

THE ESTIMATION OF OPTIMUM CONDITIONS FOR REGULATING A FISHERY WHEN GROWTH AND MORTALITY RATES ARE UNKNOWN

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The Beverton-Holt model as modified by Holt (1962) is useful for a judicious exploitation of many tropical fish populations whose elemental rates of growth and mortality are often difficult to estimate. Hence, in the light of this modification the existing methods for estimating (a) the optimum size limit and the maximum yield for a given fishing intensity, (b) the corresponding parameters for a fixed mesh size and (c) the potential yield have been examined and derived in the present paper. These derivations not only include the usefulness of limited information on some vital parameters but are also applicable to allometric growth conditions and overrule the graphical methods of estimation.

INTRODUCTION

Recently Holt (1962) has written the Beverton-Holt yield equation in a form that does not directly contain the element of time and in this form the model requires only the ratios of mortality to growth rates and the asymptotic length. Even the parameters, K and t_0 of the von Bertalanffy growth curve, are replaced from the yield equation although they may be obtained by the methods of Gulland and Holt (1959) and Diaz (1963) when age reading is difficult. Holt has thus made it possible to apply the Beverton-Holt model to many tropical fish populations where the estimates of growth and mortality rates are often not available mainly because of the difficulties in age reading. The tables of yield functions prepared by Beverton and Holt (1966) can be readily employed for drawing the eumetric fishing curve using only the ratios of mortality to growth rates. Unfortunately this table is useful only if the exponent describing the length-weight (L/Wt) relation is either three or very nearly three. Hence, in the present paper, some of the existing methods for determining the conditions of optimum exploitation have been examined in the light of Holt's substitutions so that they may also be applied to those populations where the individual estimates of the main parameters are lacking. In addition to the methods based on the Beverton-Holt model (*see* Beverton 1954; Beverton and Holt 1957; Holt 1958; Krishnan Kutty 1968a; Krishnan Kutty and Qasim 1968) those of Ricker (1945) and Allen (1953, 1954) have also been considered here. All these methods are suitable for both conditions

of growth—isometric and allometric—but the ones based on the Beverton-Holt model are more precise. The present study, however, is limited to such populations which have constant mortality rates and conform to a von Bertalanffy growth pattern.

HOLT'S EQUATION FOR ESTIMATING THE YIELD

The equation derived by Holt (1962) from the original Beverton-Holt model (see Beverton and Holt 1957) for estimating the yield (Y_w), using only the ratios of mortality to growth rates, can be written as

$$Y_w = F'W_\infty R \left(1 - \frac{l_r}{L_\infty}\right)^{-M'} \sum_{n=0}^3 \frac{\Omega_n}{Z'+n} \left(1 - \frac{l_c}{L_\infty}\right)^{M'+n} \left[1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c}\right)^{Z'+n}\right] \dots \quad (1)$$

where $F' = \frac{F}{K}$, $M' = \frac{M}{K}$, $Z' = \frac{Z}{K}$; F , M and Z are instantaneous fishing, natural and total mortality rates, K = rate of attaining the asymptotic length in the von Bertalanffy growth equation, W_∞ = asymptotic weight of the fish, R = number of recruits, l_r = the size at which fish is fully recruited to the fishery, l_c = the size at which fish becomes fully vulnerable to the gear, l_L = size at which fish disappears from the fishery, L_∞ = asymptotic length and Ω_n takes successively the values of 1, -3, +3 and -1. The ratios, F' and M' , can be calculated from estimates of Z' for two different levels of fishing intensity and Z' is obtained either from the relationship (Beverton and Holt 1956a)

$$Z = \frac{K(L_\infty - \bar{l})}{\bar{l} - l_c}, \dots \dots \dots \quad (2)$$

where \bar{l} = the mean length of fish of size l_c and above in the fishery, or by using Allen's (1967) method. When age reading is difficult, the asymptotic length may be determined fairly accurately if it is possible to apply the methods of Gulland and Holt (1959) and Diaz (1963), otherwise the less precise methods based on comparative studies of fish populations as suggested by Holt (1962) may have to be employed. If growth is not isometric, the exponent in the equation describing the length-weight relation will not be exactly three. Krishnan Kutty (1968b) has pointed out that, when the L/Wt exponent is not a positive integer, the number of summation terms in the Beverton-Holt yield equation runs to infinity, but for all practical purposes, six to ten terms would be adequate for obtaining a reasonably accurate estimate of the yield. The equivalent of this equation using only the ratios of mortality to growth rates is

