

**Abstract.**—This paper is devoted to a theoretical examination of two rules of thumb commonly used in fishery management: (I) the fishing mortality rate associated with maximum sustainable yield ( $F_{MSY}$ ) equals the natural mortality rate, and (II) the equilibrium stock biomass at maximum sustainable yield equals one-half the pristine stock biomass. Taken together, these rules of thumb are shown to be inconsistent with any simple dynamic pool model in which three conditions hold: (1) the first derivative of the stock-recruitment relationship is uniformly non-negative, (2) the second derivative of the stock-recruitment relationship is uniformly nonpositive, and (3) the first derivative of the weight-at-age relationship is uniformly positive. An example of such a model is presented and the equilibrium solution derived analytically. In this model,  $F_{MSY}$  can be either greater than or less than the natural mortality rate, while the equilibrium stock biomass at maximum sustainable yield is consistently less than one-half the pristine stock biomass. To illustrate the utility of the theoretical framework developed, the model is applied to the eastern Bering Sea stock of rock sole *Pleuronectes bilineatus*.

## Management advice from a simple dynamic pool model

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### Two rules of thumb

Despite its acknowledged shortcomings (e.g., Larkin 1977), management for maximum sustainable yield (MSY) remains a common strategy among fisheries professionals. Under a constant harvest rate policy, this strategy is implemented by exploiting the stock at the fishing mortality rate corresponding to MSY ( $F_{MSY}$ ). Alternatively, this strategy could be implemented by exploiting the stock so as to maintain its biomass at the level corresponding to MSY,  $B(F_{MSY})$ . To estimate  $F_{MSY}$  and  $B(F_{MSY})$ , fishery scientists and managers employ a variety of approaches, ranging from highly sophisticated simulation models to simple "rules of thumb." Frequently used examples of the latter can be found in the form of two hypotheses employed by Alverson and Pereyra (1969) in their analysis of the potential yield of certain fish stocks. These hypotheses (hereafter referred to as Rules I and II) are

$$\frac{F_{MSY}}{M} = 1 \quad (I)$$

and

$$\frac{B(F_{MSY})}{B(0)} = 0.5, \quad (II)$$

where  $F$  is the instantaneous rate of fishing mortality per year,  $F_{MSY}$  is the value of  $F$  that produces MSY in equilibrium,  $M$  is the instantaneous rate of natural mortality per year,  $B(F)$  is the equilibrium stock biomass corresponding to a fishing mortality

rate of  $F$ ,  $B(F_{MSY})$  is the equilibrium stock biomass when  $F = F_{MSY}$ , and  $B(0)$  is the pristine stock biomass (i.e., equilibrium stock biomass when  $F = 0$ ).

Alverson and Pereyra (1969) presented a sketchy derivation of Rules I and II, leaving open the question of which models might be capable of leading to the hypothesized relationships. A number of authors have subsequently examined specific models in this context and shown them to be inconsistent with Rules I and II. Gulland (1971) and Beddington and Cooke (1983) cast doubt on the robustness of Rules I and II in terms of their applicability to the "simple" model of Beverton and Holt (1957), but did not generalize their conclusions beyond that particular model. Likewise, Francis (1974) demonstrated inconsistencies between Rules I and II and a set of assumptions derived from the Schaefer (1954) model, although his argument was weakened somewhat by computing MSY in terms of numbers, not biomass. Deriso (1982) showed that the discrete fishing mortality rate generated by his delay-difference model at MSY was consistently higher than the discrete natural mortality rate when recruitment was constant, while under several other stock-recruitment assumptions the relationship was reversed. Shepherd (1982) also demonstrated that Rules I and II did not adequately describe the behavior of a particular surplus production model.

Since none of these authors addressed the possibility that other

models might support Rules I and II, it remains to be seen whether these rules are inconsistent only for isolated special cases, or are actually incompatible with a major class of models.

