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# SOME NOTES ON THE BASIC ELEMENTS <br> OF DYNAMIC POOL MODELS USED TO ASSESS <br> THE IMPACT OF FISHING ON YIELD 

by

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Some Notes on the Basic Elements of Dynamic Pool Models Used to Assess the Impact of Fishing on Yield<br>by Frederick W. Bell, Director Economic Research Laboratory National Marine Fisheries Service

There have been a number of models suggested to assess the impact of fishing on yield. We shall restrict our analysis to the dynamic pool variety, since the Schaefer model has been discussed elsewhere and is probably better understood by the layman. In outlining the dynamic pool model, we have used four references: M. B. Schaefer, "Methods of Estimating Effects of Fishing on Fish Populations," Transactions of the American Fisheries Society, Vol. 97, No: 3; J. A. Gulland, Manual of Methods for Fish Stock Assessment, Part 1, Fish Population Analysis, F.A.O. Fish Technical Paper No. 40; W. E. Schaaf and G. R. Huntsman, "Population Dynamics of the Atlantic Menhaden: An Analysis of the Purse Seine Fishery, 1955-1969," unpublished manuscript;
${ }^{1}$ See M. B. Schaefer, "Some Aspects of the Dynamics of Population Important to the Management of Commercial Marine Fisheries," InterAmerican Tropical Tuna Commission, Bulletin, I(2):27-56. For another exposition of the Schaefer mode1, see F. W. Bell, E. W. Carlson, and F. V. Waugh, "Production from the Sea," NMFS Conference on Fisheries Management, NMFS Special Scientific Report (forthcoming).

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and D. H. Cushing, Fisheries Biology: 'A Study in Population Dynamics, Madison, Wisc.: The University of Wisconsin Press, 1968. Before we completely formulate the dynamic pool model, let us define some important terms (or parameters) and deal briefly with their estimation.

### 1.0 Mortalities

### 1.1 General Theory

When studying mortality as applied to a fish population, it is convenient to talk in terms of instantaneous rates or the rate at which the numbers ( $N$ ) in the population are decreasing, or

$$
\begin{equation*}
\frac{\mathrm{dN}}{\mathrm{dt}}=-\mathrm{ZN} \tag{1}
\end{equation*}
$$

where $Z=$ instantaneous total mortality coefficient
From any given level of population size ( $N_{0}$ ) (i.e., numbers), the number alive at any given time is the following:

$$
\begin{equation*}
N_{t}=N_{0} e^{-Z t} \tag{2}
\end{equation*}
$$

It is, of course, paramount that we distinguish between natural (M) and fishing (F) (man-made) mortality, or

$$
\begin{equation*}
\frac{d N}{d t}=-M N \tag{3}
\end{equation*}
$$

and

$$
\begin{equation*}
\frac{d N}{d t}=-F N \tag{3'}
\end{equation*}
$$

where $M=$ natural mortality coefficient (instantaneous)
$F=$ fishing mortality coefficient (instantaneous)
In the Beverton-Holt model (i.e., dynamic pool) the estimation of these coefficients (see below) are especially critical in computing $\mathrm{F}_{\text {OPT }}$ or the optimum level of fishing mortality (i.e., that F which will maximize yield from the stock). ${ }^{2}$

For very short time intervals, we may merely add the two critical coefficients together to obtain the total mortality coefficient:

$$
\begin{equation*}
F+M=Z \tag{4}
\end{equation*}
$$

In the simplified dynamic pool model, natural mortality is assumed to be a constant (density-independent and the same at all ages).

