

## The Structure of Complex Biological Reference Points and the Theory of Replacement

BRIAN J. ROTHSCHILD\* AND YUE JIAO

*School for Marine Science and Technology, University of Massachusetts Dartmouth,  
706 South Rodney French Boulevard, New Bedford, Massachusetts 02744-1221, USA*

**Abstract.**—The percent spawning-stock biomass per recruit (PSSBR) is a commonly used biological reference point (BRP). Justification for using specific values of PSSBR as BRPs has largely been based upon graphical interrelations of (1) the dependence of recruitment on stock, (2) the dependence of stock on recruitment (i.e., replacement), and (3) the dependence of spawning-stock biomass on fishing mortality. This paper provides analytic solutions of these interdependencies. Analytic solutions are provided for equilibrium and nonequilibrium cases: (1) fixed recruitment and fixed mortality, (2) fixed recruitment and variable mortality, and (3) variable recruitment and variable mortality. The analysis is used to develop equations for both the “replacement line” and a full recruitment→stock→recruitment cycle. The analysis clarifies the connection between iteroparous and semelparous populations in both equilibrium and nonequilibrium settings. The analytic derivations provide the opportunity to conduct research on optimization of the equations and set the stage for field and laboratory studies of the dependence of stock on recruitment, complementing the much more intensive studies of the dependence of recruitment on stock.

In the 1950s, Ricker (1954), Schaefer (1954, 1957), and Beverton and Holt (1957) led the quantification of fish-population dynamics and stock assessment. Theories of production, yield per recruit, and stock–recruitment were the main components of the quantification. Each of these theories yields optimal levels of fishing mortality or stock size. For example, the theory of production yields the level of population or the level of fishing mortality that produces maximum sustained yield (MSY). The theory of yield per recruit yields the age at recruitment and level of fishing mortality that produces the maximum (or asymptotically maximum) yield per recruit. The Ricker (1954) version of stock–recruitment theory yields the stock size that maximizes recruitment, while the Beverton and Holt (1957) version yields the stock size that produces the asymptotically maximum yield per recruit.

The theoretical development created the opportunity to manage fish stocks using quantitative criteria. These quantitative criteria, the various maximal or optimum values derived from the theories of fishing, become known as biological reference points (BRPs). A large number of BRPs were developed. These included, for example, the fishing mortality rate ( $F_{\text{MSY}}$ ) that results in MSY, the fishing mortality rate ( $F_{0.1}$ , and  $F_{\text{max}}$ ) that results in maximum, or close to maximum, yield per recruit (Gulland and Boerema 1973), and the stock size

that produces maximum recruitment from stock–recruitment theory.

The large number of different BRPs requires choice of the most appropriate BRPs for the fishery management situation. The basic criteria for choosing a particular BRP should be developed from the content and structure of the theory of fishing upon which the BRPs are based. Understanding the content and structure of the production, yield-per-recruit, and stock–recruitment theories is generally straightforward since each is developed mathematically in the literature from first principles.

However, this is not the case for all BRPs. Some are based upon the more complex theoretical settings that involve combinations of the individual theories. Prominent among complex BRPs is the percent spawning-stock biomass per recruit (PSSBR), a BRP that was developed by Shepherd (1982). The PSSBR BRP is based upon combining stock–recruitment theory with yield-per-recruit theory.

The PSSBR as developed by Shepherd (1982) involves assuming that the observed slope of the recruitment–stock relationship near the origin corresponds to an “optimal” level of fishing mortality and that this optimal level of fishing mortality also corresponds to an “optimal” PSSBR. The approach is illustrated in Figure 1 (see Beverton et al. 1984:39). Operationally, as can be seen from Figure 1, the steps are:

- (1) A straight line is fit to an arbitrarily defined subset of conventional recruitment ( $R$ ) and stock ( $S$ ) data.

\* Corresponding author: brothschild@umassd.edu

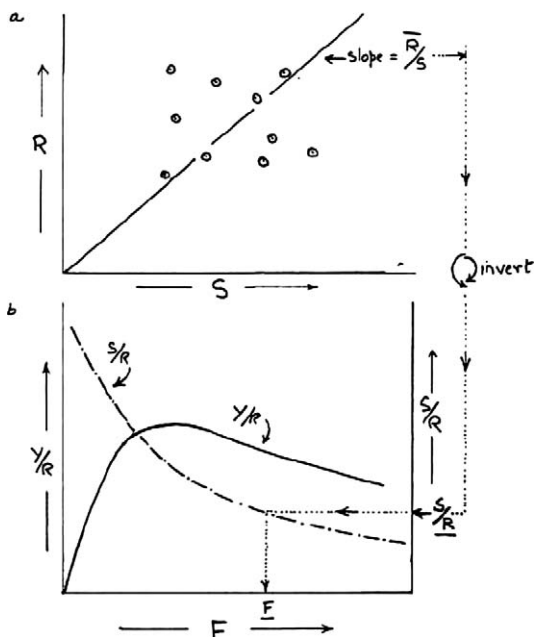


FIGURE 1.—Sissenwine and Shepherd's (1987) method for estimating the highest level of fishing mortality ( $F$ ) for persistence when the stock–recruit relationship is indeterminate. The inverse of the observed mean ratio of recruitment ( $R$ ) to stock size ( $S$ ) from (a) is entered on the  $S/R$  curve of (b), and the value of  $F$  is then determined from the  $x$ -axis. The figure is taken from Beverton et al. (1984:39).

The slope of the straight line is the  $R/S$  ratio (Figure 1a).

- (2) The  $R/S$  ratio is algebraically inverted to obtain  $(R/S)^{-1} = S/R$ . In other words, the  $R/S$  and  $S/R$  lines are identical.
- (3) The value of  $S/R$  is transferred to the  $S/R$  derived from yield-per-recruit theory to obtain an optimal value of both PSSBR and a value of  $F$  that corresponds with  $R/S$  and  $S/R$  (Figure 1b).

The PSSBR reference point is important because (1) it is commonly used in fishery management and (2) the underlying *combined* theory upon which it is based is an important scientific step toward unifying the three theories. The underlying structure of the PSSBR reference point has generally been developed using graphical analysis (e.g., Figure 1). Numerical analysis and algorithmic development of the PSSBR were accomplished by Gabriel et al. (1989). A number of papers have examined numerical properties (e.g., Shepherd 1982; Sissenwine and Shepherd 1987; Gabriel et al. 1989; Clark 1991, 1993; Mace and Sissenwine 1993; Mace 1994; Quinn and Deriso 1999; their Figures 11.8 and 11.11).

However, the combined theory of stock–recruitment and yield per recruit, and the PSSBR BRP have not been developed mathematically from first principles as have the production, yield-per-recruit, and stock–recruitment theories. This paper presents a first-principle analytic version of the combined theory of stock–recruitment and yield per recruit used to develop the PSSBR BRP. In addition to mathematically describing the combined theory, we provide three important extensions. The first relates to the basic life history, the second relates to the theory of replacement, and the third relates to equilibrium structure. With regard to life history, the interaction between recruitment and stock or between stock and recruitment is usually presented in the literature in the context of semelparous Pacific salmon *Oncorhynchus* spp. In this paper, we generalize the recruitment–stock and stock–recruitment calculations to include both the semelparous life history and the more typical lifetime multiple-spawning iteroparous fish. With regard to the theory of replacement, we develop analytic results that critically define two different approaches to replacement. The first relates to the well-known “replacement line” (e.g., see Ricker 1975), where replacement is defined as the point where the replacement line intersects the stock–recruitment curve. The second relates to the idea forwarded by Garrod (1973), where replacement is defined in terms of the relative magnitude of subsequent recruitment relative to precedent recruitment–replacement occurring when the subsequent recruitment magnitude is equal to the precedent recruitment magnitude. With regard to the equilibrium setting, it is conventional to use population-dynamic solutions that are constrained to equilibrium results. However, this is a special case as most stocks are not in equilibrium. Management advice that depends on an equilibrium setting when in fact the stock is not in equilibrium can result in overfishing or underfishing of the stock. In this paper, the equilibrium analysis is extended to the nonequilibrium setting.

In the first section of the paper, we present the “replacement equation,” reparameterizing it from the usual cohort form to a form that links the multiple-year recruitment classes to the spawning stock in the same year, explicating the  $R \rightarrow S$  part of the  $R \rightarrow S \rightarrow R$  transition (see Figure 2 for a review of the  $R \rightarrow S \rightarrow R$  transition). We then solve the reparameterized replacement equation to determine the values of  $F$  that yield any given stock size. The equation is solved in general under the conditions of (1) equilibrium: constant recruitment, constant mortality, (2) nonequilibrium: constant recruitment, variable mortality, and (3) nonequilibrium: variable recruitment, variable mortality. In the second section, the Ricker stock–recruitment

