

# New Ideas on Fish Population Dynamics

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The Beverton-Holt and Schaefer models represent two main approaches in studying the dynamics of an exploited fish population. Although both the models were developed in relation to temperate populations there is no reason why they cannot be applied to tropical fish populations for predicting conditions of optimum exploitation. The main problem is not their applicability but the difficulties of obtaining adequate data. Hence two important problems of studying tropical fish populations are, firstly, as to how to make even approximate estimations of the main population parameters so that these equations can be fitted and, secondly, how to modify these equations so that they can be applied even with limited data. Some aspects of these two problems are discussed in the paper.

## Mathematical Models and Fish Population Studies

Mathematical models used to study fish population dynamics in relation to optimum exploitation can be grouped into empirical, deductive and analytical models. Of these the deductive model and the analytical model are the most important and they are best represented by the models developed by Graham (1935) and others and later by Schaefer (1954, 1957) and that developed by Beverton and Holt (1957). The Beverton-Holt model is best applied when recruitment is fairly independent of the stock size and the growth and natural mortality

are more or less constant. But there are many populations where the assumption of steady state conditions does not hold good. Often there is a density dependent stock-recruitment relationship so that recruitment is maximum at some intermediate stock size. In such cases Schaefer's deductive model may be more appropriate to predict the optimum level of exploitation. From biological information and catch-statistics it may be possible to decide which model is more appropriate to a particular population.

Before we consider at some length what new developments can be attempted with these two models it may be worthwhile to mention one fundamental difference between the two models in relation to the concept of optimum fishing and their bearing on our understanding of overfishing. According to the Beverton-Holt theory of exploitation, under steady state conditions there can seldom be overfishing in the strict sense of the term. With increased fishing pressure the exploitable stock gets depleted but total catch increases continuously provided the mesh size is also regulated—even if such increase is negligible at high fishing pressure. Biological overfishing is said to exist only when the total catch decreases with steady or increasing fishing effort. There may be other effects of fishing on the stock such as increased growth rate, decreased mean size of the

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fish caught, decreased catch-per-unit-effort ( $C/U/E$ ), etc. But they cannot be regarded as indicative of overfishing. According to the model developed by Graham, Schaefer and others the population is said to be overfished if the fishing effort exceeds the limit that gives the maximum sustained yield. The idea of overfishing is accepted by many fishery biologists and hence they often argue that the absence of biological overfishing as per the theory of steady state conditions of Beverton and Holt is unrealistic. Similarly the main criticism of Schaefer's model is that this model ignores the age composition of the population and hence it assumes that the population responds to the effect of fishing immediately. This means that the effect of mesh size on the population cannot be studied by this model and, therefore, Schaefer's yield parabola can at best be compared only to one of the yield-intensity curves\* of Beverton and Holt. Both these criticisms are valid but they are also made partly out of contest—because these models cannot be applied blindly to any fish population. It can be applied only if the assumptions inherent in the model are reasonably satisfied by the population. Thus, if there is a fish population that satisfies the Beverton-Holt theory of steady state conditions then the conclusions based on their model will also be valid. Similarly, if fish population growth follows a sigmoid curve with maximum growth at some

intermediate stock size then Schaefer's model should be applicable to this population. This means that our concept of overfishing is more applicable to certain populations than to others. In general, where it is applicable, Schaefer's model may give a truer representation of the population and where the overfishing concept is less applicable, the Beverton-Holt model may represent the population more realistically.

One word in praise of the Beverton-Holt model should also be mentioned here, *i. e.* being an analytical model it is more rigorous and gives much more information regarding the effect of fishing on the stock size, catch-per-unit-effort, etc. than Schaefer's model. Hence even when the two models are applied to the appropriate populations the conclusions drawn from the Beverton-Holt model may be more precise than those obtained from Schaefer's model.