### 1.2 Estimation

There are a number of methods developed by the biologists to estimate $\underline{Z}, \underline{M}$, and $\underline{F}$ :
(a) Direct Abundance Statistics: Let us say that we know the abundances, say $N_{0}, N_{7}$ of any group of fish at two known times, for them the fraction surviving is $N_{7} / N_{0}=S$; therefore,

[^0]4

$$
\begin{equation*}
e^{-\hat{Z} t}=\hat{S}=N_{1} / N_{0} \tag{5}
\end{equation*}
$$

(b) Indices of Abundance (CPUE): If we assume that catch per unit of effort (CPUE), $n_{0}$ and $n_{1}$, are proportional to $N_{0}$ and $N_{7}$, then

$$
\begin{equation*}
e^{-\hat{Z} t}=\hat{S}=N_{1} / N_{0}=n_{1} / n_{0} \tag{6}
\end{equation*}
$$

(c) Estimation of M: Once $\underline{Z}$ is estimated by either (a), (b), or other techniques (e.g., Direct Census, Swept Area, Marking, Tagging, etc.), $\underline{M}$ may be estimated by the intercept of a least-squares regression of $\underline{Z}$ on effective effort (see Schaaf and Huntsman). ${ }^{3}$


Figure 1. Relation of total mortality to fishing effort
$3^{3}$ For a fuller description of methods used to estimate "Z" see Gulland, op. cit.

In the case above (Figure 1), $M=.30$ since there is no fishing effort at the intercept (i.e., F = 0). For an example, see Figure 2, which was employed by Schaaf and Huntsman to estimate M. Schaaf and Huntsman calculated the age specific total mortality $\left(Z_{i}\right)$ for ages 2, 3, and 4 using technique (b). For each year from 1955 through 1964, these age specific rates were averaged, each $Z_{i}$ being weighted by the inverse of the standard deviation of the $Z_{i}$ 's for all years. This gives the most weight to age specific total mortality rate, which is least affected by fluctuating year class strength.

Once $M$ is obtained, $F$ may be calculated easily by
$\hat{F}=\hat{Z}-\hat{M}$
(d) Estimation of $M$ from $K$ : $K$ is the rate of growth of the species (See 2.0 below). Biologists theorize that a species with a high $K$ is likely to have a high $M$ or

Clupeoids: ${ }^{4} \quad \underline{M}$ is between one and two times $K$;
Gadiformes: ${ }^{5} M$ is generally between two and three times $K$.

### 2.0 Growth

### 2.1 General Theory

There exists a considerable literature on growth equations. However, most models usually start out with the growth equation

[^1]

Figure 2. ITERATED REGRESSION: INTERCEPT IS NATURAL MORTALITY
ascribed to von Bertalanffy. If the length of a fish is plotted against age ( $t$ ), the result is usually a curve of which the shape continuously decreases with increasing age, and which approaches an upper asymptote parallel to the $X$-axis or $L_{\infty}$ (see Figure 3 below).



Curves of weight and age ( $t$ ) also approach an upper asymptote, but usually form an asymmetrical sigmoid, the inflection occurring at a weight of about one third of the asymptotic weight. This is shown in Figure 4.

We can specify that the rate of growth of the fish is linearly related to length (i.e., derivative of Figure 3).

$$
\begin{equation*}
\frac{d 1}{d t}=K\left(L_{\infty}-L_{1}\right) \tag{7}
\end{equation*}
$$

or

$$
\begin{equation*}
\frac{d l}{d t}=K L_{\infty}-L_{1} K \tag{7}
\end{equation*}
$$

$L_{\infty}=$ value where rate of growth is zero
The equation is in the general form of a common straight line ( $y=a x+b$ ) where,

$$
y=\frac{d l}{d t} ; b=K L_{\infty} ; a=-K ; x=L
$$

Equation (7) may be integrated to find the general relationship between 1 and $t$, or

$$
\begin{equation*}
i_{t}=L_{\infty}\left[1-e^{-K\left(t-t_{0}\right)}\right] \tag{8}
\end{equation*}
$$

where $\mathrm{t}_{0}=$ theoretical age where $1=0$
Equation (8) is the Bertalanffy function (i.e., see Figure 3).
The weight of a fish is usually closely proportional to the cube of its length, so that from (8) we can derive

9

$$
\begin{equation*}
W_{t}=W_{\infty}\left[1-e^{-K\left(t-t_{0}\right)}\right]^{3} \tag{9}
\end{equation*}
$$

where $W_{\infty}$ is the asymptotic weight. This is shown in Figure 4. A more general growth equation has been given by Richards ${ }^{6}$ or

$$
\begin{equation*}
w_{t}^{1-m}=w_{\infty}^{1-m}\left[1-a e^{-k t}\right] \tag{10}
\end{equation*}
$$

