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

September 21, 2010

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Abstract

We update recent work on the scientific inference and reproductive biology of steepness in three directions. First, we show how variation in natural mortality can be included in the formula for steepness, for both a biomass dynamics and age-structure models. We do this using the delta-method, so that only the mean and covariance of natural mortality rates appear in the characterization of steepness. Second, we show how to generalize the previous methods for cases in which the stock recruitment relationship is depensatory or has an Allee effect: as spawning population falls below a certain level, per capita reproduction starts to fall, rather than approach
a constant. We generally assume that the mechanism of depensation is imperfect fertilization
(and thus develop a two-sex generalization of our previous work) and determine steepness in
this case for both a biomass production model and an age-structured model and explore the
implications of such depensatory reproduction on the response of stocks to harvesting. We
briefly discuss how an increase in mortality as population size declines (as has been suggested
for penguins) could also be a mechanism for depensation. Third, we describe an improved
method for computing the maximum per capita reproduction in the age-structured model, and
show how the equivalent for the biomass dynamics model is computed.

Introduction

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

Mangel et al (2010) also assumed that as the size of the spawning population declined the
maximum per capita reproduction approached a positive constant, for example in the way that
\[ \frac{1 - \exp(-\alpha S)}{S} \] approaches \( \alpha \) as \( S \rightarrow 0 \). A population exhibits an Allee effect or a depensatory SRR
if per capita reproduction declines as the size of the population falls below a certain level (Fowler
and Baker 1991; Courchamp et al 2008, Gregory et al 2010). In fishery science, these effects are
commonly called depensation (see Iles 1994, Liermann and Hilborn 2001, Gascoigne and Lipcius
2004 for review). Since many fish, seabird, and marine mammal populations may in principle
exhibit a depensatory SRR, we show how the methods of Mangel et al. (2010) can be extended for those kinds of SRRs. In doing so, we learn a variety of interesting qualitative properties of such systems when stressed by fishing mortality (or incidental mortality for seabirds or marine mammals). To do this, we develop an explicit two sex model for the case of a structured population. Finally, we describe an improved version of the stochastic simulation used by Mangel et al. (2010) to compute maximum per capita reproduction.

**Review of The Approach**

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

**The Production Model**

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

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

(1)

where $\alpha_p$ is subscripted to note production and has units of new biomass per existing spawning (female) biomass per time, so that it is a rate, comparable to the rate of natural mortality $M$.

The steady state biomass is

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

(2)

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

\[ h = \frac{0.2 \alpha_p (1-r) B_0}{1+0.2 \beta B_0} \]  \hspace{1cm} (3)

from which we obtain

\[ h = 0.2 \cdot \frac{1 + \beta B_0}{1 + 0.2 \beta B_0} \]  \hspace{1cm} (4)

However, in light of Equation 2

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

so that we find

\[ h = \frac{\alpha_p (1-r)}{4M + \alpha_p (1-r)} \]  \hspace{1cm} (6)

which can also be rewritten as

\[ h = \frac{\alpha_p (1-r)}{4 + \frac{\alpha_p (1-r)}{M}} \]  \hspace{1cm} (7)

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

\[ h = 0.2 \left( \frac{\alpha}{M} \right)^{0.8} \]  \hspace{1cm} (8)

**The Age-Structured Model**

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

\[ B_s(t) = \sum_{a=1}^{a_{max}} N_f(a,t) W_f(a) p_{f,m}(a) \]  \hspace{1cm} (9)

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 mature and \( a_{max} \) is the maximum age that an individual can attain (with suitable modification of the dynamics of the last age class, we can incorporate a ‘plus’ group into this formulation).
If we assume that egg production is proportional to biomass then the recruited class numbers are

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

\[
N_m(0, t) = \frac{\alpha_s rB_s(t)}{1 + \beta B_s(t)} \quad (11)
\]

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

For ages \(a > 0\), in the absence of fishing mortality we have

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

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

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

We denote the steady state female biomass by \(\overline{B}_s\). This biomass produces a steady state female recruitment