#### **Applying Models to Tropical Fish Populations**

These two models are developed in relation to temperate populations. But there is no reason why they cannot be applied to tropical fish populations. The problem is not their applicability but the difficulties of obtaining adequate data. In the tropics we are not able to estimate the population parameters mainly because of the difficulties to determine the age composition of the

\* In the Beverton-Holt yield equation one can keep the mesh-size constant and study the effect of various fishing pressure on the yield or keep the fishing pressure constant and study the effect of different mesh sizes on the yield—with the result that both yield-intensity and yield-mesh curves can be drawn to find at what mesh size or fishing intensity the yield is maximum. In Schaefer's model such studies are not possible since only one yield curve can be drawn.

population. Therefore, two main problems of studying tropical fish populations are how to make even approximate estimations of the main population parameters so that these equations can be fitted and secondly, how to modify these equations so that they can be applied even with limited data. This problem has received only scanty attention from scientists so far. Holt (1962) who first considered this problem wrote the original Beverton-Holt equation in a form that does not require separate estimations of growth and mortality. He also discussed some indirect methods of evaluating the population parameters when age reading is difficult. One method he has suggested is the possibility of determining these parameters from comparative population studies. Beverton and Holt (1959) and Holt (1959, 1962) have shown that different types of comparative population studies are possible and that there is often a relationship in closely related species between maximum age and asymptotic length ( $L_{\infty}$ ), between natural mortality and  $K$  or the rate of attaining the asymptotic length, between  $K$  and the ratio  $l_m/L_{\infty}$  where  $l_m$  is the size at first maturity and between  $K$  and  $L_{\infty}$ . If a relationship can be obtained for closely related species for which sufficient data is available then these regressions can be used to obtain a rough estimate of the population parameters. Unfortunately not much information can be obtained at present from comparative population studies because of the inadequacies of the data. Besides, these growth constants estimated for short lived small tropical fishes may not be very reliable (P. 124).

### **Some Suggestions for Studying Tropical Fish Population Dynamics**

The important suggestions made by Holt are mainly with respect to the application of their model to fish populations. As already stated some populations may have to be examined by the Beverton-Holt approach while Schaefer's model may be more suitable to other populations. Therefore, the applicability of both the models to fish populations when age reading is not possible deserves examination in addition to developing new methods. Some simple ideas regarding the application of population models when data is limited are suggested below.

### **Studies with Analytical Models**

*Approximate Estimations of Growth and Mortality.* Sometimes the age could be determined approximately but the data may be insufficient to fit a von Bertalanffy growth equation either because the life span is too short or because the length-at-age-data may not be available for sufficient number of time intervals. This makes it difficult to apply the Beverton-Holt yield equation. When age determination is difficult we have to rely more on the size frequency distribution for estimating the growth and mortality rates. Even when the different modes are indistinct due to considerable overlap between adjacent age groups, it may still be possible at times to dissect the frequency distribution by the probability paper method. The accumulated biological information regarding the species might be of some help in dissec-

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ting the indistinct length frequency distribution. Once the modal groups are determined normal curves can be drawn to represent the different age groups in the population by statistical methods. After roughly delimiting the age groups in this manner age composition in the sample can be determined and this may be used for estimating the mortality rates.

It might also be possible to estimate the mortality rate if accurate estimation of the catch-per-unit-effort is possible. The C/U/E is expected to be highest in the beginning of the fishing season and it will decrease steadily with the advance of the fishing season. Assuming constant mortality rate during the fishing season, the number of fish present after a time will be described by

$$N_t = N_0 e^{-Zt} \quad (1)$$

where  $N_t$  is the number at time  $t$ ,  $N_0$  is the number at the beginning of the fishing season and  $Z$  is the instantaneous total mortality rate. From this relation by putting  $t=1$ ,

$$\ln \left( \frac{N_0}{N_t} \right) = Z \quad (2)$$

Since we can use relative number instead of absolute number,  $N_0$  and  $N_t$  may be replaced by number/unit of effort in the beginning and end of the fishing season. If such estimates of  $Z$  are available for a few years the total mortality can be separated into fishing and natural mortality from the relationship,

$$Z = M + cf \quad (3)$$

Where  $M$  is the natural mortality rate and  $f$  is the fishing intensity. Under favourable circumstances it may even be

possible to separate  $F$  and  $M$  using the data collected within the same fishing season. For instance, if effort varies within the same season, the fishing season may be divided into small periods of constant effort and the average number caught/unit effort is estimated for each time interval. If  $Z$  could be estimated for each time interval the above equation may be fitted to the data or preferably apply the iterative method of Beverton and Holt (1957) and separate  $F$  and  $M$ .

This estimate can be biased if recruitment is continuous, *i. e.*, if there is continuous immigration or if there is constant emigration or both. Nevertheless the method may be useful at least in favourable circumstances. Some correction may be necessary if recruitment is incomplete at lower size groups or if there is mesh selection.

