FACTORS CONTROLLING PHYTOPLANKTON POPULATIONS ON GEORGES BANK[1]

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A complex field such as oceanography tends to be subject to two opposite approaches. The first is the descriptive, in which several quantities are measured simultaneously and their inter-relationships derived by some sort of statistical method. The other approach is the synthetic one, in which a few reasonable although perhaps over-simplified assumptions are laid down, these serving as a basis for mathematical derivation of relationships.

Each approach has obvious virtues and faults. Neither is very profitable by itself; each requires the assistance of the other. Statistical analyses check the accuracy of the assumptioms of the theorists, and the latter lend meaning to the empirical method. Unfortunately, however, in many cases there is no chance for mutual profit because the two approaches have no common ground. Until such contact has been established no branch of oceanography can quite be said to have come of age. In this respect physical oceanography, one of the youngest branches in actual years, is more mature than the much older study of marine biology. This is perhaps partly due to the complexities of the material. More important, however, is the fact that physical oceanography has aroused the interest of a number of men of considerable mathematical ability, while on the other hand marine biologists have been largely unaware of the growing field of bio-mathematics, or at least they have felt that the synthetic approach will be unprofitable until it is more firmly backed by experimental data.

However valid the latter objection may be, the present paper will attempt, in the limited field of plankton biology, to establish continuity between some purely descriptive studies that have been made and mathematical concepts based on what seem to be logical assumptions about plankton physiology. The need for such an attempt has

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become apparent during the course of several plankton surveys in which the data were analyzed statistically with the idea of correlating plankton populations and their rate of growth with various environmental factors such as solar radiation, temperature, dissolved nutrient salts, *etc.* In each survey a reasonably high degree of correlation was found, but the empirical nature of the relationships was often confusing. For example, temperature affects plankton in several different ways, and the relative importance of these effects varies from time to time and from place to place. The statistical relationship of temperature and plankton represents an average of these different effects. Therefore, it may happen in examining sets of data for particular areas and times that the temperature constant varies widely from set to set, and study of the values of their constants does not lead easily to a universally applicable theory.

Furthermore, there is no good reason for assuming that the variations of plankton with environment are always linear. To treat them as such may introduce an error. To evolve nonlinear relationships on a purely empirical basis is possible, but this generally requires a larger set of observations than is readily available.

These limitations of the statistical method will become apparent in the pages that follow. The only way to avoid them is by the opposite approach—that of developing the mathematical relationships on theoretical grounds and then testing them statistically by applying them to observed cases of growth in the natural environment. At present this can be done only tentatively, with over-simplification of theory and without the preciseness of mathematical treatment that might be desired. It is not expected that any marine biologist, including the writer, would fully believe all the arbitrary assumptions that will be introduced. However, the purpose of the paper is not to arrive at exact results but rather to describe promising techniques that warrant further study and development.

ACKNOWLEDGMENTS

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STATISTICAL SECTION

Phytoplankton studies in the Georges Bank area of the western North Atlantic during the period from 1939 to 1941 have been described in a series of publications (Riley, 1941, 1942, 1943; Riley and Bumpus, 1946). In the first of these papers it was noted that part of

the variations that occurred in the distribution of phytoplankton from one part of the bank to another and from one month to the next could be correlated with such factors as the depth of water, temperature and dissolved phosphate and nitrate. Since that time the study of the zooplankton collections has been completed and examination of the data has shown that grazing by zooplankton is important in controlling the size of the phytoplankton population. With the inclusion of the zooplankton material, it is now possible to develop a relatively complete statistical treatment of the ecological relationships of the Georges Bank plankton.

Observations. The original observations made during the 1939–1940 cruises were listed in the papers cited above. This material is briefly summarized in Table I in the form of means and standard deviations for each cruise. Correlations of phytoplankton with its various environmental factors have also been published. These have been

TABLE I. MEANS AND STANDARD DEVIATIONS OF GEORGES BANK PLANKTON AND ENVIRONMENTAL FACTORS

		Sept.	*Jan.*	*Mar.*	*Apr.*	*May*	*June*
Mean	*Depth of water in meters*	247	209	135	209	82	206
	Mean temperature, upper 30 m.	15.24	4.61	2.60	3.81	5.14	9.66
	Mg-atoms phosphate P per m², upper 30 m.	14.4	33.7	34.7	21.9	16.6	19.2
	Mg-atoms nitrate N per m², upper 30 m.	153	209	172	129	285	155
	Number of animals, thousands per m²	135	14	24	32	106	103
	Plant pigments, thousands of Harvey units per m²	560	118	828	2303	871	478
σ	*Depth*	540	371	163	530	357	458
	Temperature	2.14	0.71	0.33	0.37	0.39	2.58
	P	7.2	11.1	8.1	8.9	3.5	8.7
	N	108	209	68	129	79	155
	Zooplankton	126	13	18	38	77	85
	Plant pigments	195	67	781	827	522	233

used to develop multiple correlation equations by which the variations in horizontal distribution of plant pigments during each cruise are calculated according to the variations in environmental factors. Comparison of calculated values with the actual determinations for plant pigments shows an average error on the different cruises of 20–40%. In other words 60–80% of the variations in phytoplankton on Georges Bank can be accounted for on the basis of variations in depth, temperature, phosphate, nitrate and zooplankton. The multiple correlation equations for each cruise are as follows:

$$\text{Sept.: } PP = -.011D - 23.8t + 5.20P + .371N - .26Z + 829$$
$$\text{Jan.: } PP = .191D - 61.2t + 7.96P + .956N + .47Z - 115$$
$$\text{Mar.: } PP = -D - 770t - 23.18P - 6.98N - .62Z + 4989$$
$$\text{Apr.: } PP = .469D - 331t - 61.4P + .197N - 5.31Z + 4954$$
$$\text{May: } PP = .007D + 236t + 15.1P - 2.316N - 3.50Z + 437$$
$$\text{June } PP = -.066D - 48.1t - 15.5P + .070N - .55Z + 1300$$

PP is thousands of Harvey units of plant pigments per m^2, D is depth of water, t is temperature, P is mg-atoms of phosphate P per m^2 in the upper 30 meters, N is mg-atoms of nitrate N, and Z is thousands of animals per m^2.

