FISHERIES RESEARCH BOARD OF CANADA

MANUSCRIPT REPORTS OF THE BIOLOGICAL STATIONS

No.

628

Title

The Mathematical Formulation of Dynamics
of Fish Populations

Author

J. E. Paloheimo

1957

Abstract

The Mathematical Formulation of Dynamics of Fish Populations

J. E. Paloheimo

Predictions of the effects of different exploitation practices are often based on data known to be insufficient. To be more realistic such predictions should be followed by an analysis to examine critical values of the parameters used and to provide a basis for the relationships employed.

A vector and matrix notation is given which is general enough to study the optimal yield conditions under different alternative assumptions. Some of the ideas presented by Ricker have been defined to permit a study of the conditions which generate permanent oscillations in the yield. The recent work on Population Dynamics by Beverton and Holt has been modified to give a non-steady state model.

Beverton and Holt have not yet published a complete account of their work. It has therefore been necessary to fill some of the gaps in published material, but which they have undoubtedly investigated. No great importance is necessarily attached to these specific solutions as our emphasis is more on the mathematical treatment. Differing from the approach by Beverton and Holt a density dependent treatment of the food population is suggested.

In formulating the different relations we have aimed at using differential equations. This results in a structural simplicity in the sense that particular sets of factors can be left out or included in many cases by simply dropping or adding the appropriate formulae. In the absence of adequate observational data this makes possible the examination of the complex of factors which may have given rise to observed conditions, and an assessment of the relative importance of various factors in the complex.

The formulation of the problem is of a type which readily lends itself to automatic machine computation by high speed electronic digital computers.

The Mathematical Formulation of Dynamics of Fish Populations

J. E. Paloheimo

Introduction

In a recent paper "Stock and Recruitment" Ricker studied different patterns of recruitment in relation to the optimal yield conditions and to the course of the fishery. He emphasized the fact that even dominant species can have a recruitment pattern which generates permanent oscillations in a strictly stable environment. He further indicated that even a species which is controlled by such recruitment or reproduction pattern that brings about, in a stable environment, an equilibrium may not proceed to the equilibrium directly but may overshoot it first. The problem is immensely complicated when the environmental conditions fluctuate and impose another series of oscillations on the one for which the recruitment is responsible. Such complications imply that high levels of density and productivity during or after short periods of reduced fishing (e.g. war time) have to be treated cautiously. All this emphasizes the importance of the study of such oscillations and the conditions which generate them.

We are concerned here with a notation and formulation of the dynamics of fish populations which is general enough to permit the study of such oscillations in relation to the conditions which bring them about. It is of particular interest to study how these ideas can be incorporated with the recent work in population dynamics by Beverton and Holt.

In laying out the notation and general principles our consideration is to aim at a framework which allows study of the optimal yield conditions, steady state or not, under (any) additional or alternative assumptions. More specifically, most of the relations are stated in the form of differential equations; this implies that some of the conditions can be left out simply by dropping the appropriate formulae, and that new relations or parameters can be added by defining them in relation to the previous ones. This is particularly important because of the tendency to base the predictions of the effect of different exploitation practices on data known to be insufficient in many respects. Decisions derived from such predictions involve a risk and a part of the analysis is to study the risk in relation to population variables.

It is realized that the inquiry into the critical values of parameters and relations employed necessitates an insight into the problem which we may or may not have. This, however, works both ways. If we need knowledge of ecology to construct a model of the fishery, the process of constructing the model and the study of the outcome will certainly clarify the complex problem. To say the most, a well chosen model can be employed to predict the course of the fishery; to say the least, it can be used to clarify our thinking and make it more precise.

For the purpose of illustrating general principles and problems involved in constructing a model and to emphasize that the mathematical formulation is hardly a problem except in the absence of factual knowledge we will modify some sections of the theory by Beverton and Holt (section "More complex theory", page 421-441 in (3)) so as to yield a non-steady state model. Some of the ideas by Ricker on cannibalism will be defined in our terminology and they can be included in the study of optimal yield conditions.