What is new in the above method is that the age composition is ignored since only the total number of fish/unit effort is required. And that is the main advantage of the method also.

*Estimation of Yield.* Once growth and mortality rates can be estimated in this manner yield estimations can be made by methods other than the Beverton-Holt yield equation. For instance the yield can be estimated either by approximate integration or by Ricker's (1945, 1958) yield equation. For estimating the yield by approximate integration (Krishnan Kutty, 1968) an estimate of the rate of change of yield at a number of equal time intervals within the fishable life span are required. The rate of change of yield is

$$\frac{dY_w}{dt} = FN_t W_t$$

where  $F$  is the fishing mortality rate,  $N_t$  is the number at time  $t$  and is easily estimated since the total mortality rate is known,  $W_t$  is the weight at time  $t$  which can also similarly be obtained. For instance if the size at one and two years of age are known an approximate growth curve can be drawn by connecting these two points with the origin so that the size at any desired age can be read from the growth curve. If the possible life span extends beyond two years of age, say, as when the fishery is comprised of three year classes, the approximate size of the three year old fish may be readily obtained by extrapolating the growth curve either by eye or after fitting a suitable equation to the curve upto age two (See Krishnan Kutty, 1973). Once the length at different time intervals is obtained in this manner, the length-weight relation may be used to obtain the corresponding weight. Sometimes we can also use the assumption that growth in weight during a period of time is exponential and calculate the weight for any intermediate age. I have found that this is a very reasonable assumption and will introduce only negligible error in our calculations.

If an approximate growth curve as the one described above can be drawn it is possible to estimate the yield by the Beverton-Holt model as well. In order to apply this model the growth curve has to be fitted by the von Bertalanffy equation. This can be done by fitting the equation to the size-at-age-data read from the growth curve. It must be mentioned here that in the tropics the growth in the first year is very rapid so that a good portion of the growth is

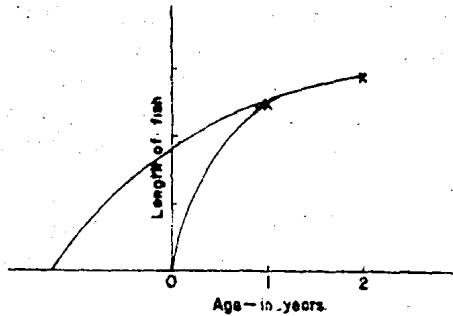


Fig. 1. Approximate growth curve obtained by connecting the origin to the known two points and the probable growth curve by fitting a Von Bertalanffy equation to the points read from the known part of the curve.

covered in the first year and we may have growth data only over a small section of the flat part of the growth curve. If the lengths at different ages within this section of the curve were estimated and a Bertalanffy curve fitted very often we will get a growth curve with low  $K$  and height  $t_0$ —very different from the actual values (Fig. 1). If the exploited size range of the population lies beyond this known, but narrow section of the growth curve it is better to use the growth parameters obtained by fitting the Bertalanffy growth equation to the growth-at-age-data read from the curve connecting the origin and the known two points. The error by doing this will be much less than by using the other growth curve represented by low  $K$  and height  $t_0$  and may even be negligible. In the absence of better information we are fully justified in using an approximate growth curve as the one obtained by connecting the origin provided we have at least two known points. In fact, Holt (1962) has pointed out that predictions of changes in yield due to changes in fishing intensity or mesh selection do not depend critically

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on the accuracy with which the growth function fits the data. If the size-at-age-data are read from the curve at equal time intervals then the Bertalanffy curve can be fitted in the usual manner, otherwise the improved method suggested by Allen (1966) may have to be applied.

Sometimes it may be possible to trace a particular mode in the size distribution for a few months. If we have such data accumulated over a period of time it can also be used to fit the von Bertalanffy curve in the usual way (Banerji—unpublished report on oil sardine). Here also, as stated earlier, if we are dealing only with the flat part of the growth curve,  $K$  may be under-estimated. Besides, the time interval is quite small here (one month) and in such cases it may be better to use the relation

$$\frac{dl}{dt} = K(L_{\infty} - l) \quad (5)$$

by approximating  $dl/dt$  to  $\Delta l/\Delta t$ .  $\Delta l/\Delta t$  is the growth in length/month. This method is developed by Diaz (1963). A somewhat similar method is also developed by Gulland and Holt (1959).