Discussion of the effect of environmental factors on the horizontal distribution of phytoplankton. The equations show, within the limits of error stated above, the amount of variation in the phytoplankton crop that is obtained by varying any one or all of the environmental factors. For example, at a particular station of the September cruise, if all the factors were found to have exactly the mean values as stated in Table I, then the plant pigments would be expected to have the mean value for September. If phosphate were increased one milligram-atom, it would increase the calculated value for plant pigments by the amount of the phosphate constant, or 5.2 thousands of units. If the phosphate varied a "normal" amount, as indicated by the limits of its standard deviation, the plant pigments would be changed ± 6.5%. Use of the standard deviation in this way is a convenient method of rating the importance of a given factor, and in Table II it is applied to all the variables in the equations. Although the standard deviation is a positive or negative variation around the mean, it serves a useful purpose to give the values in the table the same sign as the constant in the equation. The figures then represent the change in plant pigments produced by raising each factor from its mean to the upper limit of its standard deviation.

Table II shows that although one particular factor may be of outstanding significance, such as nitrate during the March cruise, phos-

TABLE II. Percentage Change in the Phytoplankton Crop Produced by Increasing the Value of Each Environmental Factor from Its Mean to the Limit of Its Standard Deviation

	Sept.	*Jan.*	*Mar.*	*Apr.*	*May*	*June*
Depth	−1	60	−20	11	0	− 1
Temperature	−9	−37	−31	− 5	10	−26
P	7	74	−23	−24	6	−28
N	7	41	−57	1	−21	1
Zooplankton	−6	5	− 1	− 9	−31	−10

phate in April, and zooplankton in May, there is no indication of complete control of the phytoplankton crop by a particular factor. It appears to be a highly complex relationship in which one factor after another gains momentary dominance. This table also shows that each variable has a vastly different significance at different times of the year, which is in accord with our present knowledge of phytoplankton ecology.

It has been shown (Riley, 1942) that the depth of water plays a significant role in the inception of the spring diatom flowering, and it is reasonable to find a strong negative relationship in March. This effect disappears later in the season when radiation becomes strong enough so that vertical turbulence is no longer able to prevent growth by dissipating the surface crop.

Temperature is generally supposed to have a negative effect on phytoplankton because increased respiration uses up part of the store of energy that would otherwise be used in the production of new plant material. The predominantly negative relationship shown in Table II is therefore expected. The positive relation in May is anomalous and not readily explainable.

The nutrient-phytoplankton relationship is one in which cause and effect are not clearly separable; although a large quantity of available nutrients is likely to stimulate growth, the growth-utilization process will reduce the quantity of nutrients so that the relationship becomes negative. The diversified results in Table II come from the complexities of this inter-relation. Probably the relationships are of three main types. First, in January, when the quantity of available nutrients was large and growth was slight because of low light intensity, the observed positive relationship is indicative of a slight stimulating effect by nutrients, which to a slight degree counteracted the inhibiting effect of insufficient light. Second, in spring, when radiation increased and growth became more abundant, negative relationships of the growth-utilization type were established. However, they did not become progressively stronger with the advance of the season, leading to complete exhaustion of nutrients; whether or not the observed partial exhaustion had an inhibiting effect on growth cannot be determined from these data. Third, a situation was established which was particularly apparent in September but which probably began early in the summer; in this situation the total quantity of plant pigments was fairly uniform all over the bank, but with certain localized areas of slightly higher crops accompanied by larger quantities of nutrients. These were sufficiently important to provide a direct relationship of a moderately low order between plankton and nutrients. They included some shallow water stations as well as four in deeper

water (50 to 100 m.) on the northern and western edges of Georges Bank. In all cases the vertical distribution of temperature, as well as nutrients, was more nearly uniform than at near-by stations that had smaller crops. It is concluded, therefore, that the observed relationship was due to localized turbulence and upwelling of the nutrient-rich lower waters. Probably such conditions were of transient nature, for it seems likely that a degree of regeneration strong enough to maintain a positive nutrient-phytoplankton relationship for any length of time would lead to a much larger growth than was observed.

The phytoplankton-zooplankton relationship has been discussed in some detail in a previous paper (Riley, 1946) and need be only briefly summarized here. It was concluded that the predominantly negative relationship was due to grazing. The quantities of animals and plants were such as to indicate that the observed relationship could have been established in a very short time, possibly in a day or in a few days. A theory was postulated that tidal currents and turbulent motion of the Georges Bank waters tended continually to destroy the horizontal gradients in phytoplankton, but that the zooplankton, because of their habit of vertical migration, would be absent part of the time from the surface waters where mixing processes are strongest, and hence they would not be so readily dispersed. Therefore, they would tend constantly to reestablish the phytoplankton gradients by their grazing activity.

Effect of Environmental Factors on the Seasonal Cycle of Phytoplankton. It is apparent from the preceding discussion that the relationship of a particular environmental factor with the horizontal distribution of phytoplankton may differ from one month to another both in quantity and in kind. Nevertheless, there are seasonal trends in these factors which are related with plankton variations, as can be observed by inspection of the data in Table I. Thus the seasonal cycle of phytoplankton can be correlated with its environment with a fair degree of accuracy, even though such treatment makes no allowance for special effects that are operative only at particular times during the year.