When $m=2 / 3$, equation (10) becomes the simple Bertalanffy curve (equation 9). When $m=2$, the equation becomes the "time honored" logistic

$$
\begin{equation*}
W_{t}=\frac{W_{\infty}}{1+b e^{-k t}} \tag{11}
\end{equation*}
$$

Hence, the difference between the logistic and the Bertalanffy growth function is the parametric value of $\underline{m}$. This is an important point to remember since the logistic is an integral part of the Schaefer model, while the Bertalanffy curve is used in most "dynamic pool models." For an exercise in the estimation of "m" the reader should see Tomlinson and Pella. ${ }^{7}$ Finally, in the simplified model, the growth rate is assumed to be density-independent.

[^2]
### 2.2 Estimation and Other Problems

(a) Age Determination Data: In fitting the growth curve, the instantaneous rate of growth will not be known, but only lengths at certain times. If $\mathrm{t}_{\boldsymbol{1}}$ and $\mathrm{t}_{2}$ are close together, a close approximation to the instantaneous rate of growth is given by

$$
\begin{equation*}
\frac{\widehat{d f}}{d t}=\frac{1_{2}-1_{1}}{t_{2}-t_{1}} \tag{12}
\end{equation*}
$$

where $l_{1}$ and $l_{2}$ are lengths at times $t_{1}$ and $t_{2}$. If this growth rate is plotted against mean length $1 / 2\left(11_{1}+1_{2}\right)$, then a plot corresponding to equation (7) is obtained; the intercept on the $X$-axis gives an estimate of $\mathrm{L}_{\infty}$ and the slope, an estimate of -K .

Figure 5 yields all the estimated parameters of (7).


Figure 5
(b) Growth of a Single Fish: The length at the end of each year of life can be obtained from measurement; or, the growth of a single year class can be followed in the same manner.
(c) Length-Weight Conversion: When growth data are given in terms of weight, fitting of growth curves is most easily done by using the cube root of the weight as an index of length, fitting this to the equations of growth in length, and finally cubing to return to weight. For example, Schaaf and Huntsman converted length to weight by empirically determined formula, or

$$
\begin{equation*}
W_{t}=.000006761_{t}^{3.18} \tag{13}
\end{equation*}
$$

for Atlantic menhaden.

### 3.0 Derivation of a Simple Yield Curve

### 3.1 General Theory

Along with the material developed above, we must also define some additional terms,
$N_{t}=$ number of fish alive at age $t$
$R=$ number of recruits to catchable stock (i.e., the number of fish alive at age $\left.t_{r}\right)^{8}$
$R^{\prime}=$ number of fish alive at the age $t_{c}$ (i.e., age of capture by fishermen)
$M=$ natural mortality coefficient (see 1.0 above)
$\mathrm{F}=$ fishing mortality coefficient (see 1.0 above)

8This exception will not consider mesh size as variable, but it should be pointed out that this variable determines age at recruitment. The dynamic pool model is especially useful for introducing mesh size problems. We shall assume it to be held constant.

The time of observation, $t$, must be

$$
\begin{equation*}
t_{r}<t<t_{c} \tag{14}
\end{equation*}
$$

or somewhere between recruitment and age at capture.

$$
\begin{equation*}
N_{t}=\operatorname{Re} e^{-M\left(t-t_{r}\right)} \tag{15}
\end{equation*}
$$

Equation (15) merely states that the number of fish alive at age $t$ is equal to the number of recruits ( $R$ ) multiplied by the instantaneous rate at which fish are dying of natural causes. Notice that equations (15) and (2) are very similar where $R=N_{0}$ and $t-t_{r}$ is necessary so we can specify the time lapsing between recruitment and the observed time period. Now, we are in an excellent position to specify the number of fish that would be alive after recruitment, natural mortality, and up to the point where capture by fishermen takes place:

$$
\begin{equation*}
R^{\prime}=R e^{-M\left(t_{c}-t_{r}\right)} \tag{16}
\end{equation*}
$$