$$Y_w = F'W_\infty R \left(1 - \frac{l_r}{L_\infty}\right)^{-M'} \sum_{n=0}^{d-1} \frac{(-1)^n \gamma(n)}{Z'+n} \left(1 - \frac{l_c}{L_\infty}\right)^{M'+n} \left[1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c}\right)^{Z'+n}\right] \dots \quad (3)$$

where $\gamma_{(n)}$ takes successively the values of

$$1, \frac{\gamma}{1!}, \frac{\gamma(\gamma-1)}{2!}, \dots, \frac{\gamma(\gamma-1)(\gamma-2) \dots (\gamma-(d-2))}{(d-1)!}$$

γ = the exponent in the equation describing the length-weight relation and d = number of terms which are taken to be sufficient for obtaining an accurate estimate of the yield. Equation (3) instead of (1) is used here to derive the method of estimating the optimum size limit for a given F' so that it can be used when growth is either isometric or allometric.

BEST SIZE LIMIT FOR A GIVEN F'

Rewriting the population parameters in terms of ratios as suggested by Holt, the details of which are given by Beverton and Holt (1966), the equation described by Krishnan Kutty (1968a) for estimating the optimum age of exploitation for a given fishing intensity can be written as

$$\left(\frac{L_\infty - l_c}{L_\infty - l_L}\right)^{Z'} \sum_{n=0}^{d-1} (-1)^n \gamma_{(n)} (M' + n) \frac{\left(1 - \frac{l_c}{L_\infty}\right)^n}{Z' + n} = -F' \sum_{n=0}^{d-1} (-1)^n \gamma_{(n)} \frac{\left(1 - \frac{l_L}{L_\infty}\right)^n}{Z' + n} \quad (4)$$

Equation (4) can be used to obtain directly the optimum size limit ($l_{c \max}$) instead of the age of exploitation when the growth and mortality rates are known or if their ratios are available. The optimum size limit ($l_{c \max}$) for a given F' can also be estimated from the equation obtained by differentiating (3) with respect to l_c and equating to zero. In this case, therefore, the substitution is made prior to differentiation. The resulting equation can be stated as

$$\begin{aligned} - \left(\frac{L_\infty - l_c}{L_\infty - l_L}\right)^{Z'} \sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} \frac{M' + n}{Z' + n} \left(1 - \frac{l_c}{L_\infty}\right)^n \left[1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c}\right)^{Z' + n}\right] \\ = \sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} \left(1 - \frac{l_L}{L_\infty}\right)^n \dots \dots \dots (5) \end{aligned}$$

By the method of successive approximation an estimate of $l_{c \max}$ to the desired accuracy can be obtained from (4) or (5). In eqn. (5), since the factors containing the term l_c are raised by n , Z' or $(Z' + n)$, the change in the value of the left-hand side (LHS) of (5) corresponding to a change in the chosen value of l_c will not be proportional. In Fig. 1 the LHS values are plotted against the values of l_c using the data of the North Sea plaice (Appendix I) which shows that their relation is exponential. Linear interpolation will not be efficient, particularly when the difference between the two chosen values of l_c is large. But from such a plot two close values of l_c within the range of which the $l_{c \max}$ lies can be read, and by successive linear interpolation between these values, $l_{c \max}$ can be calculated fairly accurately.

For the North Sea plaice $l_{c \max}$ for $F = 0.73$, as seen from Fig. 1, lies between 45 and 46 cm and two successive linear interpolations between these two values gave an estimate of 45.29 cm. This is fairly close to the actual value as the length corresponding to the optimum age of exploitation (Krishnan Kutty 1968a), for $F = 0.73$ was found to be 45.27 cm (Appendix I). The $l_{c \max}$ is now substituted in (3) to obtain an estimate of the maximum yield ($Y_{W \max F}$) for any given F' .