A multiple correlation equation was developed from the cruise averages in Table I. It is

$$PP = -153t - 120P - 7.3N - 9.1Z + 6713.$$

The symbols are the same as in previous equations. The relation between the observed cruise averages and the values determined from the equation is shown in Fig. 14. The average error between observed and calculated values is 20%, which is slightly less than that obtained in the treatment of individual cruises. Probably the errors caused by

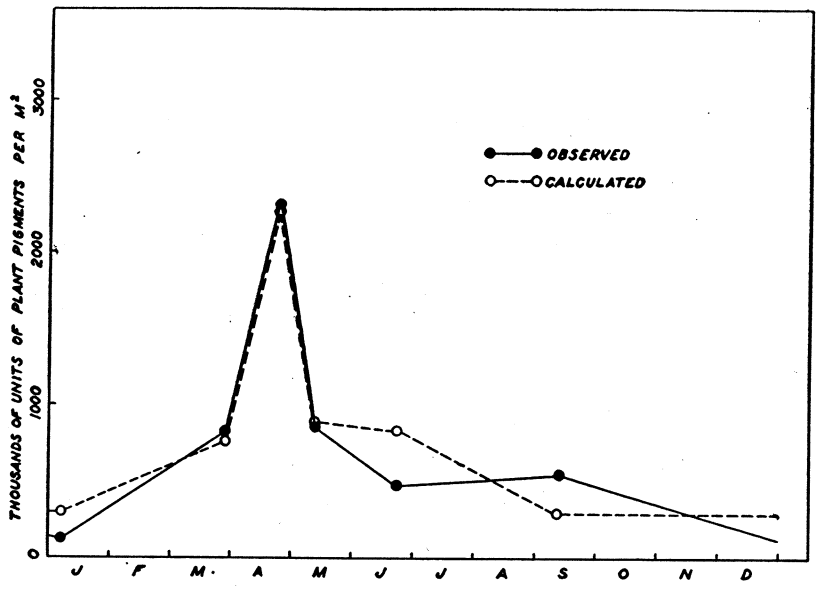

Figure 14. Comparison of the observed phytoplankton population with the calculated population as determined by a multiple correlation analysis of the relationship between phytoplankton and environmental factors.

ignoring certain special seasonal effects are more than counterbalanced by the reduction in analytical errors when averages are used for the calculation.

THEORETICAL SECTION

The rate of change of the phytoplankton population is determined by the difference in reaction rates between the process of accumulation of energy by the population and the processes of energy dissipation. It will be assumed that all the important reaction rates are included in the equation

$$\frac{dP}{dt} = P\,(P_h - R - G)\,, \tag{1}$$

in which the rate of change of the population P in respect to time is determined by the photosynthetic rate per unit of population (P_h), the rate of phytoplankton respiration (R), and the rate of grazing by zooplankton (G). Each of these rates is subject to environmental influences and therefore is continually changing with the seasons. In order to arrive at a practical solution of the equation it is necessary to examine each of its component parts in the light of present day plankton physiology.

A second major assumption will be that seasonal variations in environmental factors used in the analysis can be expressed by smooth curves drawn through the observed cruise averages. Since the latter are relatively incomplete, as far as the whole yearly cycle is concerned, there must be a certain amount of unavoidable error in the calculations.

Photosynthesis. Numerous investigators have reported that the photosynthetic rate in actively growing diatom cultures is proportional to light intensity within wide limits. The lower limit has not been determined accurately due to the insensitivity of the methods of measurement, but values of the right order of magnitude have been detected at depths where the light intensity was about 0.1–1.0% of the surface intensity in summer (Clarke, 1936). The upper limit of the proportionality is variable, depending on the species and the length of exposure; the optimum intensity for photosynthetic activity in particular situations has been reported to range from 1.8 g. cal. per cm² per hour (Jenkin, 1937) to 60 g. cal. (Curtis and Juday, 1937).

During the six cruises to Georges Bank between September 1939 and June 1940 two bottles of surface water were taken at each station and suspended in a tub of water on deck, one of them being covered with a bag of several thicknesses of dark cloth. After twenty-four hours' exposure the oxygen in the two bottles was measured and the difference in their oxygen content was used as a rough estimate of the photosynthetic activity of the surface plankton. The inset in Fig. 15 shows the average photosynthetic rate[2] obtained on each cruise plotted against the average incident solar radiation in the area at that time of year. Radiation values are obtained from data published by Kimball (1928) and reproduced in Sverdrup, Johnson and Fleming (1942: 103). The plotted points for the January, March, April and May cruises approximate a linear relationship in which the photosynthetic rate equals 2.5 times the incident radiation in g. cal. per cm² per minute. The June and September rates are lower, but it will be shown later that this can be explained as a result of nutrient depletion.

With these facts at hand the mean photosynthetic rate of the population will be estimated according to the following assumptions:

1. When nutrient depletion does not limit photosynthesis,

$$P_h = pI \qquad (2)$$

[2] The photosynthetic rate is expressed as grams of carbon produced per day per gram of carbon in the surface phytoplankton crop, using the formula photosynthetic rate = .375 × oxygen production in g/m³/day ÷ 17 × 10^{-6} Harvey units of plant pigments/m³. The conversion factor is based on analyses described in a previous paper on the plankton of Georges Bank (Riley, 1941).

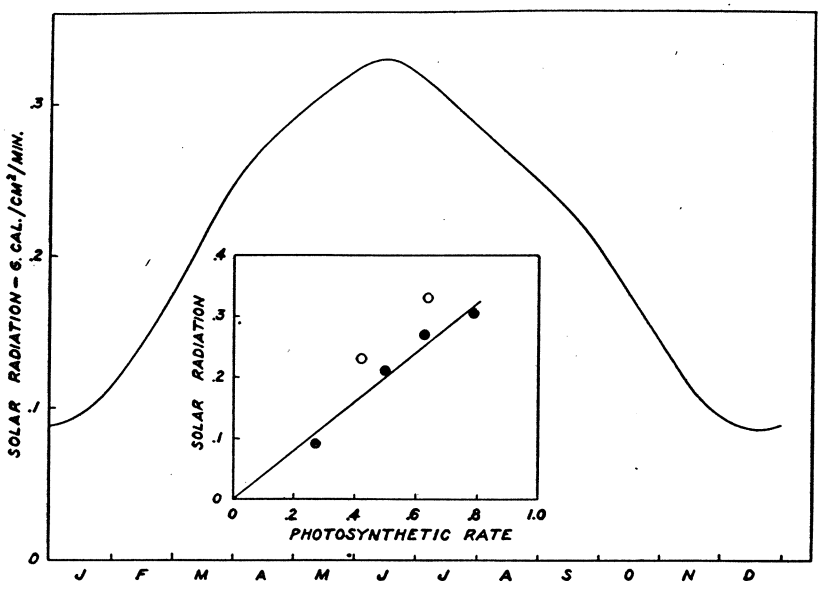

Figure 15. Seasonal variations in average incident solar radiation in the Georges Bank area. Inset shows average observed surface photosynthetic rate plotted against incident radiation. Dots are averages for January, March, April and May; circles are June and September.

