Abstract.–A simple dynamic pool model (the "base model"), defined by a linear weight-at-age relationship and a Cushing (convex power) stock-recruitment relationship, results in an explicit solution for the fishing mortality rate corresponding to maximum sustainable yield F_{MSY}. This solution's sensitivity can be examined by comparing it to solutions derived under alternative model specifications. Four such modifications are considered here: 1) replacing the Cushing stock-recruitment equation with an equation of the Beverton-Holt form; 2) generalizing from linear growth to a flexible form of von Bertalanffy growth; 3) allowing the ages of recruitment to the fishery a_f and the mature stock a_m to diverge; and 4) allowing for a finite maximum age in the stock. Exact polynomial solutions for F_{MSY} are derived for each specification (except the fourth), and the potential bias introduced by use of the base model is examined for each. In all cases, the solution to the base model is within 10% of the solution to the alternative model under a range of parameter values.

Variations on a simple dynamic pool model

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Some fishery models can be solved analytically (i.e., by mathematical manipulation of the equations), while others can be solved only numerically (i.e., by the brute force of computer simulation). One advantage of analytic models is that the generality of their solutions is more straightforwardly addressed. For example, it is easy to show that the stock size associated with maximum sustainable yield (MSY) in a Schaefer (1954) model is always one-half the pristine stock size; this property follows directly from the assumption of logistic growth upon which the model is based. Such generality is more difficult to demonstrate for simulation models, however. For instance, if a particular simulation showed that MSY was obtained at a stock size equal to one-half the pristine level, there would be no way to tell whether this result was general, except by repeated trial and error with different values for the input parameters.

Another example of an analytic solution is the one obtained by Thompson (1992) for the fishing mortality rate at MSY (F_{MSY}) in his simple dynamic pool model. Because this solution is an analytic one, it is completely general in the sense that it will hold whenever the underlying assumptions of the model hold, regardless of parameter values. Of course, the underlying assumptions may *not* hold in a particular instance, which raises the question: How sensitive is the solution to those assumptions? The purpose of this paper is thus to examine the sensitivity of Thompson's (1992) solution relative to the underlying assumptions of that model. This will be accomplished by developing four reasonable modifications to the base model proposed by Thompson and by examining the range of errors that might likely be encountered if the base model were employed in situations where one of the modifications would have been more appropriate.

Review of the base model

Thompson (1992, see also Jensen, 1973) defined a simple dynamic pool model as one that reflects the following assumptions: 1) cohort dynamics are of continuous-time form; 2) vital rates are constant with respect to time and age; 3) fish mature and recruit to the fishery continuously and at the same invariant ("knife-edge") age; 4) mean body weight at age is determined by age alone; 5) the stock (or population) consists of the pool of recruited individuals; 6) maximum age is infinite; 7) the stock is in an equilibrium state determined by the fishing mortality rate; and 8) recruitment is determined by stock biomass alone. Within the framework provided by these assumptions, particular models are distinguished by the forms assigned to the weight-at-age and stock-recruitment functions.

As an example, Thompson (1992) developed a particular simple dynamic pool model than can be solved explicitly for F_{MSY}. In terms of biomass per recruit, the model is basically

the same as that of Hulme et al. (1947), where body weight is assumed to be a linear function of age (e.g., Richards, 1969):

$$w(a) = w_r \left(\frac{a - a_r}{a_r - a_0} \right), \qquad (1)$$

where a represents age, a_r is the age of recruitment, a_0 is the age intercept, $w(a)$ represents individual weight at age, and w_r is the weight at recruitment.

For a given recruitment level, stock biomass in the model is given by

$$B(F') = \left(\frac{b(F',a_r)}{M} \right) \left(\frac{1 + K'' + F'}{(1 + F')^2} \right), \qquad (2)$$

where M is the instantaneous rate of natural mortality, $F'=F/M$, $B(F')$ is the equilibrium stock biomass obtained under a relative fishing mortality rate of F', $b(F',a_r)$ is the equilibrium biomass at $a=a_r$ obtained under a relative fishing mortality rate of F', and

$$K'' = \frac{1}{M(a_r - a_0)}, \qquad (3)$$

which can be interpreted in this model as the pristine ratio of growth to recruitment (Thompson, 1992).

Thompson (1992) extended the model described in Equation 2 by incorporating a stock-recruitment relationship of the convex power form suggested by Cushing (1971):

$$b(F',a_r) \doteq pB(F')^q, \qquad (4)$$

where p and q are constants and $0 \le q \le 1$. In the limiting case of $q=0$, recruitment is constant, while in the other limiting case of $q=1$, recruitment is proportional to biomass.

Substituting Equation 4 into Equation 2 and rearranging terms gives the following equation for equilibrium stock biomass:

$$B(F') = \left[\left(\frac{p}{M} \right) \left(\frac{1 + K'' + F'}{(1 + F')^2} \right) \right]^{\frac{1}{1-q}}. \qquad (5)$$

Multiplying both sides of Equation 5 by MF' then gives the equation for sustainable yield, which is maximized at

$$F'_{MSY} = \frac{-(q+1)K'' + 1 + \sqrt{(q+1)^2 K''^2 + (6q-2)K'' + 1}}{2q} - 1, \qquad (6)$$

where $F'_{MSY} = F_{MSY}/M$.

In the special case where $q=0$, Equation 6 reduces to the solution for F'_{max} ($=F_{max}/M$):

$$F'_{max} = \frac{K'' + 1}{K'' - 1}. \qquad (7)$$

A common rule of thumb is that F'_{MSY} should equal 1 (Alverson and Pereyra, 1969; Thompson, 1992). The locus of parameter values for which this rule holds precisely is given by

$$q = \frac{1}{K'' + 2}. \qquad (8)$$

Another behavior of interest is the ratio of $B(F'_{MSY})$ to $B(0)$. Here, this ratio has a lower limit of $(K''-1)/(4K'')$ (at $q=0$) and an upper limit of $1/e$ (at $q=1$).

The base model presented in Equations 1–6 can be modified in a number of ways. Although such modifications may make it more difficult to obtain an explicit solution for F_{MSY}, they may also provide some guidance as to the generality of the base model's behavior. Four modifications will be considered here: 1) replacing the Cushing stock-recruitment equation with an equation of the form suggested by Beverton and Holt (1957); 2) generalizing from linear growth to a flexible form of von Bertalanffy (1938) growth; 3) allowing the ages of recruitment to the fishery a_f and the mature stock a_m to diverge; and 4) allowing for a finite maximum age in the stock. For each modification (except the fourth), polynomial solutions for F'_{MSY}, F'_{max}, and the locus at which $F'_{MSY} = 1$ will be derived, and the upper limit to the ratio $B(F'_{MSY})/B(0)$ will be presented. The potential bias introduced by use of the base model will also be examined graphically for each modification.

Beverton-Holt recruitment

The choice of stock-recruitment relationship can have an appreciable impact on the resulting estimate of F_{MSY} (Kimura, 1988). For comparative purposes, the stock-recruitment relationship of Beverton and Holt (1957) can be substituted for the Cushing form used in the base model. It will prove convenient to parametrize the Beverton-Holt equation as follows:

$$b(F',a_r) = \frac{Q B(F')}{P B(F') + 1}, \qquad (9)$$

where Q represents the slope of the curve at the origin and P represents the ratio between the slope at the origin and the height of the asymptote.

Substituting Equation 9 into Equation 2 and solving for $B(F')$ gives

$$B(F') = \left(\frac{1}{P} \right) \left(\frac{Q(1 + K'' + F')}{M(1 + F')^2} - 1 \right), \qquad (10)$$

which is the analogue to Equation 5 for the Beverton-Holt recruitment case.