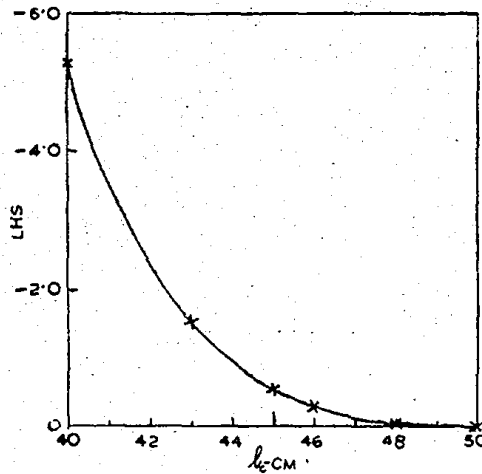


FIG. 1. Relation between the values of the left-hand side (LHS) of eqn. (5) and different values of l_c for North Sea plaice. The value of the right-hand side of the equation for equating with LHS to find $l_{c \max}$ is -0.46984 .

Newton's method of approximate solution of equations (Smail 1953) can be used to reduce the number of successive interpolations required for obtaining an accurate estimate of $l_{c \max}$. For using this method two values of l_c within which $l_{c \max}$ lies are determined from the eqns. (4) or (5) by substituting trial values for l_c . Of these, the one closer to $l_{c \max}$ may be chosen as a first approximate estimate of $l_{c \max}$, say l_{c_1} , and then the values of l_{c_2} , l_{c_3} , etc., are found out repeatedly until the desired level of accuracy is achieved from the relationship

$$l_{c_n} = l_{c_{n-1}} - \frac{f(l_{c_{n-1}})}{f'(l_{c_{n-1}})} \dots \dots \dots (6)$$

where $f(l_{c_{n-1}})$ and $f'(l_{c_{n-1}})$ are the values of the LHS of the eqns. (4) or (5) on equating to zero and the corresponding derivative obtained by substituting $l_{c_{n-1}}$ for l_c . The derivative of (4) can be written as

$$f'(l_c) = \left(\frac{L_\infty - l_c}{L_\infty - l_L} \right)^{Z'} \left[- \frac{M'}{L_\infty - l_c} + \frac{Z'}{L_\infty} \sum_{n=1}^{d-1} (-1)^{n+1} \gamma_{(n)} \frac{M'+n}{Z'+n} \left(1 - \frac{l_c}{L_\infty} \right)^{n-1} + \frac{1}{L_\infty} \sum_{n=1}^{d-1} n \left\{ (-1)^{n+1} \gamma_{(n)} \frac{M'+n}{Z'+n} \left(1 - \frac{l_c}{L_\infty} \right)^{n-1} \right\} \right] \dots \dots \dots (7)$$

and that of eqn. (5) is

$$\begin{aligned}
 f'(l_c) = & -\frac{M'}{L_\infty - l_c} + \left(\frac{L_\infty - l_c}{L_\infty - l_L}\right)^{Z'} \left[-\frac{M'}{L_\infty - l_c} \left\{ 1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c}\right)^{Z'} \right\} \right. \\
 & + \sum_{n=1}^{d-1} (-1)^n \gamma_{(n)} \frac{M' + n}{Z' + n} \left(1 - \frac{l_c}{L_\infty}\right)^{n-1} \left\{ \left(1 - \frac{l_c}{L_\infty}\right) \left(-\frac{Z' + n}{L_\infty - l_c}\right) \left(\frac{L_\infty - l_L}{L_\infty - l_c}\right)^{Z' + n} \right. \\
 & \left. \left. + \left(1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c}\right)^{Z' + n}\right) \left(\left(1 - \frac{l_c}{L_\infty}\right) \left(-\frac{Z'}{L_\infty - l_c}\right) - \frac{n}{L_\infty} \right) \right\} \right]. \quad \dots \quad (8)
 \end{aligned}$$

But from eqns. (7) and (8) it can be seen that Newton's method of solving (4) for $l_{c \max}$ is less tedious than solving (5) and does not involve any additional labour than that required for the linear interpolation. If the difference between the two chosen values of l_c is small, one or two approximations will be adequate enough for obtaining an accurate estimate of the optimum size. Newton's method may similarly be preferred over linear interpolation for finding the optimum age of exploitation ($t_{p \max}$) from the equation described by Krishnan Kutty (1968a) and the required derivative for using the equation analogous to (6) is

$$f'(t_p) = \sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} (M + nk) e^{-t_p(Z + nK) + nKt_0 + Z'l} \quad \dots \quad (9)$$

where t_p = the age of first full exploitation and t_h = the age at which the fish disappears from the fishery.

