SOME MODIFICATIONS IN THE BEVERTON AND HOLT MODEL FOR ESTIMATING THE YIELD OF EXPLOITED FISH POPULATIONS

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(Communicated by N. K. Panikkar, F.N.I.)

(*Received June 17, 1967*)

For calculating the yield of exploited fish populations a method of approximate integration of the Beverton and Holt model has been discussed. The advantage of this method is that the yield can be calculated fairly accurately even when the growth of fish is not isometric, i.e. when the exponent in the equation describing the length-weight relation deviates from three and when the population parameters such as growth and mortality are not constant within the fishable life span or when the growth pattern does not conform to the pattern of von Bertalanffy equation. The accuracy of this method of estimating yield has been checked by calculating the yield from the Beverton and Holt model after modifying it to suit instances when the power in length-weight relation is not exactly three and also by applying Newton's interpolation formula. Almost identical values were obtained by all the three methods which suggest that the method of approximate integration described here is reasonably sound.

INTRODUCTION

One of the most widely used models for studying the dynamics of exploited fish populations is that of Beverton and Holt (1957). These authors at first describe a simple model assuming that the population is in a steady state having constant parameters and then deal with more realistic models free from the assumptions of steady state conditions. Since the application of later models requires more precise data which are generally lacking for most of the fish populations, especially in the tropics, population studies are largely made by using only the simple model. It has also been pointed out by Beverton (1953) and Beverton and Holt (1957) that the general conclusions drawn from the simple model are not significantly altered when more complicated models are applied.

Although the simple model assumes the main population parameters to be constant, in many fish populations they vary with age and in this paper a method of applying the Beverton and Holt model is discussed which can be used even when the fishing and natural mortalities are not constant and when the exponent in the length-weight relationship is not exactly three. This method which involves the use of approximate integration gives a fairly accurate estimate of yield and it is greatly hoped that it would be of some general interest to fishery biologists.

The Beverton and Holt Yield Equation

The equation developed by Beverton and Holt for estimating the yield is obtained by integrating the rate of change of yield in weight between the limits of fishable life span. The rate of change of yield in weight at age t of a year class is given by

$$\frac{dY_w}{dt} = FN_tW_t, \qquad \text{(1)}$$

where F = instantaneous fishing mortality rate, N_t = number of fish of a given year class at age t and W_t = weight of an individual fish at age t. Since the mortality rates are constant N_t is described by the equation

$$N_t = R'e^{-(F+M)(t-t_{p'})}, \qquad \text{(2)}$$

where R' = number of recruits (R) of age $t_{p'}$ (years) when they become fully exploitable and M = instantaneous natural mortality coefficient. Weight of the individual fish at age t, when the exponential value in L/W relation is three and when the growth pattern conforms to the von Bertalanffy growth equation, is

$$W_t = W_\infty(1-e^{-k(t-t_0)})^3 \qquad \text{(3)}$$

where W_∞ = asymptotic weight, k = rate of deceleration in growth increments and t_0 = the age at which length of the fish is zero if its growth throughout life has followed the von Bertalanffy growth equation. On expanding (3),

$$W_t = W_\infty \sum_{n=0}^{3} \Omega_n e^{-nk(t-t_0)}, \qquad \text{(4)}$$

where n takes the value of 0, 1, 2 and 3 successively, the corresponding value of Ω_n being $\Omega_0 = +1$, $\Omega_1 = -3$, $\Omega_2 = +3$ and $\Omega_3 = -1$.

Substituting eqns. (2) and (4) for N_t and W_t respectively in (1) and integrating with respect to t between the limits of fishable life span (λ), i.e. for the period ($t_\lambda - t_{p'}$) years where t_λ is the age at which fish disappears from the fishery, the equation for yield developed by Beverton and Holt is

$$Y_w = FR'W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nk(t_{p'}-t_0)}}{F+M+nk}[1-e^{-(F+M+nk)\lambda}]. \qquad \text{(5)}$$

