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PHYTOPLANKTON-ZOOPLANKTON RELATIONSHIPS ON GEORGES BANK[1]

BY

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INTRODUCTION

Comparisons of different oceanic regions often suggest that in the largest sense there is a direct relationship between phytoplankton and zooplankton—that is, banks and coastal areas with large concentrations of phytoplankton are likely to be rich in zooplankton, while sparser crops of both occur in deep oceanic waters. On the other hand, surveys of particular areas often show an inverse relationship, with local swarms of zooplankton occurring in phytoplankton-poor waters, alternating with dense patches of phytoplankton containing few animals. Harvey, Cooper, LeBour and Russell (1935) explained the inverse relationship observed in the English Channel as a grazing phenomenon, while Hardy and Gunther (1935) advanced the theory of animal exclusion, which postulated avoidance of phytoplankton patches by the animals. Steemann Nielsen (1937) and Clarke (1939) elaborated the theory of the grazing phenomenon with particular emphasis on the time factor, pointing out that the presence of a swarm of adult copepods is the result of weeks of growth and is dependent on the quantity of phytoplankton available throughout the growth period. Thus, as described by Marshall, Nicholls and Orr (1934), it is possible for such a swarm to pass successfully through its developmental stages at the same time as (and possibly as a direct result of) a diatom flowering. In such a case two relationships between phytoplankton and zooplankton might be described: (1) a direct correlation between a diatom flowering and the swarm of copepods to which it eventually gives rise, and (2) an inverse relation obtained by comparing an area in which the zooplankton eventually grazes the phytoplankton to a low level with other localities in which this has not occurred.

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OBSERVATIONS ON GEORGES BANK

Fig. 11A shows the mean total phytoplankton and zooplankton populations of Georges Bank as determined during cruises made in 1939 and 1940 (Clarke, Pierce and Bumpus, 1943; Riley, 1941). The seasonal cycles are similar to those in numerous other localities, with spring phytoplankton and summer zooplankton maxima, mid-winter minima for both, and a gradual upward trend in the zooplankton population during the development of the spring diatom flowering; these are followed by a sharp increase in the number of animals in late April and early May, coincident with the decline of the diatom burst. Thus the seasonal trend in the phytoplankton-zooplankton relationship is direct in the early spring and inverse later.

Analysis of individual station records reveals that the horizontal distribution of plant and animal plankton varied from one month to the next in a way that reflected the general seasonal trend. During March, areas in which the spring diatom flowering was beginning were also foci of zooplankton increase. In May, on the other hand, there was little zooplankton in areas of diatom abundance, the latter being sparse in places where zooplankton growth had attained large proportions. Correlations were prepared showing the relationship between the horizontal distribution of phytoplankton and zooplankton on each of the cruises. These are plotted in Fig. 11B. They show clearly the moderately high direct relationship in March and the highly significant inverse relation in May. During the other cruises the correlations were statistically insignificant.

Further facts of interest in this connection are revealed by examination of the seasonal cycles and horizontal distribution of individual species and genera of zooplankton. Fig. 12 shows the cycles of eight of the more important groups and their correlations with total phytoplankton. Seasonal minima were generally accompanied by zero or positive correlations, and in most cases there was a positive correlation at the time when the species was beginning to increase. In each case there was a negative correlation with phytoplankton at the time when the species reached its seasonal peak. All these correlations were either statistically significant or significantly different from the preceding positive correlation, except in the case of Centropages, for which no preceding data are available. Animals such as decapod nauplii and *Pseudocalanus minutus*, which developed a peak population slowly, also showed a slowly declining correlation with phytoplankton, while in other groups both changes were more rapid. Thus, it is evident that individual zooplankton groups showed relationships with phytoplankton in their horizontal distribution that were similar to