Polynomial solution

Multiplying Equation 10 through by MF', differentiating with respect to F', and setting the resulting expression equal to zero gives the following polynomial solution for F'_{MSY}:

$$F'^3_{MSY}+3F'^2_{MSY}+[3+(K''-1)Q']F'_{MSY}+1-(K''+1)Q'=0, \quad (11)$$

where $Q' = Q/M$.

It is possible to solve Equation 11 explicitly for F'_{MSY}. For the case where $K''>1$,

$$F'_{MSY} = \left[Q'\left(\sqrt{K''^2 + Q'\left(\frac{K''-1}{3}\right)^3} + K''\right)\right]^{1/3} - \\ \left[Q'\left(\sqrt{K''^2 + Q'\left(\frac{K''-1}{3}\right)^3} - K''\right)\right]^{1/3} -1. \quad (12)$$

For the case where $K''=1$,

$$F'_{MSY} = (2Q')^{1/3} - 1. \quad (13)$$

For the case where $K''<1$,

$$F'_{MSY} = 2\sqrt{\frac{1-K''}{3}Q'} \cos\left(\left(\frac{1}{3}\right) \cos^{-1}\left[\left(\frac{3K''}{1-K''}\right)\right.\right. \\ \left.\left.\sqrt{\frac{3}{(1-K'')Q'}}\right]\right) -1 . \quad (14)$$

The parameter Q' functions inversely to q in the sense that Equations 11–14 reduce to Equation 7 as Q' approaches infinity (the F'_{max} case), whereas Equation 6 does so as q approaches zero. As Q' increases, F'_{MSY} increases monotonically, whereas F'_{MSY} decreases with increasing q in the base model.

As with the base model, Equations 11–14 contain $F'_{MSY} = 1$ as a special case. Here this is obtained when $Q' = 4$ or when K'' approaches infinity. This contrasts somewhat with the base model, where keeping F'_{MSY} at a constant value of 1.0 required an inverse relationship between q and K''. However, it should be pointed out that $F'_{MSY}= 1$ is a very special case in the Beverton-Holt form of the model, since this turns out to be the only constant value of F'_{MSY} that does not imply some sort of relationship between Q' and K''. In fact, a direct relationship between Q' and K'' is required for all constant values of $F'_{MSY} > 1$, as described below:

$$Q' = \frac{(F'_{MSY} + 1)^3}{F'_{MSY} + 1 - (F'_{MSY} - 1)K''} . \quad (15)$$

Another difference between this model and the base model is that here F'_{MSY} reaches zero at $Q'=1/(K''+1)$, whereas F'_{MSY} in the base model does not reach zero until $q=1$. Still another difference is that here the upper limit to the ratio $B(F'_{MSY})/B(0)$ is 0.5, contrasted with $1/e$ in the base model. In both models, this limit is reached as F'_{MSY} approaches zero.

Finally, the behavior of this modification differs from that of the base model in that extinction is possible here, owing to the Beverton-Holt curve's finite slope at the origin. Extinction occurs here at

$$F'_{ext} = \frac{Q' + \sqrt{(4K'' + Q')Q'}}{2} -1. \quad (16)$$

The relative fishing mortality rate described by Equation 16 need not be unrealistically high. For example, it will be less than F'_{max} whenever the following relationship holds:

$$Q' < \frac{4K''}{K''^2 - 1} . \quad (17)$$

Bias resulting from the assumption of Cushing recruitment

Assuming that the stock-recruitment relationship follows the Cushing form when it actually follows a Beverton-Holt form can lead to a biased estimate of F_{MSY}. To compare stock-recruitment curves, Kimura (1988) observed that a two-parameter function can be defined by any two points on the curve. In his example, Kimura used hypothetical stock-recruitment "observations" at the pristine biomass level and at one-half the pristine biomass level. Kimura conjectured that recruitment might be reduced to about 90% of the pristine level when biomass has been reduced by 50% relative to its own pristine level, a suggestion which has been endorsed by others (e.g., Clark, 1991). Given the other parameters used in his example, Kimura found that the F_{MSY} value under a Beverton-Holt stock-recruitment relationship was much less than the value under a Cushing relationship fit to the same two stock-recruitment points.

However, there is no reason to believe a priori that a Cushing relationship is necessarily less conservative than a Beverton-Holt relationship in terms of its associated F_{MSY} value. Note that Equation 6 can be solved explicitly for q as a function of K'' and F'_{MSY} as follows:

$$q = \frac{K'' + 1 - (K'' - 1)F'_{MSY}}{(K'' + 1 + F'_{MSY})(F'_{MSY} + 1)} . \quad (18)$$

Substituting Equation 12, 13, or 14 into Equation 18 thus gives the q value that sets F_{MSY} under a Cushing stock-recruitment relationship equal to F_{MSY} under a Beverton-Holt relationship. Assuming that both stock-recruitment curves are parametrized to pass through the same pristine stock-recruitment point $(B(0),b(0,a_r))$, this q value implies a second intersection at some lower biomass level. It turns out that this lower level is always less than about 20% of $B(0)$ (Fig. 1A) and greater than about 20% of $b(0,a_r)$ (Fig. 1B). In other words, Kimura's (1988) placement of a lower intersection at 50% of $B(0)$ would always cause the Cushing model to overestimate F_{MSY}. Placing the lower intersection at a biomass level less than 20% of $B(0)$, however, might result in either an over- or underestimate.

For example, one rule of thumb (Clark, 1991) holds that $F_{0.1}$ (the fishing mortality rate that reduces the slope of the yield-per-recruit curve to one-tenth of the slope at the origin), $F_{35\%}$ (the fishing mortality rate that reduces the level of spawning biomass per recruit to 35% of the pristine level) and M should be approximately equal. In the base model, this rule of thumb holds exactly at $K''=1.5$ (Thompson, in press). In the base model with Beverton-Holt recruitment, then, $F_{MSY}=F_{0.1}=F_{35\%}=M$ at $Q'=4$ and $K''=1.5$. These parameters imply a stock-recruitment curve in which recruitment is reduced from $b(0,a_r)$ by exactly 1/11 when biomass is reduced to 50% of $B(0)$, and in which recruitment is reduced from $b(0,a_r)$ by exactly 50% when biomass is reduced to 1/11 of $B(0)$.

In the base model with Cushing recruitment, on the other hand, $F_{MSY}=F_{0.1}=F_{35\%}=M$ at $q=2/7$ and $K''=1.5$, implying a stock-recruitment curve in which recruitment is reduced from $b(0,a_r)$ by about 18% when biomass is reduced to 50% of $B(0)$, and in which recruitment is reduced from $b(0,a_r)$ by about 50% when biomass is reduced to 1/11 of $B(0)$. Thus, in the "rule of thumb" case, the form of the stock-recruitment curve (Cushing or Beverton-Holt) has virtually no impact on the resulting estimate of F_{MSY} so long as the curve passes through $(B(0),b(0,a_r))$ and $(B(0)/11,b(0,a_r)/2)$.

More generally, to cause Cushing and Beverton-Holt curves to intersect at $(B(0),b(0,a_r))$ and at some fraction ρ of $B(0)$, set

$$q = 1 - \frac{\ln(\rho[(K''+1)Q'-1] + 1) - \ln(Q') - \ln(K''+1)}{\ln(\rho)} \quad (19)$$

and

$$p = \left(\frac{M}{K''+1}\right)\left(\frac{(K''+1)Q'-1}{P}\right)^{1-q}. \quad (20)$$

Alternatively, the lower intersection can also be defined in terms of relative recruitment (as opposed to relative biomass). To cause Cushing and Beverton-Holt curves to intersect at $(B(0),b(0,a_r))$ and at some fraction θ of $b(0,a_r)$, set

$$q = 1 - \frac{\ln(\theta)}{\ln(\theta) - \ln[(1-\theta)(K''+1)Q' + \theta]} \quad (21)$$

and p as in Equation 20.