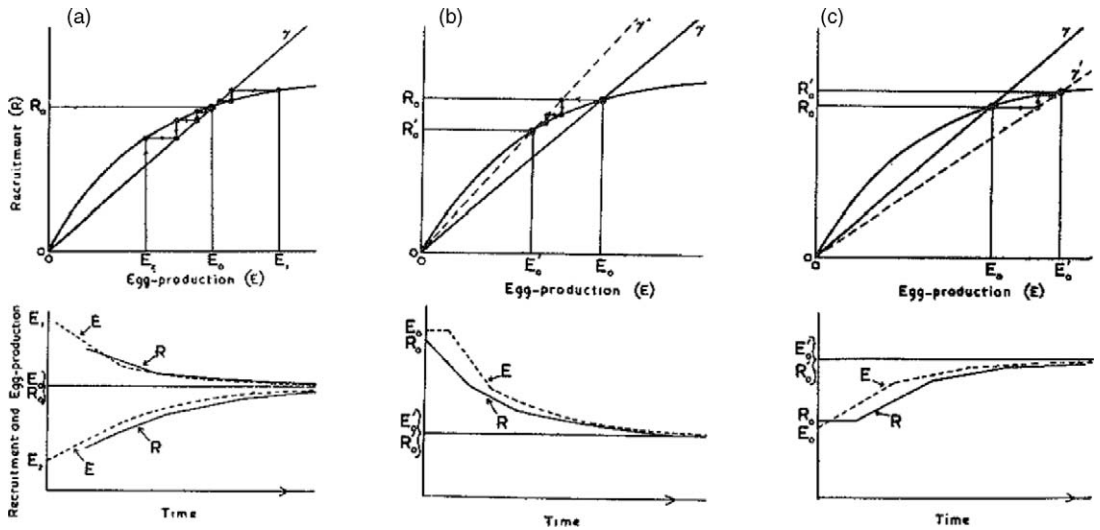


FIGURE 2.—The dynamics of a self-regenerating model with a linearly density-dependent larval mortality rate. The upper part of each panel shows successive values of recruitment and egg production following a sustained change in egg production per recruit of the adult population; in the lower part of each panel, these are plotted as a time series. With this form of larval mortality, a population is self-compensating. After a transitory change in egg production per recruit (or in larval mortality), the original steady state is regained, whereas if the change is permanent a new steady state is reached. (a) Recovery of stability following a transitory change in egg production is shown. (b) The transition from one steady state to another following a sustained decrease in egg production per recruit is illustrated. (c) The transition from one steady state to another following a sustained increase in egg production per recruit is depicted. Figure is taken from Beverton and Holt (1957:54).

relationship is included in the replacement equation to complete the  $R \rightarrow S \rightarrow R$  transition contemplated by Garrod (1973). The third and fourth sections of this paper link the combined theory with other branches of stock assessment. In the third section, we present the extension from the relation between the number of spawners and the number of recruits to the more conventional relationship between the number of recruits and the biomass of spawners. In the final section, we point out the linkage between the dynamics portrayed in this paper and the more conventional dynamics of cohort analysis. The paper concludes with a discussion of the issues associated with the simple graphical interpretation and the implications associated with our analyses. Appendix 1 includes a heuristic case study that presents calculations for a special three-dimensional case.

### The Replacement Equation

Figure 3 demonstrates the concept underlying the development of the replacement equation. Figure 3a shows a conventional depiction of the evolution of three cohorts. In Figure 3a, the cohorts are recruited at age 1 and mature at age 3. The mortality rate is such that most individuals die after age 5. Figure 3a is useful for examining cohort-specific dynamics. The usual

simplifying assumption is that the stock is in equilibrium so that recruitment is constant, and the rates are constant.

In contrast, Figure 3b exemplifies a more general structure required for the study of stock-recruitment theory, particularly if one is concerned with intra-annual variations in the effect of the environment on spawning-stock biomass. Note that three spawning age-groups are generated by recruitment from three different years. Figure 3b depicts the replacement transition, which is the transition from three recruitment groups to a single spawning-stock biomass and, in turn, the transition from the spawning stock to recruitment. The former transition is generally thought of as replacement, while the latter transition falls under stock-recruitment theory. One of the tricky problems associated with analysis of Figure 3b is the mapping of the three-element recruitment vector into the spawning-stock biomass scalar. Similarly, note that Garrod's (1973) approach for replacement involves mapping a three-element vector that represents recruitment into a scalar recruitment resulting from a single spawning. As will be shown, the mapping from vector to scalar space can only be accommodated when the stock is in equilibrium.

In discussing these issues, it is much simpler to deal

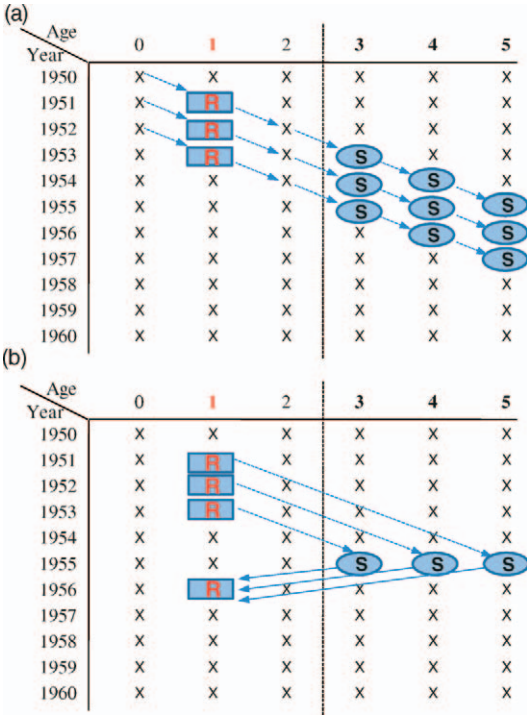


FIGURE 3.—Recruitment–stock relation in a population of fish where all individuals are recruited at age 1, become mature at age 3, and die at the end of age 5. The  $\times$  symbols represent the number of fish alive in each age-group in each year, the circled S symbols represent the spawning stock in the year, the solid arrows represent the recruitment–stock relation, and the dashed arrows represent the movement of the year-class through the population (see Rothschild 1986:107): (a) movement of 1950, 1951, and 1952 year-classes; and (b) the recruitment–stock relation. Note that recruitment in 1956 depends on the recruitment–stock relation in 1955, which is evaluated at the spawning-stock size level from 1955. The latter is a function of, among other things, the magnitude of recruitment in 1951, 1952, and 1953 (1950, 1951, and 1952 year-classes, respectively).

with the number of spawners (in contrast to the biomass of spawners), at least initially, and the number of recruits. The number of recruits and the number of individuals in each cohort are presented symbolically in Table 1. In Table 1, the stock is recruited at age 1 and matures at age 2. Most of the fish die after age  $A$ .

Mortality is fixed so that it is constant for each year. In other words, we assume knife-edge selection and knife-edge maturity. The age at knife-edge selection is the same for each cohort. In this case, the appropriate parameterization is  $Z_{2,2} = F_2 + M$ ;  $Z_{3,2} = Z_{3,3} = F_3 + M$ ;  $Z_{4,2} = Z_{4,3} = Z_{4,4} = F_4 + M$ ;  $Z_{5,2} = Z_{5,3} = Z_{5,4} = Z_{5,5} = F_5 + M$ ;  $\dots$ ; and  $Z_{A,2} = Z_{A,3} = \dots Z_{A,A} = F_A + M$  ( $M$  = natural mortality, which is held constant;  $Z$  = annual

instantaneous total mortality). The parameterization enables considering each year rather than each cohort. Thus, given the above notation, the number of individuals recruited in year  $t$  contributing to spawning stock in year  $A$  is  $R_t \exp[-\sum_{i=t+1}^A (F_i + M)]$ . Therefore, the spawning stock  $S$  (in this case, number of fish) in the  $A$ th year is represented by

$$S = \sum_{t=1}^{A-1} \left\{ R_t \exp \left[ - \sum_{i=t+1}^A (F_i + M) \right] \right\}, \quad (1)$$

which links spawning stock with different values of  $Z$  or  $F_i + M$  and the recruitment that generally comprises each spawning stock. Equation (1) is a replacement equation because it represents spawning stock biomass in year  $A$  as a function of the recruitment cohorts that comprise the spawning-stock biomass.

### Solution of Replacement Equation for the Replacement Line

We examine the  $R \rightarrow S$  transition for the replacement equation under different assumptions: (1) constant recruitment  $\bar{R}$  and constant fishing mortality  $F$ , (2) constant recruitment  $\bar{R}$  and varying fishing mortality  $F_t$ , (3) varying recruitment  $R_t$  and varying fishing mortality  $F_t$ .

#### Solution for Constant Recruitment and Constant Mortality

Solution of the replacement equation with constant recruitment and constant fishing mortality is an important special case that represents equilibrium assumptions used in most treatments. Constant recruitment enables computation of the  $S/R$  ratio. If recruitment is not constant, then the commonly used  $S/R$  ratio cannot be computed. The use of average  $R$ , calculated as  $\bar{R} = [1/(A-1)] \sum_{t=1}^{A-1} R_t$ , is permissible but will yield a different range of inferences than when the constant  $R$  is used. If we assume that  $F_t$  equals  $F$ , then we use equation (1) to write the spawning stock in the  $A$ th year as

$$S = \bar{R} \sum_{t=1}^{A-1} \{ \exp[-(A-t)(F+M)] \}. \quad (2)$$

If we are interested in the  $R \rightarrow S$  or replacement transition, we can rewrite equation (2) to obtain  $S/\bar{R}$ , or