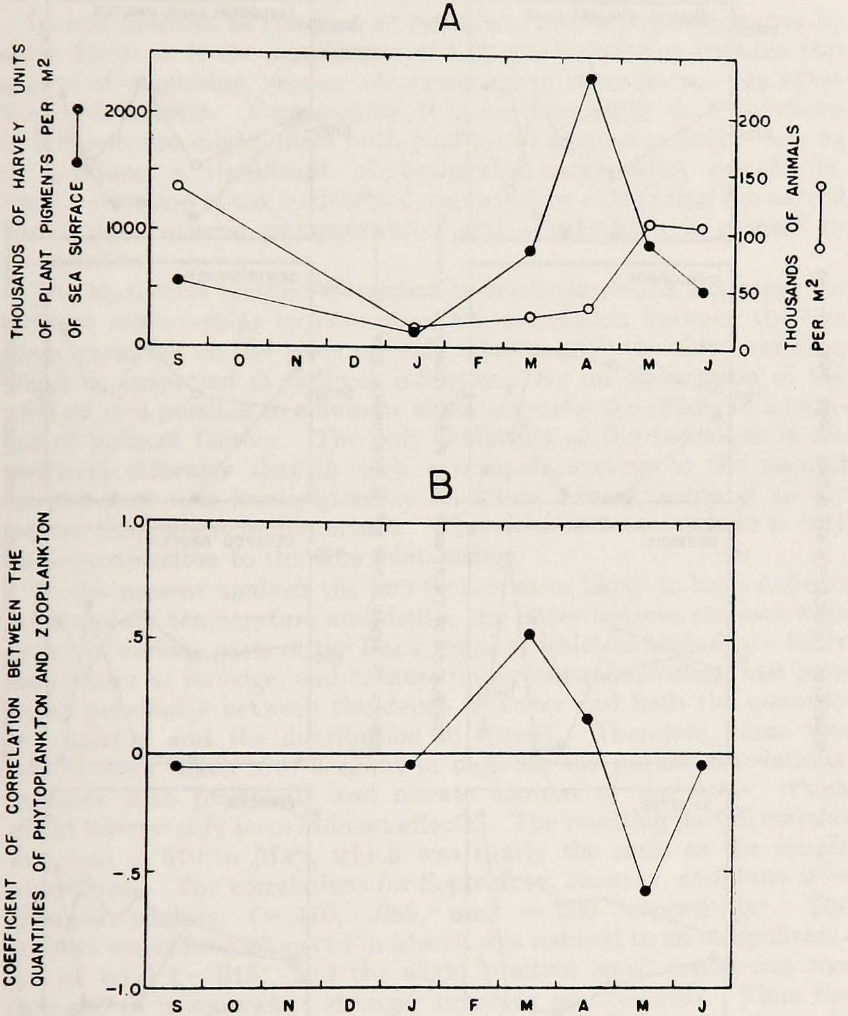
A
THOUSANDS OF HARVEY UNITS OF PLANT PIGMENTS PER M2 OF SEA SURFACE
2000
1000
0
THOUSANDS OF ANIMALS PER M2
200
150
100
50
0
S
O
N
D
J
F
M
A
M
J
B
COEFFICIENT OF CORRELATION BETWEEN THE QUANTITIES OF PHYTOPLANKTON AND ZOOPLANKTON
1.0
.5
0
-.5
-1.0
S
O
N
D
J
F
M
A
M
J

Figure 11.

