La mer 23: 153-157, 1985
Société franco-japonaise d'océanographie, Tokyo

Article spécial n°4

Varieties and properties of three recruitment curves*

W. E. RICKER**

In any population of animals some relation must exist between the abundance of the reproducing stock and the number of recruits it produces. A number of expressions have been proposed to describe this relationship. Three of them have only two parameters. These are the inverted parabola, Beverton and Holt's hyperbolic curve, and Ricker's exponential curve (Fig. 1).

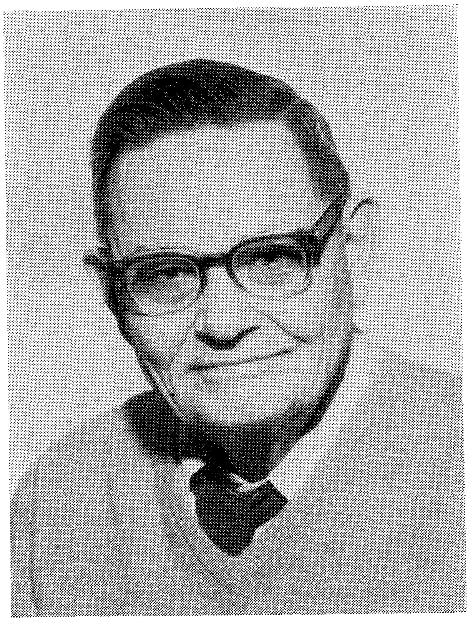
Throughout this paper recruitment (R) is defined as the number of members of a year-class that survive to the age of first maturity, or that would survive to that age (at the natural survival rate) if they had not been captured at some earlier age. Such fish are called adults. When first maturity may occur at different ages, recruitment to the median age of first maturity can be used as an approximation to R. The number of fish in the adult stock that produced any year-class is represented by P. When desirable, both P and R can be weighted by the number of eggs produced by an average fish of each of the ages represented.

In addition to P and R, the parameter symbol a appears in one or more of the expressions for all three curves. Its significance is the same in all cases, namely, the rate of recruitment, R_0/P_0, as P approaches 0. For the Beverton-Holt curve, the symbols α and β are the same as used in RICKER (1975; see especially Appendix III). For the Ricker curve note the following equivalents:

1975	α	β	a
Here	a	b	n

* Received Aqril 10, 1985

** Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B. C., Canada



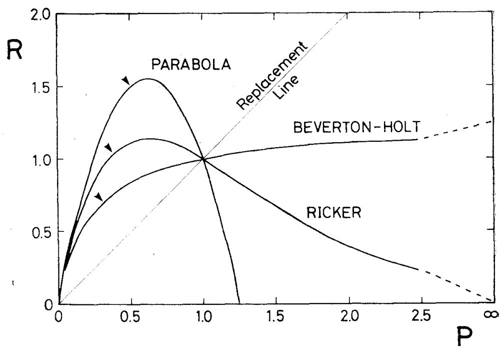


Fig. 1. Examples of the three curves considered, having an initial slope of 5 and a replacement abundance and recruitment equal to 1 in each case. For the parabola, $a=5$, $c=4$; for the Beverton-Holt curve, $\alpha=0.8$, $\beta=1/a=0.2$; for the Ricker curve, $a=5$, $b=1.609$. Maximum surplus recruitment positions are indicated by arrows.

The inverted parabola

The inverted parabola has not often been used as a recruitment curve, although it is well known as the Graham-Schaefer curve of surplus production of biomass, or sustainable yie d. It is usually written:

$$R=aP-cP^2 , \qquad (1)$$

$a=R_0/P_0$, which is the rate of recruitment as P approaches 0.
c= a parameter with the dimensions of $[1/P]$.

The positive portion of this curve, which is what interests us, starts at the graph's origin ($P=0$) and ends on the abscissa at $P=a/c$. Between the above positions there are 3 points on the curve that are of special interest.