in which P_h is the photosynthetic rate, I is radiation in g. cal./cm²/ minute at the depth of the photosynthesizing plankton, and p, the photosynthetic constant, is 2.5.

2. The intensity at the surface, I_o, may be determined for any time in the year from the curve in Fig. 15, which is based on Kimball's data, cited above.

3. The intensity at any other depth z is determined from the formula

$$I_z = I_o e^{-kz}$$

and therefore

$$P_{hz} = pI_o e^{-kz}. \qquad (3)$$

In these formulas the extinction coefficient k is defined as 1.7 divided by the depth of the Secchi disc reading, a rough conversion factor suggested by Poole and Atkins (1929). Secchi disc determinations for the Georges Bank area are shown in Fig. 16.

4. According to equation (3) the photosynthetic rate approaches zero as the depth approaches infinity. But the depth at which a measurable and significant amount of photosynthesis occurs is limited, and so is the depth at which viable phytoplankton can be found.

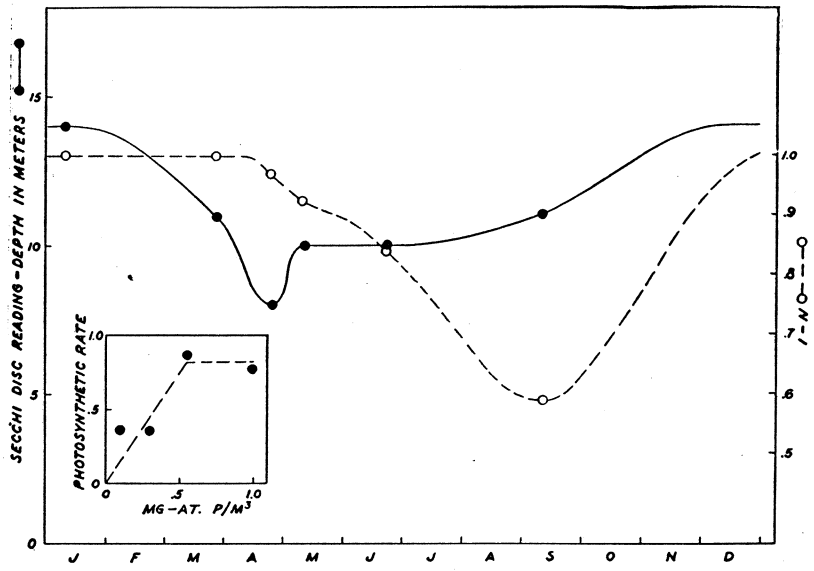

Figure 16. Solid curve is transparency as determined by Secchi disc readings. Dotted line is the estimated reduction in photosynthetic rate caused by nutrient depletion. Inset shows averages of photosynthetic rate plotted against phosphate concentration during June and September.

Therefore, it is convenient to set an arbitrary limit to the depth of the euphotic zone. This depth will be called z_1 and will be defined as the depth at which the light intensity has a value of 0.0015 g. cal./cm²/minute. This approximates the intensity at the maximum depth of photosynthesis as reported by Clarke (1936). Calculated values for z_1 are shown in Fig. 17.

5. To find the mean photosynthetic rate in the euphotic zone, equation (3) is integrated from the surface to z_1, and divided by z_1:

$$\overline{P_h} = \frac{pI_o \int_o^{z_1} e^{-kz}\,dz}{z_1} = \frac{\dfrac{pI_o}{-k}\, e^{-kz}\Big|_o^z}{z_1}$$

$$\underset{o \to z_1}{\overline{P_h}} = \frac{pI_o}{kz_1}(1 - e^{-kz_1}). \qquad (2)$$

6. It was postulated that the proportionality between photosynthesis and radiation holds only when nutrients are abundant. The fact noted previously that the ratio between the photosynthetic rate and light intensity was reduced in June and September led to an in-

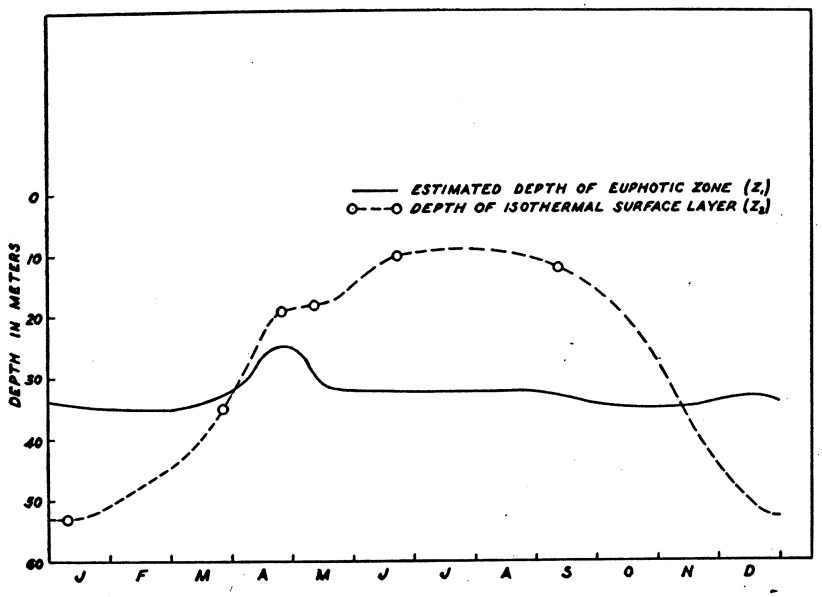

Figure 17. Estimated depth of the layer in which a measurable amount of photosynthesis occurs (z_1), and the depth of the virtually isothermal surface layer (z_2).