If, of course, both fishing and natural mortality are operating after recruitment, we have

$$
\begin{equation*}
N_{t}=R e^{-M\left(t_{c}-t_{r}\right)-(F+M)\left(t-t_{c}\right)} \tag{17}
\end{equation*}
$$

where $t>t_{c}$
The number of fish actually caught over the specified time interval ( $t, t+d t$ ) will be

$$
\begin{equation*}
\mathrm{C}=\mathrm{FN}_{\mathrm{t}} \mathrm{dt} \tag{18}
\end{equation*}
$$

So that we must, in effect, divide up the time interval between $t_{c}$ (age at first capture) and $t_{L}$ (the maximum age attainable) into short intervals and add the contribution of each.

$$
\begin{equation*}
C=\int_{t_{C}}^{t_{L}} F N_{t} d t \tag{19}
\end{equation*}
$$

or,

$$
\begin{equation*}
C=\int_{t_{C}}^{t_{L}} F R^{-M\left(t_{C}-t_{r}\right)-(F+M)\left(t-t_{C}\right)^{\prime}} d t \tag{20}
\end{equation*}
$$

or,

$$
\begin{equation*}
C=\int_{t_{c}}^{t_{L}} F R^{\prime} e^{(F+M)\left(t-t_{C}\right)^{\prime} d t} \tag{21}
\end{equation*}
$$

The weight caught, $Y$, during the time interval ( $t, t+d t$ ) may be expressed as the following:

$$
\begin{equation*}
d Y_{t}=F N_{t} W_{t} d t \tag{22}
\end{equation*}
$$

where $W_{t}=$ average weight of fish at age $t$
The total weight caught can be obtained by integrating (22):

$$
\begin{equation*}
\gamma_{t}=\int_{t_{c}}^{t_{L}} F N_{t} W_{t} d t \tag{23}
\end{equation*}
$$

Equation (23) expresses the catch (weight) from a single year class living for $\lambda$ years in a fishery. If there are $\lambda$ years in the year class, there are also $\lambda$ age groups in any one year in the fishery.

## 14

This is the case because, in all age groups in one year, the same items are being summed, as in the age group within a single year class. So (23) also expresses annual catches in a steady-state system.

As we discussed above (Section 2.0), the Bertalanffy growth function is the following:

$$
\begin{equation*}
W_{t}=W_{\infty}\left[1-e^{-K\left(t-t_{0}\right)}\right]^{3} \tag{24}
\end{equation*}
$$

If we substitute (24) and (17) into (23) and integrate over a period of time, the total yield function can be easily obtained:

$$
\begin{equation*}
Y=F \cdot e^{-M\left(t_{c}-t_{r}\right)} W_{\infty} \sum_{n=0}^{3} \frac{U_{n} e^{-n K\left(t_{c}-t_{0}\right)}}{F+M+n K} \tag{25}
\end{equation*}
$$

where $U_{0}=1 ; U_{1}=-3 ; U_{2}=3 ; U_{3}=-1$
Equation (25) may be expressed in terms of yield per recruit. Simplifying by using (23), we can express yield per recruit as

$$
\begin{equation*}
\frac{Y_{t}}{R}=\int_{t_{c}}^{t_{L}} \frac{F N_{t}}{R} W_{t} d t \tag{26}
\end{equation*}
$$

This is shown in Figure 6. The reason the dynamic pool model is expressed in terms of catch (yield) per recruit is that it avoids the problem of specifying the relationship between stock and recruitment. In this way, we can separate the relationship between catch and fishing intensity from that between stock and recruitment. According to Cushing, it is wrong for fishermen to exploit stock at a point beyond or to the right of the maximum yield per recruit.


Figure 6. Yield curves for plaice calculated with density-dependent growth; it was assumed that $L_{\infty}$ varied inversely with stock density. If growth is reduced with increased stock, the peak of the curve is reduced, as might be expected. Curve (a) is that with constant parameters; curve (b) is that with density-dependent values of $L_{\infty}$. Adapted from Beverton and Holt, 1957.