The Estimation of Yield by the Method of Approximate Integration

The requirements for the use of eqn. (5) to calculate the yield are: (*a*) that the fishing and natural mortalities should be constant, (*b*) the growth pattern of the species should conform to the von Bertalanffy growth equation and (*c*) the growth should be isometric, i.e. the exponent in L/W relation should be three. These conditions may not be met by all the fish populations. There are many instances when the mortality rates have been found to vary with age. Moreover, many authors have reported the exponential value in the equation describing the L/W relation to deviate considerably from three (Alverson and Westrheim 1961; Hatanaka and Iwahashi 1953; Hennemuth 1959; Krishnan Kutty and Qasim 1968; Pantulu 1962; Pillay 1954; and others). In such cases, i.e. when the growth is allometric, the calculation of yield, assuming the exponent to be three, might introduce serious errors in the yield estimate (*see* Paulik and Gales 1964). Jones (1957) gave a simplified version of the Beverton and Holt yield equation involving the use of the Incomplete Beta Function. Wilimovsky and Wicklund (1963) have prepared tables of the Incomplete Beta Function using which the yield can be calculated from Jones's version of the Beverton and Holt model when the exponent in L/W relation deviates from three. Recently Paulik and Gales (1964) also wrote this equation in the form of an Incomplete Beta Function to calculate the yield when growth is allometric and the integration was accomplished by approximating this function to a polynomial. Both these equations, however, assume the population parameters such as growth and mortality to be constant.

Krishnan Kutty (1963) pointed out that, when the mortality varies with age or when the growth pattern within the fishable life span is such that the von Bertalanffy growth equation has to be applied to different periods separately, the exploitable phase can be divided into shorter time intervals within which the population parameters are constant and the yield is calculated for each period using the Beverton and Holt model. But this method has been found to be rather tedious especially when the mortality rates vary within short intervals. Besides, it is only applicable when the power in L/W relation is three.

The calculation of yield by the method of approximate integration makes the Beverton and Holt model more flexible since the population parameters such as growth and mortality need not be constant and the exponent in L/W relation could be any value. Another advantage of this method is that the growth pattern may follow any mathematical formula, including the von Bertalanffy equation. The method can be described as follows:

In place of integrating the rate of change of yield in weight between the limits of fishable life span for a continuous age distribution, as has been done by Beverton and Holt, the exploitable phase of the population is to be divided into suitable numbers of equal time intervals (h) so that

$$h = \frac{t_\lambda - t_{p'}}{\text{number of intervals}}. \qquad \ldots \quad \ldots \quad \ldots \quad (6)$$

For the sake of accuracy the number of intervals is to be kept sufficiently large particularly when the parameters are not constant. After dividing the fishable life span let $T_0, T_1, T_2, \ldots T_{n-1}$ denote the age of the fish at the beginning of the successive time intervals so that $T_0 = t_{p'}$ and $T_n = t_\lambda$. The rates of yield Y_0, Y_1, Y_2, etc., at T_0, T_1, T_2, etc., are calculated from the function $Y_t = F_t W_t N_t$. The curve obtained by joining Y_0, Y_1, Y_2, etc., describes the relation between the rate of change of yield in weight and age and the area under this curve gives the total yield during the entire exploitable phase of the population, which can be obtained either by applying Simpson's rule or by the Trapezoidal rule of approximate integration. Simpson's rule of approximate integration can be applied only if the number of intervals are even but the Trapezoidal rule can be used in all cases. By applying Simpson's rule, the yield

$$Y_w = \frac{h}{3}\{Y_0 + Y_n + 2(Y_2 + Y_4 + Y_6 + \ldots Y_{n-2}) + 4(Y_1 + Y_3 + Y_5 + \ldots Y_{n-1})\} \quad \ldots \quad (7)$$

and by using the Trapezoidal rule, the yield

$$Y_w = \frac{h}{2}\{Y_0 + Y_n + 2(Y_1 + Y_2 + Y_3 + \ldots Y_{n-1})\}. \quad \ldots \quad \ldots \quad (8)$$