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

The steady state female biomass is

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

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 \(\overline{N}_f(0)\) from the last expression in Eqn 15, define \(\overline{W}_f = \sum_{a=1}^{a_{max}} S_f(a)W_f(a)p_{f,m}(a)\) and thus write

\[
\overline{B}_s = \overline{N}_f(0)\overline{W}_f \quad (16)
\]
We now rewrite Eqn 14 as
\[ N_f(0) = \frac{\alpha_s(1 - r)N_f(0)W_f}{1 + \beta B_s} \]  
(17)
from which we conclude
\[ 1 + \beta B_s = (1 - r)\alpha_s W_f \]  
(18)
Since reproduction is assessed counting both males and females, steepness is given by
\[ h = 0.2\alpha_s B_s \cdot \frac{1 + \beta B_s}{\alpha_s B_s} \cdot \frac{0.2(1 + \beta B_s)}{1 + 0.2\beta B_s} \]  
(19)
We now use Eqn 18 in the last expression in Eqn 19 and simplify to obtain
\[ h = \frac{(1 - r)\alpha_s W_f}{4 + (1 - r)\alpha_s W_f} \]  
(20)
For the case of Ricker density dependence, Eqns 12 and 13 are replaced by
\[ N_f(0, t) = \alpha_s (1 - r)B_s(t)e^{-\beta B_s(t)} \]  
(21)
\[ N_m(0, t) = \alpha_s rB_s(t)e^{-\beta B_s(t)} \]  
(22)
Following the steps above leads to
\[ h = 0.2 \left( (1 - r)\alpha_s W_f \right)^{0.8} \]  
(23)
Comparing Eqns 7 and 8 with Eqns 20 and 23 we see that the functional form is the same
and that with the exception of \( \alpha_s \) in the latter replacing \( \alpha_p \) in the former we can make them
“identical” by setting \( W_f = \frac{1}{M} \). Mangel et al. (2010) explicitly show the conditions under which
the result for the age-structured model becomes the result for the production model.

**Imperfect Fertilization as a Mechanism for Depensation**

Both the Ricker SRR
\[ R = \alpha S e^{-\beta S} \]
and the Beverton-Holt SRR
\[ R = \frac{\alpha S}{1 + \beta S} \]
have the property that as \( S \rightarrow 0 \), \( R \rightarrow \alpha S \). A depensatory SRR will arise if for small \( S \) recruitment becomes sublinear. For example, Myers et al (1995) modify the Beverton-Holt SRR to

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

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

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

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

Similarly, modifying the Ricker SRR to

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

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

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

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

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

and consider two forms the probability of fertilization. When the biomass of the population is \( B \) the biomass of males is \( rB \); for the algebraic representation of probability of fertilization we write

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

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

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

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

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

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

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

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

In summary, there are four cases: 1) Beverton-Holt density dependence of recruitment and algebraic probability of fertilization; 2) Ricker density-dependence of recruitment and algebraic probability of fertilization; 3) Beverton-Holt density dependence of recruitment and exponential probability of fertilization; and 4) Ricker density-dependence of recruitment and exponential probability of fertilization. Each of these cases may apply for the biomass dynamics model or the age-structured model.
Including Variation in Natural Mortality in the Equations for Steepness

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

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

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

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

In light of Eqn 28

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

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

We thus conclude

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

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

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

$$h = \frac{\alpha W_f}{4 + \alpha W_f} \quad (33)$$

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

$$W_f = \sum_{a=1}^{a_{\text{max}}} \exp\left(\sum_{a'=1}^{a-1} -M(a')\right) W_f(a) p_{f,m}(a) \quad (34)$$
We recognize that each of the $M(a')$ in this equation may have its own probability distribution.

