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International Council for the
Exploration of the Sea

C.M. 1963

Symposium on the Measurement
of Abundance of Fish Stocks

No. 2o

Att. Comparative Fishing Committee

On the Biological Basis of Mathematical Models for the Dynamics of Fish Populations

by

G. V. Nikolsky
Institute of Animal Morphology
Academy of Sciences, USSR

One of the most important tasks facing the modern fishery science is to improve methods of predicting possible catches and to calculate optimal exploitation regimes for the stocks of commercial fish providing for the highest, reiterated from year to year, productivity of the populations fished. With this aim in mind it is extremely desirable that the process of compiling predictions of catches and calculations of the regime of fish stock exploitation should be simplified as far as possible. Substantial assistance in this matter can, undoubtedly, be achieved with application of electronic computers. However, to provide a possibility for the application of computers in the analyses of populations it is necessary to develop appropriate mathematical models which should represent the process of the dynamics of populations in a proper way.

Many attempts to develop mathematical models for the fish population dynamics have been made including the first endeavours of R. Ross (1911), V. Kevdin (1915), F. Baranov (1918) and modern works of R. J. H. Beverton & S. Holt (1957), W. Ricker(1958), T. Doi (1959), G. Hempel & D. Sahrhage (1961), J. Gulland (1962) and many other investigators.

All the available mathematical models of the dynamic of fish populations can, to a certain extent, be divided into the following four groups:-

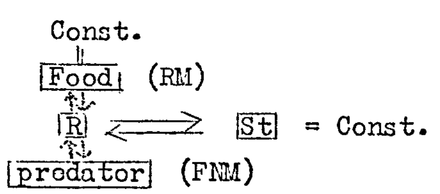
a) Models based on the food-consumer relation where the fish are represented as consumers. One of the founders of such a type of models is Gunnar Alm;

b) Models based on the predator-prey relation where the fish play the role of prey. This group also comprises models where the fishery is represented as "predator". Such a type of models was initially suggested by B. Ross, V. Kevdin, F. Baranov, A. Lotka, V. Volterra and others. At the time being this type of models is most widely spread;

c) Models based on the regular quantitative relation between the stocks of spawners and broods. These models seem to be most comprehensively elaborated by W. Ricker;

d) Models which include some interacting values, such as recruitment, growth and mortality; particularly Russell's model (1942) should be referred to.

It is quite obvious that the division suggested is very schematic, and, of course, there are many other intermediate or combined models. But the most characteristic feature of the majority of models, as stated by Hempel & Sahrhage (1961), is that they are derived from a notion suggesting one variable with other factors being constant; for example, if the model is based on the predator-prey relation the bonds will be as follows:-



i.e., it is the predator-prey relation that is assumed the only variable.

However, it should be borne in mind that in nature, including commercial organisms, any change in the predator-prey relationship is inevitably connected with changes in the relation of prey and their food supply. As it was clearly shown by B. P. Manteufel (1961) we are dealing with at least a three-linked relation or so-called triotrophus, where the mean term of chain bears direct connections through adaptive dependencies with the extreme terms, that is we mean a relation consisted of at least two interrelated binomials:-

$$F \overset{\pm}{\underset{\pm}{\rightleftarrows}} St \overset{\pm}{\underset{\pm}{\rightleftarrows}} Pred.$$

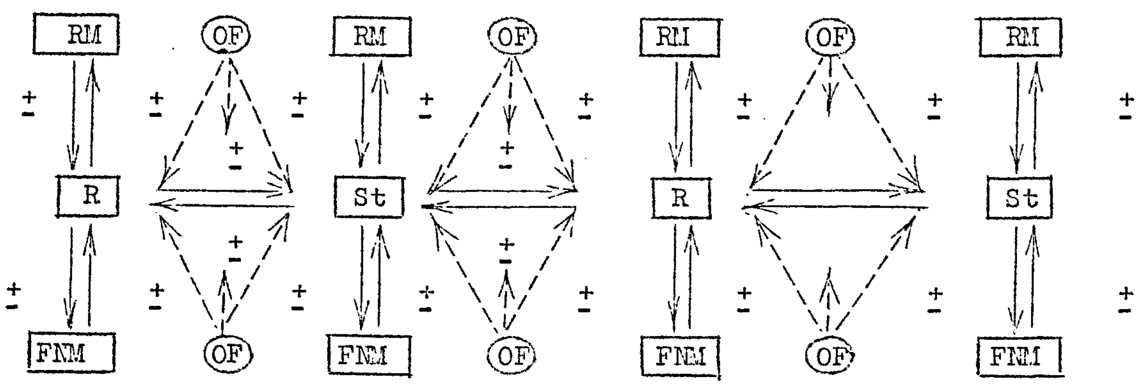
The triotrophus does not seem actually to be a completely closed system due to its interactions with other environmental factors, the system of relations may be affected by such factors or factors gradients which the species are not adapted to.

It is worth mentioning that a possibility of occurrence of such "hindrances" in the triotrophus relationship, as a rule, increases with moving away from the biological centre of the area inhabited by the species to its extremities.