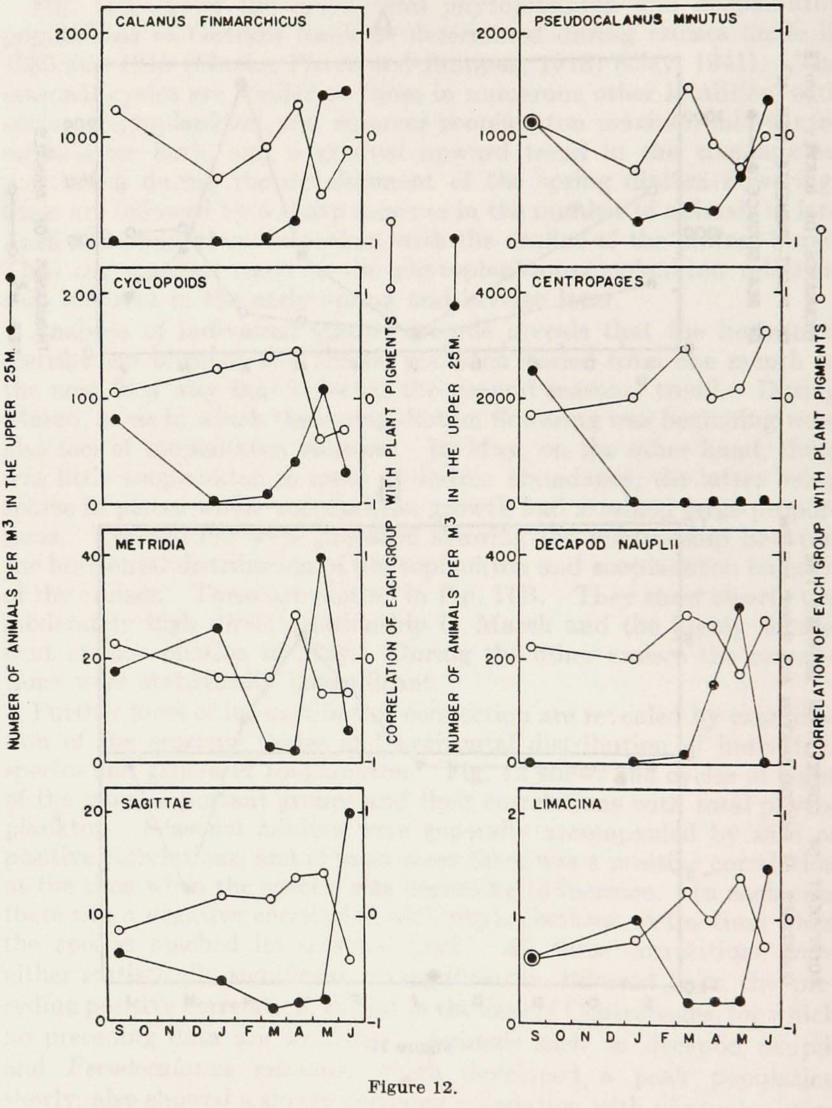
CALANUS FINMARCHICUS
PSEUDOCALANUS MINUTUS
CYCLOPOIDS
CENTROPAGES
METRIDIA
DECAPOD NAUPLII
SAGITTAE
LIMACINA
NUMBER OF ANIMALS PER M3 IN THE UPPER 25M.
CORRELATION OF EACH GROUP WITH PLANT PIGMENTS
2000
1000
0
200
100
40
20
20
10
4000
2000
400
200
2
1
1
0
-1
S O N D J F M A M J
S O N D J F M A M J

Figure 12.

those of the total population, and this is particularly significant in that their seasonal peaks appeared at different seasons of the year.

In any problem as complex as plankton relationships there may be some doubt as to the significance of a simple correlation between two groups of organisms, because obviously many other factors can affect their relationship. For example, it is not impossible that variations in temperature might affect both plants and animals in such a way as to produce a significant phytoplankton-zooplankton correlation. Such a situation could be detected, however, by calculating the partial correlation between phytoplankton and zooplankton in respect to temperature.

The statistical method of partial correlations makes allowance for indirect relationships by correcting the correlation between the two main variables on the basis of their relation with the third variable, which is suspected of indirect influence. By an elaboration of the method it is possible to eliminate simultaneously the effects of a number of indirect factors. The only limitation of the technique is the practical difficulty that in such a complex system as the natural environment it is hardly possible to obtain measurements of all the factors that might be important. Therefore such an analysis is only an approximation to the true relationship.

In the present analysis the two factors most likely to have indirect influence are temperature and depth, the latter because stations were made on various parts of the Bank, some of which extended into fairly deep water at its edge, and because important relationships had been noted previously between the depth of water and both the quantity of plankton and the distribution of species. Therefore, these two factors were taken into account in deriving the partial correlations, together with phosphate and nitrate content of the water, which might conceivably have indirect effects. The resulting partial correlation was −.510 in May, which was nearly the same as the simple correlation. The correlations for September, January, and June were changed slightly (−.170, .089, and −.200 respectively). The positive correlation observed in March was reduced to an insignificantly low level (−.015), and the slight positive April correlation was changed to a somewhat stronger negative one (−.246). Thus the direct relation between phytoplankton and zooplankton in the early spring can be explained as the product of other factors of the environment, but there is nothing in the available data that denies the biological significance of the negative correlation observed in May.