When the length-weight exponent deviates from being three, the above methods of estimating the optimum size limit for a particular F' becomes slightly tedious. Since the estimation of yield (Y_w) is now to be made from the eqn. (3), reading the modal size from a yield-mesh curve as suggested by Beverton (1954) is also not easy and the optimum size read from this curve will only be a close approximation. However, computational labour required for drawing the yield curve can be reduced by dividing the post-exploitable phase into sufficiently small time intervals (Δt) and summing up the yield during each time period as discussed by Beverton so that

$$Y_w \simeq \sum Y_{N_{\Delta t}} \bar{W}_{\Delta t} \quad \dots \quad (10)$$

where $Y_{N_{\Delta t}}$ = the yield in number during the period between t_n and t_{n-1} years of age, and $\bar{W}_{\Delta t}$ = the average weight of the individual fish during the same time interval which can be obtained by taking the arithmetic mean or preferably the exponential average of the initial and final weights attained during the period. The equation described by Beverton and Holt (1957) for $Y_{N_{\Delta t}}$ is

$$Y_{N_{\Delta t}} = R e^{-M(t_p - t_p)} \cdot e^{-Z(t_{n-1} - t_p)} \left[\frac{F}{Z} \left\{ 1 - e^{-Z(t_n - t_{n-1})} \right\} \right] \quad \dots \quad (11)$$

where t_p is the age of recruitment. Equation (11) using Holt's substitution becomes

$$Y_{N_{\Delta t}} = R \left(\frac{L_{\infty} - l_r}{L_{\infty} - l_c} \right)^{-M'} \left(\frac{L_{\infty} - l_c}{L_{\infty} - l_{t_{n-1}}} \right)^{-Z'} \left[\frac{F'}{Z'} \left\{ 1 - \left(\frac{L_{\infty} - l_{t_{n-1}}}{L_{\infty} - l_{t_n}} \right)^{-Z'} \right\} \right] \dots \quad (12)$$

where $l_{t_{n-1}}$ and l_{t_n} denote the size of the fish of age t_{n-1} and t_n years respectively. The above equation enables the calculation of $Y_{N_{\Delta t}}$ in terms of the size of the fish instead of its age. Hence, the total yield in weight (Y_w) can easily be obtained from eqn. (10) using only the ratios of mortality to growth rates.

The methods of Ricker (1945) and Allen (1953, 1954), after appropriate modifications, can also similarly be used for obtaining close approximations to the optimum size limit when ageing is difficult, provided that the average growth of the individuals conforms to the von Bertalanffy pattern. Ricker's original method is to read the optimum size corresponding to the mode in a yield-mesh curve, assuming exponential growth and mortality. Since the growth in length over the fishable life span as a whole is seldom exponential, Ricker divides the exploitable phase into a number of smaller units thus restricting the use of the exponential growth function only to short time intervals. Ricker's *weight change factor* for any period can be written as

$$e^{(G_{\Delta t} - M - F)(t_n - t_{n-1})} = \left(\frac{L_{\infty} - l_{t_{n-1}}}{L_{\infty} - l_{t_n}} \right)^{G'_{\Delta t} - M' - F'} \dots \dots \quad (13)$$

where $G_{\Delta t}$ like M and F is an instantaneous rate on a yearly basis. The ratio, $G'_{\Delta t}$ or $G'_{\frac{\Delta t}{K}}$, is obtained from

$$G'_{\Delta t} \log \left(\frac{L_{\infty} - l_{t_{n-1}}}{L_{\infty} - l_{t_n}} \right) = \log \left(\frac{W_{t_n}}{W_{t_{n-1}}} \right) \dots \dots \dots \quad (14)$$

where $W_{t_{n-1}}$ and W_{t_n} are the weights of the fish at ages t_{n-1} and t_n years respectively. The *weight change factor* can thus be obtained for estimating the biomass at the end of each time interval without any knowledge of the latter's duration. Since only F' is known Ricker's yield equation will now give

$\left(\frac{Y_w}{K} \right)$ instead of Y_w . But as $\left(\frac{Y_w}{K} \right)$ is proportional to Y_w , the size limit corresponding to $\left(\frac{Y_w}{K} \right)_{\max}$ will be optimum. The corresponding maximum yield may be obtained by determining the growth constant K , which requires a knowledge of the duration of at least one time interval. Since, $G'_{\Delta t}$ is already evaluated and

$$G_{\Delta t} = \frac{\ln \left(\frac{W_{t_n}}{W_{t_{n-1}}} \right)}{(t_n - t_{n-1}) \text{ years}} \dots \dots \dots \quad (15)$$

a reliable estimate of K is possible by taking the mean of a number of estimations based on the available data. The quantity $\left(\frac{Y_w}{K}\right)$ can also be obtained rather easily when the L/Wt exponent is not three, by using the method of approximate integration suggested by Krishnan Kutty (1968b).