There is no complete account of the recent work by Beverton and Holt, and this will bring about some difficulties. There are several points in (3) which have been left open with a reference to the forthcoming paper. These include the relationship between food utilization and maintenance coefficients (ε and ζ) and the level of food, and the dependance of the grazing coefficient on the population size. In what follows a solution is obtained to both of these problems; the dependance relation of the grazing coefficient on the population size appears to be logical one, while the problem of food utilization and maintenance coefficients depending on food has been treated by making a distinction between food consumed and food available, and by assuming, quite arbitrarily, that ε and ζ are constants. No great importance is necessarily attached to these solutions as we do not have any data. Differing from the approach by Beverton and Holt it is shown that the supply of food, understood as a separate population liable to predation by fish, can easily be considered to follow density-depending population laws.

In constructing his reproduction curves Ricker (13) restricts the compensatory mortalities to the immature section of the stock, and only the joint effect of all such mortalities is considered. To quote his own words "...... the average resultant of their action, over the existing range of environmental conditions, is represented by the average size f maturing brood, or recruitment, which each stock density produces. A graph of this relationship between an existing stock, and the future stock which the existing stock produces, will be called a reproduction curve". Strictly speaking, of course, such a relationship can be specified only when the stock is at equilibrium or when the effect of the compensatory mortalities extends only over the period (one year) during which the stock does not change appreciably. To formulate the problems precisely the effect of the density of the adult stock on young fish, and the effect of the density of immature stock on itself has to be defined at any given time. This results in a relationship where the future stock does not depend only on the stock which produces it, but on the (composition of the) stock during all years it is liable to compensatory mortalities. This more precise formulation of the problem presents, however, several difficulties. We cannot any more be content with a joint relation but each type of mortality has to be treated separately, at least as far as the analysis is concerned. The only compensatory mortality we consider here is cannibalism.

Notations and Basic Formulae

Population size. To describe the population at time t we will use the notation

$$N_t = (n_{ot}, n_{1t}, \ldots, n_{\lambda t})$$

where n_{it} $(i = o, \ldots, \lambda)$ refers to the numbers of fish in the i^{th} age group at time t. λ is the maximum age fish can obtain. As the time unit we will use the period between successive spawnings. We take it as one year. Whenever no confusion results we use simpler notation

$$N_t = (n_o, n_1, \ldots, n_\lambda)_t$$

The total population size (the number of fish in all age groups) is denoted by $|N_t|$, called the norm of N_t, i.e.

$$|N_t| = \sum_{i=o}^{\lambda} n_{it} = \left(\sum_{i=o}^{\lambda} n_i\right)_t$$

When we wish to refer to a sub-population an appropriate subscript is given to N_t, e.g. N_{Mt} refers to the population of all mature fish, $|N_{Mt}|$ to the total number of all mature fish. If p_i denotes the fraction of the i^{th} age group which are mature then

$$N_{Mt} = N_t \begin{pmatrix} p_o & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & p_1 & \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & & & & \cdot \\ \cdot & \cdot & & & & \cdot \\ \cdot & \cdot & & & & \cdot \\ 0 & 0 & & & & p_\lambda \end{pmatrix} = N_t P$$

and

$$|N_{Mt}| = \left(\sum_{i=o}^{\lambda} p_i n_i\right)_t = |N_t P|$$

The array at p_i's and 0's, P is called a diagonal matrix. Above we have used the rule for matrix multiplication. The reader who is not familiar with it may take the results as such.

Growth. The average weight of the i^{th} age group at time t is denoted by w_{it}. The aggregate of the average weights of all age groups at time t is denoted by W_t. We write

$$W_t = \begin{pmatrix} w_o & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & w_1 & \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & & & & \cdot \\ \cdot & \cdot & & & & \cdot \\ \cdot & \cdot & & & & \cdot \\ 0 & 0 & \cdot & \cdot & \cdot & w_\lambda \end{pmatrix}_t$$