vestigation of nutrients as a possible cause. Large individual variations were found, and the correlation between photosynthetic rate and phosphate concentration was poor; nevertheless, when the rates were averaged for different ranges of phosphate concentration, there was a pronounced reduction in the average rate when the phosphate fell below about 0.5 to 0.6 mg-atom of P per m³ (Fig. 16, inset). Ketchum (1939) reported a decrease in the growth rate of experimental cultures of *Nitschia closterium* when the phosphate concentration was less than 50 gamma of PO_4 per liter (0.55 mg-atom per m³). Therefore it seems reasonable to assume that the mean photosynthetic rate as determined in equation (4) should be multiplied by a factor $(1 - N)$, in which N is the reduction in rate due to nutrient depletion. According to the facts above,

$$N = \frac{0.55 - \textit{mg-at. } P/m^3}{0.55} \qquad \text{when } P \leq 0.55.$$

Mean values for $(1 - N)$ are shown in Fig. 16.

7. Several investigators have pointed out the importance of vertical turbulence in reducing phytoplankton crops by carrying the breeding stock below the euphotic zone. That this is an important phenomenon on Georges Bank has been demonstrated (Riley, 1942). If turbulence

is such that each phytoplankton cell spends only a certain proportion of its time in the euphotic zone, then the mean photosynthetic rate of the population as a whole will be reduced. Therefore equation (4) should be multiplied by still another factor $(1 - V)$, in which V is the reduction in rate produced by vertical water movements. It is impossible to define V in any simple way that will be entirely satisfactory, but as an approximation,

$$(1 - V) = \frac{z_1}{z_2} \text{ when } z_1 \leqq z_2,$$

in which z_1 is the depth of the euphotic zone as previously defined and z_2 the depth of the mixed layer, which is arbitrarily defined as the maximum depth at which the density is no more than 0.02 of a σ_t unit greater than the surface value. Fig. 17 shows the estimated values for z_1 and z_2 for Georges Bank.

The final equation for the mean photosynthetic rate is now

$$P_h = \frac{pI_o}{kz_1}(1 - e^{-kz_1})(1 - N)(1 - V). \tag{5}$$

The application of the equation to the Georges Bank data is shown in Fig. 18. The upper curve shows the primary calculation of the photo-

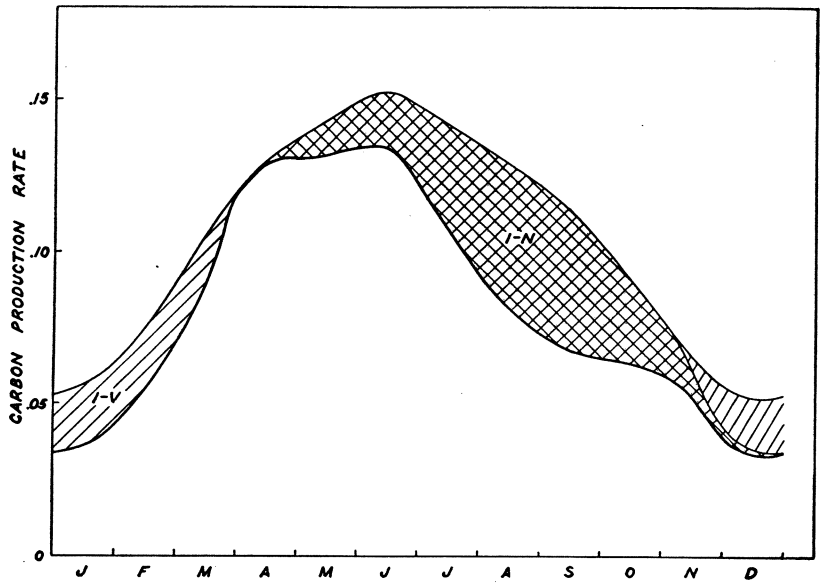

Figure 18. Estimated mean photosynthetic rate. Upper curve is the maximum possible rate as determined by incident radiation and transparency. Lower curve is the estimate obtained by introducing correction factors for the effects of vertical turbulence and nutrient depletion.

synthetic rate based on light intensity. The reduction obtained by introducing $(1 - N)$ and $(1 - V)$ is indicated by hatched areas. The heavy lower curve is the final estimate of the mean photosynthetic rate.

Phytoplankton respiration. The few available measurements of the respiration of pure diatom cultures have not yielded precise results. Observed rates have varied from one species to another as well as during different stages of growth of the same culture. The recorded values differ by a factor of 10 to 20, and there are not enough of them to draw a good average.

No direct measurements have been made of the respiration of a natural phytoplankton population, since the measured oxygen consumption also includes zooplankton and bacterial respiration. Statistical estimates have been made by the writer on the basis of the observed correlation between phytoplankton and total oxygen consumption. The best of these, judging by quantity and homogeneity of data, was obtained in Long Island Sound (Riley, 1941a). It was estimated that in winter (average temperature 2.05° C.) the respiration rate was 0.024 ± 0.012 mg. of carbon consumed per day per mg. of phytoplankton carbon. Calculations based on summer observations suggested that the respiration increased with higher temperatures (0.110 ± 0.007 at 17.87° C.), the rate being approximately doubled by a 10° increase in temperature.

On the basis of these rather scanty data it will be assumed that:

1. The temperature effect can be stated as

$$R_T = R_o e^{rT} \qquad (6)$$

in which R_T is the respiratory rate at any temperature T, R_o is the rate at 0° C. and r is a constant expressing the rate of change of the respiratory rate with temperature. The value of r is 0.069 when the rate is doubled by a 10° increase in temperature. The seasonal cycle of Georges Bank surface temperatures used in computing respiratory rates is shown in Fig. 19.