Allen's method (1953, 1954) is to find the optimum weight of the fish using the relation that the weight of the fish at the optimum size (W_{max}) equals the product of the fraction, p of the fish reaching this size that are ultimately caught and the mean weight of the individual fish in the catch (\bar{W}_y). Thus assuming natural and fishing mortality rates to be constant

$$W_{max} = p \bar{W}_y \quad \dots \quad (16)$$

where $p = \frac{F'}{Z}$. If the existing mesh size does not correspond to the optimum size limit, then W_{max} is to be obtained by successive approximation, i.e., with each value of the size limit chosen, \bar{W}_y has to be estimated separately until W_{max} equals $p \bar{W}_y$. The mean weight in the catch (\bar{W}_y) may be estimated in different ways. The method described by Beverton and Holt (1957) becomes elaborate when the growth is not isometric, but it may easily be obtained by using eqns. (10) and (12) since the mean weight of the individual fish in the catch is the total yield in weight divided by the total yield in number. Allen and Forrester (1966) have used an empirically determined \bar{W}_y based on catch samples for estimating the optimum size limit but the latter will now be subjected to errors arising from sampling variations and fluctuations in abundance.

POTENTIAL YIELD AND THE CORRESPONDING SIZE LIMIT

Potential yield can be realized by catching all the fish just when the brood attains its greatest biomass (Ricker 1945; Allen 1954; Beverton and Holt 1957; Holt 1958). Krishnan Kutty and Qasim (1968) have pointed out that the equation for estimating the biomass (P_{W_t}) at time, t , in the absence of fishing becomes

$$P_{W_t} = W_{\infty} R e^{-M(t-t_p)} [1 - e^{-K(t-t_0)}]^{\gamma} \quad \dots \quad (17)$$

and the optimum age of exploitation (t_y) when the size of the brood is greatest can be obtained from the relationship

$$e^{K(t-t_0)} = \frac{\gamma K + M}{M} \quad \dots \quad (18)$$

Removing the element of time from these equations by means of Holt's substitutions, the equation for estimating the biomass ($P_{W_{l_0}}$) at size l_0 for all values of the L/Wt exponent can be written as

$$P W_{l_0} = R W_{\infty} \left(\frac{l_0}{L_{\infty}}\right)^{\gamma} \left(\frac{L_{\infty} - l_0}{L_{\infty} - l_{\gamma}}\right)^{M'} \quad \dots \quad (19)$$

and the optimum size limit (l_{cy}) corresponding to t_y is obtained from

$$l_{cy} = L_{\infty} \left(1 - \frac{M'}{\gamma + M'} \right) \dots \dots \dots (20)$$

The equation for P_{Wt_c} can also be derived from (3) by putting $F' = \infty$ so that

$$P_{Wt_c} = W_{\infty} R \left(1 - \frac{l_r}{L_{\infty}} \right)^{-M'} \sum_{n=0}^{d-1} (-1)^n \gamma_{(n)} \left(1 - \frac{l_c}{L_{\infty}} \right)^{M'+n} \dots \dots (21)$$

By differentiating (21) with respect to l_c and equating to zero, an estimate of l_{cy} can be obtained. Thus we get the relationship

$$\sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} (M'+n) \left(1 - \frac{l_c}{L_{\infty}} \right)^n = 0 \dots \dots \dots (22)$$

from which l_{cy} is calculated. Substituting l_{cy} in (21), an estimate of the greatest biomass which the brood can attain may be arrived at. This is also equal to the potential yield (Y) since all fish of this size have to be captured to obtain this yield.