$$S/\bar{R} = \sum_{t=1}^{A-1} \{ \exp[-(A-t)(F+M)] \}. \quad (3)$$

The solution for  $F$  given  $M$  and  $S/R$  is

$$F = -\log_e(x) - M, \quad (4)$$

where  $x$  is the positive real root of the polynomial

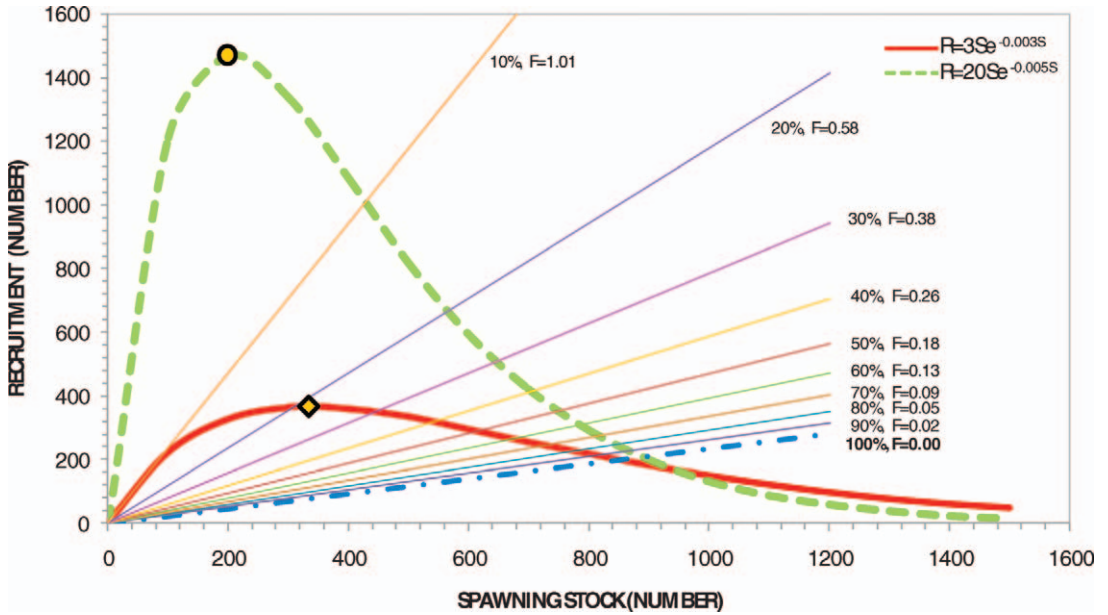


FIGURE 4.—The ratio of stock size ( $S$ ) to average recruitment ( $\bar{R}$ ), inverse of the slopes of the straight lines, are calculated using equation (3) and indicated as a percentage of the maximum  $S/\bar{R}$  for the base case with constant recruitment and constant mortality (equilibrium case). Natural mortality ( $M$ ) is 0.2; the largest age-class is  $A = 15$  ( $\approx 3/M$ ). The maximum  $S/\bar{R}$  (100%) is represented by the slope of the dot-dash line. The corresponding fishing mortality ( $F$ ), calculated using equation (4), is indicated. Two Ricker stock–recruitment curves (solid and dashed curves) are superposed on the graph. The diamond symbol and circle symbol indicate the maximum recruitment  $R_{\max|S=333.33} = 367.88$  and  $R_{\max|S=200} = 1,471.52$  for each Ricker model, respectively.

$P(x) = \sum_{t=1}^{A-1} x^t - (S/\bar{R})$  that satisfies the constraint  $F \geq 0$ , or  $-\log_e(x) \geq M$ . The positive real root can be obtained numerically; specific values are presented in Table A.1 (Appendix 2).

There are at least three applications of equation (4). First, setting  $F$  equal to 0 yields the maximum value of  $S/\bar{R}$ , the 100% PSSBR. This is the unfished biomass per recruit. We do not believe that this analytic result (which depends on  $A$ ) has been presented before (see Gabriel et al. 1989).

Second, equilibrium  $F$  can be obtained for any stock and recruitment values subject to the constraint of  $F \geq 0$ . Two applications are that (1) the equilibrium  $F$  can be obtained for any point on the  $S/\bar{R}$  plane and (2)  $F$  can be obtained for any point of an  $S$ – $\bar{R}$  curve, such as the maximum in the Ricker curve or near the asymptote in a Beverton–Holt curve (Figure 4).

Third, the formalism represented by equation (3) means that there is an upper bound on  $S/\bar{R}$  under  $F = 0$ , for example. As an example, when  $F$  equals 0 and  $M$  equals 0.1,  $S/\bar{R} \leq 9.508$ ; when  $M$  equals 0.2,  $S/\bar{R} \leq 4.517$ ; when  $M$  is equal to 0.3,  $S/\bar{R} \leq 2.858$ ; when  $M$  is 0.4,  $S/\bar{R} \leq 2.033$ ; and when  $M$  equals 0.5,  $S/\bar{R} \leq 1.541$  (see Figure 5).

It is important to observe that the value of  $F$

determined using equation (4) requires only an assumption of a particular value of  $R$  or a particular value of  $R/S$ . It is not necessary to rely on any functional relationship that relates  $R$  to  $S$ .

As a further illustration of the application of equation (2) or (3), we can determine the optimum value in a Ricker stock–recruitment relationship. If we insert the optimum values that we denote ( $R_{\text{opt}}$  and  $S_{\text{opt}}$ ) in the stock–recruitment relationship, we can determine the value of  $F$  that yields the maximum recruitment. This value of  $F$  might be considered as a “new” reference point.

#### Solution for Constant Recruitment Variable Mortality Rates

To generalize from the conventional strict equilibrium approach, we fix recruitment at a constant or average value, letting mortality vary among years. In this case, equation (1) becomes:

$$S = \bar{R} \sum_{t=1}^{A-1} \left\{ \exp \left[ - \sum_{i=t+1}^A (F_i + M) \right] \right\}. \quad (5)$$

Given a value of  $\bar{R}$  and some target for  $S$ , we can solve equation (5) to obtain the values of mortality



TABLE 1.—Notation used to develop theoretical results. Each cell contains the number of individuals at the  $t$ th year and the  $a$ th age. The variable  $R_t$  is the recruitment in the  $t$ th year. The stock is recruited at age 2, the largest age-class is  $A$ , and there are virtually no individuals in the population that are older than age  $A$ . The total mortality of the  $a$ th age-class at the  $t$ th year is  $Z_{t,a}$ .  $S$  is the spawning stock at year  $t = A$ . The subsequent year recruitment at year  $t = A + 1$  is  $R_{A+1}$ , which is the function of spawning stock at previous year  $t = A$ . In consideration of the assumption of the largest age-class  $A$  the maximum year  $A + 1$  is used, which completes one  $R \rightarrow S \rightarrow R$  transition.

Year	Age-class		
	1	2	3
1	$R_1$		
2	$R_2$	$R_1 \exp(-Z_{2,2})$	
3	$R_3$	$R_2 \exp(-Z_{3,2})$	$R_1 \exp(-Z_{2,2} - Z_{3,3})$
4	$R_4$	$R_3 \exp(-Z_{4,2})$	$R_2 \exp(-Z_{3,2} - Z_{4,3})$
5	$R_5$	$R_4 \exp(-Z_{5,2})$	$R_3 \exp(-Z_{4,2} - Z_{5,3})$
...	...	...	...
$A$	$R_A$	$R_{A-1} \exp(-Z_{A,2})$	$R_{A-2} \exp(-Z_{A-1,2} - Z_{A,3})$
$A + 1$	$R_{A+1} = f(S)$		

coefficients that will produce  $S$ . Specific values of  $\bar{R}$  and  $S$  could arise from some management goals or from examination of  $S$ – $R$  theory (Figure 6). The solution for any specified positive values of  $F_t$  (where  $t = 2, 3, \dots, A - 1$ ) is

$$F_{t=A} = \log_e \left\{ \frac{\bar{R}}{S} \left[ 1 + \sum_{i=2}^{A-1} \exp \sum_{i=2}^t (F_i + M) \right] \right\} - \sum_{i=2}^{A-1} (F_i + M) - M. \tag{6}$$

In other words, equation (6) gives the values of fishing mortality (i.e.,  $F_{t=A}$  given the previous years  $F_t$ ,  $t = 2, 3, \dots, A - 1$ ) that would result in a specific value of  $S$  given  $\bar{R}$  and  $M$ . Note that we can specify  $F_t$  ( $t = 2, 3, \dots, A - 1$ ) to be some values, and the magnitude of  $F_{t=A}$  then depends upon  $F_t$  ( $t = 2, 3, \dots, A - 1$ ).

The solution is constrained by the fact that  $F_t \geq 0$ . The condition  $F_{t=A} \geq 0$  requires that

$$\log_e \left\{ \frac{\bar{R}}{S} \left[ 1 + \sum_{i=2}^{A-1} \exp \sum_{i=2}^t (F_i + M) \right] \right\} \geq \sum_{i=2}^{A-1} (F_i + M) + M.$$

Since

$$\frac{\bar{R}}{S} \left[ 1 + \sum_{i=2}^{A-1} \exp \sum_{i=2}^t (F_i + M) \right] > 0,$$

then we have

$$\begin{aligned} \frac{\bar{R}}{S} \left[ 1 + \sum_{i=2}^{A-1} \exp \sum_{i=2}^t (F_i + M) \right] \\ \geq \exp \left[ \sum_{i=2}^{A-1} (F_i + M) + M \right], \end{aligned}$$

and therefore

$$\frac{S}{\bar{R}} \leq \frac{1 + \sum_{i=2}^{A-1} \exp \sum_{i=2}^t (F_i + M)}{\exp \left[ \sum_{i=2}^{A-1} (F_i + M) + M \right]}. \tag{7}$$

So the assumption of variable mortality has a direct application because, from a management perspective, tradeoffs can be made on the magnitude of the mortality rates among years, while at the same time maintaining the vector of  $F$ -values that maintains the replacement value. Again, it is important to note that the assumption of variable mortality rate results in a different constraint on the  $S/R$  ratio than the constraint when mortality and recruitment are fixed (equations 4 and 7).