(Mathematically speaking, $\overline{W}_f$ is a functional, since it takes a vector of mortality rates and returns a scalar. There is a large literature on functional derivatives, but we can do all that is needed here using elementary calculus). For simplicity, we use the notation $M_1 = M(1), M_2 = M(2)$ etc to denote the rate of mortality at age, $\overline{M}_a, \text{Var}(M_a)$ and $\text{Cov}(M_a, M_{a'})$ to denote the mean, variance, and covariance of the mortality rates and $<\overline{W}_f>$ to denote the value of $\overline{W}_f$ obtained when the means of the rates of mortality are used. The analogue of Eqn 31 is now

$$E_M[h] = <\overline{W}_f> + \frac{1}{2} \sum_a \frac{\partial^2 h}{\partial^2 M_a} \text{Var}(M_a) + \sum_a \sum_{a' \neq a} \frac{\partial^2 h}{\partial M_a \partial M_{a'}} \text{Cov}(M_a, M_{a'})$$

(35)

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

$$\frac{\partial h}{\partial M_a} = \frac{\partial h}{\partial \overline{W}_f} \cdot \frac{\partial \overline{W}_f}{\partial M_a}$$

(36)

$$\frac{\partial^2 h}{\partial M_a \partial M_{a'}} = \left[ \frac{\partial^2 h}{\partial \overline{W}_f^2} \cdot \frac{\partial \overline{W}_f}{\partial M_a} \cdot \frac{\partial \overline{W}_f}{\partial M_{a'}} + \frac{\partial h}{\partial \overline{W}_f} \cdot \frac{\partial^2 \overline{W}_f}{\partial M_a \partial M_{a'}} \right]$$

(37)

The easiest part in the next step is to show that

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

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

(38)

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

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

(40)

from which we can see the pattern of first derivatives

$$\frac{\partial \overline{W}_f}{\partial M_1} = -\overline{W}_f$$

$$\frac{\partial \overline{W}_f}{\partial M_2} = -\overline{W}_f + e^{-M_1}W_1p_{f,m}(1)$$

$$\frac{\partial \overline{W}_f}{\partial M_3} = -\overline{W}_f + e^{-M_1}W_1 + e^{-M_1-M_2}W_2p_{f,m}(2)$$

$$\vdots$$

(41)

(42)

(43)

(44)
Similarly, the pattern of second derivatives is

\[
\frac{\partial^2 W_f}{\partial M_1^2} = - \frac{\partial W_f}{\partial M_1} = W_f 
\]

(45)

\[
\frac{\partial^2 W_f}{\partial M_1 \partial M_2} = W_f - e^{-M_1} W_1 p_{f,m}(1) 
\]

(46)

\[
\frac{\partial^2 W_f}{\partial M_2^2} = W_f 
\]

(47)

\[
\frac{\partial^2 W_f}{\partial M_1 \partial M_3} = W_f - e^{-M_1} W_1 p_{f,m}(1) - e^{-M_1 - M_2} W_2 p_{f,m}(2) 
\]

(48)

\[
\vdots 
\]

(49)

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

**Steepness for a Production Model with Depensatory SRR**

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

**Beverton-Holt density dependence and algebraic probability of fertilization**

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

\[
\frac{\alpha_p \cdot (1 - r) \cdot B}{(B + B_c)(1 + \beta \cdot B)} = M 
\]

(50)

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

\[
h = \frac{0.2 \alpha_p (1-r) \cdot B}{(B_c + 0.2B)(4 + \alpha_p (1-r) B / M(B_c + B))} 
\]

(51)

As \( B_c \to 0 \), this equation becomes Eqn 7, as it must. Note the important differences, however, between Eqns 7 and 51: the former only involves \( \alpha \) and \( M \) whereas the latter includes \( B_c \) and \( B \).

**Ricker density-dependence and algebraic probability of fertilization**

In this case the steady state biomass \( B \) satisfies

\[
\frac{\alpha_p (1-r)}{M} \cdot \frac{B}{B_c + B} = e^{\beta B} 
\]

(52)
Although this equation does not have an analytical solution, $\bar{B}$ can easily be found using Newton’s method (Mangel 2006). Steepness is given by

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

(53)

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

**Beverton-Holt density dependence and exponential probability of fertilization**

In this case the steady state biomass satisfies

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

(54)

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

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

(55)

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

**Ricker density-dependence and exponential probability of fertilization**

In this case, $\bar{B}$ satisfies

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

(56)

and steepness is given by

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

(57)

