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A THEORETICAL ANALYSIS OF THE ZOOPLANKTON POPULATION OF GEORGES BANK

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Studies by Fleming (1939), Riley and Bumpus (1946), and Riley (1946) of the seasonal variations of marine phytoplankton populations have resulted in the development of a growth budget in which the rate of change of the population is balanced against the rates of all the processes that increase or decrease the organic content of the population. The fundamental basis of this type of analysis is a differential equation in which the rate of change of the carbon content of the phytoplankton at any time is equal to the difference between the rate of accumulation of carbon by photosynthesis and the rates of dissipation by respiration, grazing, and natural death. Furthermore, since interest is centered in the seasonal cycle rather than long period fluctuations, it is assumed for practical purposes that over a period of one year the sum of the variations expressed by the equation is equal to zero. In the first two papers cited above, a study was made of the period of the spring diatom flowering in the Georges Bank area of the Gulf of Maine and in the English Channel where the budgets proved useful in describing quantitatively the phytoplankton-zooplankton grazing relationship. In the third paper, a more elaborate but somewhat empirical treatment of the same general type was used to evaluate the entire yearly phytoplankton cycle on Georges Bank.

The advantage of this method is that the balancing of the budget permits an estimate of the overall accuracy of the results. It is therefore a useful tool in putting ecological theories to a quantitative test. The disadvantage is that it requires detailed quantitative information about many processes, some of which are only poorly understood. Therefore, until more adequate knowledge is obtained, any application of the method must contain some arbitrary assumptions and many errors due to over-simplification.

This type of treatment is not necessarily limited to phytoplankton studies. Any population that is ecologically homogeneous may be

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considered in an analogous way. For example, the animals which live by grazing on phytoplankton may be analyzed by an equation such as:

\[ \frac{dH}{dt} = H(A-R-C-D), \]  

(1)

in which:

- \( H \) = the herbivore population;
- \( A \) = the rate of assimilation of food by the herbivores;
- \( R \) = their respiration rate;
- \( C \) = the rate of consumption of herbivores by their predators;
- \( D \) = the herbivore death rate.

Then the size of the population at the end of time \( t \) is determined by the equation:

\[ H_t = H_0e^{(A-R-C-D)t}. \]  

(2)

While the theory is simple enough, the practical application is full of uncertainty because we know so little about the physiology of herbivores and about their predators. The writer feels that it is worthwhile to include such an analysis in the general study of Georges Bank plankton, but the available information is only a small fraction of what is needed for the work, and the results are therefore to a large degree speculative.

The data in the present analysis are derived largely from the two papers referred to previously. The zooplankton population on Georges Bank, shown in Fig. 27, was estimated as grams of carbon per m\(^2\) of sea surface, determined by applying a conversion factor to the measurements of zooplankton volume. Herbivores constitute the main bulk of the zooplankton. Since there is no simple and accurate method of quantitatively allowing for that part of the zooplankton which is carnivorous, it will be assumed that the population of herbivores is equal to the total zooplankton.

**Assimilation.** The assimilation rate is strictly defined as grams of carbon taken into the herbivore tissues (and therefore available for growth or energy) per day per gram of carbon in the herbivore population. Since the assimilation rate does not readily lend itself to quantitative measurement, it is necessary to use indirect evidence to derive a practical definition which is at best an approximation. This definition is as follows:

The assimilation rate is 0.0075 \( P \), where \( P \) represents grams of phytoplankton carbon per m\(^2\), except when this value exceeds 8 per cent of the animals' weight per day, which is set as the maximum limit of the assimilation rate.
The definition is based on the following line of reasoning: It is generally believed that a unit quantity of zooplankton filters the food from a constant volume of water per unit time and therefore eats a constant fraction of the phytoplankton population per day irrespective of the absolute size of the population. This presupposes that the feeding rate is not affected by seasonal changes in temperature, which may not be strictly true, although previous discussion of the subject (Riley, 1946) indicated that on Georges Bank the feeding rate was probably independent of temperature. In the paper just referred to, it was estimated that the fraction of the phytoplankton consumed by a unit quantity of zooplankton (1 g. carbon per m²) was 0.0075. Therefore, the daily rate of consumption of food by herbivores is 0.0075 P, where P represents grams of phytoplankton carbon. The phytoplankton population is shown in Fig. 27, and the consumption rate derived from it is the upper curve in Fig. 28A.

In a study of the plankton of the English Channel, Harvey, Cooper, Lebour and Russell (1935) concluded that utilization (the ratio of assimilation to consumption) was very near unity through most of the year, but that the spring diatom flowering provided the animals with more food than they could use, so that some was excreted in a semidigested condition. The same thing appears to occur in the
Georges Bank area, for although the growth budget for phytoplankton indicates that consumption continues at a constant rate through the spring flowering, the amount consumed is at least twice as much as is needed to account for the observed rate of animal growth. Furthermore, the zooplankton appears to have attained its maximum rate of spring growth in late March before the phytoplankton reached its peak and to have maintained this rate until about the middle of May, when the diatom flowering was largely finished. It seems likely, therefore, that the assimilation rate during the whole of the spring flowering was no larger than the consumption rate of 0.080 observed at the beginning and end of this period. The definition therefore sets 0.080 (8 per cent per day) as the maximum rate of assimilation, and during the remainder of the year it is assumed that assimilation approximately equals consumption. The final result is shown by the broken curve in Fig. 28A.
Respiration. It will be assumed that the respiratory rate increases with an increase in temperature and is not affected by any other factor. Thus

\[ R = r f(T) \]

in which:

- \( R \) = the respiratory rate in g. carbon consumed per g. of herbivore carbon per day;
- \( r \) = the respiratory rate at 0° C = 0.019 (1.9% of the animals' weight per day);
- \( T \) = Temperature (°C), the seasonal cycle of which is shown in Fig. 29;
- \( f(T) \) = the ratio of the respiratory rate at any temperature \( T \) to the rate at 0°, as shown in Fig. 29, inset.