## Review of simple dynamic pool models

One place to start in the search for models that might be compatible with Rules I and II is within the family of simple dynamic pool models. As distinguished from surplus production models such as those of Schaefer (1954) and Pella and Tomlinson (1969), dynamic pool models describe stock dynamics in terms of the individual processes of recruitment, growth, and mortality, and incorporate age structure at least implicitly (e.g., Pitcher and Hart 1982). Within the broad class of dynamic pool models, a model will be referred to here as "simple" if it reflects the following assumptions: (A) Cohort dynamics are of continuous-time form, (B) vital rates are constant with respect to time and age, (C) fish mature and recruit to the fishery continuously and at the same invariant ("knife-edge") age, (D) mean body weight-at-age is determined by age alone, (E) the stock (or population) consists of the pool of recruited individuals, (F) maximum age is infinite, (G) the stock is in an equilibrium state determined by the fishing mortality rate, and (H) 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.

Assumptions (A–C) imply that simple dynamic pool models conform to the following pair of equations:

$$\frac{\partial n(F, a)}{\partial a} = -n(F, a)Z, \quad (1)$$

and

$$n(F, a) = n(F, a_r) e^{-Z(a-a_r)}, \quad (2)$$

where  $a$  = age,  $n(F, a)$  is the stationary population distribution (in numbers) by ages  $a$  when the stock is exploited at a fishing mortality rate of  $F$ ,  $Z$  is the instantaneous rate of total mortality ( $F + M$ ), and  $a_r$  is the age of recruitment.

Equation (1) gives the instantaneous rate of change, by age, of the distribution  $n$ . When integrated with  $Z$  constant (Assumption B), Equation (1) gives Equation (2), numbers as a function of age. Assumption (D) implies that Equation (2) can be cast in terms of biomass by multiplying both sides of the equation by the weight-at-age function  $w(a)$ :

$$b(F, a) = W(a) n(F, a_r) e^{-Z(a-a_r)}, \quad (3)$$

where  $b(F, a)$  is the stationary population distribution (in biomass) by ages  $a$  when the stock is exploited at a fishing mortality rate of  $F$ .

Assumptions (B), (C), (E), and (F) imply that total equilibrium stock numbers can be obtained by integrating Equation (2) from  $a = a_r$  to  $a = \infty$ , giving

$$N(F) = \frac{n(F, a_r)}{Z}, \quad (4)$$

where  $N(F)$  represents total equilibrium numbers when the stock is exploited at a fishing mortality rate of  $F$ .

Likewise, equilibrium stock biomass is obtained by integrating Equation (3) from  $a = a_r$  to  $a = \infty$ :

$$B(F) = n(F, a_r) \int_{a_r}^{\infty} w(a) e^{-Z(a-a_r)} da. \quad (5)$$

In the case where  $a = a_r$ , Assumptions (G) and (H) imply that the left-hand side of Equation (3), recruitment biomass, is a deterministic function of equilibrium stock biomass  $r(B(F))$ :

$$b(F, a_r) = r(B(F)). \quad (6)$$

Average weight of individuals in the stock  $W(F)$  can be written

$$\begin{aligned} W(F) &= \frac{\int_{a_r}^{\infty} w(a) e^{-Z(a-a_r)} da}{\int_{a_r}^{\infty} e^{-Z(a-a_r)} da} \\ &= Z \int_{a_r}^{\infty} w(a) e^{-Z(a-a_r)} da. \end{aligned} \quad (7)$$

Equation (5) can then be rewritten

$$B(F) = \frac{W(F) n(F, a_r)}{Z}. \quad (8)$$

For the case of a pristine stock ( $F = 0$ ), Equations (4) and (8) imply that equilibrium stock size (in terms of

numbers and biomass, respectively) is given by

$$N(0) = \frac{n(0, a_r)}{M}, \quad (9)$$

and

$$B(0) = \frac{W(0) n(0, a_r)}{M}. \quad (10)$$

## Inconsistency of Rules I and II

The argument of Francis (1974) can be generalized to address more fully the compatibility of Rules I and II. The method to be used is as follows: First, it will be shown that if Rules I and II were to hold simultaneously with the properties of simple dynamic pool models, these rules would imply a particular result. It will then be shown that this result is incompatible with a major subset of the family of simple dynamic pool models, thus proving that Rules I and II are also incompatible with this subset.