**Numerical Results When Maximum Productivity is Known**

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

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

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

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

Beverton-Holt density dependence and algebraic probability of fertilization

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

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

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

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

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

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

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

The Probability Density for Steepness

As described in Mangel et al (2010) in detail, uncertainty in $M$ itself can induce a probability distribution on steepness. That is, all of the equations characterizing steepness are conditioned on a particular value of $M$. Then if $f_m(m)$ denotes the probability density for $M$, since the
relationship between steepness and rate of mortality is unique, we are easily able to compute
the probability density for steepness, \( f_h(h) \). All of this can be done for the production model
without simulation if \( \alpha_p \) is treated as a constant.

For example, we assume that the rate of mortality follows a gamma density with mean
0.2 and coefficient of variation \( \frac{1}{3} \). This frequency distribution is shown in Figure 4a and the
resulting frequency distributions for steepness in Figure 4b for Ricker density dependence and
Figure 4c for Beverton-Holt density dependence when the probability of fertilization at \( B_0 \) is
0.887. We note two observations about these figures. First, that for Ricker density dependence,
steepness can be arbitrarily large but in this particular case there is little probability of it being
larger than about 2.0. Second, although in the absence of Allee effects, steepness for Beverton
Holt density dependence cannot fall below 0.2, when there are Allee effects steepness can be less
than 0.2.

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

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

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

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

\[
B_m = \sum_{a=1}^{a_{max}} N_m(a,t)W_m(a)p_{m,m}(a) \tag{61}
\]
where the terms in the latter equation have the obvious interpretations based on the case without
depensation. We assume that the probability of fertilization depends upon the relative mature
biomasses. Thus, the analogue of Eqn 25 is

$$p_f(B_f, B_m) = \frac{B_m/B_f}{B_c/B_f + B_m/B_f} = \frac{B_m}{B_c + B_m}$$  \hspace{1cm} (62)

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

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

so that $\gamma$ has exactly the same interpretation as before. Readers who would prefer to think of
probability of fertilization in terms of mature numbers rather than mature biomass are encour-
eged to reproduce the calculations that follow using mature numbers.

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

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

We begin with Beverton-Holt density dependence and algebraic probability of fertilization for
two reasons. First, the calculations are the simplest ones possible – there are no transcendental
equations and all quantities can be determined using no more than the quadratic formula.
Second, in the absence of Allee effects, steepness for this case ranges between 0.2 and 1, so results are more easily interpreted than for Ricker density dependence. If density dependence is caused by the entire biomass (not just spawning biomass) the production of young of the year females and males in the steady state is

\[
N_f(0) = (1 - r) \alpha_s B_f \cdot \frac{1}{1 + \beta B} \cdot B_m \cdot \frac{B_m}{B_c + B_m}
\]

(64)

\[
N_m(0) = r \alpha_s B_f \cdot \frac{1}{1 + \beta B} \cdot B_m
\]

(65)

and in analogy with Eqn 16 we have

\[
B_f = N_f(0) W_f
\]

(66)

\[
B_m = N_m(0) W_m
\]

(67)

\[
B = N_f(0) < W_f > + N_m(0) < W_m >
\]

(68)

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

Note from Eqns 64 and 65 that

\[
\frac{N_m(0)}{N_f(0)} = \frac{r}{1 - r}
\]

(69)

so that it is helpful to define \(\rho = \frac{r}{1 - r}\) and compactly write \(N_m(0) = \rho_r N_f(0)\).

We now use Eqns 65, 67 and 68 to rewrite Eqn 64 as a single equation for \(N_f(0)\)

\[
N_f(0) = (1 - r) \alpha_s N_f(0) W_f \cdot \frac{1}{1 + \beta N_f(0) (< W_f > + \rho_r < W_m >)} \cdot \rho_r N_f(0) W_m
\]

(70)

which can be re-arranged to give

\[1 + \beta N_f(0) (< W_f > + \rho_r < W_m >) = \frac{(1 - r) \alpha_s W_f \rho_r N_f(0) W_m}{B_c + \rho_r N_f(0) W_m}\]