As an example the yield per recruit $\left(\frac{Y_w}{R}\right)$ has been calculated below by using the data of the North Sea plaice given by Beverton (1954). But the exponent in L/W relation is taken to be 3·5. The values of the various parameters used for calculating yield are: $F_t = 0{\cdot}05$, $M = 0{\cdot}1$, $W_\infty = 3000$ gm, age of recruitment, $t = 3{\cdot}7$ years, $t_0 = -0{\cdot}8$ years, $t_\lambda = 15$ years, $k = 0{\cdot}1$ and $\lambda = (t_\lambda - t_{p'})$ or 11·3 years. The λ is divided into 10 equal intervals, hence $h = 1{\cdot}13$ years, $T_0 = 3{\cdot}7$ years and $T_n = 15$ years. The rates of yield, Y_0, Y_1, etc., at various ages beginning from T_0 are given in Table I. The total yield per recruit during the entire period of exploitation using Simpson's rule is 129·5695 gm and by using the Trapezoidal rule is 130·2877 gm.

Validity of the Method of Approximate Integration for calculating Yield

In the above example, yield has been calculated by the method of approximate integration for the plaice data assuming that the parameters are constant. The only change made in the data is the assumption that the power in the equation describing the length-weight relation is 3·5 instead of 3. Hence, for testing the accuracy of the method of approximate integration, one would expect that the yield calculated by this method should be compared with the values obtained by applying either the method of Jones (1957) or that of Paulik and Gales (1964) to the same data. But the difficulty is that Jones's version of the Beverton and Holt model requires the use of

TABLE I

The estimated rates of yield at various ages beginning from $T_0 = 3 \cdot 7$ years from the function $Y = F_t N_t W_t$

Age in years ..	3·70	4·83	5·96	7·09	8·22	9·35	10·48	11·61	12·74	13·87	15·00
N_t ..	1·0	0·8437	0·7118	0·6005	0·5066	0·4274	0·3606	0·3042	0·2567	0·2165	0·1836
W_t ..	85·958	154·880	253·120	361·283	482·890	627·071	765·933	907·460	1049·70	1202·41	1338·09
$F_t N_t W_t$ ..	4·2979	6·5337	9·0085	10·8475	12·2316	13·4005	13·8098	13·8025	13·4729	13·0161	12·2837

a table of the Incomplete Beta Function and that of Paulik and Gales is very tedious and involves the use of a digital computer. Hence, the accuracy of the calculated yield is tested by using the following two methods instead: (*a*) modified Beverton and Holt model and (*b*) Newton's interpolation formula. The advantage of both these methods is that they require only a log table and a desk calculator.

Estimation of Yield using the Modified Beverton and Holt Model:

Equation (5) can be used as such only if the exponent in L/W relation is exactly three. The general form of eqn. (3) for any value of the exponent may be written as

$$W_t = W_\infty(1-e^{-k(t-t_0)})^{\underline{c}}, \quad .. \quad .. \quad .. \quad (9)$$

where $\underline{c}$ is the exponent in the equation describing L/W relation. When eqn. (9) in the expanded form using the binomial theorem is inserted in eqn. (1) and integrated, the general form of the Beverton and Holt equation is obtained for any value of $\underline{c}$ when it is a positive integer. This can be written as

$$Y_w = FR'W_\infty \sum_{n=0}^{\underline{c}} \frac{\Omega_n e^{-nk(t_{p'}-t_0)}}{F+M+nk}[1-e^{-(F+M+nk)\lambda}], \quad .. \quad (10)$$

where for values of $n = 0, 1, 2, \ldots \underline{c}$, Ω_n takes the values of the successive coefficients of the various terms obtained by the binomial expansion of eqn. (9). If $\underline{c}$ is a positive integer, then on expanding (9) the binomial series will terminate after $(\underline{c}+1)$ terms. If $\underline{c}$ is not a positive integer, then the series will not terminate and the expansion has to be discontinued after certain number of terms depending on the accuracy required in yield values. In this case the upper value in the summation term, $\sum\limits_{n=0}^{\underline{c}}$ in eqn. (10), is one less than the number of binomial terms considered sufficient for calculating the yield. Applying the binomial theorem, eqn. (9) can be written as