In the construction of appropriate models for the relations in the triotrophus chain it is necessary to proceed from a notion of the population as a self-regulating system which by means of its regulatory mechanisms adjust itself to a certain regime of living. The review of the mechanisms observed was made at the Symposium in Durham in 196o (Nikolsky, 1962).

Alongside with this the parents' stock seems to adjust themselves by means of their regulatory adaptive mechanism to a certain reproducing intensity suitable to certain conditions of life.

The range of self-adjustment cannot actually be infinite. There are many cases referred to in literature, for example, the bream of the Aral Sea, the Amur autumn chum, the red from Alaska, the North Sea herring and some other species, when the regulatory mechanisms were found disturbed. This is a grave signal that the conditions of life for the population are also disturbed, particularly it is too high fishing activities that are responsible for the disturbances in the autumn chum of the Amur River and herring of the southern North Sea. The system of relations governing the process of the dynamics of populations can be represented in the following way:-



where RM = food supply,

FNM = total mortality,

R = recruitment,

St = stock,

OF = occasional factors or phenomena which the population is not adapted to.

The central horizontal links reflect the relationship of the stocks of spawners and broods, the vertical links mean food relations and the predator-prey relation including fishing. Bonds or "occasional phenomena" as they might be called, which the population is not adapted to are shown by broken lines.

The representation is based on the relation between the stocks of spawners and broods, but the relation is expressed not by a simple function, but by a correlation, i.e., by a ratio of such a type as: $R = \sigma_r St$

Furthermore, the relation is expressed not by a linear system of co-ordinates, viz., the numbers of spawners - the number of broods, but by a three-linked relation:- the quantity and quality of spawners the quantity and quality of broods.

By "quality" we mean suitability to the conditions of life. It is evident that those factors which are favourable under some conditions, viz., eggs of different quality, may prove damaging under other conditions. However, the relation should be supplemented by a certain coefficient to show a level of reproduction. The coefficient will depend on the vertical bonds (predator-prey, food-consumer) which appear in the population investigated.

These data should be used as a basis in the construction of a model of the population dynamics. Further corrections should be introduced from data obtained in the analyses of the process of growth of year-classes from which recruitment to the stock and mortality are formed.

At the Moscow Session of ICES (196o) the author showed that the earlier opinion that the mortality rate should be taken as a decisive factor affecting the formation of the age composition of the population, does not seem to be true, and, furthermore, that the models of F. Baranov (1918) and Thompson (1937) are most unlikely to reflect actual biological phenomena. The connection between the rate of growth of individuals, age at the first maturity and wide variations in the recruitment composition are of great importance to the formation of the composition of the spawning population. Besides, as it was clearly shown on the example of a number of species by G. D. Polyakov (1962), the intereffect of adjacent year-classes to each other, i.e., their growth and maturation, is of great significance. The mutual influence of the adjacent year-classes to form the recruitment can, undoubtedly, be well expressed mathematically.

The second group of corrections, bound to a certain extent with the first one, specifies the mortality rate of the population. In the estimate of the mortality in the population, particularly in fish with wide fluctuations, the early methods suggested by F. Baranov (1918) on the basis of the relation between the age composition of the population and the mortality rate cannot be used. A detailed discussion of modern methods of biological analysis and mathematical interpretation of the mortality process are beyond the scope of the present paper. In this respect the suggestions made by Beverton & Holt (1959), Tiurin (1962) and Boiko, Paper No. lo, Comparative Fishing Committee, 1963) should be taken into consideration.

The formation of the prediction of a possible yield seems to remind the operation of a decorating weaving machine. The warp will be a relation between the stocks of spawners and broods which is of a non-linear character, and further corrections on the size and composition of the recruitment should be made from the two interrelated processes of growth and mortality, this may be done by means of punch cards.

The scheme suggested can be mathematically treated with the aid of modern technique,and at the same time it does not seem to simplify very much the biological phenomena trying to keep the biological peculiarities in the mathematical interpretation, so it may secure the reliability of the prediction estimated in this way.

At present, researches are being carried out to apply the above-mentioned scheme to some populations of commercial fish, the most grave difficulties arising due to lack of reliable data on the relation between the qualitative indices of the parents' stock and survival of recruitment.

<u>Summary</u>

1. Difficulties which arise in the practical use of mathematical models to the dynamics of populations, are firstly connected with some unsatisfaction of the biological basis when one variable organism-environment is accepted, while other factors are considered constant.

2. At the construction of mathematical models of the dynamics of populations it is necessary to proceed from an idea of a population as a self-regulating system which adjust itself to a certain regime of reproduction in compliance with the food supply.

3. As a basis of prediction of the yield it is suggested to take the relation between the parents stocks and recruitment expressed by equations of a correlative relation with non-linear correlation (at least it should be a three-linked correlation).

4. While constructing a model of the stock-recruitment relation it is necessary to have in mind that both terms of relation are within a triotrophic system: food-consumer (prey) predator. When some changes occur in the system both the stock and recruitment make an adaptive response by changing their biological indices.

5. Occasional effects which the populations investigated are not adapted to, should be included in the mathematical model of the dynamics of population proceeding from the hydrometeorological forecast.

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