Rule II and Equation (10) imply

$$B(F_{MSY}) = \frac{W(0) n(0, a_r)}{2M}. \quad (11)$$

Equation (8) implies that  $B(F_{MSY})$  must also conform to

$$B(F_{MSY}) = \frac{W(F_{MSY}) n(F_{MSY}, a_r)}{F_{MSY} + M}. \quad (12)$$

Solving Equations (11) and (12) for  $F_{MSY}$  gives

$$F_{MSY} = \left( \frac{2W(F_{MSY}) n(F_{MSY}, a_r)}{W(0) n(0, a_r)} - 1 \right) M. \quad (13)$$

Next, Rule I and Equation (13) imply

$$\frac{n(F_{MSY}, a_r)}{n(0, a_r)} = \frac{W(0)}{W(F_{MSY})}. \quad (14)$$

The left-hand side of Equation (14) can be rewritten

$$\frac{n(F_{MSY}, a_r)}{n(0, a_r)} = \frac{w(a_r) n(F_{MSY}, a_r)}{w(a_r) n(0, a_r)}$$

$$\begin{aligned} &= \frac{b(F_{MSY}, a_r)}{b(0, a_r)} \\ &= \frac{r(B(F_{MSY}))}{r(B(0))}. \end{aligned} \quad (15)$$

Now let the discussion be restricted to models in which the first derivative of the stock-recruitment relationship is uniformly nonnegative. In such cases, Equation (15) indicates that the left-hand side of Equation (14) is less than or equal to 1 if equilibrium stock biomass decreases as a function of  $F$  [i.e., if  $B(F_{MSY}) < B(0)$ , then  $r(B(F_{MSY})) < r(B(0))$ ]. To examine the conditions under which this occurs, let Equation (8) be rewritten

$$B(F) = \frac{W(F) r(B(F))}{w(a_r) Z}. \quad (16)$$

Equation (16) can be differentiated as follows:

$$\frac{dB(F)}{dF} = \frac{r(B(F)) \left[ Z \left( \frac{dW(F)}{dF} \right) - W(F) \right]}{Z \left[ w(a_r) Z - W(F) \left( \frac{dr(F(F))}{dB(F)} \right) \right]}. \quad (17)$$

The numerator in Equation (17) is negative whenever  $dW(F)/dF < 0$ , which is easily shown to be true whenever  $w(a)$  is monotone increasing, a characteristic typical of all commonly used growth functions (Schnute 1981).

Thus, it follows that  $dB(F)/dF$  will likewise be negative whenever the denominator in Equation (17) is positive; that is, whenever

$$\frac{w(a_r) Z}{W(F)} > \frac{dr(F(F))}{dB(F)}. \quad (18)$$

By Equation (16), the left-hand side of (18) can be rewritten as the ratio of  $r(B(F))$  to  $B(F)$ , giving

$$\frac{r(B(F))}{B(F)} > \frac{dr(B(F))}{dB(F)}. \quad (19)$$

Given that the discussion has been restricted to models with stock-recruitment relationships that are nondecreasing (nonnegative first derivative), a sufficient condition for Equation (19) to hold is for  $dr(B(F))/dB(F)$  to be nonincreasing (nonpositive second

derivative). Therefore, for all simple dynamic pool models in which  $r(B(F))$  is nondecreasing and  $dr(B(F))/dB(F)$  is nonincreasing, the left-hand side of Equation (14) is less than or equal to 1.0.

Turning to the right-hand side of Equation (14), note that this expression is necessarily greater than 1.0 whenever  $dW(F)/dF < 0$ , a condition which has already been noted to hold whenever  $w(a)$  is monotone increasing.

Summarizing the argument, then, it has been shown that Rules I and II cannot hold simultaneously for any simple dynamic pool model in which the first derivative of the stock-recruitment relationship is uniformly non-negative, the second derivative of the stock-recruitment relationship is uniformly nonpositive, and the first derivative of the weight-at-age relationship is uniformly positive.

## Example of a simple dynamic pool model

### Growth, biomass, recruitment, and yield

As an alternative to Rules I and II, it is possible to examine the behavior of  $F_{MSY}/M$  and  $B(F_{MSY})/B(0)$  explicitly for a particular model. The model to be examined here incorporates a linear weight-at-age function (Schnute 1981). Let

$$w(a) = w(a_r) \left( \frac{a - a_0}{a_r - a_0} \right), \quad (20)$$

where  $a_0$  represents the age intercept.