Biases resulting from placement of the lower intersection at 50% and 10% of $B(0)$ are compared in Figure 2, A and B, respectively. Note that use of the 50% value (as in Kimura's [1988] example) causes large and uniformly positive biases in the base model's estimate of F_{MSY}. On the other hand, use of the 10% value constrains bias to the +/− 10% range over a large portion of parameter space.

Biases resulting from placement of the lower intersection at 90% and 50% of $b(0,a_r)$ are compared in Figure 2, C and D, respectively (the 50% reference point has been suggested by Mace[1] and Myers et al.[2]). As with the relative biomass reference level, use of Kimura's (1988) relative recruitment reference level (90%) causes large and uniformly positive biases in the base model's estimate of F_{MSY} over a large portion of parameter space. On the other hand, use of the 50% value constrains bias to the +/− 10% range over a sizable region.
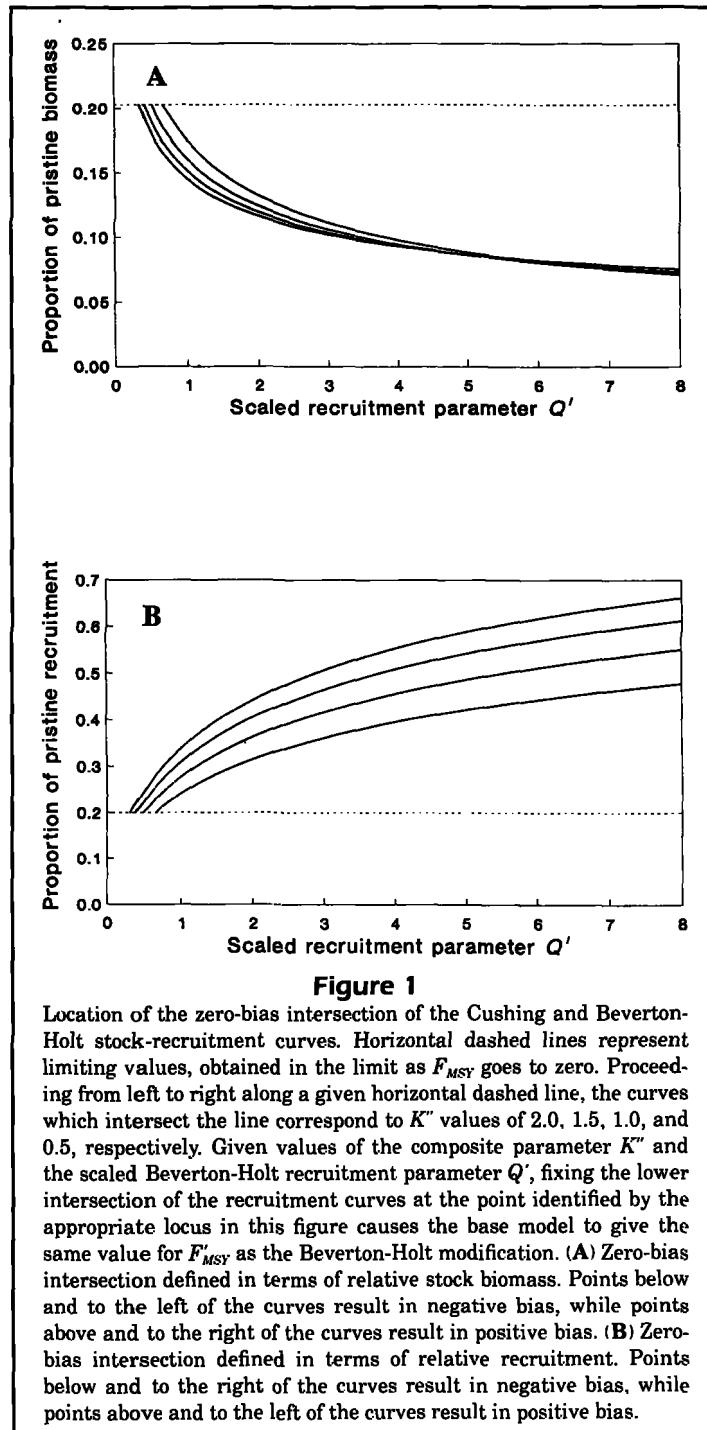
As Figure 2 illustrates, then, there is reason to believe that the form of the stock-recruitment curve (Cushing or Beverton-Holt) may not be particularly important in terms of the resulting estimate of F_{MSY} so long as the candidate curves intersect at a fairly low level. In other words, fishery managers need not always view an estimate of F_{MSY} as being critically dependent on the form of the stock-recruitment curve.

A general growth function

The linear growth function used by Thompson (1992) may be viewed as a special case of the following more

[1]Mace, P. M. 1993. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., 1335 East-West Highway, Silver Spring, MD 20910.

[2]Myers, R. A., A. A. Rosenberg, P. Mace, N. Barrowman, and V. Restrepo. 1993. In search of thresholds for recruitment overfishing. Dep. Fisheries and Oceans, St. John's, New Foundland. Unpubl. manuscr., 14 p.

Figure 1

Location of the zero-bias intersection of the Cushing and Beverton-Holt stock-recruitment curves. Horizontal dashed lines represent limiting values, obtained in the limit as F_{MSY} goes to zero. Proceeding from left to right along a given horizontal dashed line, the curves which intersect the line correspond to K'' values of 2.0, 1.5, 1.0, and 0.5, respectively. Given values of the composite parameter K'' and the scaled Beverton-Holt recruitment parameter Q', fixing the lower intersection of the recruitment curves at the point identified by the appropriate locus in this figure causes the base model to give the same value for F_{MSY} as the Beverton-Holt modification. (A) Zero-bias intersection defined in terms of relative stock biomass. Points below and to the left of the curves result in negative bias, while points above and to the right of the curves result in positive bias. (B) Zero-bias intersection defined in terms of relative recruitment. Points below and to the right of the curves result in negative bias, while points above and to the left of the curves result in positive bias.

general form:

$$w(a) = w_r \left(\frac{1 - e^{-K(a-a_r)-K'/K''}}{1 - e^{-K'/K''}} \right)^n, \qquad (22)$$

where K is Brody's growth coefficient, $K' = K/M$, and n is a positive integer. In different parametrizations, Equation 22 corresponds to (or is a special case of) a

number of general growth functions, including those of Richards (1959, see also Fletcher, 1975), Savageau (1980), and Schnute (1981). Schnute described his parametrization of Equation 22 as "generalized von Bertalanffy growth" (although he did not restrict n to integer values). When $n=3$, Equation 22 corresponds to the common ("specialized") von Bertalanffy (1938) curve, and, when $n=1$, the "monomolecular" curve of Pütter (1920) and Brody (1928) is obtained.

In the limit as K approaches zero, Equation 22 gives an nth-degree polynomial in age:

$$w(a) = w_r \left(\frac{a - a_0}{a_r - a_0} \right)^n, \qquad (23)$$

which has been used to describe growth (though not always in weight) by Mendelsohn (1963), Dethlefsen et al. (1968), Knight (1968), Rafail (1972), Roff (1980), Geoghegan and Chittenden (1982), Standard and Chittenden (1984), and Chen et al. (1992). Equation 1 thus represents the special case of Equation 22 where K approaches zero and $n=1$.

Polynomial solution

The polynomial solution for this model is partitioned into two cases ($K=0$ and $K>0$) and derived in the Appendix.

When $K=0$, the solution for F'_{max} can be written as a polynomial of degree n, and the solution for F'_{MSY} can be written as a polynomial of degree $n+1$. When $K>0$, the solution for F'_{max} can be written as a polynomial of degree $2n$, and the solution for F'_{MSY} can be written as a polynomial of degree $2n+1$. As with the base model, the solution in either case indicates that maintaining an F'_{MSY} value of 1.0 requires an inverse relationship between q and K'' (which, as in the base model, can be written explicitly). Likewise, the upper limit to the ratio $B(F'_{MSY})/B(0)$ is the same as in the base model ($1/e$) in both cases.