The population by weight is denoted by $N(w)_t$ where

$$N(w)_t = (n_o w_o, n_1 w_1, \ldots, n_\lambda w_\lambda)_t$$

Using matrix multiplication we get

$$N(w)_t = N_t W_t$$

The total weight of the population is denoted by

$$\left| N(w)_t \right| = \left(\sum_{i=o}^{\lambda} n_i w_i \right)_t$$

The weight of all mature fish is

$$\left| N_M(w)_t \right|$$

Recruitment. To describe the recruitment (by birth) we have to have a way to indicate the spawning time. For this reason we will let $\lfloor t \rfloor$ denote the highest integer less than t (e.g. $t = 2.3$, $\lfloor t \rfloor = 2$). The time just before fish change their age groups is denoted symbolically by $\lceil t - o \rceil$. In this notation $n_{o\lfloor t \rfloor}$ is the number of eggs laid at the beginning of the year t. We may assume that the number of eggs is proportional to the weight of mature stock, i.e.

$$n_{o\lfloor t \rfloor} = \xi \left| N_M(w)_{\lfloor t \rfloor} \right| \tag{1}$$

The total effects of weather, etc. which are in no way predictable at the present time have to be considered as random variables in a sense. As such one questions whether this randomness cannot be counted for by letting such population characteristics which change with them have this randomness built right into them. Indeed, because the weather may have a different effect on recruitment than on growth this appears to be the only way to handle such effects. Ricker has already treated some of his theories in this fashion in (13). Some others, e.g. K. E. F. Watt include in the yield equation a term called total quantitive impact of weather, etc. To introduce random variation we may put, following Ricker

$$n_o[t] = r\{N_M(w)[t]\} \tag{2}$$

where r, according to a random choice, follows a positive half of the normal variate with mean one, or is the inverse of such a variate.

For convenience we often indicate the recruitment by $R[t]$ where

$$R[t] = (n_o, 0, \ldots, 0)[t]$$

Similarly

$$R_t = (n_o, 0, \ldots, 0)_t$$

__Aging and survival.__ The percentage survival fraction from time t to time t + 1 of fish in the i^{th} age group at time t is denoted by s_{it}

To describe the process of fish changing age group each year we arrange the survival fractions s_{it} in a matrix as follows

$$S_t = \begin{pmatrix} 0 & s_1 & 0 & \ldots & 0 \\ 0 & 0 & s_2 & \ldots & 0 \\ \cdot & \cdot & & & \cdot \\ \cdot & \cdot & & & \cdot \\ \cdot & \cdot & & & s_{\lambda-1} \\ 0 & 0 & 0 & \ldots & 0 \end{pmatrix}_t$$

If the instantaneous rates of fishing and natural mortality are (approximately) constants, let F_i and M_i be the mortality rates of the i^{th} age group then

$$s_i = \exp. - (F_i + M_i)$$

The population at time t + 1 is given now by the formula

$$N_{t+1} = R_t + N_t S_t \tag{3}$$

__Yield.__ If the fishing and natural mortalities are regarded as constants during the year then the yield in the year $[t], [t+1]$ denoted by $Y[t]$ is obtained, in most cases accurately enough, from

$$Y_{[t]} = \left| \tfrac{1}{2}(N_{[t]} - N_{[t+1-o]})\ (W_{[t]} + W_{[t+1-o]}) \left(\frac{F}{F+M}\right) \right| \tag{4}$$

where $\left(\frac{F}{F+M}\right)$ stands for the diagonal matrix

$$\left(\frac{F}{F+M}\right) = \begin{pmatrix} \frac{F_o}{F_o + M_o} & 0 & \cdots & 0 \\ 0 & \frac{F_1}{F_1 + M_1} & & \cdot \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ 0 & 0 & \cdots & \frac{F_\lambda}{F_\lambda + M_\lambda} \end{pmatrix}$$

with F_i and M_i referring to the instantaneous fishing and natural mortality rates of the i^{th} age group respectively.

In the case (4) is a too coarse approximation more refined formulae may be used. For the reason that the fishing and/or natural mortality as well as growth may interact with other variables we will give only the differential equations. We may write

$$\frac{dY}{dt} = \left| \left(\frac{\partial n_i}{\partial t_F} \frac{dF(t)_i}{dt} w_i \right)_t \right| \tag{5}$$

The right hand size refers to the norm of the diagonal matrix of the elements

$$\left(\frac{\partial n_i}{\partial t_F} \frac{dF(t)_i}{dt} w_i \right)_t ,$$

the derivative $\frac{\partial n_i}{\partial t_F}$ refers to the rate at which the size of the i^{th} age group decreases due to fishing, and $\frac{dF(t)_i}{dt}$ to the rate at which the fishing mortality changes with time. If for instance the instantaneous fishing mortality rate is constant, say F, then

$$F(t) = Ft, \quad \frac{\partial n_i}{\partial t_F} = -n_{it} F \quad \text{and} \quad \frac{dF(t)_i}{dt} = F$$

In most cases (5) is an unnecessarily refined estimate particularly if we are using the average growth curve. For discussion of the suitable approximations over the selection range of the gear we refer to the Appendix.