Biomass at age is then

$$b(F, a) = \frac{b(F, a_r) (a - a_0) e^{-Z(a - a_r)}}{a_r - a_0}, \quad (21)$$

For a given value of  $b(F, a_r)$ , biomass at age can be integrated from  $a = a_r$  to  $a = \infty$  to obtain the corresponding equilibrium stock size. Equation (21) can be integrated by parts, giving the following expression for equilibrium stock biomass (Hulme et al. 1947):

$$\begin{aligned} B(F) &= \left( \frac{b(F, a_r)}{a_r - a_0} \right) \int_{a_r}^{\infty} (a - a_0) e^{-Z(a - a_r)} da \\ &= \left( \frac{b(F, a_r)}{Z} \right) \left( 1 + \frac{1}{Z(a_r - a_0)} \right). \end{aligned} \quad (22)$$

The stock-recruitment relationship of Cushing (1971) will be used to complete the model, giving recruitment as a power function of stock size:

$$b(F, a_r) = pB(F)^q, \quad (23)$$

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

The Cushing stock-recruitment relationship has the advantage of rendering Equation (22) explicitly solvable. Substituting Equation (23) into Equation (22) and rearranging terms gives the following equation for equilibrium stock biomass:

$$B(F) = \left[ \frac{p}{Z} \left( 1 + \frac{1}{Z(a_r - a_0)} \right) \right]^{\frac{1}{1-q}}. \quad (24)$$

Multiplying both sides of Equation (24) by  $F$  then gives the equation for yield  $Y(F)$  shown below:

$$Y(F) = F \left[ \frac{p}{Z} \left( 1 + \frac{1}{Z(a_r - a_0)} \right) \right]^{\frac{1}{1-q}}. \quad (25)$$

### A partitioning of stock production

From this point on, it will prove helpful to make use of a new parameter  $K''$ , defined as follows:

$$K'' = \frac{1}{M(a_r - a_0)}. \quad (26)$$

The parameter  $K''$  has a special biological interpretation in the context of the present model. To develop this interpretation, first multiply Equation (22) through by  $Z$ , yielding:

$$Z B(F) = b(F, a_r) \left( 1 + \frac{1}{Z(a_r - a_0)} \right). \quad (27)$$

Assuming no immigration or emigration, stock losses due to mortality must equal stock gains due to recruitment and growth at equilibrium (Russell 1931). Since the left-hand side of Equation (27) represents losses due to mortality, the right-hand side must equal the sum of equilibrium recruitment and growth. Therefore, Equation (27) can be rearranged to define equilibrium stock growth  $G(F)$  as follows:

$$G(F) = Z B(F) - b(F, a_r) = \frac{b(F, a_r)}{Z(a_r - a_0)}. \quad (28)$$

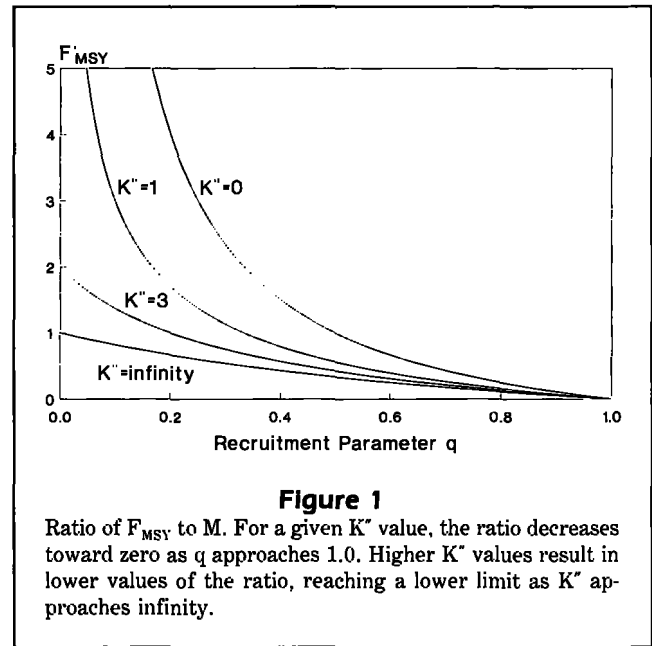
Dividing Equation (28) through by  $b(F, a_r)$  gives the ratio between the two components of stock production, i.e., growth and recruitment:

$$\frac{G(F)}{b(F, a_r)} = \frac{1}{Z(a_r - a_0)} \tag{29}$$

In the case of a pristine stock, Equation (29) reduces to

$$\frac{G(0)}{b(0, a_r)} = \frac{1}{M(a_r - a_0)} = K'' \tag{30}$$

In other words,  $K''$  is simply the pristine ratio of growth to recruitment. At values of  $K'' > 1$  pristine production is dominated by growth, while at  $K'' = 1$  the two components of pristine production are equal, and at values of  $K'' < 1$  pristine production is dominated by recruitment.



**Figure 1**  
Ratio of  $F_{MSY}$  to  $M$ . For a given  $K''$  value, the ratio decreases toward zero as  $q$  approaches 1.0. Higher  $K''$  values result in lower values of the ratio, reaching a lower limit as  $K''$  approaches infinity.

**Fishing mortality at maximum sustainable yield**

Differentiating Equation (25) with respect to  $F$  and setting the resulting expression equal to zero gives the following equation for  $F_{MSY}$ :

$$F_{MSY} = \frac{-\left(\frac{q+1}{a_r - a_0}\right) + M + \sqrt{\left(\frac{q+1}{a_r - a_0}\right)^2 + \left(\frac{(6q-2)M}{a_r - a_0}\right) + M^2}}{2q} - M \tag{31}$$

Using  $F'$  to denote the ratio  $F/M$ , Equation (31) can be simplified via Equation (26) to

$$F'_{MSY} = \frac{-(q+1)K'' + 1 + \sqrt{(q+1)^2 K''^2 + (6q-2)K'' + 1}}{2q} - 1 \tag{32}$$

Figure 1 illustrates the behavior of  $F'_{MSY}$  as a function of  $q$  for four values of  $K''$  (0, 1, 3, and  $\infty$ ). Note that  $F'_{MSY}$  can deviate substantially from the value of 1.0 suggested by Rule I. The locus of parameter values for which Rule I holds under Equation (32) is

$$q = \frac{1}{K'' + 2} \tag{33}$$

implying that  $q$  must be less than 0.5 in order for Rule I to hold.

When  $q=1$ , Equation (32) falls to zero. As  $q$  approaches zero, Equation (32) approaches an upper limit  $F'_{max}$  defined by

$$F'_{max} = \frac{K'' + 1}{K'' - 1} \tag{34}$$

The limits of Equation (32) as  $K''$  approaches zero and infinity are, respectively,

$$\lim_{K'' \rightarrow 0} F'_{MSY} = \frac{1-q}{q} \tag{35}$$

and

$$\lim_{K'' \rightarrow \infty} F'_{MSY} = \frac{1-q}{1+q} \tag{36}$$

When pristine growth and recruitment are exactly balanced ( $K'' = 1$ ), Equation (32) reduces to

$$F'_{MSY} = \sqrt{\frac{1}{4} + \frac{2}{q}} - \frac{3}{2}. \quad (37)$$

In the case of Equation (34), Rule I is always an underestimate (i.e.,  $F'_{MSY}$  is always greater than 1.0). In the case of Equation (35), Rule I is an underestimate whenever  $q < 0.5$  and an overestimate whenever  $q > 0.5$ . In the case of Equation (36), Rule I is always an overestimate, except in the limiting case where  $q = 0$ . In the case of Equation (37), Rule I is an underestimate whenever  $q < 1/3$  and an overestimate whenever  $q > 1/3$ .

### Biomass at MSY relative to pristine biomass

Substituting  $M + F_{MSY}$  for  $Z$  in Equation (24) gives  $B(F_{MSY})$ . Likewise, substituting  $M$  for  $Z$  in Equation (24) gives  $B(0)$ . Forming a ratio from these two biomasses gives

$$\frac{B(F_{MSY})}{B(0)} = \left( \frac{K'' + F'_{MSY} + 1}{(K'' + 1)(F'_{MSY} + 1)^2} \right)^{1-q}, \quad (38)$$