The polynomial solution can be manipulated easily to show how it varies across the range of possible K', q, and K'' values. For example, several limiting values of F'_{max} and F'_{MSY} are shown in Table 1.

Bias resulting from the assumption of linear growth

Assuming that growth is linear when it actually follows a generalized von Bertalanffy form can lead to a
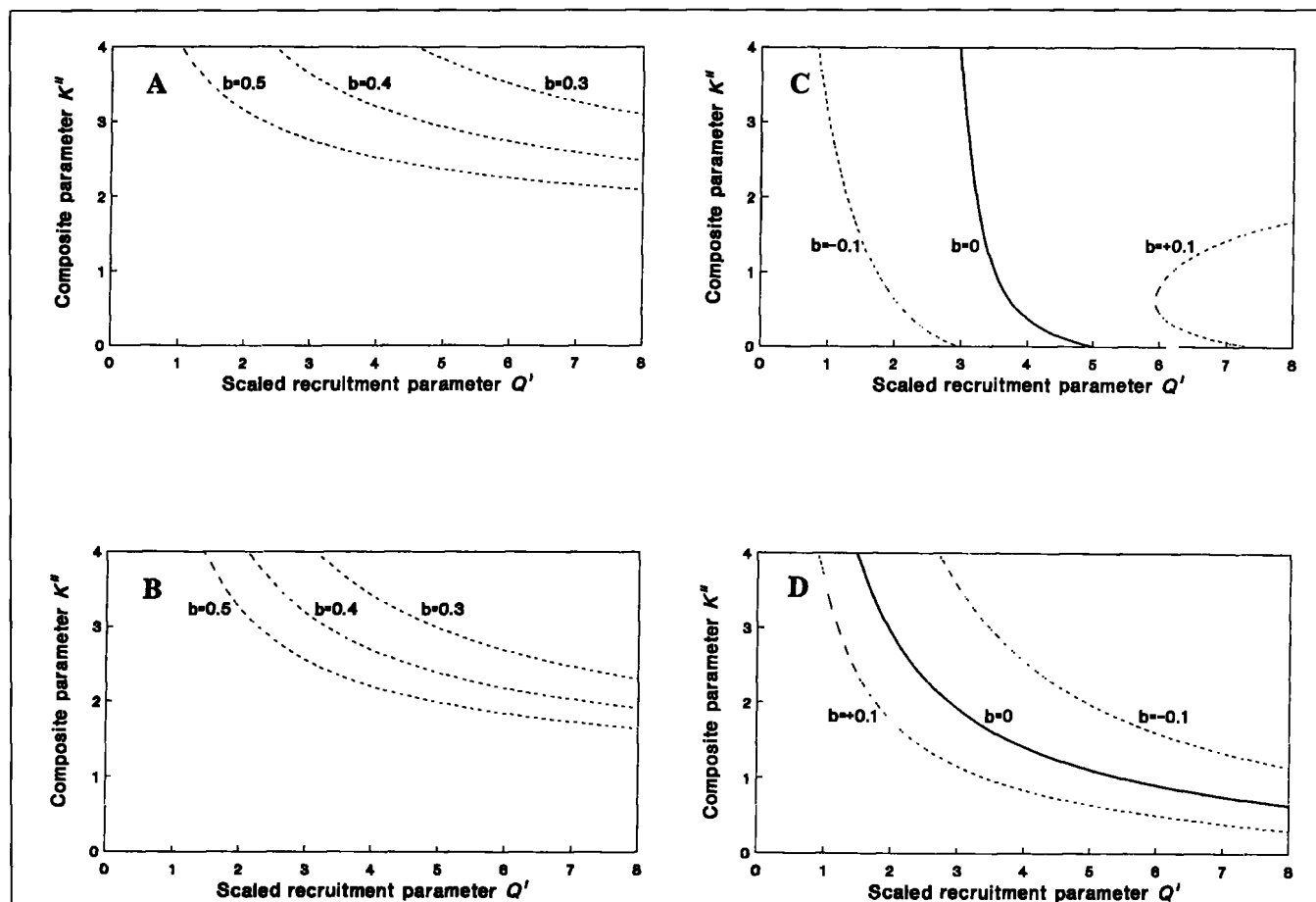
Figure 2

Isobias loci obtained when the base model is used to approximate the Beverton-Holt modification under four calibration methods. (A) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 50% of pristine biomass. Loci corresponding to biases in F'_{MSY} of 30% (b=0.3), 40% (b=0.4), and 50% (b=0.5) are shown. (B) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 10% of pristine biomass. Loci corresponding to biases in F'_{MSY} of -10% (b=-0.1), 0% (b=0), and +10% (b=+0.1) are shown. (C) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 90% of pristine recruitment. Loci corresponding to biases in F'_{MSY} of 30% (b=0.3), 40% (b=0.4), and 50% (b=0.5) are shown. (D) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 50% of pristine recruitment. Loci corresponding to biases in F'_{MSY} of +10% (b=+0.1), 0% (b=0), and -10% (b=-0.1) are shown.

biased estimate of F_{MSY}. One way to compare the two types of curve is to require that they intersect at w_r and that they imply the same pristine biomass-per-recruit level. In the base model, stock biomass per recruit is obtained by multiplying Equation 2 through by $w_r/b(F'',a_r)$. When Equation 22 or 23 is used to represent growth, stock biomass per recruit is given by Appendix Equation 5 or Appendix Equation 11. When growth curves are forced to intersect at w_r and pristine biomass per recruit levels are equated, the following parametrization is defined:

$$\hat{K}'' = (1 - e^{-K''/K''})^{-n}\left(\sum_{k=0}^{n}\frac{(-1)^k\binom{n}{k}e^{-kK''/K''}}{kK''+1}\right) - 1, \quad (24)$$

where $\binom{n}{k}$ is the binomial coefficient (Appendix) and $\hat{K}''$ is the estimated value of K'' used to define the linear growth relationship (assuming that M and a_r are the same under both weight-at-age relationships, $\hat{K}''$ is distinguished from K'' by the fact that the age intercepts of the two curves differ—Equation 3).

Substituting Equation 24 for K'' in Equation 6 gives F'_{MSY} in the base model when the linear growth function is fit in the manner described above. This F'_{MSY} value can be either higher or lower than the value given by the solution derived in the Appendix. For the case where $n=3$, Figure 3 shows the range of +/- 10% bias for four values of K'', along with the loci of zero bias. Note that at low values of K'' (e.g., 0.5), the two

Table 1
Limits on F'_{max} and F'_{MSY} under generalized von Bertalanffy growth.

	$K' = 0$	$K' \to \infty$
Limits on F'_{max}		
$K'' \to \infty$	$F'_{max} = \dfrac{1}{n}$	$F'_{max} \to \infty$
$F'_{max} \to \infty$	$K'' = \lim\limits_{K' \to 0}\left(\dfrac{K'}{\ln(nK'+1)}\right) = \dfrac{1}{n}$	$K'' \to \infty$
Limits on F'_{MSY}		
$K'' \to \infty$	$F'_{MSY} = \dfrac{1-q}{n+q}$	$F'_{MSY} = \dfrac{1-q}{q}$
$K'' = 0$	$F'_{MSY} = \dfrac{1-q}{q}$	$F'_{MSY} = \dfrac{1-q}{q}$

F'_{MSY} values tend to be close over a large portion of parameter space, but that as K'' increases, the base model's estimate of F'_{MSY} is more likely to be significantly biased.