Food and growth. Recently noticeable changes in growth of fish have been observed in a number of stocks. To quote some examples: the 1949 haddock year-class on St. Pierre Bank was very abundant and also very slow growing; during recent years Gulf of St. Lawrence cod have grown exceptionally fast, associated with a concurrent herring disease and high herring mortality; similar changes in growth have been observed at the North Sea as a result of the changes in density of fish during war time. It indeed becomes apparent that landing statistics did not supply quite enough information for population dynamics studies.

An extremely intereating attempt to meet the situation is that by Beverton and Holt in (3). To modify it for our present purposes we will recapitulate some of it. Let χ_A stand for the amount of food required by fish for maintenance, and ζ for a constant. They assume, referring to experiments by Dawes in 1929-1931, that

$$\frac{d\chi_A}{dt} = \zeta w^{2/3} \tag{6}$$

It is furthermore assumed that a fixed proportion of food in excess of the food required for maintenance is converted into growth. If χ_B specifies food in excess of the maintenance requirements and ε the food utilization coefficient then we may write

$$\varepsilon \frac{d\chi_B}{dt} = \frac{dw}{dt} \tag{7}$$

This equation is not given in the text but that it is implied follows easily.

In addition, the validity of van Bertalanffy's growth equation is assumed. We may write this growth equation in the form

$$\frac{dw}{dt} = Hw^{2/3} - Dw \tag{8}$$

where H refers to the anabolism and D to catabolism, or in the form

$$\frac{dl}{dt} = \frac{D}{3}(l_{\infty} - l)$$

where l stands for the length of fish and l_{∞} for the maximum length. Beverton and Holt assume that H but not D or, what is the same thing, that l_{∞} but not D changes with the abundance of food.

The rate of total food consumption of fish of weight w follows from (6) and (7), and we get

$$\frac{d\chi}{dt} = \zeta w^{2/3} + \frac{1}{\varepsilon}\frac{dw}{dt} \tag{9}$$

$$= \left(\zeta + \frac{H}{\varepsilon}\right) w^{2/3} - \frac{Dw}{\varepsilon}$$

where χ denotes the food consumed.

Let us now denote by $\left(\frac{d\chi}{dt}\right)_t$ the diagonal matrix, the elements of which are

$$\left(\zeta + \frac{H}{\varepsilon}\right) w_{it}^{2/3} - \frac{D}{\varepsilon} w_{it}$$

Then the rate of food consumption of the population is given by $\left| N_t \left(\frac{d\chi}{dt}\right)_t \right|$ providing that H is known. We denote it by $\frac{dX_t}{dt}$, i.e.

$$\frac{dX_t}{dt} = \left| N_t \left(\frac{d\chi}{dt}\right)_t \right|$$

where the matrix

$$\left(\frac{d\mathcal{X}}{dt}\right)_t = \left(\left(\zeta + \frac{H}{\varepsilon}\right) w_i^{2/3} - \frac{D}{\varepsilon} w_i\right)_t$$

The above equation can be written

$$(9)' \qquad \frac{dX_t}{dt} = \left| \left(\zeta + \frac{H}{\varepsilon}\right) N_t W_t^{2/3} - \frac{D}{\varepsilon} N_t W_t \right|$$

where $W_t^{2/3}$ is a diagonal matrix the elements of which are $w_{it}^{2/3}$, i.e.

$$W_t^{2/3} = (w_i^{2/3})_t$$

Conversely if the rate at which food is available is known, H can be calculated from

$$(10) \qquad (H =)\ H_t = \frac{\frac{dX_t}{dt} - \zeta \left| N_t W_t^{2/3} \right| + \left| \frac{D}{\varepsilon} N_t W_t \right|}{\frac{1}{\varepsilon} \left| N_t W_t^{2/3} \right|}$$

This implies that H changes continuously. Therefore we replaced H by H_t. Equation (10) together with (9) define H_t and W_t completely as soon as W_t and N_t are given at the beginning of the year t and $\frac{dX_t}{dt}$ is known.