*Solution of Replacement Equation with Variable Recruitment and Mortality*

Generalizing further, we now consider the case where recruitment and mortality vary among years. This in fact is the case that is most likely to occur in actual practice. We solve equation (1) for this general

TABLE 1.—Extended.

Year	Age-class			
	4	5	...	A
1				
2				
3				
4	$R_1 \exp(-Z_{2,2} - Z_{3,3} - Z_{4,4})$			
5	$R_2 \exp(-Z_{3,2} - Z_{4,3} - Z_{5,4})$	$R_1 \exp(-Z_{2,2} - Z_{3,3} - Z_{4,4} - Z_{5,5})$		
...	...	...	...	
A	$R_{A-3} \exp\left(-\sum_{\substack{t=A-2, \dots, A, \\ a=t-A+4}} Z_{t,a}\right)$	$R_{A-4} \exp\left(-\sum_{\substack{t=A-3, \dots, A, \\ a=t-A+5}} Z_{t,a}\right)$	...	$R_1 \exp\left(-\sum_{\substack{t=2, \dots, A, \\ a=t}} Z_{t,a}\right)$
A + 1				

case and any specific value of  $F_t$  ( $t=2, 3, \dots, A-1$ ) to obtain

$$F_{t=A} = \log_e \left\{ \frac{1}{S} \left[ R_1 + \sum_{t=2}^{A-1} R_t \exp \sum_{i=2}^t (F_i + M) \right] \right\} - \sum_{t=2}^{A-1} (F_t + M) - M. \tag{8}$$

Similarly, we have the condition  $F_t \geq 0$  (where  $t=2, 3, \dots, A$ ). The condition  $F_{t=A} \geq 0$  requires that

$$\log_e \left\{ \frac{1}{S} \left[ R_1 + \sum_{t=2}^{A-1} R_t \exp \sum_{i=2}^t (F_i + M) \right] \right\} \geq \sum_{t=2}^{A-1} (F_t + M) + M.$$

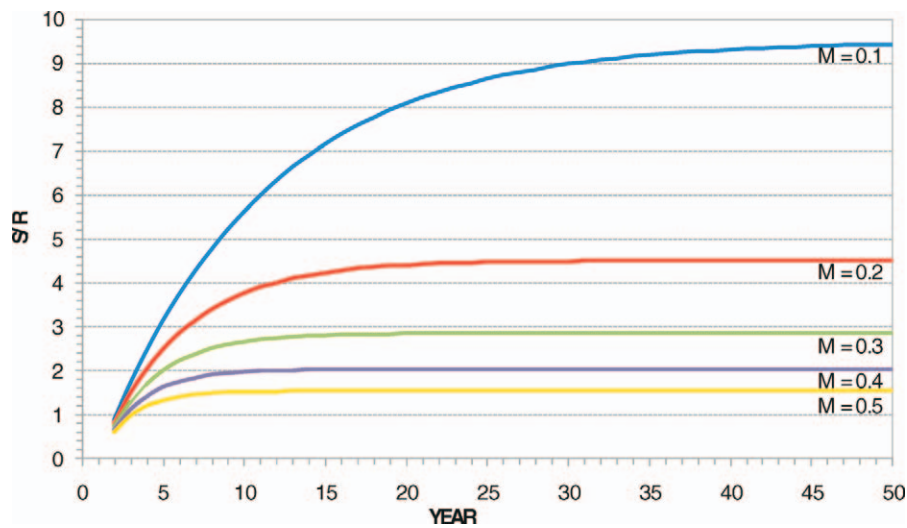


FIGURE 5.—The upper bound of the ratio of stock size ( $S$ ) to average recruitment ( $\bar{R}$ ) under fishing mortality ( $F$ )=0, calculated using equation (3). The population is recruited at age 1 and matures at age 2 with knife-edge selection and knife-edge maturity. The age at knife-edge selection is the same for each cohort. Natural mortality ( $M$ ) is constant. When  $F=0$  and  $M=0.1$ ,  $S/\bar{R} \leq 9.508$ ; when  $M=0.2$ ,  $S/\bar{R} \leq 4.517$ ; when  $M=0.3$ ,  $S/\bar{R} \leq 2.858$ ; when  $M=0.4$ ,  $S/\bar{R} \leq 2.033$ ; and when  $M=0.5$ ,  $S/\bar{R} \leq 1.541$ .

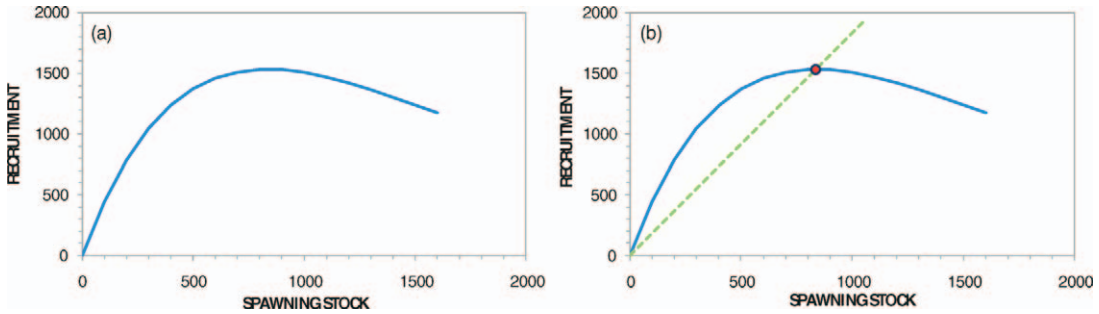


FIGURE 6.—Illustration of equilibrium mortality that results in stock equilibrium: (a) Ricker stock–recruitment model and (b) stock–recruitment curve (solid line), showing maximum recruitment point (dot) and the replacement line (dashed line) through the maximum point.

Since

$$\frac{1}{S}\left[R_1 + \sum_{i=2}^{A-1} R_i \exp \sum_{i=2}^t (F_i + M)\right] \geq 0,$$

then we have

$$\begin{aligned} \frac{1}{S}\left[R_1 + \sum_{i=2}^{A-1} R_i \exp \sum_{i=2}^t (F_i + M)\right] \\ \geq \exp \left[ \sum_{i=2}^{A-1} (F_i + M) + M \right], \end{aligned}$$

and therefore

$$S \leq \frac{R_1 + \sum_{i=2}^{A-1} R_i \exp \sum_{i=2}^t (F_i + M)}{\exp \left[ \sum_{i=2}^{A-1} (F_i + M) + M \right]}. \tag{9}$$

The main feature of this solution that distinguishes it from the previous solutions is that equation (1) is solved for variable recruitment. This, of course, is the most realistic assumption. However, we can see that if recruitment is variable, then the ratios between  $R/S$  and  $S/R$ , as shown in Figure 1 and implicit in subsequent publications (e.g., Sissenwine and Shepherd 1987; Gabriel et al. 1989; Mace and Sissenwine 1993; Mace 1994) related to PSSBR, are not defined. In other words, the simple graphical connection between  $R/S$  and  $S/R$  (as shown in Figure 3) is not defined. Also, note that the constraints on the solution change. In other words, under these conditions, the calculus implied in Figure 4 is not valid.

If we set  $A$  equal to 4, we can interpret departures from equilibrium graphically (Figure 7). In order to do this, we set  $Z_{2,2} = \alpha + M$ ,  $Z_{3,2} = Z_{3,3} = \beta + M$ , and  $Z_{4,2} = Z_{4,3} = Z_{4,4} = \gamma + M$  with constant  $M$  (see Appendix 1). Figure 7a is the result that can be interpreted in terms of

fixed recruitment and variable or fixed mortality rates. We can see that fixed mortality is the collection of points in the three-dimensional space where  $\alpha = \beta = \gamma$ . For example,  $\alpha = \beta = \gamma = 0.5$  would represent a particular point in three-dimensional space. However, as  $\alpha$ ,  $\beta$ , and  $\gamma$  vary, different levels of spawning stock arise. As Figure 7a shows, different combinations of  $\alpha$ ,  $\beta$ , and  $\gamma$  result in the same fixed spawning stock (e.g., in this case, 1,000 individuals). Note that the gray plane is coincident with the green color. Figures 7b and 7c contrast the effect of increasing and decreasing recruitment. Even though  $\bar{R}$  is the same for all panels, the gray plane in the increasing recruitment case lies above the gray plane in the constant recruitment case and below the gray plane in the declining recruitment case. This shows that the appropriate replacement levels of fishing mortality are overpredicted or underpredicted relative to those in the conventionally used equilibrium populations depending upon the variability of recruitment. It is interesting to observe that if we can anticipate the levels of recruitment from virtual population analysis (VPA) or surveys, and we have some estimate of  $\gamma$  in the first year, then the combination of  $\alpha$  and  $\beta$  required to maintain 1,000 units in the second year can be obtained, and so on for subsequent years.

**Solution for Linking Subsequent Recruitment with Precedent Recruitment**

Up to this point, we have concentrated on the  $R \rightarrow S$  transition leading to a replacement line. In this section, we use Ricker stock–recruitment model  $R = aSe^{-bS}$  to derive the  $R \rightarrow S \rightarrow R$  transition, an idea forwarded by Garrod (1973). We let the recruitment equal replacement recruitment ( $R_{\text{rep}}$ ): that is,  $R_{A+1} \equiv R_{\text{rep}}$  ( $R_{A+1}$  in the  $R \rightarrow S \rightarrow R$  transition as shown in Table 1). Similarly, we examine the replacement recruitment under different assumptions: (1) constant recruitment  $\bar{R}$  and constant fishing mortality  $F$ , (2) constant recruitment



$\bar{R}$  and varying fishing mortality  $F_t$  and (3) varying recruitment  $R_t$  and varying fishing mortality  $F_t$ .