Divergent ages of recruitment and maturity

As defined by Thompson (1992), all simple dynamic pool models assume that fish recruit to both the fishery and the mature stock at a single age a_r. However, in more complicated dynamic pool models, it is common for the age (or size) of recruitment to the fishery to be treated as a management variable.
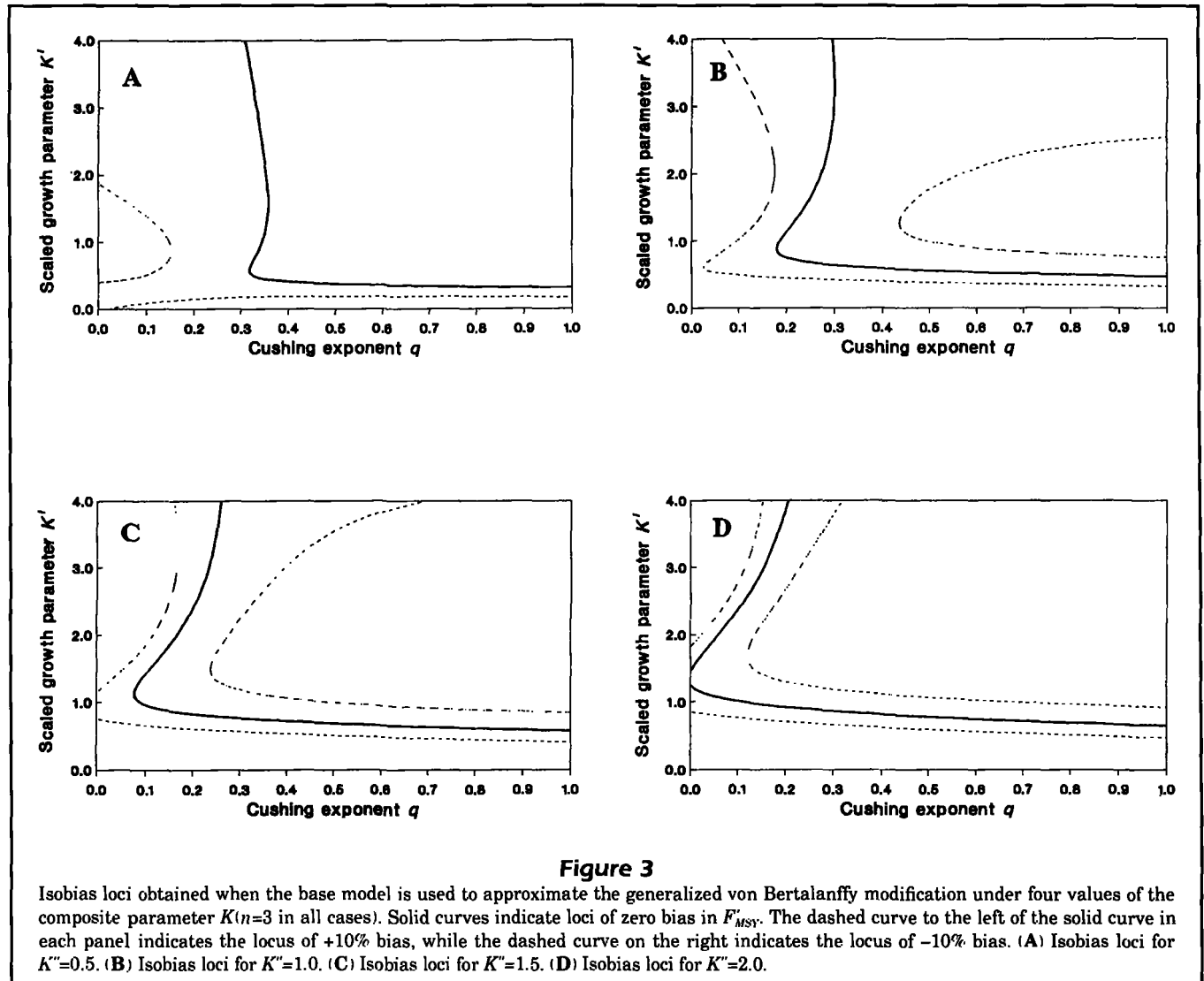

Figure 3
Isobias loci obtained when the base model is used to approximate the generalized von Bertalanffy modification under four values of the composite parameter $K(n=3$ in all cases). Solid curves indicate loci of zero bias in F'_{MSY}. The dashed curve to the left of the solid curve in each panel indicates the locus of +10% bias, while the dashed curve on the right indicates the locus of −10% bias. (A) Isobias loci for $K''=0.5$. (B) Isobias loci for $K''=1.0$. (C) Isobias loci for $K''=1.5$. (D) Isobias loci for $K''=2.0$.

To accommodate this change, the Cushing stock-recruitment relationship (Equation 4) has to be re-written to specify that only the mature biomass $B_m(F')$ contributes to recruitment:

$$b(F',a_f) = p B_m(F')^q. \tag{25}$$

Equation 2 can be rewritten to express total fishable biomass as

$$B_f(F') + \left(\frac{b(F',a_f)}{M}\right)\left(\frac{1 + K_f'' + F'}{(1 + F')^2}\right), \tag{26}$$

where $K_f'' = 1/[M(a_f - a_0)]$, after Equation 3.

Polynomial solution

Age at recruitment exceeds age at maturity
In the case where a_f exceeds a_m, recruitment to the fishery and to the mature stock are related as follows:

$$b(F',a_f) = b(F',a_m)\left(\frac{w(a_f)}{w(a_m)}\right) e^{-M(a_f - a_m)} =$$

$$b(F',a_m)\left(\frac{K_m''}{K_f''}\right) e^{-\left(\frac{1}{K_f''} - \frac{1}{K_m''}\right)}, \tag{27}$$

where $K_m'' = 1/[M(a_m - a_0)]$, after Equation 3.
Total mature biomass can then be expressed as

$$B_m(F') = \left(\frac{b(F',a_m)}{a_m - a_0}\right) \int_{a_m}^{a_f}(a - a_0)e^{-M(a - a_m)}da + B_f(F')$$

$$=\left(\frac{b(F',a_m)}{M}\right)\left[\left(1 + \frac{1}{M(a_m - a_0)}\right)\right.$$

$$\left. - e^{-M(a_f - a_m)}\left(\frac{a_f - a_0}{a_m - a_0} + \frac{1}{M(a_m - a_0)}\right)\right] + B_f(F') \tag{28}$$

$$=\left(\frac{b(F',a_m)}{M}\right)\left[1 + K_m'' - e^{-\left(\frac{1}{K_f''} - \frac{1}{K_m''}\right)}\left(\frac{K_m''}{K_f''} + K_m''\right)\right] + B_f(F')$$

$$= \frac{b(F',a_m)(1 + K_m'') - b(F',a_f)(1 + K_f'')}{M} + B_f(F').$$

Equations 25–28 constitute a set of four equations in four unknowns $[b(F',a_f), b(F',a_m), B_f(F'),$ and $B_m(F')]$. Solving simultaneously gives

$$B_f(F') = \left(\frac{p}{M}\right)\left(\frac{1+K_f''+F'}{(1+F')^2}\right)\left[\left(\frac{p}{M}\right)\left(\frac{1+K_m''+F'}{(1+F')^2}\right)+\alpha(K_f'')\right]^{\frac{q}{1-q}}, \tag{29}$$

where

$$\alpha(K_f'') =\left(\frac{K_f''}{K_m''}\right)\left(\frac{1 + K_m''}{e^{-\left(\frac{1}{K_f''} - \frac{1}{K_m''}\right)}}\right) - K_f'' - 1. \tag{30}$$

Multiplying Equation 29 through by MF', differentiating with respect to F', and setting the resulting expression equal to zero gives the following polynomial solution for F_{MSY}' (which collapses to Equation 6 when $K_f'' = K_m''$):

$$((1- q)[\alpha(K_f'')(1-K_f'')+1]-1)F_{MSY}'^3+$$

$$((1-q)[\alpha(K_f'')(3-K_f'')+2K_f''+3]-3K_f''-2)F_{MSY}'^2+$$

$$(1-q)[\alpha(K_f'')(3+K_f'')+K_f''^2+4K_f''+3]-2K_f''^2-3K_f''-1)F_{MSY}'+ \tag{31}$$

$$(1-q)[\alpha(K_f'')(1+K_f'')+K_f''^2+2K_f''+1] = 0.$$

The solution for F_{max}' in this model is the same as in the base model (Equation 7).