Equation (9) as such does not set any limits to potential growth. Beverton and Holt correct this absurdity by assuming that ε and ζ depend on the amount of food consumed (and by placing restrictions on the food supply). The same thing would be achieved by making a distinction between food consumed and food available. Indeed this seems necessary even if ε and ζ vary with the amount of food. To express a restriction on the amount of food that fish can eat we may simply put $0 \leq H_t \leq H$ in (9). This, of course, is at the best only a rough approximation.

Suppose again that the total amount of food consumed is given. This determines H, and therefore the amount of food eaten by each individual fish.

This amount is given by (9). In other words, from the total food supply, fish of weight w have been able to secure that amount of food. Equation (9) assigns therefore the "searching power" or the "grazing coefficient" for fish of given weight. Furthermore, the grazing coefficient of the total population must therefore be proportional to (9)'. We denote the grazing coefficient by g_t, i.e.

$$(11) \qquad g_t = c\left|N_t\left(\frac{d\varkappa}{dt}\right)_t\right| = c\left|N_t\left(\left(S + \frac{H}{S}\right) W_t^{2/3} - DW_t\right)\right|$$

where c is a constant.

Let me remark that Beverton and Holt have not published this conclusion but they may have had it in their minds when they left this question open as too complicated.

The conclusion (11) appears first quite odd. One would rather think that $g_t \sim |N(w)_t|$ or $g_t \sim A\,|N(w)_t| + B|\,N(w^{2/3})_t|$ with $A \geq 0$, $B \geq 0$. It is not quite obvious why the grazing coefficient should decrease in proportion to the total weight.

Furthermore, g_t should not depend on the amount of food available at any particular time as it does in (11), i.e. the level of food supply should factor out from the expression $\left|N_t\left(\frac{d\varkappa}{dt}\right)_t\right|$. In this sense the result (11) is an absurdity; and in its present form it will lead to insoluble equations. This can be remedied if we regard H as constant in (11). For this reason we already used H instead of H_t.

The searching power or the grazing coefficient of the animal together with the equations (6) and (7) determine the growth curve. If we assume that $\frac{d\varkappa}{dt} \sim w$ then this together with the equations (6) and (7) are not compatible with the van Bertalanffy growth equation. However, with slight modification of (6) and (7) the assumption $\frac{d\varkappa}{dt} \sim w$ gives realistic growth curves.

Cannibalism. To define cannibalism in precise terms we first have to consider all such groups of adults which prey on different age groups of young fish. For this purpose we denote by $N_{c_1 t}$, $N_{c_2 t}$, . . . , etc. the part of the adult population which, on account of their size and habitat, prey on the one year olds, on the two year olds, etc. We may put

$$N_{c_1 t} = N_t P_{c_1}, \; N_{c_2 t} = N_t P_{c_2} \;\text{ etc.}$$

where P_{c_1}, P_{c_2}, etc. are diagonal matrices, elements of which express the fraction of potential predators in an age group; they do not depend on the population size.

The measure of the predator density must be based on the (grazing) efficiency of the sub-population to catch the particular age group as well as its capacity to eat quantities of young fish. In the absence of any emperical evidence almost any argument could be advanced here. However, to get a starting point and to choose the assumption so as to satisfy common sense we suppose that the grazing (searching, fishing) efficiency of the sub-population and as well as its capacity to consume young fish depends on its weight. From these assumptions it follows that we can write

$$\frac{1}{n_{it}} \frac{dn_{it}}{dt} = - g \left| N_{c_i}(w)_t \right|$$

where g is a constant. If there exists a natural mortality operating independently of cannibalism then we may write

$$\frac{1}{n_{it}} \frac{dn_{it}}{dt} = - g \left| N_{c_i}(w)_t \right| - M \tag{12}$$

It follows that

$$s_{it} = \exp - \int_t^{t+1} \left(g \left| N_{c_i}(w)_t \right| + M \right) dt$$

Instead of the equation (12) we could take

(12)' $$\frac{1}{n_{it}} \frac{dn_{it}}{dt} = - g_{c_i t} - M$$

where $g_{c_i t}$ is given by (11) with $N_{c_i t}$ instead of N_t.