2. The value chosen for R_o will be 0.0175. This is the mean of the two estimates derived from the Long Island Sound data mentioned above, in which the calculated values of R_o for winter and for summer are respectively 0.020 and 0.015.

Grazing. The greater part of the zooplankton population consists of filter-feeding organisms which tend to strain a relatively constant volume of water in a given time irrespective of the quantity of food material in it. Therefore a fixed proportion of the phytoplankton population will be consumed in successive units of time. This is stated as

$$G = gZ\,, \qquad (7)$$

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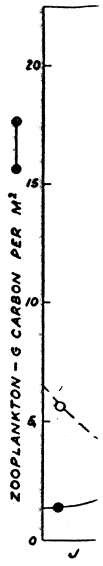

Figure 19. volume by th vol. in cc.) to temperature.

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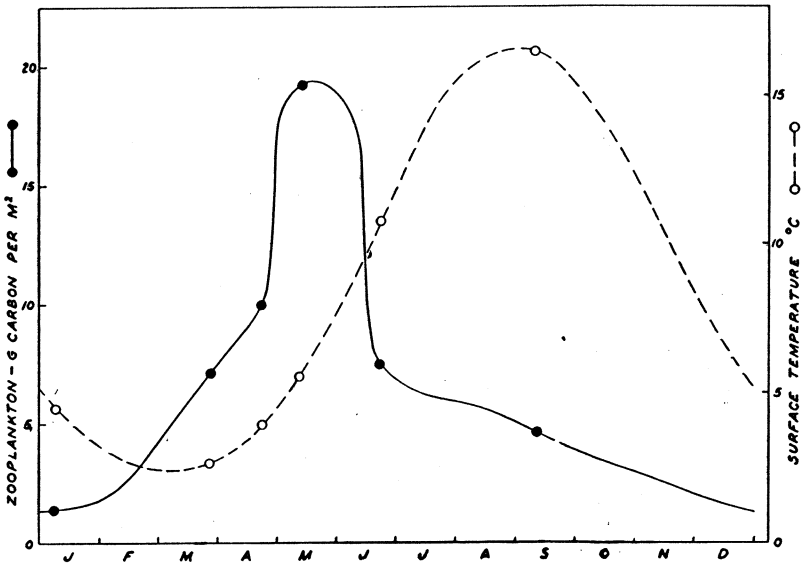

Figure 19. Solid line is the seasonal cycle of zooplankton. Measurements of zooplankton volume by the displacement method are treated by a conversion factor (wt. in g. = 12.5% × vol. in cc.) to derive a rough estimate of the carbon content. Dotted line is the mean surface temperature.

in which G is the rate of grazing, g is the rate of reduction of phytoplankton by a unit quantity of animals and Z is the quantity of zooplankton in grams of carbon per m².

There is some question as to whether g is nearly constant over long periods of time or undergoes a marked seasonal change. On the one hand there are the experiments of Marshall, Nicholls and Orr (1935) which showed that the respiratory rate of *Calanus finmarchicus* increases with increasing temperature, implying a greater food requirement at higher temperatures and possibly an increased filtering rate. On the other hand, feeding experiments by Fuller (1937) showed variations of a more complex nature. The grazing rate of *Calanus finmarchicus* was greater at 8° C. than at 3° or 13° C., and animals captured in the late summer, when the natural breeding stock was declining, had lower feeding rates than those studied earlier in the summer. Thus a factor that can be called "depressed physiological state" for want of a more precise term appears to counterbalance the expected effect of high temperature late in the summer. It is clear that the whole process of zooplankton feeding requires much more thorough study. However, lacking the necessary information to de-

scribe the process accurately, it is believed that it can best be approximated by the simple form of equation (7).

The value of g must be of an order of magnitude which will at least satisfy the minimum respiratory requirements of the zooplankton population at times when the latter is stable. According to Marshall, Nicholls and Orr (1935), the daily food requirement of *Calanus* in winter (5° C.) lies between 1.3 and 3.6% of the carbon content of the animals. This estimate applied to the January plankton on Georges Bank yields a grazing constant of 0.0091 to 0.0252. In summer (15° C.), these authors suggest a food requirement of 1.7–7.6%, for which the corresponding values of g are 0.0084 to 0.0374 in September on Georges Bank. The latter estimates are perhaps too high, since the zooplankton was decreasing at a rate of 0.5% per day and therefore probably was not getting enough food to satisfy the minimum respiratory requirements. If it is assumed that the food intake equaled the food requirement minus the rate of population decrease, then the food intake was 1.2–7.1% of the animals' carbon content per day, and the corresponding values for g are 0.0059 and 0.0350.

Within these wide limits it is difficult to choose a correct value for the grazing constant, and again the need for more experimental work is apparent. On a purely empirical basis, a good fit for the data is obtained by using the average of the minimum values of g for the September and January cruises, namely 0.0075. This factor, multiplied by the quantity of zooplankton, shown in Fig. 19, estimates the Georges Bank grazing rate.

Conclusions. The original equation

$$\frac{dP}{dt} = P\,(P_h - R - G)$$

can now be expanded by substituting the right hand terms of equations (5), (6) and (7):

$$\frac{dP}{dt} = P\left[\frac{pI_o}{kz_1}\,(1 - e^{-kz_1})\,(1 - N)\,(1 - V) - R_o e^{rT} - gZ\right]. \quad (8)$$

The rate of change of the population is dependent on six ecological variables: the incident solar radiation, transparency of the water, the quantity of phosphate, the depth of the mixed layer, the surface temperature and the quantity of zooplankton. The results of the application of equation (8) to the Georges Bank data are shown graphically in Fig. 20. The curve at the top is the photosynthetic rate previously illustrated (Fig. 18). The second curve is the photosynthetic rate minus the respiratory rate of the phytoplankton, or in other words the