*Assumption of Constant  $R$ , Constant  $F$*

For the base case with constant recruitment and constant mortality, the spawning stock  $S$  is obtained by equation (2), so using the Ricker stock–recruitment model, we have the subsequent year recruitment ( $R_{A+1}$ ),

$$R_{A+1} = a\bar{R} \sum_{t=1}^{A-1} \left\{ \exp[-(A-t)(F+M)] \right\} \times \exp \left( -b\bar{R} \sum_{t=1}^{A-1} \left\{ \exp[-(A-t)(F+M)] \right\} \right). \quad (10)$$

Letting  $R_{A+1} = R_{\text{rep}}$ , we solve the above equation for  $F$  to obtain

$$F = -x - M, \quad (11)$$

where  $x$  is the negative real root of

$$P(x) = -x + b\bar{R} \sum_{t=1}^{A-1} (e^x)^t + \log_e \left\{ R_{\text{rep}} / \left[ a\bar{R} \sum_{t=0}^{A-2} (e^x)^t \right] \right\}$$

that satisfies the constraint  $F \geq 0$ , or  $-x \geq M$ .

*Assumption of Constant  $R$ , Varying  $F$*

Consider the case of constant recruitment and variable mortality as described by equation (5), we have the subsequent year recruitment ( $R_{A+1}$ ) as

$$R_{A+1} = a\bar{R} \sum_{t=1}^{A-1} \left\{ \exp \left[ - \sum_{i=t+1}^A (F_i + M) \right] \right\} \times \exp \left( -b\bar{R} \sum_{t=1}^{A-1} \left\{ \exp \left[ \sum_{i=t+1}^A (F_i + M) \right] \right\} \right). \quad (12)$$

Again, letting  $R_{A+1} = R_{\text{rep}}$ , we solve the above equation for  $F_t$ . For any specific value of  $F_t$  ( $t = 2, 3, \dots, A-1$ ), we have

$$F_{t=A} = W \left( -\frac{bR_{\text{rep}}}{a} \right) + \log_e \left\{ \frac{a\bar{R}}{R_{\text{rep}}} \left[ 1 + \sum_{t=2}^{A-1} \exp \sum_{i=2}^t (F_i + M) \right] \right\} - \sum_{t=2}^{A-1} (F_t + M) - M, \quad (13)$$

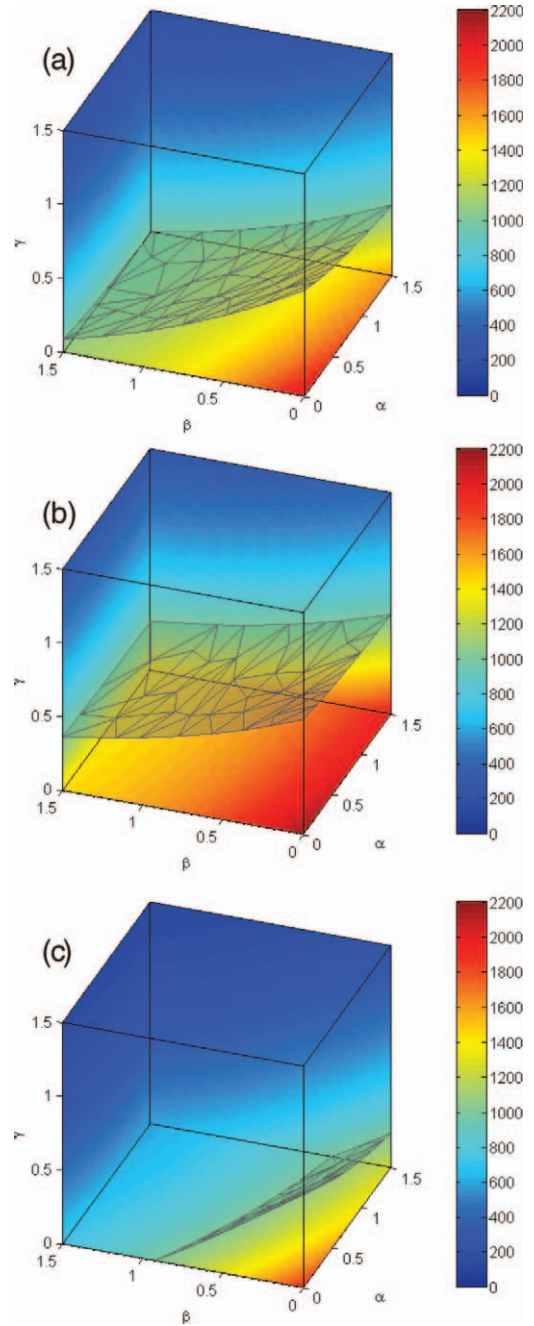


FIGURE 7.—Spawning stock (color bar) is a function of variable recruitment ( $R$ ) at various levels of instantaneous fishing mortality (solution of equation A.1): (a)  $R_1 = R_2 = R_3 = 1,000$ ; (b)  $R_1 = 500$ ,  $R_2 = 1,000$ , and  $R_3 = 1,500$ ; and (c)  $R_1 = 1,500$ ,  $R_2 = 1,000$ , and  $R_3 = 500$ . Natural mortality ( $M$ ) is 0.2. Note that mean recruitment ( $\bar{R} = 1,000$ ) is the same for each scenario. The gray plane is the constant surface where spawning stock ( $S$ ) = 1,000 fish. The maximum  $S$ ,  $S_{\text{max}}|_{\alpha=\beta=\gamma=0, M=0.2}$ , is 2,037.1, 2,172.8, and 1,902.9 for panels a, b, and c, respectively.

where  $W(x)$  refers to the Lambert  $W$  function (Wolfram MathWorld 2008). The Lambert  $W$  function is real for  $x \geq (-1/e)$ . Thus, for the feasible solutions, we have  $F_t \geq 0$  ( $t = 2, 3, \dots, A$ ) and  $(-bR_{\text{rep}}/a) \geq (-1/e)$ . The last constraint,  $(-bR_{\text{rep}}/a) \geq (-1/e)$  or  $R_{\text{rep}} \leq (ae^{-1}/b)$ , actually demonstrates the maximum recruitment that can be achieved for a given Ricker stock–recruitment model. If we let  $R_{\text{rep}}$  equal  $\bar{R}$ , then we have

$$F_{t=A} = W\left(-\frac{bR_{\text{rep}}}{a}\right) + \log_e \left\{ a \left[ 1 + \sum_{t=2}^{A-1} \exp \sum_{i=2}^t (F_i + M) \right] \right\} - \sum_{t=2}^{A-1} (F_t + M) - M. \quad (14)$$

#### Assumption of Varying $R$ , Varying $F$

Consider the case where recruitment varies among years, we have the subsequent year recruitment ( $R_{A+1}$ ) as

$$R_{A+1} = a \sum_{t=1}^{A-1} \left\{ R_t \exp \left[ - \sum_{i=t+1}^A (F_i + M) \right] \right\} \times \exp \left( -b \sum_{t=1}^{A-1} \left\{ R_t \exp \left[ - \sum_{i=t+1}^A (F_i + M) \right] \right\} \right). \quad (15)$$

Letting  $R_{A+1}$  equal a replacement recruitment  $R_{\text{rep}}$  (i.e.,  $R_{A+1} = R_{\text{rep}}$ ), we solve the above equation for  $F_t$ . For any specific value of  $F_t$  ( $t = 2, 3, \dots, A-1$ ), we have

$$F_{t=A} = W\left(-\frac{bR_{\text{rep}}}{a}\right) + \log_e \left\{ \frac{a}{R_{\text{rep}}} \left[ R_1 + \sum_{t=2}^{A-1} R_t \exp \sum_{i=2}^t (F_i + M) \right] \right\} - \sum_{t=2}^{A-1} (F_t + M) - M. \quad (16)$$

where  $W(x)$  again refers to the Lambert  $W$  function. Thus, for the feasible solutions, we have  $F_t \geq 0$  ( $t = 2, 3, \dots, A$ ) and  $(-bR_{\text{rep}}/a) \geq (-1/e)$ . Once again, the last constraint,  $(-bR_{\text{rep}}/a) \geq (-1/e)$  or  $R_{\text{rep}} \leq (ae^{-1}/b)$ , demonstrates that the replacement recruitment is limited by a given Ricker stock–recruitment model. In other words, the maximum replacement recruitment is  $R_{\text{rep}} = (ae^{-1}/b)$ .

We can relax the knife-edge selectivity and knife-edge maturity assumptions. If we assume that selectivity of age  $a$  at year  $t$  is  $s_{t,a}$  and  $\bar{F}_t$  is fully recruited fishing mortality at year  $t$ , then we can substitute  $F_t$  with  $F_{t,a} = s_{t,a} \bar{F}_t$  in the above equations. Also, we assume

that maturity of age  $a$  at year  $t$  is  $m_{t,a}$ , then we can calculate the spawning stock at year  $t = A$  as

$$S = \sum_{t=1}^{A-1} \left\{ R_t \prod_{\substack{i=t+1, \dots, A, \\ j=i-t+1}} [m_{i,j} \exp(-s_{i,j} \bar{F}_i - M)] \right\} \quad (17)$$

or

$$S = \sum_{t=1}^{A-1} \left\{ R_t \prod_{\substack{i=t+1, \dots, A, \\ j=i-t+1}} (m_{i,j}) \times \exp \left[ \sum_{\substack{i=t+1, \dots, A, \\ j=i-t+1}} (-s_{i,j} \bar{F}_i - M) \right] \right\}. \quad (18)$$

#### Extension from Numbers of Spawners to Biomass of Spawners

It is important to emphasize again that the calculations in this paper are based on the *number* of recruits and the *number* of spawners, in contrast to the more typical approach that considers the relationship between the number of recruits and the biomass of spawners. Comparing the number of recruits with the number of spawners greatly simplifies calculations. The introduction of biomass into the calculations requires taking into account the growth rate of the individual fish and perhaps the length–weight relationship. Inclusion of growth requires additional assumptions and calculations beyond those needed in a numbers-only approach.