(71)

and cross-multiplying by the denominator on the right hand side, we see that Eqn 71 – as complicated as it looks — is simply a quadratic equation for the single unknown \(N_f(0)\). Once we find that, we know all the other steady state population numbers and biomasses from Eqns 65-68.
Assuming that 20% of unfished biomass is understood as equivalent reductions in female and male populations, steepness is computed from

\[
h = \frac{0.2\alpha_s B_f 0.2B_m}{\alpha_s B_f 0.2B_m} \frac{1}{B_f + B_m} \frac{0.2B_m}{B_f + 0.2B_m}
\]  

(72)

which simplifies to

\[
h = 0.04 \left[ \frac{1 + \beta \overline{B}}{1 + 0.2\beta \overline{B}} \left( \frac{B_c + B_m}{B_c + 0.2B_m} \right) \right]
\]  

(73)

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

\[
h = 0.2 \left[ \frac{(1 - r)\alpha_s W_f \rho_r N_f(0)W_m}{4 + (1 - r)\alpha_s W_f \rho_r N_f(0)W_m} \right] \left[ \frac{B_c + \rho_r N_f(0)W_m}{B_c + 0.2\rho_r N_f(0)W_m} \right]
\]  

(74)

Note that if we set \(B_c = 0\) then we recover Eqn 20 as must happen.

The Deterministic Estimate of Steepness of Bigeye Tuna *Thunnus obesus*

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

\[
M_m(a) = \frac{k_m}{k_f} M_f(a)
\]  

(75)

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

The two parameters that remain to be specified are \(\beta\) and \(B_c\). In principle, \(\beta\) can be computed from the dynamics underlying the Beverton-Holt recruitment function, in which per
capita larval mortality is a linear function of larval numbers (Mangel 2006, pg 213) but for illustration here we proceed differently. Note from Eqn 71 that in the absence of Allee effects we have

\[ 1 + \beta N_f(0)[< W_f > + \rho_r < W_m >] = (1 - r)\alpha_s W_f \]  

(76)

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

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

\[ p_f = \frac{\rho_r N_f(0) W_m}{B_c + \rho_r N_f(0) W_m} \]  

(77)

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

**An Improved Approach for Estimating \( \alpha_s \)**

The stochastic simulation used in Mangel et al (2010) is not appropriate for case in which the mechanism of depensation is reduced probability of fertilization, because we must track the
size of both male and female populations. In this section, we introduce an improved stochastic
simulation, which can be used for either the depensatory case or the non-depensatory case.

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

**The Cohort Based Computation of $\alpha_s$**

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

Next we compute the number of females and males of age $a$ using the survival functions, so
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
the probabilities that a female or male survives to age $a$. In this way we uniquely identify the
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 $a$.

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

In order to account for fertilization based depensation, we must specify the size of the mating
group, $G$. We let $B_m$ and $B_f$ respectively denote the biomass of males and females in the
currently simulated mating group and $E_T$ denote the number of eggs that survive to recruit to
the population produced by females in the currently simulated mating group. One can imagine
a variety of means of assembling the mating group. For example, mature individuals may join
matting groups randomly (the pseudocode for this situation is given below) or they may join
through size association (so that larger fish are paired with larger fish; smaller fish are paired
with smaller fish).

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

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

Step 2. Draw a test value, $i_{test}$ that is uniformly distributed across the total number of fish.
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
the fish is mature, proceed to Step 3.

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

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

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

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

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

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

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

Step 9. If current group size is less than $G$ return to Step 2.
Increased Mortality as the Depensatory Mechanism

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

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

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

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

which is once again a quadratic equation for $B$.

Empirical Assessment for the Depensatory Mechanism

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

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

Some very simple statistical methods can be applied to estimate $B_c$ in Eqn 25 or $\gamma$ in Eqn 26. Inverting Eqn 25 and simplifying shows that (suppressing the dependence of the probability
of fertilization on biomass)

\[
\frac{1}{p_f} - 1 = B_c \cdot \frac{1}{B}
\]  

(80)

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 methods for estimating the rate constant in Michaelis-Menten enzyme kinetics). Similarly, Eqn 26 can be simply manipulated to give

\[
\log(1 - p_f) = \gamma \cdot B
\]  

(81)

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

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

Finally, it is natural to consider Bayesian methods by introducing appropriate priors for either \( B_c \) or \( \gamma \). All of this remains to be done.