If the exponent, which describes the L/Wt relation, is not an integer, the estimates of Y and l_{cy} from eqns. (21) and (22) will only be close approximations and hence (19) and (20) are preferred over eqns. (21) and (22). The solution of l_{cy} from (22) is by successive approximation as described earlier for $l_{c \max}$. The derivative of (22) for applying Newton's method is

$$f'(x) = \sum_{n=1}^{d-1} (-1)^n \gamma_{(n)} \frac{n(M'+n)}{L_{\infty}} x^{n-1} \dots \dots \dots (23)$$

where $x = \left(1 - \frac{l_c}{L_{\infty}} \right)$. Once the value of x to the desired level of accuracy is obtained, l_{cy} can easily be found. If γ is a positive integer, an exact solution of (22) for l_{cy} is possible and this can be made much simpler by substituting x for $\left(1 - \frac{l_c}{L_{\infty}} \right)$ and factorizing (22). It has been found that $(x-1)$ is a factor when $\gamma = 2$, but occurs repeatedly $(\gamma-1)$ times when γ is 3 or a higher integer. Since $(x-1)$ is a factor, one value of l_c , which will satisfy the eqn. (22), is zero. Since the main interest is to find the l_c when the biomass is greatest, it becomes necessary to find the other possible values of x . Thus, factorizing (22), we get the relationship

$$(M'+\gamma)x - M' = 0 \dots \dots \dots (24)$$

for all integer values of γ except that the terms $(M'+\gamma)x$ and M' in (24) alternate their signs if γ is an even number. Solution of (24) is direct and does not require any interpolation.

Appendix I gives the values of the potential yield and the corresponding l_{c_y} for the North Sea plaice obtained from the eqns. (21) and (24) respectively along with one of the estimates based on the methods given by Krishnan Kutty and Qasim (1968). It can be seen that both the methods give almost identical results.

MAXIMUM YIELD WHEN THE MESH SIZE CANNOT BE REGULATED

The methods discussed above are applicable to the fishery where the selectivity of the gear can be controlled. If, for any reason, the mesh size cannot be regulated the maximum yield can be obtained only by adjusting F' (Gulland—private communication), although, according to the principles of *eumetric fishing* (Beverton and Holt 1956b, 1957), this yield can be obtained at a lower fishing intensity if it is possible to adjust the mesh. Hence, regulatory measures based on the eumetric fishing curve permit maximum utilization of the fishing effort. Nevertheless, the estimation of the maximum yield and the corresponding fishing intensity for a fixed mesh size may at times be useful in setting a practical limit on the fishing effort. The F' maximizing the yield at a fixed mesh size is estimated by any of the methods of successive approximation suggested earlier using the relationship derived from (3),

$$\left[\ln \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right) \right] \left[\sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} \left(1 - \frac{l_c}{L_\infty} \right)^n \left(\frac{F'}{Z'+n} \right) \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right)^{Z'+n} \right] + \sum_{n=0}^{d-1} (-1)^n \gamma_{(n)} \left(1 - \frac{l_c}{L_\infty} \right)^n \left(\frac{M'+n}{(Z'+n)^2} \right) \left\{ 1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right)^{Z'+n} \right\} = 0. \quad (25)$$

The above equation can be used to find the optimum F' or F'_{\max} when the recruits are either fully vulnerable to the gear ($l_r = l_c$) or exploited only after they grow to a larger size ($l_r < l_c$). It should be mentioned, however, that since the regulation of F' involves changes in fishing effort an accurate estimate of F'_{\max} which can be obtained from the above method is more desirable than that read from the yield-intensity curve. Hence, eqn. (25) may be solved by using Newton's method for which the required derivative is

$$f'(F') = \left[\ln \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right) \right]^2 \sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} \left(1 - \frac{l_c}{L_\infty} \right)^n \left(\frac{F'}{Z'+n} \right) \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right)^{Z'+n} + 2 \left[\ln \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right) \right] \sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} \left(1 - \frac{l_c}{L_\infty} \right)^n \left(\frac{M'+n}{(Z'+n)^2} \right) \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right)^{Z'+n} + \sum_{n=0}^{d-1} (-1)^{n+1} \gamma_{(n)} \left\{ 1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c} \right)^{Z'+n} \right\} \left(1 - \frac{l_c}{L_\infty} \right)^n \frac{2(M'+n)}{(Z'+n)^3}. \quad (26)$$

To obtain the maximum yield ($Y_{W \max} l_c$) the estimated F'_{\max} is substituted in eqns. (3) or (28) depending on whether l_c is greater than or equal to l_r .

Once the F'_{\max} is calculated, the corresponding fishing intensity (\bar{f}_{\max}) should also be known for regulating a fishery. This is possible by estimating k from the relationship

$$\bar{f} = kF' \dots \dots \dots (27)$$

using known values of F' and the corresponding fishing intensity (\bar{f}). If there are two or more independent estimates of F' , a better estimate of k is possible by fitting (27) to the data.