$$W_t = W_\infty[1-\underline{c}_{(1)}e^{-k(t-t_0)}+\underline{c}_{(2)}e^{-2k(t-t_0)}-\underline{c}_{(3)}e^{-3k(t-t_0)}$$
$$+\underline{c}_{(4)}e^{-4k(t-t_0)}-\ldots], \quad .. \quad .. \quad .. \quad .. \quad .. \quad (11)$$

where $\underline{c}_{(1)} = \frac{\underline{c}}{1!}$, $c_{(2)} = \frac{\underline{c}(\underline{c}-1)}{2!}$ and so on. Since we require to calculate yield for $\underline{c} = 3{\cdot}5$, eqn. (9) on expansion will not terminate. Taking the first six terms in the binomial expansion, (9) can be written as

$$W_t = W_\infty[1-3{\cdot}5e^{-k(t-t_0)}+4{\cdot}375e^{-2k(t-t_0)}-2{\cdot}1875e^{-3k(t-t_0)}$$
$$+0{\cdot}2734e^{-4k(t-t_0)}+0{\cdot}0820e^{-5k(t-t_0)}]. \quad .. \quad .. \quad .. \quad (12)$$

Equation (12) now can be written in the form,

$$W_t = W_\infty \sum_{n=0}^{5} \Omega_n e^{-nk(t-t_0)}, \quad .. \quad .. \quad .. \quad (13)$$

where n takes the value of 0, 1, 2, 3, 4 and 5 with corresponding Ω_n values of $+1$, $-3{\cdot}5$, $+4{\cdot}375$, $-2{\cdot}1875$, $+0{\cdot}2734$ and $+0{\cdot}0820$—these being the successive binomial coefficients taken from (12). On substituting (2) and (13) for N_t and W_t in (1) and integrating with respect to t between the limits of fishable life span, as has been done by Beverton and Holt, we get an equation identical to eqn. (10) except that the summation term $\sum\limits_{n=0}^{\underline{c}}$ is replaced by $\sum\limits_{n=0}^{5}$ where for values of n ranging from 0 to 5 the corresponding Ω_n values are the same as given for eqn. (13). Using eqn. (10) in this form the yield can be calculated in exactly the same manner as has been done by Beverton (1954) for $\underline{c} = 3$.

By slightly rearranging eqn. (10) a less tedious procedure can be adopted to calculate the yield (*see* Krishnan Kutty 1961). When $\underline{c} = 3{\cdot}5$ and taking the first six terms of the binomial expansion, eqn. (10) can be written as

$$Y_w = FR'W_\infty \sum_{n=0}^{5} \Omega_n U_n, \qquad \ldots \quad \ldots \quad \ldots \quad (14)$$

where

$$U_n = \frac{[e^{-k(t_{p'}-t_0)}]^n - e^{-\lambda(F+M)}[e^{-k(\lambda+t_{p'}-t_0)}]^n}{F+M+nk}.$$

Putting $e^{-k(t_{p'}-t_0)} = A$, $e^{-\lambda(F+M)} = B$ and $e^{-k(\lambda+t_{p'}-t_0)} = D$, U_n is now written as $\dfrac{A^n - BD^n}{F+M+nk}$.

The steps in calculation are to get U_n values for $n = 0, 1, 2, 3, 4$ and 5. These U_n values, i.e. U_0 to U_5, are then multiplied by the corresponding Ω_n values given for eqn. (13) and on adding them, $\sum\limits_{n=0}^{5} \Omega_n U_n$ is obtained which is then multiplied by $FR'W_\infty$ to get the required yield in weight. The yield per recruit calculated in this way from the data of the North Sea plaice when $\underline{c} = 3{\cdot}5$ is found to be 129·705 gm.