Equation 31 contains $F_{MSY}' = 1$ as a special case, obtained when the following relationship holds:

$$q = 1 - \frac{(K_f'' + 2)(K_f'' + 1)}{4\alpha(K_f'') + (K_f'' + 2)^2}. \tag{32}$$

Just as the base model required an inverse relationship between q and K'' in order for F_{MSY}' to equal 1.0 (Equation 8), this model requires an inverse relationship between q and K_f''. Likewise, the upper limit to the ratio $B(F_{MSY}')/B(0)$ is the same as in the base model $(1/e)$.

Age at maturity exceeds age at recruitment
Another possible modification is to allow a_m to exceed a_f. This requires rewriting Equation 27 as follows:

$$b(F',a_f) = b(F',a_m)\left(\frac{K_m''}{K_f''}\right) e^{-1+F'\left(\frac{1}{K_f''} - \frac{1}{K_m''}\right)}. \tag{33}$$

The previous expressions for recruitment (Equation 25) and equilibrium fishable biomass (Equation 26) can be applied without modification. However, because the entire mature stock is subject to both fishing and natural mortality, the previous expression for equilibrium mature biomass (Equation 28) is simplified to

$$B_m(F') =\left(\frac{b(F',a_m)}{M}\right)\left(\frac{1 + K_m'' + F'}{(1 + F')^2}\right). \tag{34}$$

Solving Equations 25, 26, 33, and 34 simultaneously gives

$$B_f(F') = \left(\frac{p}{M}\right)\left(\frac{1+K_f''+F'}{(1+F')^2}\right)\left[\left(\frac{p}{M}\right)\left(\frac{1+K_m''+F'}{(1+F')^2}\right)\times\right.$$
$$\left.\left(\frac{K_f''}{K_m''}\right)e^{-(1+F')\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)}\right]^{\frac{q}{1-q}}. \quad (35)$$

The fact that F' appears in the exponent in Equation 35 complicates the solution for F_{MSY}' somewhat, increasing the degree of the polynomial solution to four:

$$\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)qF_{MSY}'^4 + \left[(K_f''+K_m''+3)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)+1\right]qF_{MSY}'^3 +$$
$$\left[(K_f''K_m''+2K_f''+2K_m''+3)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)q +\right.$$
$$\left.(2K_m''+3)q + K_f''-1\right]F_{MSY}'^2 + \quad (36)$$
$$\left[(K_f''+1)(K_m''+1)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)q + (K_f''+3)(K_m''+1)q +\right.$$
$$\left. K_f''K_m''-K_m''-2\right]F_{MSY}' - (K_f''+1)(K_m''+1)(1-q) = 0.$$

The solution for F_{max}' is the same as in the base model (Equation 7).

Equation 36 contains $F_{MSY}'=1$ as a special case, obtained when the following relationship holds:

$$q = \frac{K_m''+2}{(K_f''+2)(K_m''+2)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)+K_f''(K_m''+1)+3K_m''+4}. \quad (37)$$

As with the base model (Equation 8), the above expression implies an inverse relationship between q and K_f''. Likewise, the upper limit to the ratio $B(F_{MSY}')/B(0)$ remains the same $(1/e)$.

Bias resulting from the assumption of $a_f = a_m$

When $a_f > a_m$, Equation 6 tends to underestimate F_{MSY}'. Loci of -10% bias are shown in Figure 4A for four values of K_m''. Parameter combinations above a particular curve and below the horizontal line $K_f'' = K_m''$ result in an F_{MSY}' estimate that is within 10% of the value given by Equation 31. Note that the base model's solution is fairly sensitive to K_f'' when K_m'' is low. For example, when $K_m''=0.5$, almost any value of $K_f''<K_m''$ will result in Equation 6 underestimating F_{MSY}' by more than 10%. At higher K_m'' values (e.g., $K_m''>1$), the base model's solution is less sensitive.

The results for the case where $a_f < a_m$ are similar, except that here Equation 6 tends to overestimate rather than underestimate F_{MSY}'. Loci of $+10\%$ bias are shown in Figure 4B for four values of K_m''. Parameter combinations below a particular curve and above the horizontal line $K_f''=K_m''$ result in an F_{MSY}' estimate that is within 10% of the value given by Equation 31. Again, the base model's solution is fairly sensitive to K_f'' when K_m'' is low (e.g., $K_m''=0.5$), while at higher values (e.g., $K_m''>1$), the base model's solution is less sensitive.

Finite maximum age

As defined by Thompson (1992), all simple dynamic pool models exhibit mortality and growth rates which are independent of age (above the age of recruitment). This implies that there is no maximum age. However, in more complicated dynamic pool models, it is common to specify a maximum age above which all remaining fish die in knife-edge fashion. As noted by Fletcher (1987), misspecification of maximum age can introduce significant bias into some models. When the base model is modified so as to exhibit a finite maximum age (a_{max}), Equation 5 will tend to overestimate true equilibrium stock biomass, which can be written as
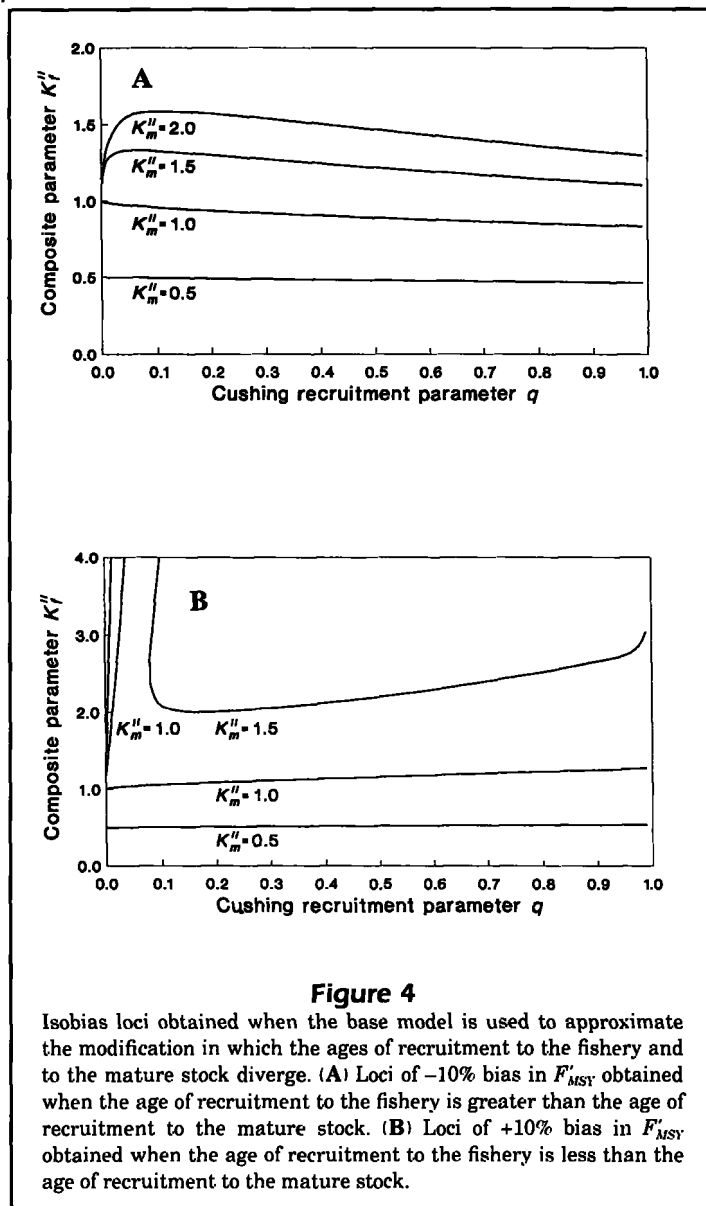
$$B(F') = \left[\left(\frac{p}{M}\right)\left(\frac{K''+1+F'}{(1+F')^2} - \right.\right.$$
$$\left.\left.\left(\frac{K_{max}''+1+F'}{(1+F')^2}\right)\left(\frac{K''}{K_{max}''}\right)e^{-(1+F')\left(\frac{1}{K_{max}''}-\frac{1}{K''}\right)}\right]^{\frac{1}{1-q}}, \quad (38)$$

where $K_{max}''=1/[M(a_{max}-a_0)]$, after Equation 3. The difference inside the exterior parentheses in Equation 38 is proportional to the difference between two calculations of stock biomass per recruit in a population with infinite maximum age, where the first calculation begins the integral (over age) at age a_r and the second begins at age a_{max}. Subtracting the second term from the first adjusts for the assumption of a maximum age at $a=a_{max}$.