(i) Because parabolas are symmetrical about a central axis, the point of maximum recruitment (R_m, P_m) must lie half way between the two zero points on the abscissa, i.e. at $P_m=a/2c$. Maximum recruitment is then:

$$R_m=a^2/4c . \qquad (2)$$

(ii) When R and P are in comparable units such that $R=P$ at the replacement level of stock, that replacement point is found by putting $R=P$ in expression (1); hence it is:

$$R_r=P_r=(a-1)/c . \qquad (3)$$

(iii) With R and P in comparable units, the maximum surplus recruitment (MSR) is the maximum value of $R-P$. This occurs at the point where the curve has a slope of $+1$, and its parameters will be identified by the subscript s. The slope or differential of expression (1) is $a-2cP$. Equating this to 1 we obtain P_s; putting P_s in (1) gives R_s; and their difference is the MSR:

$$P_s=(a-1)/2c , \qquad (4)$$

$$R_s=(a^2-1)/4c , \qquad (5)$$

$$MSR=R_s-P_s=(a-1)^2/4c . \qquad (6)$$

A preliminary or approximate fit of a parabola to recruitment data can be made by eye. Choose what seems the best position for the maximum point, and equate its parameters to $a/2c$ and $a^2/4c$, respectively.

Expression (1) can be fitted mathematically by solving the simultaneous equations:

$$a\Sigma P^2-c\Sigma P^3=\Sigma PR$$
$$a\Sigma P^3-c\Sigma P^4=\Sigma P^2R \qquad (6a)$$

for a and c. This procedure assumes that P is without error, so that all the variability in the data is in the recruitment observations; but this is usually at least approximately true.

The Beverton-Holt curve

A hyperbolic recruitment curve introduced by BEVERTON and HOLT (1957) has been written in several forms, some of which are:

$$R=\frac{1}{\alpha+\beta/P} , \qquad (7)$$

$$R=\frac{P}{\alpha P+\beta} , \qquad (8)$$

$$\frac{1}{R}=\alpha+\frac{\beta}{P} , \qquad (9)$$

$$R=\frac{aP}{1+P/K} , \qquad (10)$$

$$R=\frac{P}{1-A(1-P/P_r)} , \qquad (11)$$

Expressions (7)-(9) are merely algebraic transformations using the same parameters. Expression (10) has the form of the 3-parameter curve proposed by SHEPHERD (1982), with his $\beta=1$. Expression (11) was suggested by RICKER (1958) as a form of the Beverton-Holt relationship in which replacement abundance (P_r) would appear explicitly and the single parameter A would describe the shape of the curve with values ranging from 0 to 1.

The parameters used above are as follows:
α= the reciprocal of maximum recruitment, $1/R_m$.
β= the reciprocal of the slope of the curve at the origin, 1/a.
a= the slope of the curve at the origin, R_0/P_0.
K= the magnitude of P if recruitment were linear and $R=aP/2$.
A= the complement of the reciprocal of the slope of the curve at the origin, $1-1/a$.

P_r=stock size at the replacement level, if $R=P$ at replacement.

Table 1 gives the corresponding values of the parameters for the three notations used in expressions (7)-(11). In a stock that conforms to the Beverton-Holt relationship maximum recruitment would occur only if the stock became indefinitely large, but for practical purposes a finite value of P can be used, corresponding to (say) 0.95 R.

Expressions for replacement (P_r) and the point of maximum surplus recruitment (P_s, R_s) are found in the same way as for the parabola. P_r is obtained by putting $R=P$ in any one of expressions (7)-(11), and the result is shown in line 6 of Table 1. To obtain maximum surplus recruitment, the differential of, for example, expression (8) is:

$$\beta/(\beta+\alpha P)^2 . \qquad (12)$$

With R and P in comparable units this can be equated to 1, giving:

$$P_s=(\sqrt{\beta}-\beta)/\alpha . \qquad (13)$$

Substituting this in expression (8):

$$R_s=(1-\sqrt{\beta})/\alpha , \qquad (14)$$

$$MSR=R_s-P_s=(1-\sqrt{\beta})^2/\alpha . \qquad (15)$$

Corresponding expressions for expressions (10) and (11) are obtained by substituting the equivalent parameters from Table 1.

For an approximate fit of a Beverton-Holt curve to data it is usually easiest to estimate by eye the level of maximum recruitment ($=1/\alpha$) and the slope of the curve at the origin ($=1/\beta$). However, if the maximum is not available because the R observations are not close to constant at the largest observed P values, it may be possible to estimate the replacement point, which is $R=P=(1-\beta)/\alpha$ provided R and P are in comparable units.