It is to be noted that in expanding (9) when $\underline{c} = 3{\cdot}5$, the constants of the first few terms are alternately positive and negative but later on all constants become positive. As a result, when only the first few terms are considered in incorporating (9) into the yield equation, the yield will be slightly underestimated. If $\underline{c}$ is 2·5 then, after the first few terms which are alternately positive and negative, the rest would be all negative. In this case the selection of the first few terms in incorporating (9) into the yield equation will overestimate the yield. Thus, depending on the value of $\underline{c}$, when it is not a positive integer, the Beverton and Holt equation may slightly under- or overestimate the yield. In this respect, therefore, the application of the Beverton and Holt model, as described here when growth is allometric, is slightly less precise than those of Jones, and Paulik and Gales. But this error in the above example seems to be negligible since the yield per recruit obtained using this method is nearly the same as has been obtained by using the method of approximate integration.

Estimation of Yield by Newton's Interpolation Formula:

Newton's interpolation with equal intervals (Freeman 1960) can be applied when there are $\underline{b}$ equidistant terms and it is required to find an intermediate term.* According to this formula the intermediate term,

$$U_{0+\underline{d}} = U_0 + \underline{d}_{(1)} \Delta U_0 + \underline{d}_{(2)} \Delta^2 U_0 + \underline{d}_{(3)} \Delta^3 U_0 + \ldots \underline{d}_{(p)} \Delta^p U_0, \quad .. \quad (15)$$

where U_0 is the first given term; ΔU_0 is the first term of the first difference or $(U_1 - U_0)$, $\Delta^2 U_0$ is the first term of the second difference or $(U_2 - U_1)$–$(U_1 - U_0)$ and so on; $\underline{d}$ is the value of the multiple of interval to be taken; $\underline{d}_{(1)} = \frac{\underline{d}}{1!}$, $\underline{d}_{(2)} = \frac{\underline{d}(\underline{d}-1)}{2!}$ and so on. To obtain the accurate value of $U_0 + \underline{d}$, successive differences should be taken until $\Delta^p U_1 - \Delta^p U_0$ becomes zero. But for ordinary purposes it is sufficient to take successive differences until $\underline{d}_{(p)} \Delta^p U_0$ becomes insignificant.

TABLE II

Data required to calculate yield using Newton's interpolation formula

$\underline{c}$	$\frac{Yw}{R}$	ΔU_0	$\Delta^2 U_0$	$\Delta^3 U_0$	$\Delta^4 U_0$
2	267·57(U_0)				
		$\underline{-103{\cdot}92}$			
3	163·65(U_1)		$\underline{44{\cdot}13}$		
		− 59·79		$\underline{-20{\cdot}16}$	
4	103·86(U_2)		23·97		$\underline{9{\cdot}8}$
		− 35·82		−10·36	
5	68·04(U_3)		13·61		
		− 22·21			
6	45·83(U_4)				

To calculate $\frac{Yw}{R}$ when $\underline{c} = 3{\cdot}5$, $\frac{Yw}{R}$ for various values of $\underline{c}$ at equidistant intervals are to be calculated using eqn. (10). Further steps in calculating yield are given in Table II. The first value of $\frac{Yw}{R}$ pertains to $\underline{c} = 2$ and hence $\underline{d}$ or the multiple of unit interval between this value and $\underline{c} = 3{\cdot}5$ is 1·5. Applying eqn. (15) the yield when $\underline{c}$ is 3·5,

* This method can be used to find the value of $f(x)$ for any intermediate value of x when values of $f(x)$ are available for values of x spaced at equal intervals. Whatever may be this interval, $\underline{d}$ or the difference between the first and the intermediate value of x is always expressed as a multiple of the unit interval taking the interval between two adjacent values of x as the unit.

$$\frac{Yw}{R} = 267{\cdot}57 + 1{\cdot}5(-103{\cdot}92) + \frac{1{\cdot}5(0{\cdot}5)}{2}(44{\cdot}13) + \frac{1{\cdot}5(0{\cdot}5)(-0{\cdot}5)}{3\times 2}(-20{\cdot}16)$$
$$+ \frac{1{\cdot}5(0{\cdot}5)(-0{\cdot}5)(-1{\cdot}5)}{4\times 3\times 2}(9{\cdot}8)$$
$$= 129{\cdot}7281 \text{ gm.}$$

Since $\frac{Yw}{R}$ is calculated only for five values of $\underline{c}$ ranging from 2 to 6 at unit intervals it is assumed that the fourth differences are constant and hence $(\Delta^4 U_1 - \Delta^4 U_0)$ is zero. This assumption seems to be reasonable since the yield obtained agrees very closely with the estimates from the previous two methods. The error in calculating the yield when more differences are not considered seems insignificant.