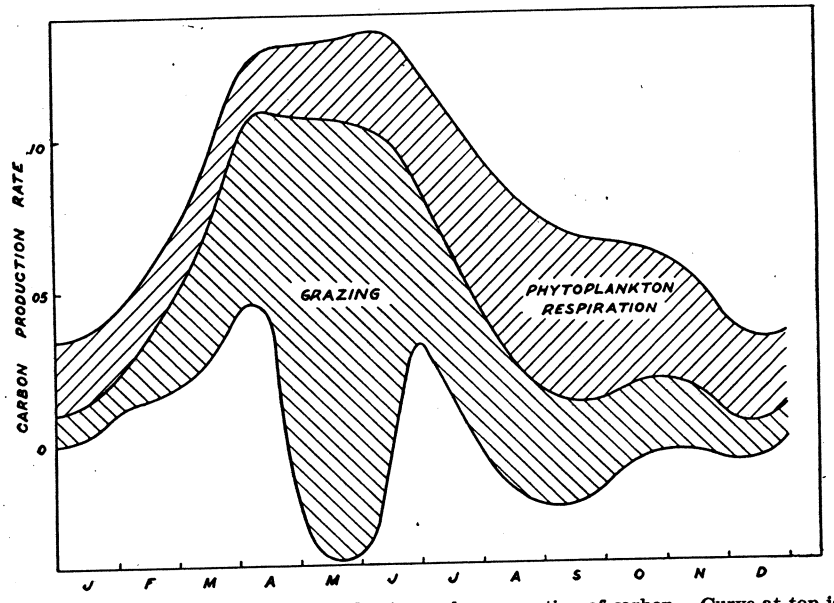

Figure 20. Estimated rates of production and consumption of carbon. Curve at top is the photosynthetic rate. By subtracting the respiratory rate the second curve is obtained, which is the phytoplankton production rate. From this is subtracted the zooplankton grazing rate, yielding the curve at the bottom, which is the estimated rate of change of the phytoplankton.

phytoplankton production rate. By subtracting the grazing rate from the production rate, the rate of change of the population is obtained. This is the bottom curve of Fig. 20. Numerical values used in drawing these curves are shown in the appendix.

Equation (8) cannot be integrated readily, but an approximation is obtained by integrating over successive short intervals of time and assuming for each variable a constant, average value during that time. Thus the change in population in the time interval 0 to t is determined by

$$lnP_t - lnP_o = \overline{P_h} - \overline{R} - \overline{G}.$$

Therefore, by a series of integrations the quantity $lnP_t - lnP_o$ can be approximated for the whole seasonal cycle. This quantity indicates the relative size of the population from one part of the cycle to another. To convert to absolute terms requires evaluation of the integration constant P_o (the size of the population at the minimum point in the cycle), which is readily obtained if the quantity of plankton (P_t) is measured at one or more times during the year. In the present case, in which six cruise averages are available, P_o was statistically deter-

mined so as to give the best fit for the data. The results are shown in Fig. 21, in which the theoretical population cycle is shown by a smooth curve, and the observed cruise averages are indicated by dots. The average error is 27%.

It is now apparent that a few simple and commonly measured environmental factors can be used with a fair degree of accuracy to evaluate the quantitative aspects of the seasonal cycle of phytoplankton. Furthermore, this can be done in two different ways: first by statistical comparison of the simultaneous variations of phytoplankton and environmental characteristics in a particular locality; second, by theoretical evaluation of the way in which changes in the environment might affect growth as evidenced by the results of various physiological experiments. Each of these methods has something to contribute to plankton biology. The statistical method is useful in determining whether a particular factor is significant; the theoretical method carries on from there, discriminating between cause and effect and helping to establish certain quantitative relationships that are not likely to be derived empirically.

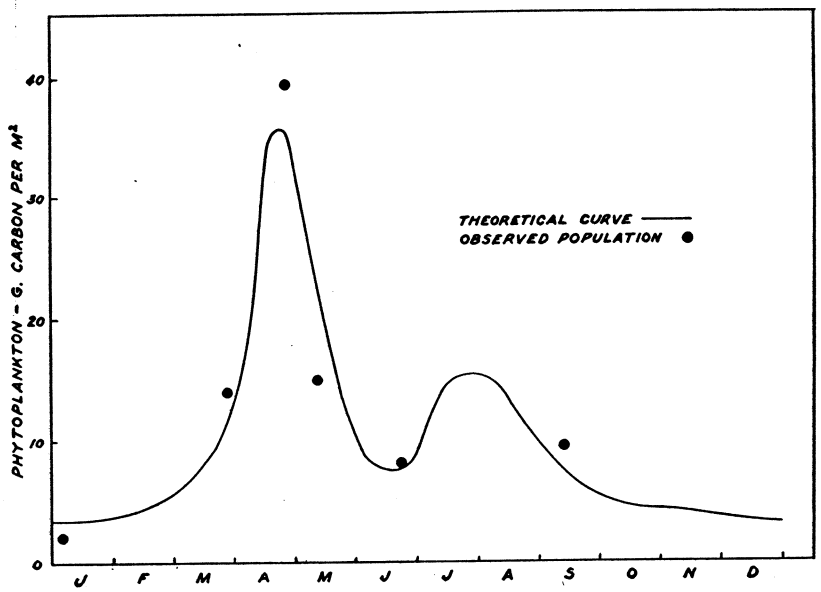

Figure 21. Curve shows the calculated seasonal cycle of phytoplankton, determined by approximate integration of the equation for the rate of change of the population. For comparison the observed quantities of phytoplankton are shown as dots.

While these methods are obviously crude at the present time and need to be developed further, both by examination of other areas and by better experimental evaluation of constants, it does not seem too much to hope that they will eventually solve some of the problems of seasonal and regional variations that puzzle marine biologists today.

SUMMARY

1. Variations in the phytoplankton population of the Georges Bank area are correlated with various environmental factors. Equations are developed statistically by which the size of the population can be calculated on the basis of such factors as temperature, depth of water, and the quantities of nitrate, phosphate and zooplankton. Calculated horizontal variations in the plankton crop at various times in the year differ from observed values by about 20–40%. Calculations of the seasonal variation of the average crop in the area are accurate within about 20%.

