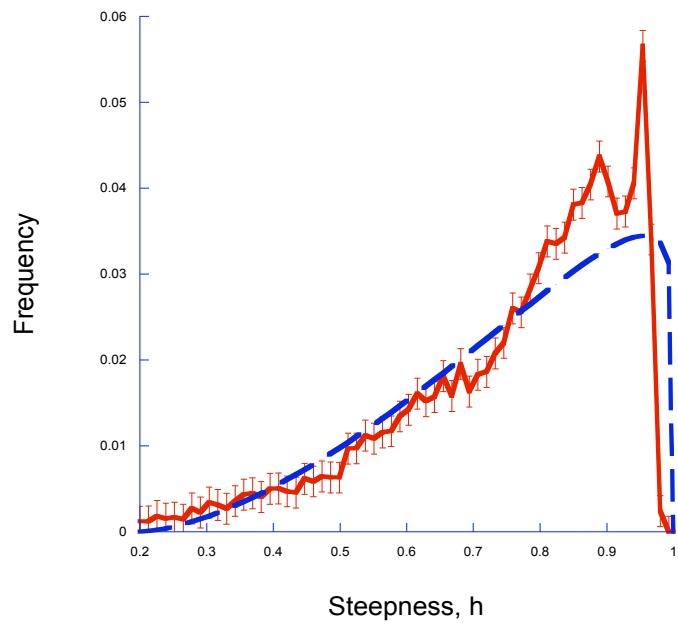
523 Figure 1f.pdf

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525 Figure 2a.pdf





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