The simplest way to fit a Beverton-Holt curve mathematically, if P is substantially without error, is to use expression (9) and regress $1/R$ on $1/P$. The slope of the line is an estimate of the quantities in line 2 of Table 1, while the ordinate intercept gives those in line 1. However, an R value computed from such a fit is the harmonic mean of actual values of R at the given P. This can be adjusted to an arithmetic mean by multiplying each of the computed values of R by the ratio of the sum of the observed values to the sum of the computed values.

Table 1. Relationships among the parameters of 3 forms of the Beverton-Holt curve; also the maximum value of recruitment (obtained when $P\to\infty$). Expressions for or containing A and P_r require that $R_r=P_r$ at the replacement level of stock.

	Symbol	Corresponding symbol for expression			Line
		No. 7-9	No. 10	No. 11	No.
Expressions(7)-(9)	α	—	$1/aK$	A/P_r	1
	β	—	$1/a$	$1-A$	2
Expression (10)	a	$1/\beta$	—	$1/(1-A)$	3
	K	β/α	—	$P_r(1-A)/A$	4
Expression (11)	A	$1-\beta$	$1-1/a$	—	5
	P_r	$(1-\beta)/\alpha$	$K(a-1)$	—	6
Maximum R	R_m	$1/\alpha$	aK	P_r/A	7

The Ricker curve

A possible type of recruitment curve for animal populations was suggested by RICKER in 1954. The same curve was discussed by BEVERTON and HOLT (1957), using different parameters, and RICKER (1958) introduced still another version. In order of appearance these three forms of the curve were:

$$\frac{R}{R_m}=\frac{P}{P_m}e^{1-P/P_m} , \qquad (16)$$

$$R=aPe^{-bP} , \qquad (17)$$

$$R=Pe^{n(1-P/P_r)} , \qquad (18)$$

Table 2. Relationships among the three forms of the Ricker curve shown in expressions (16)-(18). Exqression (18) requires that $R=P$ at replacement. (ln=natural logarithm)

Expr.	Symbol	Corresponding parameter in symbols of expression			Line
No.		No. 16	No. 17	No. 18	No.
16	R_m	—	a/be	P_re^{n-1}/n	1
	P_m	—	$1/b$	P_r/n	2
17	a	R_me/P_m	—	e^n	3
	b	$1/P_m$	—	n/P_r	4
18	n	$1+\ln(R_m/P_m)$	$\ln a$	—	5
	P_r	$P_m(1+\ln(R_m/P_m))$	$(\ln a)/b$	—	6

R_m = maximum recruitment,
P_m = parental stock needed for maximum recruitment,
a $= R_0/P_0$, the rate of recruitment as $P \rightarrow 0$,
P_r = stock size at the replacement level, if $R = P$ at replacement,
b $= 1/P_m$,
n $= P_r/P_m$.

The relationships among the three pairs of parameters above are shown in Table 2. Note that the quantities P_m, R_m, and P_r are all included. The point of maximum surplus recruitment on a RICKER curve is found, as usual, by equating the differential to 1, provided $R = P$ at replacement. In the symbols of expression (17) this is:

$$(1-bP)ae^{-bP}=1. \qquad (19)$$

Unfortunately this expression can be solved for P only by iteration (successive approximations). The P_s value obtained is substituted in (17) to get R_s, and MSR is $R_s - P_s$.

Expression (16) can often be used for preliminary or approximate fitting of this relationship to data. On the graph of R plotted against P, simply select a best position for the apex of the curve by eye, and read R_m and P_m from the axes. The other forms of the curve can then be written, using the transformations in the No. 16 column of Table 2. Your eye will presumably endeavour to select an arithmetic mean position for the maximum point in the vertical direction, so the result will be an AM curve (see below). This method is of course not available if the data do not include a recognizable maximum.

However, the usual way of fitting any of these expressions has been to compute the ordinary regression of the natural logarithm of R/P against P. The slope of this line is negative; with sign changed, it is an estimate of the quantity represented by the symbols in line 4 of Table 2. The ordinate intercept of the fitted line is an estimate of the quantity represented by the symbols in line 5. This method implies that P is known without error, so that all the variability in the data is in the recruitment R. This will usually be at least approximately true; but if not, it means that the estimated slope is numerically too small (i.e. it should be steeper), so that both b and a are underestimated.

The R values computed by this method of fitting are the geometric means (GM) of R at any value of P. The corresponding arithmetic means (AM) can be computed by one of the methods described in RICKER (1975, Section 11. 4. 2). Simplest is to compute for each observed P the GM value of R, then multiply these by the ratio of the sum of the observed values of R to the sum of the computed values.