If we use weight of spawners, we need to consider the spawning-stock biomass. We would use

$$S_{\text{biomass}} = \sum_{t=1}^{A-1} \left\{ R_t W_{A-t+1} \times \prod_{\substack{i=t+1, \dots, A, \\ j=i-t+1}} [m_{i,j} \exp(-s_{i,j} \bar{F}_i - M)] \right\} \quad (19)$$

or

$$S_{\text{biomass}} = \sum_{t=1}^{A-1} \left\{ R_t W_{A-t+1} \times \prod_{\substack{i=t+1, \dots, A, \\ j=i-t+1}} (m_{i,j}) \times \exp \left[ \sum_{\substack{i=t+1, \dots, A, \\ j=i-t+1}} (-s_{i,j} \bar{F}_i - M) \right] \right\}, \quad (20)$$

where  $W_a$  is the spawning-stock weight at age  $a$ . For example,  $W_a$  can be calculated using the growth equation  $W(a) = W_\infty \{1 - \exp[-\kappa(a - a_0)]\}^\beta$ , which is derived from the allometric weight-length relationship and von Bertalanffy length-age relationship, where  $\kappa$  is a growth parameter,  $a_0$  is the theoretical age at a length of zero,  $W_\infty = \alpha L_\infty^\beta$  and represents the asymptotic weight (see Quinn and Deriso 1999:140), and  $S_{\text{biomass}}$  is the equation for spawning-stock biomass at year  $t = A$ .

### Relationship between Recruitment–Stock and Stock–Recruitment Calculations

The  $R \rightarrow S$  or replacement transition, as depicted in this paper, is analogous with the VPA as recognized by Garrod (1973). This can easily be seen from using Pope's (1972) approximation of the VPA. Pope's approximation of the VPA is an alternative method for deriving stock abundance from recruitment. With constant  $M$ , using Pope's approximation, we have Pope's forward equation  $N_{a+1} = N_a e^{-M} - C_a e^{-M/2}$  at the start of age  $a$ , where  $C_a$  is catch at age  $a$ . Thus, for an example with largest age-class  $A$ , we have

$$\begin{aligned} SS_{A-1} &= N_{A,2}^{R_{A-1}} = R_{A-1} e^{-M} - C_{A-1,1} e^{-M/2}, \\ SS_{A-2} &= N_{A,3}^{R_{A-2}} = R_{A-2} e^{-2M} - C_{A-2,1} e^{-3M/2} \\ &\quad - C_{A-1,2} e^{-M/2}, \\ &\dots\dots \\ SS_t &= N_{A,A-t+1}^{R_t} = R_t e^{-(A-t)M} \\ &\quad - \sum_{\substack{i=t, \dots, A-1, \\ j=i-t+1}} C_{i,j} e^{-(A-i-1/2)M}, \\ &\dots\dots \\ SS_1 &= N_{A,A}^{R_1} = R_1 e^{-(A-1)M} \\ &\quad - \sum_{\substack{i=1, \dots, A-1, \\ j=i}} C_{i,j} e^{-(A-i-1/2)M}, \end{aligned}$$

and

$$\begin{aligned} S &= \sum_{t=1}^{A-1} SS_t \\ &= \sum_{t=1}^{A-1} \left[ R_t e^{-(A-t)M} - \sum_{\substack{i=t, \dots, A-1, \\ j=i-t+1}} C_{i,j} e^{-(A-i-1/2)M} \right] \end{aligned} \quad (21)$$

where  $SS_t$  indicates the spawning stock from recruitment  $R_t$ , the subscripts of the  $N$  and  $C$  terms follow the above definition (i.e.,  $N_{t,a}$  or  $C_{t,a}$  is the abundance or catch, respectively, of age  $a$  at year  $t$ ). Note that these equations are fundamentally different than the ones used in the paper inasmuch as VPA calculations are aligned with cohorts rather than with years.

### Discussion

The development of the theories of fishing—stock–recruitment, yield per recruit, and production—was essentially completed in the 1950s as evidenced by the works of Ricker (1954), Schaefer (1954, 1957), and Beverton and Holt (1957). These mathematical expressions could be used to generate optimal or asymptotic values of fishing mortality or stock size that resulted in maximum recruitment, yield per recruit, or production.

These optimal or asymptotic values became known as BRPs. In the 1990s, authors using the same theories of fishing developed many different BRPs. Mace (1994), for example, lists the constant fishing mortality rate that produces MSY ( $F_{\text{MSY}}$ ), the fishing mortality rate that equals the natural mortality rate ( $F = M$ ), the reference fishing mortality rates from yield-per-recruit theory ( $F_{0.1}$  and  $F_{\text{max}}$ ), the reference fishing mortality rates from stock–recruitment theory (e.g.,  $F_{20\%}$  and  $F_{35\%}$ ), the threshold fishing mortality rate associated with extinction of the stock ( $F_c$ ), the equilibrium biomass levels corresponding to the reference fishing mortalities ( $B_{\text{MSY}}$ ,  $B_{F=M}$ ,  $B_{0.1}$ , and  $B_{\text{max}}$ ), virgin biomass ( $B_0$ ), and virgin recruitment ( $R_0$ ). As a result, the manager must choose from a long list of different reference points in managing any particular fishery. Clearly, the foundation for the choice must be related to an understanding of the underlying theory. Understanding the underlying theory is not always straightforward. Understanding is relatively simple when a particular BRP is based solely on one of the well-known theories of fishing. However, the setting becomes more complex when a BRP derived from one theory of fishing is used as a substitute or “proxy” for a reference point derived from a different theory of fishing. A good example of this is Clark's (1991) suggestion that the  $F_{35\%}$  spawning-stock biomass per recruit (an intermediate variable in calculating yield per recruit) can be used a substitute or proxy for MSY.

Yet another complex approach involves combining theories of fishing. Such a combination can be thought of as an innovation to the standard theories of fishing. Shepherd (1982) combined stock–recruitment and yield-per-recruit theories to obtain optimal  $F$  and PSSBR and to obtain yield per recruit (Figure 1). The sense of Shepherd's (1982) work is that stock–recruitment theory could produce a “comfortable” ratio between recruitment and stock size and that this  $R/S$  ratio could be translated into an optimal level of fishing mortality and spawning-stock biomass or percent of unharvested spawning-stock biomass consistent with the stock–recruitment ratio. It is important to make the distinction between Shepherd's (1982) work, which estimates an optimal  $F$  by combining two

theories, and the simple depiction of SSBR as an intermediate result in the calculation of the Beverton–Holt yield-per-recruit theory. In the latter case, only the relationship between SSBR and  $F$  is considered; optimal  $F$  is not taken into account.

It turns out, however, that the simple graphical interpretation as depicted in Figure 1 and various numerical results does not generally apply. The graphical results and numerical results are valid only in the simplest circumstances. Shepherd's (1982) work, nevertheless, leads to understanding the SSBR that results from the more complex and more realistic settings (e.g., nonequilibrium), while also providing a "scientific" opportunity to study the specific complex interrelationships between two commonly used theories. An interesting bonus from this study is the opportunity to examine the problem of replacement, which is central in the population dynamics theory but virtually not addressed in the literature, particularly regarding iteroparous fish. In this regard, we have solved the traditional replacement problem for iteroparous fish and clarified Garrod's (1973) analysis of this problem, resulting in two different but complementary definitions of replacement in both equilibrium and nonequilibrium settings.

Beyond graphical conjecture and numerical results, the combined theory has not been fully set out in analytic terms as contrasted with the other three theories of fishing. A particular difficulty in doing this is that the complete version of the stock–recruitment theory as specified by Ricker (1954) and Beverton and Holt (1957; see also the review by Rothschild 1986) is based on two separate population dynamic transitions, which need to be interrelated. One transition involves recruitment depending on spawning stock, and another transition involves stock depending on recruitment. The dependence of stock on recruitment is called *replacement*. Even though the concept of replacement is central to stock–recruitment theory, it is scarcely treated in the literature. In fact, most discussions of replacement refer only to the atypical semelparous fish that spawn only once and then die. Our analytic description of replacement enables extensions to study the density-dependent features of the replacement process.

A full analytic articulation of the combined theory enables the definitions of various BRPs based on the combined theory. Analysis of the combined theory facilitates the study of the graphical and numeric interpretations. To organize the discussion, we rely on the Beverton et al. (1984) depiction of Shepherd's (1982) work as an organizing theme. Referring directly to Figure 1, we can see how four sets of assumptions motivated the analytic solution.

First, the computational procedure for selecting points to calculate the "straight line," the  $R/S$  ratio, is not well defined because it is not evident which points should be used in the calculation and which should be excluded. Standard stock–recruitment theory suggests that data points associated with low stock sizes contain little density-dependent influences (apart from depensation), while points associated with relatively large stock sizes contain strong density-dependent influences. The number of points included can contain a mixture of relatively density-dependent and relatively density-independent points. There is obviously a tradeoff, particularly in data-limited fisheries, between the number of points included in an analysis and the extent to which they are density independent.