This definition is derived from a study of the respiration of the copepod *Calanus finmarchicus* by Marshall, Nicholls and Orr (1935). They found that the increase in the respiratory rate with temperature did not have an easily defined form such as the van't Hoff law; hence in the present treatment it is necessary to use a graphical definition of the type shown in the inset in Fig. 29. Each point on the curve is
obtained by averaging their experiments with stage V copepodites and adult males and females. Using this average curve as a basis, a value for the constant \( r \) can now be derived from each of the experiments, regardless of the temperature at which it was conducted. The experiments yield a large range of values, from 0.006 to 0.029, which average 0.019. This average value for the constant is used in the present report. The seasonal change in the estimated respiratory rate is shown in Fig. 28B.

**Predation and loss by other causes.** It will be assumed that herbivore predators expend a constant feeding effort irrespective of the amount of food available. Then the total amount of food eaten will be proportional to the product of predators and prey, and the rate of consumption of the prey will be proportional to the number of predators. This is similar to the assumption previously made about the phytoplankton-zooplankton grazing relationship, and it leads to an equation such that:

\[
C = cs
\]

where:

- \( C \) = the rate of consumption of herbivores;
- \( c \) = a constant;
- \( S \) = the quantity of herbivore predators.

It seems likely that sagittae are the most important herbivore predators in the Georges Bank area, since they are numerically very abundant and since, according to LeBour (1922, 1923), they commonly feed on copepods, although fish larvae and other sagittae also constitute part of their diet. Other predators, such as mackerel, the pelagic young of various other fishes, decapod larvae and jellyfish are much less numerous than the sagittae; moreover, the quantitative aspects of their part in the food chain are very uncertain, and therefore, they are not included in the analysis of predation.

Fig. 30 is the seasonal cycle of *Sagitta elegans*, the only quantitatively important species of sagittae on Georges Bank, based on data published by Clarke, Pierce and Bumpus (1943). The curve shows a minimum point in early spring and a maximum in early or midsummer. The maximum is poorly defined due to the lack of summer data. However, it is clear that the time when the sagittae increased most rapidly coincided with the seasonal peak in total zooplankton, just as the latter increased most rapidly at the time of the diatom flowering. Thus there was a lag period of roughly a month in successive constituents of the food chain.

Little is known about the feeding rate of sagittae, or about the quantity of organic material involved. It is not possible, therefore,
to assign an experimentally determined value for the constant $c$ in equation (4). An approximation can be obtained by statistical methods as will be shown later. However, it is first necessary to consider the herbivore death rate.

It will be assumed that the death rate $D$ is constant. In this category are lumped several processes, such as natural death, predation by animals other than sagittae, and dilution of the population by water movements. None of these factors is actually constant, with the possible exception of natural death, although there is a slight factual basis in that the net loss is more uniform than any one of its component factors, for predation is certain to be more important during the summer season and loss by water transport more important during the winter.

On the basis of these assumptions, equation (1) is rearranged so that the terms that have already been evaluated are on the left, with predation and death on the right:

$$A - R - \frac{1}{H} \left( \frac{dH}{dt} \right) = cS + D.$$

Numerical values for the left-hand side of the equation are determined for various times of the year, and corresponding values for $S$ are read.
from the curve in Fig. 30. The constants $c$ and $D$ can then be estimated statistically by the least squares method, and it is found that

$$A - R + \frac{1}{H} \left( \frac{dH}{dt} \right) = 0.0016S + 0.006,$$

where $S$ is the number of sagittae per m$^3$.

*Seasonal change in the herbivore population.* Fig. 31A is a graphical summation of the various factors that are believed to affect the seasonal rate of change of the herbivore population. The upper curve is the estimated rate of assimilation $A$. When the respiration rate $R$ is sub-
tracted from the assimilation rate, the result is the second curve. From it are subtracted successively the rate of consumption $C$ and the death rate by other causes $D$, yielding the bottom curve which is the estimated rate of change of the population. This curve can be approximately integrated by assigning a mean value for the rate of change during successive short intervals of time and by applying these mean rates to equation (2). The absolute size of the population, of course, depends on the integration constant $H_c$, and this constant is arbitrarily chosen so that the average population will approximate the observed one. The results are shown in Fig. 31B, in which the solid line is the theoretical population curve, and the observed population is indicated by dots connected with a broken line. The curves differ in that the ratio of maximum to minimum population is greater in the theoretical curve, and growth in the late winter and early spring is much slower than that of the observed population. Otherwise fair agreement is obtained, and it appears likely that the general mode of attack is correct, although each step in the analysis would be much improved by further study.

**SUMMARY**

1. A theoretical analysis of the seasonal cycle of zooplankton in the Georges Bank area is presented. An equation is set up in which the rate of change of the herbivore population in respect to time is equal to the difference between the rate of assimilation of organic material by feeding on the phytoplankton and the rate of dissipation by respiration, predation, and loss by various other causes.

2. With the aid of experimental data and statistical procedures, numerical values are assigned to the constants in the equation. It is then possible to construct a theoretical curve for the herbivore seasonal cycle which is in general agreement with the observed population.

3. This type of analysis is particularly useful in plankton work, since it utilizes all the available quantitative information on the biology of a particular group of organisms in a way that permits testing the overall accuracy of the results.
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