A method of fitting the curve directly by iteration, using a computer, was used by CUSHING and HARRIS (1973), which provides an AM curve. It of course weights the observations somewhat differently, but it too assumes that P is free of error. Other computer programs are available, for example by P. K. TOMLISON in ABRAMS (1971). If a computer program is used, care should be taken to discover what kind of curve it estimates (AM, GM or other), and on what basis.

Discussion

1. For most fish stocks the point of maximum surplus recruitment (MSR) is not the same as the point of maximum sustainable yield (MSY), the principal exceptions being Pacific salmon (*Oncorhynchus*) that are fished only in or near their spawning river. To estimate MSY, the gains made by the growth of the fish during each year, or part thereof, must be balanced against the losses from natural mortality during the same period, in order to identify a best rate of fishing. For example, one of the methods suggested by BARANOV (1918), RICKER (1945) or BEVERTON and HOLT (1957)—all described in RICKER (1975)—can be used to estimate the rate of fishing that will produce greatest yield per unit recruitment. However, the rate of fishing that produces maximum yield per recruit is not necessarily the one that will generate the abundance of spawners that produces MSR. Thus to estimate the rate of fishing that gives a true MSY there will usually have to be a trade-off between having most recruits, and getting maximum yield from a unit number of them.

2. SCHNUTE (1985) showed that all three of the curves described above, as well as intermediate types, can be represented by a single

3-parameter expression:

$$R=aP(1-\beta\gamma P)^{1/\gamma}. \qquad (20)$$

When $\gamma=+1$ this becomes a parabola; when $\gamma=-1$ it is the Beverton-Holt hyperbola; and when $\gamma=0$ it is the Ricker exponential curve (because $(1-\beta\gamma P)^{1/\gamma}\rightarrow e^{-\beta P}$ as $\gamma\rightarrow 0$). By using 3 parameters a much greater variety of shapes can be obtained than with only two. For example, the maximum level of recruitment, relative to the replacement level, can be made independent of the initial slope (a), whereas with the Ricker curve R_m/R_r has a minimum value of 1 when $a=e=2.718$ (provided R and P are in comparable units), and increases when a is either larger or smaller.

Unfortunately, even with a good computer the mathematical fitting of a 3-parameter curve can be tedious, and it may pose serious problems because the observed values of R at a given P usually vary widely, and because the data may include only a part of the total region of interest. It may be necessary to put constraints on one or more of the parameters to avoid obtaining a biologically ridiculous result. There is of course no objection to doing this; if a 2-parameter curve is chosen it automatically puts a major constraint on the kinds of results obtainable. However, it may come to a point where a freehand curve is about as representative as anything fitted mathematically. In fact, SHEPHERD (1982) has described an empirical method of fitting an expression somewhat similar to expression (20) that differs little from a freehand approach. With a mathematical expression, however, it is possible to compute limits of variability about the central trend.

References

ABRAMSON, N. J. (1971): Computer programs for fish stook assessment. FAO Fish. Tech. Paper **101**, 1-154.

BARANOV, F. I. (1918): On the question of the biological basis of fisheries. Nauchnyi Issledovatelskii Ikhtiologicheskii Institut, Izvestiya, **1**, 81-128. (In Russian).

BEVERTON, R.J.H. and S.J. HOLT (1957): On the dynamics of exploited fish populations. U.K. Min. Agr. Fish., Fish. Invest. (Ser. 2), **19**, 533 pp.

CUSHING, D.H., and J.G.K. HARRIS (1973): Stock and recruitment and the problem of density-dependence. Rapp. Procès-Verb. Conseil Explor. Mer, **164**, 142-155.

RICKER, W. E. (1945): A method of estimating minimum size limits for obtaining maximum yield. Copeia 1945 (**2**), 84-94.

RICKER, W.E. (1954): Stock and recruitment. J. Fish. Res. Board Canada, **11**, 559-623.

RICKER. W.E. (1958): Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Canada, 119, 300 pp.

RICKER, W.E. (1975): Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Canada, 191, 382 pp. Also available in French and Russian.

SCHNUTE, J. (1985): A general theory for analysis of catch and effort data. Can. J. Fish. Aquatic Sci., **42**, 414-429.

SHEPHERD, J. G. (1982): A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Conseil Expl. Mer, **40**, 67-75.