Conclusion

When the growth is not isometric, calculation of yield using the Beverton and Holt model taking the exponent in length-weight relation to be three might introduce serious errors depending on the actual value of the exponent. When the population parameters vary within the exploitable phase this model can still be used for estimating the yield by dividing the fishable life span into shorter time intervals within which the parameters are constant. But this method is tedious especially when the parameters vary within short intervals and can be applied only if the growth pattern conforms to the von Bertalanffy equation. These difficulties do not arise if yield is calculated by the Beverton and Holt model using approximate integration. The method of approximate integration makes this model more flexible and gives fairly accurate estimate of yield.

Acknowledgements

I wish to thank Dr. N. K. Panikkar, Director, National Institute of Oceanography, for his interest in this work and Dr. S. Z. Qasim for critically going through the manuscript of this paper. Thanks are also due to Sri K. V. Achuthan Kutty and Sri E. N. Vasudevan Namboodiri for their assistance in mathematics.

References

Alverson, D. L., and Westrheim, S. J. (1961). A review of the taxonomy and biology of the Pacific Ocean perch and its fishery. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer.*, **150**, 12–27.

Beverton, R. J. H. (1953). Some observations on the principles of fishery regulation. *J. Cons. perm. int. Explor. Mer*, **19**, 56–68.

——— (1954). Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. *U.S. Fishery Lab. Beaufort, N.C., Misc. Contr.*, No. 2, 181 pp.

Beverton, R. J. H., and Holt, S. J. (1957). On the dynamics of exploited fish populations. *Fishery Invest., Lond.*, Ser. 2, **19**, 533 pp.

Freeman, H. (1960). Finite differences for Actuarial students. Camb. Univ. Press, 228 pp.

Hatanaka, M., and Iwahashi, S. (1953). Studies on the populations of the flat-fishes in Sendai Bay. 3. The biology of *Limanda yokohamae* (Gunther). *Tohoku J. agric. Res.*, 3, 303–309.

Hennemuth, R. C. (1959). Additional information on the length-weight relationship of skipjack tuna from the eastern tropical Pacific Ocean. *Bull. inter-Am. trop. Tuna Commn.*, 4, 23–37.

Jones, R. (1957). A much simplified version of the fish yield equation. *Lisbon Joint meeting of ICNAF/ICES/FAO*, Document No. P. 21, 8 pp.

Krishnan Kutty, M. MS. (1961). Some aspects of the theoretical models in the estimation of yield per recruit and deductions from isopleth diagrams under various postulated situations. In: *Population dynamics, Inst. Fish., Univ. B.C., Canada*, 107–131.

——— (1963). An ecological study and theoretical considerations of butter sole (*Isopsetta isolepis*) population in Hecate Strait. *Ph.D. Thesis, Dept. Zool., Univ. B.C., Canada*, 168 pp.

Krishnan Kutty, M., and Qasim, S. Z. (1968). Theoretical yield studies on the large-scaled tongue sole, *Cynoglossus macrolepidotus* (Bleeker), from the Arabian Sea. (*In press*).

Pantulu, V. R. (1962). On the use of pectoral spines for the determination of age and growth of *Pangasius pangasius* (Hamilton-Buch). *J. Cons. perm. int. Explor. Mer*, 27, 192–216.

Paulik, G. J., and Gales, L. E. (1964). Allometric growth and the Beverton and Holt yield equation. *Trans. Am. Fish. Soc.*, 93, 369–381.

Pillay, T. V. R. (1954). The biology of the grey mullet, *Mugil tade* Forskal, with notes on its fishery in Bengal. *Proc. natn. Inst. Sci. India*, 20, 187–217.

Wilimovsky, N. J., and Wicklund, C. (1963). Tables of the Incomplete Beta Function for the calculation of fish population yield. *Inst. Fish., Univ. B.C., Canada*, 291 pp.