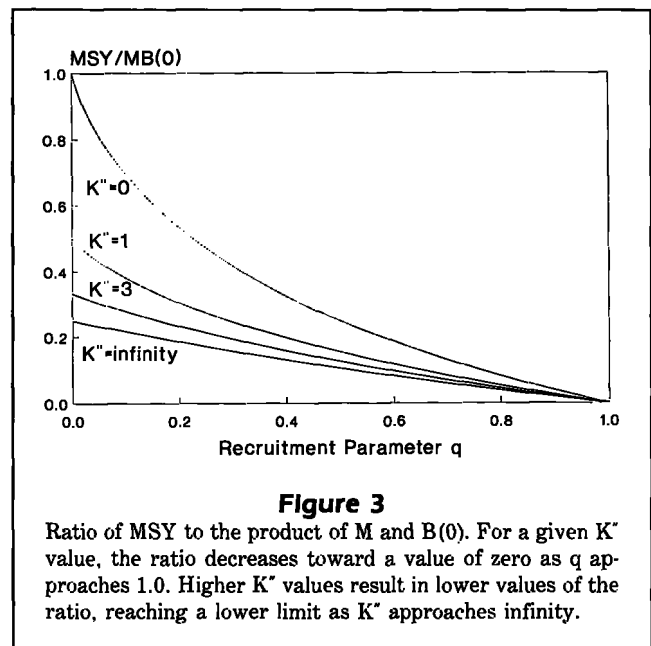
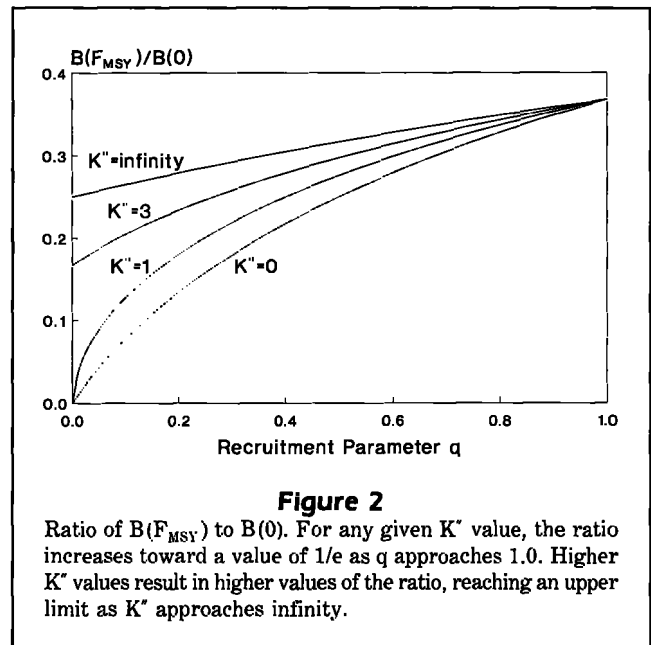
where  $F'_{MSY}$  is given by Equation (32).

Equation (38) is illustrated in Figure 2. Note that all of the curves in Figure 2 exhibit the same upper bound ( $1/e$ , about 0.37), which is reached in the limit as  $q$  approaches 1.0. Thus, Rule II always overestimates Equation (38) by a minimum of about 36%. At values of  $q > 0.5$ , the biomass ratio is always greater than 0.25, but at lower values of  $q$  the ratio can be much smaller.

Multiplying Equations (32) and (38) gives the ratio  $MSY/MB(0)$ , which is plotted in Figure 3. This ratio describes a stock's maximum sustainable fishery-induced losses as a proportion of its pristine losses. Alverson and Pereyra (1969) suggested that the  $MSY/MB(0)$  ratio should equal 0.5, a figure obtained by multiplying Rules I and II together. Note that this suggestion errs on the high side whenever  $K''$  exceeds 1.0, as well as whenever  $q$  exceeds  $\sim 0.23$ .

### Applying the model to rock sole

As an illustration of the approach suggested above, the model can be applied to the eastern Bering Sea stock of rock sole *Pleuronectes bilineatus*. This stock is exploited by a multispecies flatfish fishery, and is also the target of an important roe fishery (Walters and Wilderbuer 1988).