Second, the conversion of  $R/S$  to  $S/R$  through simple inversion is only applicable for the special case when a stock is in equilibrium (as can be seen from equations 1, 3, and 5). When the stock is not in equilibrium, the transformations indicated in Figure 1 are not correct. The nonequilibrium condition, which is generally applicable, generates the vector→scalar problem and requires the analytical rather than graphical analysis. The consequences of assuming equilibrium when in fact the stock is not in equilibrium can be detected from equation (A.1) (Appendix 1) and demonstrated in Figure 7 using  $A = 4$  as an example.

Third, the conversion of  $R/S$  to  $S/R$  represents conceptual difficulties as well. The  $R \rightarrow S$  transition, which is the subject of extensive literature, is nonlinear, and so an  $R/S$  ratio is not defined (a "ratio" is a straight line that passes through the origin) unless it is conditional on some particular value of  $S$ . The  $S \rightarrow R$  transition (i.e., replacement transition) has received relatively miniscule study, but it is generally represented as being linear, so an  $S/R$  ratio can be defined. On the other hand, it is obvious but not generally recognized that commonly observed density-dependent growth or mortality in juveniles and adults would result in a curvilinear replacement line. The nature of curvilinear replacement is an important, virtually unresearched topic in fish population dynamics. Density-dependent growth used in replacement would require calculation in spawning-stock biomass rather than in numbers (see Jones 1973; Rothschild 1986).

Fourth, the final step in calculating PSSBR is to convert the  $S/R$  ratio to  $F$ . It is worth noting here that three arbitrary assumptions need to be used. These include assuming a level of  $M$  in the assessment model, a level of  $M$  in the yield per recruit, and a level of PSSBR that is greater than 20% (see Mace and Sissenwine 1993). Actually, Mace and Sissenwine (1993) showed that an average of 80 stocks reflected a PSSBR of 20%, suggesting that the use of high levels

of PSSBR (e.g., 40%) might need to be refined. We need to recall that use of the PSSBR was motivated by the hypothetical situation where MSY could not be calculated (Clark 1993); therefore, in such instances, if a PSSBR could be calculated, then some level of a PSSBR might serve as a proxy for MSY. The problem with this assertion is that there are potentially greater sources of error owing to the larger number of calculations in the PSSBR than in calculating the MSY directly.

Finally, we have pointed out the connection (1) between number of recruits and number of spawners and between number of recruits and biomass of spawners and (2) between the replacement calculus in this paper and the VPA. Highlighting the number versus biomass issue is particularly important since number–number issues are linked to stock overfishing, while number–biomass issues are linked to recruitment overfishing. The latter type of overfishing is more important from a conservation point of view, suggesting the need for additional focus on the calculations made in this paper. Highlighting the connection between the replacement calculus and the VPA is important because the contrast between the two different calculations places an important focus on the biological mechanisms that affect replacement.

In summary, the PSSBR is a commonly used BRP. It has its roots in graphic interpretation and conjecture. The analytic mathematical development enables extension of the basic concept from semelparous populations to iteroparous populations. However, the extensions also clarify the fact that the conventional equilibrium calculations need to be applied with caution to the more typical case where populations are not in equilibrium. The analysis provides a rich opportunity for research on optimization of the replacement equations and the biological phenomena that relate to the dependence of spawning-stock biomass on recruitment rather than the conventional focus on the dependence of recruitment on spawning-stock biomass.

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### Appendix 1: Example of Model Application

For expository purposes, a heuristic example with a population of  $A = 4$  age-classes and characterized by knife-edge selection and knife-edge maturity is presented in this section. The reduced number of age-classes places the problem in three-dimensional space that can be easily visualized. The stock is recruited at age 1 and matures at age 2, and the age at knife-edge selection is the same for each cohort. There are virtually no individuals in the population that are older than age 4. In this case, the appropriate parameterization of total mortality of age  $a$  at year  $t$  ( $Z_{t,a}$ ) is  $Z_{2,2} = \alpha + M$ ,  $Z_{3,2} = Z_{3,3} = \beta + M$ , and  $Z_{4,2} = Z_{4,3} = Z_{4,4} = \gamma + M$  (with constant natural mortality  $M$ ). Thus, three recruitment years or cohorts contribute to each spawning stock in year 4 according to  $SS_1 = R_1 e^{-(\alpha+\beta+\gamma+3M)}$ ,  $SS_2 = R_2 e^{-(\beta+\gamma+2M)}$ , and  $SS_3 = R_3 e^{-(\gamma+M)}$ . The spawning stock in the 4th year is represented by

$$S = R_1 e^{-(\alpha+\beta+\gamma+3M)} + R_2 e^{-(\beta+\gamma+2M)} + R_3 e^{-(\gamma+M)}, \quad (A.1)$$

which gives the equation that links spawning stock with different values of  $Z$  represented by  $\alpha$ ,  $\beta$ ,  $\gamma$ , and multiple recruitments that generally comprise each spawning stock. We present the replacement equation and solution for linking subsequent recruitment with precedent recruitment derived for this heuristic example under different assumptions: (1) constant recruitment  $\bar{R} = (R_1 + R_2 + R_3)/3$  and constant mortality  $\alpha = \beta = \gamma = F$ ; (2) constant recruitment  $\bar{R} = (R_1 + R_2 + R_3)/3$  and varying mortality  $\alpha$ ,  $\beta$ , and  $\gamma$ ; and (3) variable recruitment  $R_1$ ,  $R_2$ , and  $R_3$  and varying mortality  $\alpha$ ,  $\beta$ , and  $\gamma$ .

#### Solution of Replacement Equation for the Replacement Line

For case (1) with constant recruitment and constant mortality, by substituting  $A = 4$  in equation (4), we have the solution for  $F$  given  $M$  and  $S/\bar{R}$ :

$$F = -\log_e \left\{ \frac{[f(S/\bar{R}) + 2][f(S/\bar{R}) - 4]}{6f(S/\bar{R})} \right\} - M, \quad (A.2)$$

where

$$f(S/\bar{R}) = \sqrt[3]{28 + 108S/\bar{R} + 12\sqrt{9 + 42S/\bar{R} + 81(S/\bar{R})^2}}.$$

To have a feasible solution, we should have constraints  $F \geq 0$ ,  $f(S/\bar{R}) \neq 0$ , and  $(\{[f(S/\bar{R}) + 2][f(S/\bar{R}) - 4]\}/[6f(S/\bar{R})]) > 0$ . The constraint  $f(S/\bar{R}) \neq 0$  is satisfied as  $f(S/\bar{R}) > 0$  for  $(S/\bar{R}) \geq 0$ . The function  $(\{[f(S/\bar{R}) + 2][f(S/\bar{R}) - 4]\}/[6f(S/\bar{R})])$  is monotonically increasing when  $(S/\bar{R}) \geq 0$  and is equal to 0 at  $(S/\bar{R}) = 0$ ; thus, the constraint  $(\{[f(S/\bar{R}) + 2][f(S/\bar{R}) - 4]\}/[6f(S/\bar{R})]) > 0$  is satisfied for  $(S/\bar{R}) > 0$  as well. The function  $-\log_e(\{[f(S/\bar{R}) + 2][f(S/\bar{R}) - 4]\}/[6f(S/\bar{R})])$  is monotonically decreasing when  $(S/\bar{R}) > 0$  and is equal to 0 at  $(S/\bar{R}) = 3$ . Therefore, if  $M = 0$ , we will have  $F \geq 0$  under the condition  $0 < (S/\bar{R}) \leq 3$ .

Consider case (2) of constant recruitment and varying mortality, substituting  $F_2$ ,  $F_3$ ,  $F_4$ , and  $A$  by  $\alpha$ ,  $\beta$ ,  $\gamma$ , and age 4, respectively, in equation (6), we have

$$\gamma = \log_e \left\{ \frac{\bar{R}}{S} \left[ 1 + e^{(\alpha+M)} + e^{(\alpha+\beta+2M)} \right] \right\} - \alpha - \beta - 3M. \quad (A.3)$$

In other words, equation (A.3) gives the values of fishing mortality (i.e.,  $\gamma$  given  $\alpha$  and  $\beta$ ) that would result in a specific value of  $S$  given  $\bar{R}$  and  $M$  for a population with the largest age-class of 4. Note that we can specify  $\alpha$  and  $\beta$  to be some values, and the magnitude of  $\gamma$  then depends upon  $\alpha$  and  $\beta$ .

The solution is constrained by the fact that  $\alpha \geq 0$ ,  $\beta \geq 0$ , and  $\gamma \geq 0$ . The condition  $\gamma \geq 0$  requires

$$\frac{S}{\bar{R}} \leq \frac{1 + e^{(\alpha+M)} + e^{(\alpha+\beta+2M)}}{e^{(\alpha+\beta+3M)}}. \quad (A.4)$$

Again, it is important to note that the assumption of variable mortality rate results in a different constraint on the  $S/\bar{R}$  ratio than the constraint when mortality and recruitment are fixed.