Food. The food supply can be considered as a population in the same manner as the fish stock while probably immensely more complex. If the food is a critical factor which restricts the population growth an equal importance should be given to its study as to that of the fish population. Nevertheless the only publication I know of where the food population has been considered explicitly in the optimal yield study is in that by Beverton and Holt. It is noticeable that they treat the food supply in the same fashion as they first did the fish population, assuming constant recruitment and natural mortality. This approach may not, of course, be any more acceptable than the first density independent models of fish populations. As a better alternative while still probably not acceptable, we may take the Verhulst-Pearl equation. If we denote the amount of food at time t by ϕ_t (not including the young brood eaten), the maximum food population level by ϕ, and the reproduction rate at minimum population density by r we can write

(13) $$\frac{d\phi_t}{dt} = r\phi_t (\phi - \phi_t) - \phi_t g_t$$

where g_t expresses the grazing action of fish as given in (11). The rate of food consumption is now given by

(14) $$\frac{dX_t}{dt} = \phi_t g_t$$

providing that $\frac{dX}{dt}$ does not exceed the upper limit as given in (9)' with the maximum H. If it does, we substitute (14) by (9)' and make the corresponding correction in (13).

Completion of model. The equations (1) (or alternatively (2)), (3), (4), (9), (10), (11), (13), and (14) define a type of model where growth and recruitment depend on the density. To include the compensatory type of mortality which controls the survival of young eggs the effect of such mortality has to be expressed as a differential equation; this equation can then be added to the set above. To include cannibalism within the factors controlling the population the equations (12) or (12)' have to be added and some changes have to be made in the equations specifying food consumption and food supply. For each of N_{c_i} there must exist a corresponding equation of the form

$$\frac{dX_i}{dt} = \phi_t \, g_{c_i t} + n_{it} \, g_{c_i t} \tag{15}$$

where $g_{c_i t}$ is the grazing coefficient corresponding to N_{c_i}. In most cases we may take $N_{c_1} = N_{c_2} = \ldots$ In this case we have only two equations to specify the food consumption, the one referring to the part of the population being preyed upon and the other to the adult predators. Furthermore, these sub-populations of young and adults may have quite different basic diets and consequently two different food populations have to be considered. The food supply of the young fish might follow the equation of the type (14), that of adult stock might then follow the equation of the type (15). This division of food or an even more complicated one might, of course, be necessary whether there is any cannibalism or not.

Comments

The formulation of the problem is of type which easily lends itself for automatic machine computation by high speed electronic digital computers. To carry out the calculations involved with more conventional methods when the growth is adjusting itself continuously to account for new recruits and to the variations in food supply, when the recruitment is changing with the population size and indeed when the conditions in general may be such that they generate permanent oscillations of the population, is almost too formidable to contemplate. On the other hand, however, if a (medium size) general purpose electronic computer is used the formulae as presented or even a more complex one can easily be programmed. The computer can then approximate, with any degree of accuracy the differential equations given, continuously checking, if instructions call for it, that the upper limits we have set for certain parameter will not be exceeded, and if exceeded the computer will choose the upper limit instead of the calculated one or sound an alarm depending on instruction. It can calculate the expected number of recruits, change the age group of fish, and make, if desired, a random adjustment to recruitment. The operation speed of the most medium size electronic computers being from 1 - 17 milliseconds the annual yields (or population sizes) will be printed at the intervals from a few seconds to a few minutes depending on a machine and on the type of population model employed.