References


Appendix: The Production Model as a System of Stochastic Differential Equations

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

\[ dM = M[\lambda - \mu \cdot M]dt + \sigma_M MdW_1 \]  \hspace{1cm} (A1)

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

\[ E[dM] = m(\lambda - \mu m)dt + o(dt) \]  \hspace{1cm} (A2)

and variance

\[ Var[dM] = \sigma_M^2 m^2 dt + o(dt) \]  \hspace{1cm} (A3)

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

This observation suggests that we can interpret Eqn 1 or the equivalent using Ricker density dependence and the probability density for gamma in the context of stochastic differential equations. If we let \( g(B) \) denote the density dependence, then if the source of stochasticity for
changes in biomass is a birth and death process, the stochastic version of either equation is
(Mangel 1994, 2006)
\[ dB = [\alpha_p (1 - r) B g(B) p_f (B) - M \cdot B] dt + \sqrt{\alpha_p (1 - r) B g(B) p_f (B) + M \cdot B} \cdot dW_2 \quad (A4) \]

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

If \( f(m, b) \) is the stationary probability density for \( M \) and \( B \), then under the assumptions in
Eqns A1-A4, it will satisfy the equation
\[
\frac{1}{2} \left[ \sigma^2_M m^2 \frac{\partial^2 f}{\partial m^2} + (\alpha_p (1 - r) B g(b) p_f (b) + m \cdot b) \frac{\partial^2 f}{\partial b^2} \right] \\
- [m(\lambda - \mu) \frac{\partial f}{\partial m}] - [(\alpha_p (1 - r) B g(b) p_f (b) - m \cdot b) \frac{\partial f}{\partial b}] = 0 \quad (A5)
\]

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

References for the Appendix


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Captions for Figures

Figure 1. Results for the production model with illustrative parameters. a) The steady state biomass in the presence of an Allee effect as a function of the probability of fertilization $p_f(B_0)$ when biomass is $B_0 = 1000$; b) Steepness for the production model with Ricker density dependence and algebraic probability of fertilization as a function of the probability of fertilization $p_f(B_0)$; c) Graphical determination of the unstable steady state biomass as the solution of the associated transcendental equation. d) Per capita growth rate at 20% of steady state biomass as a function of the probability of fertilization $p_f(B_0)$.

Figure 2. Similar calculations for Beverton Holt density dependence and algebraic probability of fertilization. a) Steepness as a function of the probability of fertilization when biomass is 1000, $p_f(B_0)$; b) Illustration of graphical determination of the unstable steady state. c) Per capita growth rate at 20% of steady state biomass as a function of the probability of fertilization when biomass is 1000, $p_f(B_0)$.

Figure 3. When there is an Allee effect, otherwise sustainable harvesting may become unsustainable. We show, as a function of the probability of fertilization when biomass is 1000, $p_f(B_0)$ the biomass trajectory for fishing mortality $F = M$ (panel a) or fixed catch $C = 0.5MB$ (panel b).

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

Figure 5. The point estimate of steepness for bigeye tuna as a function of the probability that an egg is fertilized when the population is in the stable age distribution.
Figure 1a.pdf
Figure 1b.pdf
Exponential or saturating curve

Biomass, $B$

\[ \exp(\beta r B) \]

$p_f(B_0) = 0.94$

$p_f(B_0) = 0.85$

$p_f(B_0) = 0.76$
Per capita growth rate

$p_f(B_0)$
Figure 2b.pdf

Line or saturating function

Biomass, B

$p_f(B_0) = 0.9878$

$p_f(B_0) = 0.9542$

$p_f(B_0) = 0.971$
Figure 2c.pdf
Figure 3a.pdf
Figure 4a.pdf
Figure 5. The point estimate of steepness for the age structured model.