For case (3) with variable recruitment and mortality, substituting  $F_2$ ,  $F_3$ ,  $F_4$ , and  $A$  with  $\alpha$ ,  $\beta$ ,  $\gamma$ , and 4, respectively, in equation (8), we obtain

$$\gamma = \log_e \left[ \frac{R_1 + R_2 e^{(\alpha+M)} + R_3 e^{(\alpha+\beta+2M)}}{S} \right] - \alpha - \beta - 3M. \quad (\text{A.5})$$

Similarly, we have the conditions  $\alpha \geq 0$ ,  $\beta \geq 0$ , and  $\gamma \geq 0$ . The condition  $\gamma \geq 0$  requires

$$S \leq \frac{R_1 + R_2 e^{(\alpha+M)} + R_3 e^{(\alpha+\beta+2M)}}{e^{(\alpha+\beta+3M)}}. \quad (\text{A.6})$$

*Solution for Linking Subsequent Recruitment with Precedent Recruitment*

For the base case with the assumption of constant recruitment and constant mortality, we let  $A = 4$  and  $R_5 \equiv R_{\text{rep}}$  in equation (10), and solve the equation for  $F$  to obtain

$$F = -\log_e \left\{ \frac{[f(a, b, \bar{R}, R_{\text{rep}}) + 2][f(a, b, \bar{R}, R_{\text{rep}}) - 4]}{6f(a, b, \bar{R}, R_{\text{rep}})} \right\} - M, \quad (\text{A.7})$$

where

$$f(a, b, \bar{R}, R_{\text{rep}}) = \sqrt[3]{\frac{1}{b\bar{R}} \left[ 28b\bar{R} - 108W\left(-\frac{bR_{\text{rep}}}{a}\right) + 12\sqrt{9b^2\bar{R}^2 - 42b\bar{R}W\left(-\frac{bR_{\text{rep}}}{a}\right) + 81W\left(-\frac{bR_{\text{rep}}}{a}\right)^2} \right]}$$

and where  $W(x)$  refers to the Lambert  $W$  function. Thus, for the feasible solutions, we have constraints  $F \geq 0$ ;  $(-bR_{\text{rep}}/a) \geq (-1/e)$ ;  $f(a, b, \bar{R}, R_{\text{rep}}) \neq 0$ , and  $(\{[f(a, b, \bar{R}, R_{\text{rep}}) + 2][f(a, b, \bar{R}, R_{\text{rep}}) - 4]\}/[6f(a, b, \bar{R}, R_{\text{rep}})]) > 0$ . As presented above,  $(-bR_{\text{rep}}/a) \geq (-1/e)$  or  $R_{\text{rep}} \leq (ae^{-1}/b)$  demonstrates that the replacement recruitment is limited by a given Ricker stock–recruitment model.

Comparing equation (A.7) with equation (A.2), we notice that the two equations are essentially the same. Equation (A.2) represents the fishing mortality as a function of the  $S/\bar{R}$  ratio, not including the stock–recruitment relationship. Equation (A.7) represents the obtained fishing mortality as a function of the parameters of the Ricker stock–recruitment model and replacement recruitment.

For case (2) of constant recruitment and variable mortality, we let  $A = 4$  and  $R_5 \equiv R_{\text{rep}}$  and solve the above equation for  $\alpha$ ,  $\beta$ , and  $\gamma$ . For any specific value of  $\alpha$  and  $\beta$ , we have

$$\gamma = W\left(-\frac{bR_{\text{rep}}}{a}\right) + \log_e \left\{ a\bar{R} \left[ e^{-(\alpha+\beta+2M)} + e^{-(\beta+M)} + 1 \right] \right\} - \log_e(R_{\text{rep}}) - M. \quad (\text{A.8})$$

If we let  $R_{\text{rep}} = \bar{R}$ , then we have

$$\gamma = W\left(-\frac{bR_{\text{rep}}}{a}\right) + \log_e \left\{ a \left[ e^{-(\alpha+\beta+2M)} + e^{-(\beta+M)} + 1 \right] \right\} - M. \quad (\text{A.9})$$

Considering case (3) where recruitment varies among years, we let  $R_5$  equal a replacement recruitment  $R_{\text{rep}}$  (i.e.,  $R_5 \equiv R_{\text{rep}}$ ) and solve the above equation for  $\alpha$ ,  $\beta$ , and  $\gamma$ . For any specific value of  $\alpha$  and  $\beta$ , we have

$$\gamma = W\left(-\frac{bR_{\text{rep}}}{a}\right) + \log_e \left\{ a \left[ R_1 e^{-(\alpha+\beta+2M)} + R_2 e^{-(\beta+M)} + R_3 \right] \right\} - \log_e(R_{\text{rep}}) - M. \quad (\text{A.10})$$

Again, in equations (A.8) to (A.10),  $W(x)$  refers to the Lambert  $W$  function. Thus, for the feasible solutions, we have constraints  $\alpha \geq 0$ ,  $\beta \geq 0$ ,  $\gamma \geq 0$ , and  $(-bR_{\text{rep}}/a) \geq (-1/e)$  or  $R_{\text{rep}} \leq (ae^{-1}/b)$ .

Appendix 2: Calculation of Values for  $S/\bar{R}$ .

APPENDIX 2.—Explicit definitions of the positive real root  $x$  for polynomial  $P(x) = \sum_{t=1}^{A-1} x^t - S/\bar{R}$ , and  $-\log_e(x)$ . It should be noted that for a given  $M$  the ratio  $S/\bar{R}$  should be within a certain range to satisfy the constraint  $F = -\log_e(x) - M \geq 0$ .

Age	$S/\bar{R}$					
	0.5	1	1.5	2	2.5	3
$x$						
4	0.342508	0.543689	0.691414	0.810536	0.911569	1.000000
5	0.336197	0.518790	0.644471	0.741271	0.820599	0.888180
6	0.334263	0.508660	0.623501	0.709011	0.777307	0.834323
7	0.333640	0.504138	0.613012	0.691994	0.753796	0.804554
8	0.333435	0.502017	0.607412	0.682328	0.739968	0.786666
9	0.333367	0.500994	0.604299	0.676568	0.731398	0.775304
10	0.333345	0.500493	0.602522	0.673023	0.725891	0.767800
11	0.333337	0.500245	0.601491	0.670791	0.722257	0.762701
12	0.333335	0.500122	0.600886	0.669363	0.719814	0.759161
13	0.333334	0.500061	0.600528	0.668440	0.718147	0.756663
14	0.333333	0.500031	0.600316	0.667837	0.716997	0.754878
15	0.333333	0.500015	0.600189	0.667441	0.716197	0.753589
$-\log_e(x)$						
4	1.071460	0.609378	0.369017	0.210060	0.092589	0.000000
5	1.090059	0.656256	0.439325	0.299389	0.197721	0.118581
6	1.095826	0.675975	0.472405	0.343884	0.251920	0.181135
7	1.097692	0.684905	0.489371	0.368177	0.282634	0.217467
8	1.098307	0.689121	0.498548	0.382245	0.301148	0.239952
9	1.098511	0.691161	0.503687	0.390723	0.312797	0.254500
10	1.098578	0.692161	0.506631	0.395976	0.320356	0.264226
11	1.098601	0.692656	0.508343	0.399298	0.325374	0.270889
12	1.098609	0.692902	0.509350	0.401428	0.328763	0.275541
13	1.098611	0.693025	0.509945	0.402809	0.331081	0.278837
14	1.098612	0.693086	0.510299	0.403711	0.332684	0.281200
15	1.098612	0.693117	0.510511	0.404304	0.333799	0.282908

APPENDIX 2.—Extended.

Age	<i>S/R</i>							
	3.5	4	4.5	5	6	7	8	9
<i>x</i>								
4	1.079082	1.150911	1.216927	1.278163	1.389194	1.488302	1.578220	1.660802
5	0.947295	1.000000	1.047673	1.091281	1.168960	1.236910	1.297526	1.352395
6	0.883380	0.926519	0.965083	1.000000	1.061402	1.114338	1.160993	1.202794
7	0.847650	0.885128	0.918316	0.948121	1.000000	1.044213	1.082813	1.117121
8	0.825871	0.859648	0.889320	0.915783	0.961453	1.000000	1.033389	1.062870
9	0.811808	0.843002	0.870214	0.894338	0.935660	0.970246	1.000000	1.026122
10	0.802349	0.831657	0.857067	0.879473	0.917595	0.949265	0.976346	1.000000
11	0.795790	0.823679	0.847723	0.868822	0.904503	0.933944	0.958980	0.980748
12	0.791138	0.817932	0.840915	0.860993	0.894759	0.922447	0.945872	0.966154
13	0.787779	0.813714	0.835856	0.855121	0.887353	0.913630	0.935757	0.954840
14	0.785319	0.810571	0.832038	0.850644	0.881627	0.906749	0.927810	0.945907
15	0.783497	0.808200	0.829119	0.847186	0.877138	0.901299	0.921472	0.938745
$-\log_e(x)$								
4								
5	0.054145	0.000000						
6	0.124000	0.076320	0.035541	0.000000				
7	0.165288	0.122023	0.085214	0.053273	0.000000			
8	0.191316	0.151233	0.117299	0.087975	0.039310	0.000000		
9	0.208491	0.170786	0.139016	0.111671	0.066503	0.030206	0.000000	
10	0.220212	0.184335	0.154239	0.128433	0.085999	0.052067	0.023938	0.000000
11	0.228420	0.193974	0.165201	0.140617	0.100370	0.068339	0.041885	0.019440
12	0.234283	0.200976	0.173264	0.149669	0.111201	0.080726	0.055648	0.034432
13	0.238538	0.206146	0.179298	0.156513	0.119512	0.090330	0.066399	0.046211
14	0.241665	0.210017	0.183877	0.161761	0.125986	0.097890	0.074929	0.055611
15	0.243988	0.212946	0.187392	0.165835	0.131091	0.103918	0.081783	0.063212