Because of the presence of F' in the exponential term in Equation 38, it is not possible to solve for F_{MSY}' explicitly in this modification.

Bias resulting from the assumption of infinite maximum age

Note that as K_{max}'' becomes small (e.g., as a_{max} becomes large), the proportion surviving to the maximum age (the exponential term in Equation 38) goes to zero and

Figure 4

Isobias loci obtained when the base model is used to approximate the modification in which the ages of recruitment to the fishery and to the mature stock diverge. (A) Loci of −10% bias in F'_{MSY} obtained when the age of recruitment to the fishery is greater than the age of recruitment to the mature stock. (B) Loci of +10% bias in F'_{MSY} obtained when the age of recruitment to the fishery is less than the age of recruitment to the mature stock.

Equation 38 collapses to Equation 5. However, at any positive value of K'''_{max}, Equation 5 will tend to overestimate the true value of $B(F')$ to some extent. Conversely, Equation 6 will tend to underestimate the true value of F'_{MSY}. Figure 5 shows loci of −10% bias in Equation 6's estimate of F'_{MSY}. Points above and to the left of the curves result in a bias of less than 10% (absolute value). For example, a stock with $M=0.2$, $a_0=-1$, and $a_{max}=24$ would have a K'''_{max} value of 0.2. For such a stock, Equation 6's estimate of F'_{MSY} would be within 10% of the correct value for any value of $K''>0.5$ so long as q was less than about 0.53.

Conclusion

Four modifications to the base model presented by Thompson (1992) have been considered (Beverton-Holt recruitment, generalized von Bertalanffy growth, divergent ages of recruitment and maturity, and finite maximum age). The first three modifications all increase the degree of the polynomial solution for F_{MSY} (Table 2), while the fourth modification renders a polynomial solution impossible.

In order to make the Cushing stock-recruitment form of the model comparable to the Beverton-Holt form, an acceptable approximation can often be made by equating the pristine stock-recruitment points and placing the other (non-zero) intersection of the stock-recruitment curves at a fairly low level (e.g., at 10% of the pristine biomass level or at 50% of the pristine recruitment level).
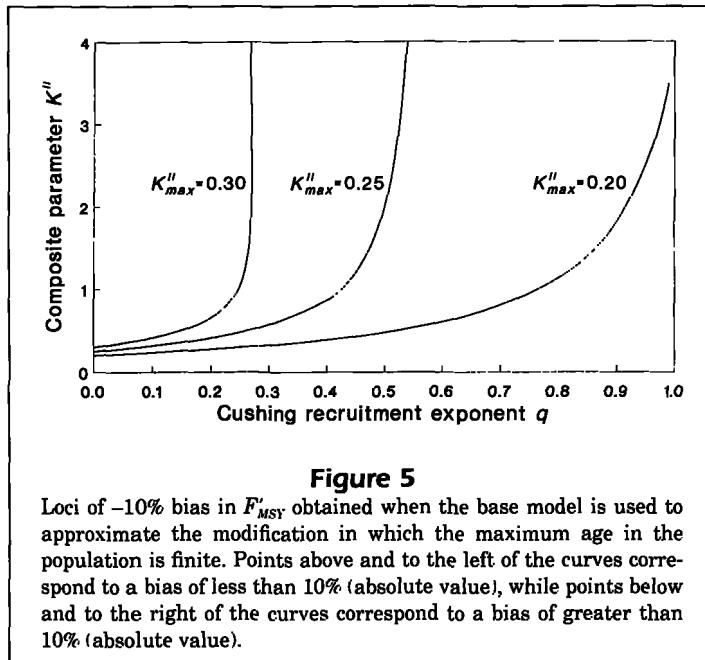
In order to make the linear growth form of the model comparable to the generalized von Bertalanffy growth form, an acceptable approximation can often be made by equating the weights at recruitment and the pristine biomass-per-recruit ratios.

When the ages of recruitment to the fishery and to the mature stock diverge sufficiently or when the maximum age in the stock is sufficiently low, the base model can produce a significantly biased estimate of F_{MSY}. Except for the case in which the age of recruitment to the fishery precedes the age of recruitment to the mature stock, though, it is helpful to note that the base model always errs on the conservative side.

In conclusion, it appears that simple models (at least the base model considered here) may often perform adequately even when the true dynamics of the system follow more complicated formulae. This tends to confirm the results of studies by Silliman (1971), Roff (1983), and Ludwig and Walters (1985), who also found that simple models could perform at least as well as more complex versions in a variety of situations.

Acknowledgments

Figure 5

Loci of –10% bias in F'_{MSY} obtained when the base model is used to approximate the modification in which the maximum age in the population is finite. Points above and to the left of the curves correspond to a bias of less than 10% (absolute value), while points below and to the right of the curves correspond to a bias of greater than 10% (absolute value).

Table 2

Degree of polynomial solutions for F'_{MSY} under various modifications.

Modification	Degree
Beverton-Holt stock-recruitment	3
Generalized von Bertalanffy growth	
$K=0$	$n+1$
$K>0$	$2n+1$
Divergent ages of recruitment and maturity	
$a_r > a_m$	3
$a_r < a_m$	4

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Appendix

Some combinatoric terms

In order to incorporate Equations 22 or 23 into the model, it is helpful to define a few concepts taken from combinatorial theory (the notation used here follows Riordan [1980]). First, the number of permutations of n objects taken k at a time is given by

$$(n)_k = \frac{n!}{(n-k)!},$$ (A1)

with $(n)_k$ defined as zero for $k<0$ or $k>n$.

The number of combinations (i.e., permutations without regard to order) of n objects taken k at a time is given by the binomial coefficient

$$\binom{n}{k} = \frac{(n)_k}{k!} = \frac{n!}{k!\,(n-k)!},$$ (A2)

with $\binom{n}{k}$ defined as zero for $k<0$ or $k>n$.