The parameters to be estimated are  $q$  and  $K''$ . The parameter  $q$  can be determined from data on stock biomass and recruitment. Trawl survey estimates of rock sole stock biomass are available for the years 1979–88 (Walters and Wilderbuer 1988). In addition, age composition of the stock has been determined for the years 1979–87. In order to obtain an estimate of age composition for 1988, the “iterated age-length key” approach of Kimura and Chikuni (1987) was applied to the 1986 age-length key and the 1988 length-

frequency distribution. Assuming that rock sole recruit at age 3 (Walters and Wilderbuer 1988), these data provide seven years of information on the stock-recruitment relationship. Fitting Eq. (23) to these seven points (assuming lognormal error, Fig. 4) gives  $q = 0.235$ .

The composite parameter  $K'$  can be estimated from its constituent parameters  $a_r$ ,  $a_0$ , and  $M$  (Eq. 26). Walters and Wilderbuer (1988) set  $a_r = 3$  and  $M = 0.2$ . The parameter  $a_0$  can be derived by regressing a line through the mean weights-at-age, as shown in Figure 5 ( $R^2 = 0.904$ ). This gives an  $a_0$  value of 1.475 years, implying a  $K'$  value of 3.279.

With these parameter values, Equation (32) gives  $F'_{MSY} = 0.880$ , or  $F_{MSY} = 0.176$ . This estimate of  $F_{MSY}$  compares favorably with the value of 0.155 that Walters and Wilderbuer (1988) derived from a surplus production model. It is relatively close to (within 12% of) the value indicated by Rule I.

However, Rule II does not fare so well in this example. Equation (38) estimates the ratio between  $B(F_{MSY})$  and  $B(0)$  at a value of 0.245, 51% below the value predicted by Rule II.

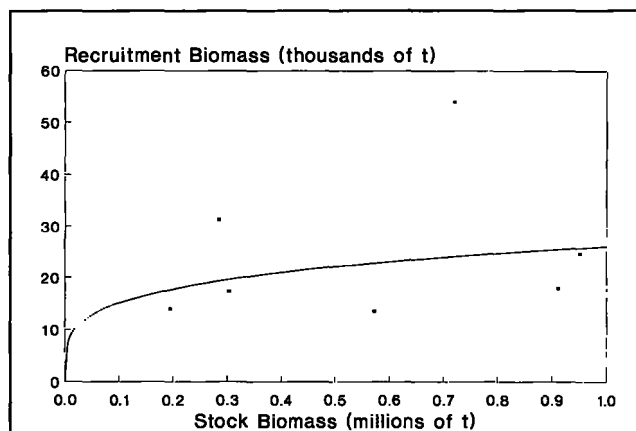
## Discussion

The topic of this paper, management advice from a simple dynamic pool model, has been considered from the perspective of how two commonly used rules of thumb compare with simple dynamic pool models in general, and how they compare with one such model in particular.

### Choice of functional forms

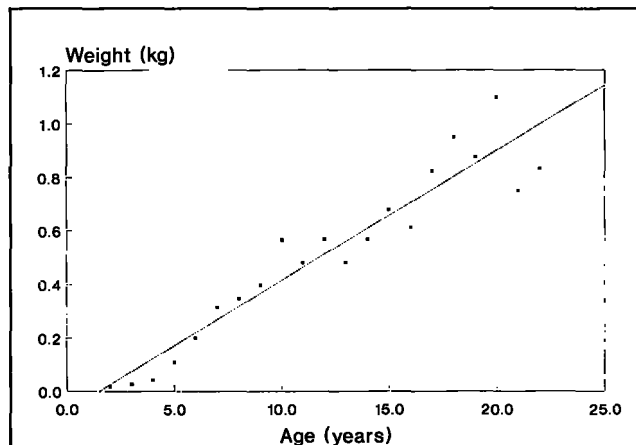
Within the family of simple dynamic pool models, a particular model is defined by its stock-recruitment and growth functions. As Paulik (1973) and Ricker (1979) state, the choice of functional form for these two processes is largely a matter of convenience. The linear growth and Cushing stock-recruitment functions have been chosen for the proposed model, in part because of the tractability they confer. For example, their use permits explicit specification of  $F_{MSY}$  (impossible in other known examples of simple dynamic pool models, except in the special case where  $F_{MSY} = F_{max}$ ). Another advantage is economy of parametrization: only two parameters ( $K'$  and  $q$ ) are required. The main disadvantage is the possibility that the simplicity of these functional forms might ignore critical behaviors.