*Allen's Method of Estimating the Optimum Size Limit.* If we have no estimate of the growth data but a reasonably accurate values of fishing and natural mortality rates are available then Allen's (1953, 1954) simple method of determining the optimum size limit for obtaining the maximum yield can be used. Allen has pointed out that when the size limit is correctly set

$$W_c = E\bar{W} \quad (6)$$

where  $W_c$  = weight of the typical fish at the limiting size,  $\bar{W}$  = mean weight of fish caught and  $E = F/Z$  or proportion of fish reaching the size  $W_c$  which are

ultimately caught. This method can be readily applied if size composition data for a number of years and average estimates of total and fishing mortality rates are available (See Allen and Forrester, 1966). This approximation is subject to errors if the existing limit is not optimal. But Allen (1954) has described methods of overcoming these errors within reasonable limits.

This method is equivalent to reading the mode from Beverton-Holt's yield-mesh curve for a particular value of  $F$ . It is, however, worth examining whether or not this method can be extended to study optimum size limit for any fishing level provided we have an estimate of  $M$ . In this case we may not be dealing with the actual size distribution but a theoretical distribution calculated from a knowledge of the age at recruitment and the total mortality rate. But some knowledge of the growth rate is needed for constructing a theoretical size distribution. If an approximate growth curve can be drawn like the one discussed in the previous section then it must be possible to extend this method to study the optimum size limit for any fishing level.

#### **Possible Changes in the Deductive Model**

Let us now examine Schaefer's model and see whether any modification is possible here. The basic assumption underlying the theory of optimum exploitation of Schaefer and others is that the population growth follows a symmetrical sigmoid curve. Hence, when the population is small the actual increase is also small. The increase is maximum at an intermediate level of population abundance and this increase one can afford

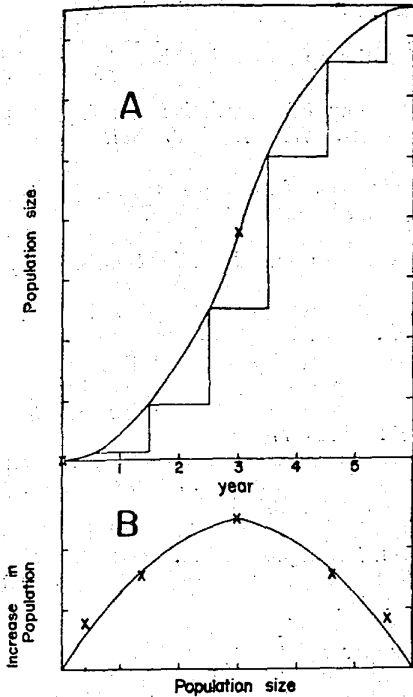


Fig. 2. A: Hypothetical growth curve of a population showing the increase at different population sizes.  
 B: The increase in population plotted against the mean population size.  
 (Adapted from Graham, 1939).

to catch every year (Fig. 2). This is called the maximum equilibrium catch. Hence by maintaining the population at this level the maximum sustained yield is obtained. If this increase in the population is plotted against the corresponding levels of population abundance or fishing intensity it will follow a symmetrical parabola (Fig. 2). Therefore what Schaefer does is first to estimate this increase in the population, also called the equilibrium yield, at different fishing levels using the catch-effort data and fit a parabola to this data. Schaefer's method of estimating the

maximum sustained yield is a significant improvement over the methods of fitting the same model suggested by Graham and others. By developing a method of estimating the equilibrium yield at different population densities he has made the fitting of this curve much simpler. However, plotting the equilibrium yield against the population biomass in the exploited phase may introduce errors in the estimate of the maximum yield especially if the species is not short lived.

This method requires an estimate of the catchability or the proportion of the population caught by one unit of effort. Population is also assumed to follow a symmetrical sigmoid curve. Ricker (1958) has pointed out that due to time lag and other factors population does not respond immediately to the effect of fishing and hence the sigmoid curve is often asymmetrical. Recently, Pella and Tomlinson (1969) have described a complicated procedure of fitting the right kind of parabolic curve to the data but this method can be used only if a computer is available.

As per this model the equilibrium yield/unit effort is linearly related to fishing intensity whereas according to Beverton and Holt the curve declines exponentially. This is due to the fundamental difference in the assumptions involved in the two models. A critical study of these models might help in developing better methods of estimating maximum yield.

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