The number of ways in which an n-element set can be partitioned into k subsets is given by Stirling numbers of the second kind, written

$$S(n, k) = \left(\frac{1}{k!}\right) \sum_{\lambda=0}^{k} (-1)^{(k-\lambda)} \binom{k}{\lambda} \lambda^n.$$ (A3)

The coefficients of the polynomial expansion of $(x)_n$ are given by Stirling numbers of the first kind, written

$$s(n, k) = \sum_{\lambda=0}^{n-k} (-1)^{\lambda} \binom{n-1+\lambda}{n-k+\lambda}\binom{2n-k}{n-k-\lambda} S(n-k+\lambda, \lambda).$$ (A4)

Polynomial solution for a generalized growth function

$K=0$ Beginning with the simpler case where $K=0$ (Equation 23), stock biomass per recruit can be written

$$BPR(F') = \int_{a_r}^{\infty} w_r \left(\frac{a-a_r}{a_r-a_0}\right)^n e^{-M(1+F')(a-a_r)}\, da$$

(A5)

$$= \left(\frac{w_r}{M}\right) \sum_{k=0}^{n} \frac{(n)_k K''^k}{(1+F')^{k+1}}.$$

In general, stock biomass in any simple dynamic pool model with Cushing recruitment can be written as the following function of biomass per recruit:

$$B(F') = \left(\frac{pBPR(F')}{w_r}\right)^{\frac{1}{1-q}}.$$ (A6)

Substituting Appendix Equation 5 (A5) into Appendix Equation 6 (A6), multiplying through by MF', and differentiating gives the following expression:

$$\frac{dY(F')}{dF'} = \left(\frac{pB(F')^q}{(1-q)(1+F')^{n+2}}\right) \times$$

$$\left(\sum_{k=0}^{n} [(n)_k K''^k (1-kF')(1+F')^{n-k}] - \right.$$ (A7)

$$\left. q \sum_{k=0}^{n} [(n)_k K''^k (1+F')^{n+1-k}]\right).$$

The solution to Equation A7 can be written as a polynomial of degree $n+1$ as follows:

$$\sum_{i=0}^{n}\left(\sum_{k=0}^{n}\left[\binom{n-k}{i}-k\binom{n-k}{i-1}\right](n)_k K''^k - \right.$$

$$\left.\left[\sum_{k=0}^{n}\binom{n+1-k}{i}(n)_k K''^k\right]q\right)F'_{MSY}{}^i - qF'_{MSY}{}^{n+1} = 0. \quad \text{(A8)}$$

In the special case where $q=0$, Equation A8 gives the following polynomial solution for F'_{max}:

$$\sum_{i=0}^{n}\left(\sum_{k=0}^{n}\left[\binom{n-k}{i}-k\binom{n-k}{i-1}(n)_k K''^k\right]\right)F'_{max}{}^i = 0. \quad \text{(A9)}$$

Equation A7 can be solved explicitly for q. The locus at which $F'_{MSY}=1$ is given by

$$q = \left(\frac{1}{2}\right)\left(1 - \frac{\sum_{k=0}^{n}\left[k\,(n)_k\left(\frac{K''}{2}\right)^k\right]}{\sum_{k=0}^{n}\left[(n)_k\left(\frac{K''}{2}\right)^k\right]}\right). \quad \text{(A10)}$$

Note that Equations 6–8 constitute the special cases of Equations A8–A10 where $n=1$.

K>0 When growth follows the form of Equation 22, stock biomass per recruit can be written

$$BPR(F') = \int_{a_r}^{\infty} w_r\left(\frac{1-e^{-K(a-a_r)-K'/K''}}{1-e^{-K'/K''}}\right)^n e^{-M(1+F')(a-a_r)}\,da \quad \text{(A11)}$$

$$= \left(\frac{w_r}{M(1-e^{-K'/K''})^n}\right)\left(\sum_{k=0}^{n}\frac{(-1)^k\binom{n}{k}e^{-kK'/K''}}{kK'+1+F'}\right).$$

Substituting Equation A11 into Equation A6, multiplying through by MF', and differentiating gives the following expression:

$$\frac{dY(F')}{dF'} = MB(F')\left(1-\left(\frac{F}{(1-q)\sum_{k=0}^{n}\dfrac{(-1)^k\binom{n}{k}e^{-kK'/K''}}{kK'+1+F'}}\right)\times\right.$$

$$\left.\sum_{k=0}^{n}\frac{(-1)^k\binom{n}{k}e^{-kK'/K''}}{(kK'+1+F')^2}\right). \quad \text{(A12)}$$

Letting

$$z(F') = \frac{MB(F')}{(1-q)\left(\sum_{k=0}^{n}\dfrac{(-1)^k\binom{n}{k}e^{-kK'/K''}}{kK'+1+F'}\right)\prod_{k=0}^{n}(kK'+1+F')^2}, \quad \text{(A13)}$$

Equation A12 can be rewritten as

$$\frac{dY(F')}{dF'} = z(F')\left[\sum_{k=0}^{n}\left((-1)^k\binom{n}{k}e^{-kK'/K''}[(1-q)\times\right.\right.$$

$$\left.\left.(kK'+1)-qF']\left(\prod_{m\neq k}(mK'+1+F')^2\right)\right)\right]. \quad \text{(A14)}$$

The term enclosed in large square brackets in Equation A14 can be expanded to polynomial form. Proceeding in steps, first note that

$$\prod_{m=0}^{n-1}(mK'+1) = \sum_{m=0}^{n-1}(-1)^m s(n, n-m)K'^m. \quad \text{(A15)}$$

Letting

$$\alpha_{k,m} = \sum_{\lambda=0}^{m}(-1)^{m+\lambda}(n-k)_\lambda s(n-\lambda, n-m) \quad \text{(A16)}$$

(except for $\alpha_{0,n}=n!$), Equation A15 can be extended to

$$\sum_{k=0}^{n}\left(\prod_{m\neq k}(mK'+1)\right) = \sum_{k=0}^{n}\left(\sum_{m=0}^{n}\alpha_{k,m}K'^m\right). \quad \text{(A17)}$$

Next, let

$$\beta_{k,l,m} = \alpha_{k,m}\binom{n-m}{l}, \quad \text{(A18)}$$

in which case Equation A17 can be extended to

$$\sum_{k=0}^{n}\left(\prod_{m\neq k}(mK'+1+F')\right) = \sum_{k=0}^{n}\left(\sum_{l=0}^{n}\left(\sum_{m=0}^{n}\beta_{k,l,m}K'^m\right)F'^l\right). \quad \text{(A19)}$$

Then, let

$$\gamma_{i,j,k} = \sum_{l=0}^{i}\left(\sum_{m=\min(0,j-n)}^{j}\beta_{k,l,m}\beta_{k,i-l,j-m}\right), \quad \text{(A20)}$$

in which case Equation A19 can be extended to

$$\sum_{k=0}^{n}\left(\prod_{m\neq k}(mK'+1+F')^2\right) = \sum_{i=0}^{2n}\left(\sum_{j=0}^{2n-1}\left(\sum_{k=0}^{n}\gamma_{i,j,k}K'^j\right)F'^i\right). \quad \text{(A21)}$$

Finally, the solution to Equation A14 can be written as a polynomial of degree $2n+1$ as follows:

$$\sum_{i=0}^{2n}\left[\sum_{j=0}^{2n-i}\left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}(k\gamma_{i,j-1,k}+\gamma_{i,j,k})e^{-kK'/K''}\right)K'^j - \right.$$

$$\left(\sum_{j=0}^{2n-i}\left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}(k\gamma_{i,j-1,k}+\gamma_{i,j,k}+\right.\right.$$

$$\left.\left.\left.\gamma_{i-1,j,k})e^{-kK'/K''}\right)K'^j\right)q\right]F'_{MSY}{}^i - \left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}e^{-kK'/K''}\right)qF'_{MSY}{}^{2n+1} = 0. \quad \text{(A22)}$$

In the special case where $q=0$, Equation A22 gives the following polynomial solution for F'_{max}:

$$\sum_{i=0}^{2n}\left[\sum_{j=0}^{2n-i}\left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}(k\gamma_{i,j-1,k}+\gamma_{i,j,k})e^{-kK'/K''}\right)K'^j\right]F'^i_{max}=0. \quad (A23)$$

Equation A14 can be solved explicitly for q. The locus at which $F'_{MSY}=1$ is given by

$$q = \frac{\displaystyle\sum_{k=0}^{n}\left[(-1)^k\binom{n}{k}e^{-kK'/K''}\left(\prod_{m\neq k}(mK'+2)^2\right)(kK+1)\right]}{\displaystyle\sum_{k=0}^{n}\left[(-1)^k\binom{n}{k}e^{-kK'/K''}\left(\prod_{m\neq k}(mK'+2)^2\right)(kK+2)\right]}. \quad (A24)$$