The linear growth assumption is probably the more controversial of the two choices. The primary criticism of the linear growth equation is that it implies a con-



**Figure 4**

Stock-recruitment data and curve for eastern Bering Sea rock sole *Pleuronectes bilineatus*. Age-3 biomass (lagged 3 yr) is plotted against stock biomass for the years 1979-88.



**Figure 5**

Weight-at-age data and relationship for eastern Bering Sea rock sole *Pleuronectes bilineatus*. Data are from the 1986 trawl survey conducted by the Alaska Fisheries Science Center.

stant growth rate, whereas other commonly used functions exhibit decreasing growth rates at upper ages (Beverton and Holt 1957), usually manifested in the form of an upper asymptote. In practice, however, the absence of an asymptote may be inconsequential or even preferable (Knight 1968, Ricker 1979) for two reasons: (1) In exploited populations, individuals may only rarely survive to reach the portion of the growth curve where a marked decrease in growth rate would be most discernible; and (2) in functional forms that incorporate an asymptote, this parameter is often poorly estimated, being highly correlated with at least one other parameter in the equation.

## Robustness of the rules of thumb

Neither Rule I nor Rule II is particularly robust when applied to simple dynamic pool models in general or to the model developed here in particular. Rule I can drastically over- or underestimate the true relationship between  $F_{MSY}$  and  $M$ . When  $q$  exceeds 0.5, Rule I consistently overestimates the ratio between  $F_{MSY}$  and  $M$ , whereas when  $q$  is less than 0.5, the ratio can range both well above and well below the value suggested by Rule I.

Although these results do not provide much theoretical support for Rule I, it is still possible that Rule I holds as an empirical generalization (it turned out to be fairly close in the case of eastern Bering Sea rock sole, for example). If Rule I does hold as an empirical generalization, Equation (33) indicates that this implies an inverse relationship between the relative importance of growth in pristine production ( $K''$ ) and the degree of density-dependence in the stock-recruitment relationship ( $q$ ). Further work is necessary to see if such an inverse relationship is supported on the basis of life history or other theory.

Rule II consistently overestimates the ratio between  $B(F_{MSY})$  and  $B(0)$  in the model presented here (Eq. 38, Fig. 2). In the case of eastern Bering Sea rock sole, Rule II was off by 51%. The problem with Rule II stems from the "diminishing returns" nature of the relationship between  $F$  and  $B(F)$ , wherein successive increases in  $F$  result in less and less of an impact on biomass. Rule II, on the other hand, was inspired by the Schaefer (1954) model, in which the relationship between  $F$  and  $B(F)$  is linear (i.e., it exhibits constant returns to scale).

Interestingly, the upper asymptote displayed in Figure 2 corresponds exactly to the asymptote observed in a pair of surplus production models proposed by Pella and Tomlinson (1969, reparametrized by Fletcher 1978) and Fowler (1981), models that are conceptually very different from the one presented here. Mathematically, the isomorphism stems from the fact that all three models involve functions that raise a parameter  $x$  to an exponent of the form  $1/(1-x)$ . The fact that this result can be obtained from both surplus production and dynamic pool models indicates that it may be worthy of further investigation.

Since the rule of thumb setting  $MSY/MB(0)$  equal to 0.5 was derived by multiplying Rules I and II, it is affected by the upward bias inherent in Rule II. This is reflected in the eastern Bering Sea rock sole example, where the estimated value for the  $MSY/MB(0)$  ratio was only 0.216. It appears that the "MSY/MB(0) rule" can be a good approximation only when Rule I results in a major underestimate, which in the context of the model developed here requires two things: (1) Recruitment must be relatively independent of stock

size, and (2) pristine production must be relatively dependent on recruitment (Fig. 3). Another consequence of this relationship is that Rule I can never hold when  $MSY/MB(0) = 0.5$ , and vice-versa. This conclusion stands in stark contrast to the traditional view which holds that the  $MSY/MB(0)$  rule derives from Rule I. Instead, it seems more likely that the two are mutually exclusive, at least in the context of simple dynamic pool models.

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