2. The seasonal cycle of phytoplankton is also evaluated from a more theoretical standpoint. It is postulated that the rate of change of the phytoplankton population is equal to the photosynthetic rate minus the phytoplankton respiratory rate minus the grazing rate of the zooplankton. Factors affecting these rates are discussed, and the ones that are considered particularly important are solar radiation, temperature, transparency of the water, the depth of the isothermal surface layer, phosphate, and zooplankton. The observed variations of these factors are combined with appropriate constants derived from experimental data to develop an equation that expresses the seasonal rate of change of the phytoplankton population. Approximate integration of the equation yields a population curve of the same order of accuracy as the statistical estimate.

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APPENDIX

NUMERICAL VALUE OF QUANTITIES USED IN THE CALCULATION OF THE SEASONAL RATE OF CHANGE OF THE GEORGES BANK PHYTOPLANKTON POPULATION AS DEVELOPED IN THE THEORETICAL SECTION OF THIS PAPER

Date	I_o	k	z_1	$1-N$	z_2	$1-V$	P_h	T	R_T	Z	G	dP/dt	$lnP_t - lnP_o$	lnP_t	P_t
1/1	.088	.121	34	1.00	53	.64	.034	5.2	.024	1.3	.010	.000	.000	1.217	3.4
1/15	.094	.121	34	1.00	53	.64	.036	4.1	.023	1.4	.011	.002	.030	1.247	3.5
2/1	.112	.124	35	1.00	51	.69	.044	3.2	.021	1.7	.013	.010	.180	1.397	4.0
2/15	.138	.128	35	1.00	48	.73	.055	2.7	.021	2.6	.020	.014	.390	1.607	5.0
3/1	.174	.136	35	1.00	45	.78	.071	2.4	.021	4.2	.031	.019	.675	1.897	6.7
3/15	.212	.145	34	1.00	40	.85	.091	2.5	.021	5.8	.043	.027	1.080	2.297	10.0
4/1	.247	.159	32	1.00	32	1.00	.120	2.7	.021	7.5	.056	.043	1.725	2.942	19.1
4/15	.272	.200	26	1.00	23	1.00	.130	3.4	.021	8.9	.067	.042	2.355	3.572	35.5
5/1	.290	.205	25	.95	19	1.00	.131	4.5	.024	17.2	.129	−.022	2.025	3.242	25.7
5/15	.306	.170	31	.92	18	1.00	.132	5.9	.026	19.3	.145	−.039	1.440	2.657	14.2
6/1	.321	.170	32	.90	15	1.00	.134	7.6	.030	18.8	.141	−.037	.885	2.102	8.2
6/15	.329	.170	32	.88	11	1.00	.134	9.7	.035	14.0	.105	−.006	.795	2.012	7.5
7/1	.319	.170	32	.82	10	1.00	.122	11.8	.038	6.9	.052	.032	1.275	2.492	12.1
7/15	.302	.170	31	.76	9	1.00	.108	13.9	.045	6.2	.047	.016	1.515	2.732	15.4
8/1	.284	.165	32	.69	9	1.00	.093	15.5	.051	6.0	.045	−.003	1.470	2.687	14.8
8/15	.267	.162	32	.63	10	1.00	.081	16.3	.054	5.7	.043	−.016	1.230	2.447	11.5
9/1	.250	.159	32	.60	11	1.00	.073	16.6	.056	5.1	.038	−.021	.915	2.132	8.4
9/15	.230	.154	33	.59	13	1.00	.067	16.4	.054	4.5	.034	−.021	.600	1.817	6.1
10/1	.204	.145	34	.63	16	1.00	.065	15.5	.051	3.9	.029	−.015	.375	1.592	4.9
10/15	.174	.138	34	.69	20	1.00	.063	14.2	.045	3.3	.025	−.007	.270	1.487	4.4
11/1	.144	.131	35	.77	27	1.00	.060	12.4	.040	3.2	.024	−.004	.210	1.427	4.2
11/15	.115	.126	35	.85	37	.95	.053	10.5	.037	2.6	.020	−.004	.150	1.367	3.9
12/1	.094	.121	34	.92	45	.76	.039	8.5	.031	2.0	.015	−.007	.045	1.262	3.5
12/15	.086	.121	33	.97	50	.66	.033	6.7	.028	1.6	.012	−.007	−.060	1.157	3.2

I_o = incident solar radiation in g. cal./cm² 1 /cm²/minute

k = extinction coefficient = 1.7/Secchi disc reading in meters

z_1 = depth of euphotic zone in meters, defined as depth where the light intensity is .0015 g. cal.

$1 - N$ = correction factor for nutrient depletion = mg-at. phosphate P/0.55 when $P \leqq 0.55$.

z_2 = depth of mixed layer = maximum depth at which $\sigma_{tz} - \sigma_{t_o} \leqq 0.02$.

$1 - V$ = correction factor for vertical turbulence = z_1/z_2 when $z_1 \leqq z_2$.

P_h = estimated mean photosynthetic rate according to equation (5) in text.

T = mean surface temperature.

R_T = estimated phytoplankton respiration according to equation (6).

Z = g. of zooplankton carbon/m², estimated on the assumption that the weight of carbon in grams = 12.5% of the volume (by displacement) in cubic centimeters.

G = grazing rate = $0.0075Z$

dP/dt = rate of change of the phytoplankton population = $Ph - R - G$.

$lnP_t - lnP_o$ = the summation of 15 × dP/dt (since the rate determinations are at approximately 15-day intervals)

$lnP_t = lnP_t - lnP_o + 1.217$. The latter is a value for P_o determined statistically as the best fit for the observed population data.

P_t = estimated population in g. of phytoplankton carbon/m² (considered equivalent to 17 × Harvey units of plant pigments × 10^{-6}/m²).