For many years to come we shall not have the data which are required to confirm or reject all the assumptions inherent in any population dynamics model. Because of this, present studies should be conducted so as to examine all possible conditions, the joint effort of which, over a limited range of variations in the environment, may have resulted in the existing observation data. It will be obvious from the foregoing treatment that we can create ecological conditions with a few "paper-bound" symbols and that the effect of hypothetical relations upon the course of the fishery can be easily determined by taking, if necessary, a refuge in automatic computation by electronic computers. Theoretical analysis does not have to be contended any more, as it has been in the past, with the study of the implications of vast statistical generalities of the type the observation data represents, but it can be directed toward the study of the underlying population laws as well. Indeed, the theoretical work has an important role in indicating the type of data which is relevant and not only in trying to fit the models to the available data. At least, in such an undertaking we have nothing to lose as the theoretical investigation is practically free.

Acknowledgement

This paper has been written in response to the demands of the analysis of ICNAF sub-area 4 fish stocks. At the Biological Station in St. Andrews the study of the area is being primarily conducted by W. R. Martin, F. D. McCracken and A. C. Kohler. W. R. Martin and L. M. Dickie have kindly read the paper and made several suggestions which have been incorporated in the text.

Literature

1. Baranov, F. I. 1918. On the question of the biological basis of fisheries. N. -i Ikhtiologisheskii Inst. Izvestiia, 1 (1): 81-288.

2. Beverton, R. J. H. 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. U.S. Fish. Lab., Beaufort, North Carolina, Misc. Contr. No. 2.

3. Beverton, R. J. H. and Holt, S. J. 1956. The theory of fishing. Sea Fisheries and their investigations in United Kingdom by M. Graham. London.

4. Cole, LaMont C. 1951. Population cycles and random oscillations. J. Wildlife Management, 15: 233-252.

5. ______ 1954. Some features of random population cycles. Ibid. 18: 2-24.

6. Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33: 183-212.

7. ______ 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35: 213-245.

8. Logistics Research Inc. Description of operations, Alwac III -E, Electronic Digital Computer (Programming Manual).

9. Lotka, A. J. 1925. Elements of physical biology. Williams and Williams, Baltimore. 460 pp.

10. Martin, W. R. 1957. The status of evidence bearing on optimum size for first capture of ICNAF sub-area 4 cod, the 7th Ann. Meeting of ICNAF, Lisbon.

11. Nicholson, A. J. and Bailey, V. A. 1935. The balance of animal populations. Proc. Zool. Soc. Lond. 33: 551-598.

12. Ricker, W. E. 1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Publ. Sc. Series No. 15, pp. 101.

13. _____ 1954. Stock and recruitment. J. Fish. Res. Bd. Canada 11: 559-623.

14. Riley, G. A. 1953. Theory of growth and competition in natural populations. J. Fish. Res. Bd. Canada, X, 211-223.

15. Schaefer, M. B. 1954. Some aspect of the dynamics of population important to the dynamics of the commercial marine fisheries. Inter-American Tropical Tuna Comm., Bull., 1: 25-56.

16. Slobodkin, L. B. 1953. An algebra of population growth. Ecology 34: 513-519.

17. _____ 1953. On social single species populations. Ecology 34: 430-434.

18. Templeman, W. 1955. Groundfish stocks of the West North Atlantic. Trans. 20, N. Amer. Wildlife Conf. 454-476.

19. Watt, K. E. F. 1955. Studies on population productivity. I Three approaches to the optimum yield problem in populations of Tribolium confusum. Ecol. Monogr., 25: 269-290.

20. _____ 1956. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. J. Fish. Res. Bd. Canada XIII, 613-645.

Appendix

Approximation of the sigmoid shape selection curve in the yield equations

Let us denote by t_o the time when a year-class first enters the fishery, by t_1 when fish are fully catchable by the net used, and by $l(t)$ the average length of fish. Accordingly $l_o = l(t_o)$ and $l_1 = l(t_1)$ specify the 0% and 100% selection points of the net used.

Within the selection range of the net, only a fraction of the total mortality is operating. We approximate the sigmoid shape selection curve by a segment of a line. The percentage selection is given by

$$k(l - l_o), \ l_o \leq l \leq l_1, \text{ where k equals } \frac{1}{l_1 - l_o}$$

The differential equation which describes the population is

$$\frac{dn_t}{n_t dt} = - Fk(l - l_1) - M; \ t_o \leq t \leq t_1 \tag{16}$$

where F and M are assumed to be constant.