### 3.2 Simulation

The dynamic pool model presented above can be used for simulation purposes. Values of the parameters may be changed, and the sensitivity of the model determined. The most useful simulation is in deriving an estimate of the maximum catch per recruit.

### 4.0 The Stock-Recruitment Problem

As Cushing has indicated, the coefficient of variation of recruitment to the East Anglian herring stock is 250 percent, and that for the Arctic cod stock is perhaps from two to four times greater. Therefore, specifying any mathematical or systematic relationship between stock and recruitment may be very difficult, if not impossible. Ricker has formulated the following relationship between stock and recruitment:

$$
\begin{equation*}
\frac{R}{R_{r}}=\frac{P}{P_{r}}\left(P_{r}-P\right) / P_{m} \tag{27}
\end{equation*}
$$

```
where R = recruitment
    P = parent stock
    Pr = replacement size of the stock
    Rr}=\mathrm{ number of recruits from. Pr
    Pm}= stock producing maximum recruitment
```

If recruitment and stock are expressed in the same units, $R_{r}=P_{r}$, so

$$
\begin{equation*}
R=P e^{(P r-P) / P m} \tag{28}
\end{equation*}
$$

Schaefer showed a simplified version of (28):

$$
\begin{equation*}
R=P e^{a-b P} \tag{29}
\end{equation*}
$$

The form of (27) and (28) is shown in Figure 7. An empirical fit of the Ricker equation is shown in Figures 8 and 9.


Figure 7. The stock and recruitment curves of Ricker for various conditions. The curves A-E represent different "stock and recruitment relationships." They pass through the bisector (where recruitment and stock are equal, and hence recruitment can replace stock) at the same point, an equilibrium point. The dashed lines represent different rates of exploitation. Adapted from Ricker, 1958.


Figure 8. The relationship between recruitment and stock for the Tillamook Bay chum salmon. Adapted from Ricker, 1958.


Figure, $9 . \quad$ CURVE SHOWS FIT OF RICKER MODEL

Once the yield per recruit equation has been specified along with the stock recruitment relationships, we are in a position to derive the steady-state yields (catch) given various levels of fishing mortality and starting from a particular population size. 9 Schaaf and Huntsman have generated such relationships using Atlantic menhaden. This is shown in Figure 10. A stock-recruitment relationship of a form similar to Ricker's brings the results of the dynamic pool model into line with those of the logistic model according to Schaefer. An example for the yellowfin tuna fishery is given in Figure 11.

### 5.0 Conclusion

The exposition is not intended for the professional population dynamicist. It should be recognized that the dynamic pool model is basically a simulation type approach. It is critically based on the estimate of crucial parameters such as $F, M$, and $K$. The model differs from the Schaefer approach in that the parameters are not estimated simultaneously via least-squares. The dynamic pool model

[^3]


Figure 11. Catch-per-recruit from Beverton-Holt model and total catch from logistic model, as functions of fishing effort. Age at recruitment 1.5 years, natural mortality rate 0.80 , fishing mortality rate 0.95 at 25,000 units of effort.
is especially useful in dealing with circumstances where the initial population deviates from steady-state results and one wishes to obtain long-run steady-state implications of holding fishing mortality constant.


[^0]:    ${ }^{2}$ R. J. H. Beverton and S. J. Holt, "On the Dynamics of Exploited Fish Populations," London: Her Majesty's Stationery Office, 1957.

[^1]:    ${ }^{4}$ Any fish of the herring family.
    ${ }^{5}$ Cod or cod-like species.

[^2]:    ${ }^{6}$ F. J. Richards, "A Flexible Growth Function for Empirical Use," Journal of Experimental Biology, X(29):1959, 290-300.

    7Jerome J. Pella and Patrick K. Tomlinson, "A Generalized Stock Production Model," Inter-American Tropical Tuna Commission, Bulletin, XIII(3), 1969.

[^3]:    ${ }^{9}$ It should be pointed out that Beverton and Holt have used a stock-recruitment relationship of the form

    $$
    R=\frac{1}{\alpha+\beta / P}
    $$

    so as R approaches an asymptote, $1 / \alpha$, P becomes larger.