If the recruits are exploited as soon as they enter the fishing ground, the eqn. (1) for yield becomes (Gulland—private communication)

$$Y_W = F'W_{\infty}R \sum_{n=0}^3 \frac{\Omega_n}{Z'+n} \left(1 - \frac{l_c}{L_{\infty}}\right)^n \left[1 - \left(\frac{L_{\infty}-l_L}{L_{\infty}-l_c}\right)^{Z'+n}\right] \dots (28)$$

By changing the summation terms to $\sum_{n=0}^{d-1}$ and the Ω_n term to $(-1)^n \gamma_{(n)}$ as is

done in the eqn. (3), (28) also can be adjusted for all values of the L/Wt exponent. If the fishery is dependent on the recruits alone, as for instance, when the older age groups are scarce in the fishery due to the peculiar distribution and behaviour pattern of the population, the maximum yield under steady state conditions is obtained only by catching all the recruits. This yield ($Y_{W \max_R}$) is estimated from the equation

$$Y_{W \max_R} = W_{\infty}R \sum_{n=0}^{d-1} (-1)^n \gamma_{(n)} \left(1 - \frac{l_r}{L_{\infty}}\right)^n \dots (29)$$

which also gives the biomass of the recruits. A better estimate of $Y_{W \max_R}$, when growth is not isometric, can be obtained by putting $l_c = l_r$ in eqn. (19) so that

$$Y_{W \max_R} = RW_{\infty} \left(\frac{l_r}{L_{\infty}}\right)^{\gamma} \dots (30)$$

Similarly, if the fishery depends only on a population of a particular size, l_c which is greater than l_r , then the maximum yield is obtained from (19) or (21).

Since the eqn. (25) is derived from Holt's version of the Beverton-Holt model it can be applied equally well to cases where the individual estimates of the growth and mortality rates are available. However, the fishing mortality (F'_{\max}) needed to produce the maximum yield for a fixed mesh size can also be estimated from the relation

$$\sum_{n=0}^{d-1} (-1)^n \gamma_{(n)} e^{-nk(t_p' - t_0)} \left[\frac{\lambda F'}{Z+nk} e^{-(Z+nk)\lambda} + \frac{M+nk}{(Z+nk)^2} (1 - e^{-(Z+nk)\lambda}) \right] = 0 \dots (31)$$

where $\lambda = (t_\lambda - t_p)$ years. Equation (31) is derived from the original Beverton-Holt model.

DISCUSSION

The methods discussed above are developed under the assumption that the population is in a steady state having constant growth, mortality and recruitment. Hence these methods are useful for the regulation of such exploited fish populations with constant parameters and a stable recruitment or when the fluctuations in the population biomass are purely random. However, Beverton and Holt (1956b) have indicated that the stock density is relatively stable over a wide range of fishing intensity and hence over this range the density dependant effect on the population is at a minimum. It may therefore be possible to apply regulatory measures based on the simple model to many fish populations. If the density dependant effects are significant then these should also be considered for adopting the necessary management policies. Beverton and Holt (1957), Ricker (1958) and Larkin and Ricker (1964) have discussed the effects of random variation on the population and their results indicate that the best long-term average yield can be obtained from deterministic models even when the population fluctuates randomly.

When the population is in a steady state, but with age-specific natural mortality, the exact methods based on the simple Beverton-Holt model discussed above cannot be used for estimating the optimum conditions of exploitation. This is because the original Beverton-Holt yield equation is a continuous time model with constant parameters.

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APPENDIX I

Comparison of the optimum size limit and the maximum yield for North Sea plaice. The values in parentheses refer to the lengths calculated from the corresponding optimum ages of exploitation taken from the sources cited. The data (Beverton 1954) are:

$M = 0.1$, $t_p = 3.72$ years, $t_1 = 15$ years, $t_0 = -0.815$ years, $K = 0.095$, $W_\infty = 2867$ g, $L_\infty = 69$ cm, $\gamma = 3$, $l_r = 24.15228$ cm and $l_L = 53.64129$ cm.

Source	Present paper	Krishnan Kutty 1968a	Krishnan Kutty and Qasim 1968
		$F = 0.73$	
$l_{0 \max}$	45.2883 cm	(45.2726 cm)	
$Y_{W \max F'}$	414.3389 g	414.42 g	
l_{cy}	51.0779 cm		(51.0346 cm)
Y	442.8597 g		442.84 g