Before these equations can be integrated we have to express them by one variable only, i.e. by l or t. After substituting t or l by means of the growth curve $l = l(t)$ and after making the necessary transformations, we arrive at the equations for n_t which can be integrated. The formula for n_t is rather complicated. When these solutions are substituted in (6), we get the yield from the given number of recruits. The yield integral is apparently not integrable; the integration has to be taken numerically and it is rather laborous and even then we do not get but an approximation. Our constants F and M are subject to the error; indeed they may not be constants at all. Further, the equations give the yield only for the part of the year-class having the average growth $l = l(t)$. For the relative yield, however, this may be adequate.

If instead of the growth curve $l = ab^t + c$ a simple linear equation $l = at + c$ is used within the selection range of the net, we get in place of (16)

$$\frac{dn_t}{n_t dt} = At - B;\ t_1 \leq t \leq t_2$$

where $A = -Fk$ and $B = FKat_o - M$.

By solving for n_t we get

(17) $$n_t = n_{t_o} e^{A \frac{t^2 - t_o^2}{2} + B(t - t_o)};\ t_o \leq t \leq t_1$$

The exponent in the formula of n_t when $t_1 \leq t \leq t_2$ can be put in the form

$$A \frac{t^2 - t_o^2}{2} + B(t - t_o) = (t - t_o)\ (A \frac{t_o + t}{2} + B)$$

It means that at any given interval within the selection range of the net the instantaneous mortality rate can be regarded as constant having the same value as the true mortality rate in the middle of the interval.

To get the total yield from the given number of recruits (having the given growth), we insert (17) in (5) and integrate the obtained formulae. The integration has to be taken numerically for the selection range of the net.

To give an idea of the range of accuracy using different approximations a hypothetical example will be considered, and the annual yield from an age group will be estimated with three different methods. In the first two cases, the fishing mortality is assumed constant during the year and having the same value as the true fishing mortality in the middle of the year. In the third case, the estimation is done by means of the equation (5). To be exact, the methods are as follows:

1. We approximate the growth curve by

(18) $$w_t = w_o \exp. kt;\ (0 \leq t \leq 1)$$

the average weight at the end of the year is $w_1 = w_o \exp. k$.

By substituting (18) in (5) and assuming that F and M are constant we get

$$Y = \frac{Fn_o}{k - F - M} (1 - \text{exp. } k - F - M) \qquad (19)$$

where n_o is the number of fish in the age group at the beginning of the year. These formulae have been used by Ricker.

2. We assume not only the fishing mortality to be constant but the weight (i.e. the growth) too. As a weight we will use the average weight, the arithmetical mean at the initial weight and the weight at the end of the year. Accordingly the yield is given by

$$\frac{Fn_o}{F + M} (1 - \text{exp. } - (F + M)) \frac{w_o + w_1}{2}$$

This is slightly more expedient to use than (19).

3. As a third alternative we shall estimate the yield by means of the equation (17). The weight is assumed to increase as the third power of the length.

The following values will be inserted

$t_1 = 0$ $\quad w_o = 1$ $\quad M = .19$ $\quad$ at $t_1 = 0$ $\quad F = 0$

$t_2 = 1$ $\quad w_1 = 2$ $\quad$ at $t_2 = 1$ $\quad F = .32$

$n_{t_1} = 1{,}000$

The estimates of the yield are $Y_1 = 192$, $Y_2 = 203$, and $Y_3 = 210$ according to the first, second and third method, respectively. The third figure, $Y = 210$, should be regarded as a best approximation of the yield. Let it be noted that the second method which is slightly simpler than the first gave better approximation within the selection range of the net.

[illegible]

where n is the number of [illegible] in the [illegible]. These formulae have been used by [illegible].

[illegible] it is seen that only the [illegible] to the [illegible] and [illegible] the [illegible] value of the [illegible] points [illegible] the [illegible]

[illegible]

yields [illegible]

[illegible] alternative [illegible] the yield [illegible] equation (17). [illegible] length.

[illegible] following [illegible] with the [illegible]

[illegible]

[illegible] regarded as a [illegible] of the yield. It [illegible] noted that the [illegible] method [illegible] length [illegible]