DISCUSSION

Negative Phytoplankton-Zooplankton Correlation and Grazing Effect. It is apparent that the plant-animal relationship on Georges Bank is similar to that observed in many other regions in the springtime and therefore might be described as a grazing or animal exclusion phenomenon. There are two reasons, however, for believing that the latter cannot be applied in this particular case. First, the vertical distribution of phytoplankton on Georges Bank was too nearly constant to favor the method of avoidance by vertical migration postulated by Hardy. Second, the time of greatest negative correlation varied from one species to another. It apparently had nothing to do with the richness of the phytoplankton crop which supposedly sets up the avoidance reaction. Rather, the negative correlation, both in total zooplankton and in individual species, was greatest when the zooplankton reached its peak, irrespective of the quantity of phytoplankton in the water at that time. This points to the grazing phenomenon as the cause of the relationship.

The quantitative aspects of the relationship are further elaborated in Tables I and II. The first two columns of Table I show the average values for phytoplankton and zooplankton during each cruise. The values for phytoplankton were determined according to the Harvey plant-pigment method and are listed as thousands of "Harvey units" per m². The partial correlations are used to calculate regression equations for the phytoplankton-zooplankton relationship. By this means a quantitative estimate of grazing is derived from the observed negative correlations, and the constants for the regression equations are listed in the third column in terms of phytoplankton (Harvey units x 1000) consumed per 1000 animals. The product of the constants and the mean quantity of animals is an estimate of the total amount of grazing during the time required to develop the correlation,

TABLE I. Mean Quantities of Plankton on Georges Bank and Estimates of the Grazing Phenomenon

Month	*Mean plant pigments*	*Mean number of animals per m²*	*Estimate of plant pigment consumption per 1000 animals*	*Estimated total consumption*	*Mean phytoplankton crop and grazing estimate*
Sept	560	135,000	0.26	35	595
Jan.	120	14,000	−0.47	−7	113
Mar.	830	24,000	0.62	15	845
Apr.	2,300	32,000	5.3	170	2,470
May	870	106,000	3.5	371	1,241
June	480	103,000	0.55	56	536

and this is shown in column 4. The sum of columns 1 and 4 suggests what the phytoplankton would be if no animals were present.

The relationship between phytoplankton and zooplankton can be understood more clearly if an attempt is made to convert the estimates into directly comparable terms. This is done in Table II. Figures for zooplankton volume (column 1) were determined by the displacement method. The second column was derived on the assumption that the dry weight of organic matter in the zooplankton averages 25% of the volume in cubic centimeters. The phytoplankton figures in the third column are based on measurements from a previous paper (Riley, 1941) which gave a conversion factor of 35 mgs. of dry organic matter per thousand units of plant pigments. The fourth column utilizes the same factor together with data from Table I to determine the weight of phytoplankton consumed during the course of development of the observed correlation between phytoplankton and zooplankton. Finally, the last two columns list the data on consumption as percentages of the plant and animal weights.

TABLE II. QUANTITATIVE COMPARISONS OF PHYTOPLANKTON AND ZOOPLANKTON

Month	*Zooplankton volume cc/m²*	*Dry weight of zooplankton g/m²*	*Dry weight of phytoplankton g/m²*	*Estimated total consumption g/m²*	*Per cent of phytoplankton crop consumed*	*Food requirement, % of zooplankton weight*
Sept.	38.1	9.5	19.6	1.2	6	13
Jan.	11.1	2.8	4.2	−0.2	−5	−7
Mar.	58.2	14.5	29.0	0.5	2	3
Apr.	81.3	20.3	80.5	6.0	7	30
May	152.6	38.1	30.4	13.0	43	34
June	60.1	15.0	16.8	2.0	12	13

The gradual development of the negative correlation during the spring months might suggest a static situation in which a swarm of zooplankton developed in a particular local water mass and gradually reduced the phytoplankton crop during a period of two or three months. However, reference to Table II indicates that this is very unlikely since the increment in the weight of zooplankton during the spring months exceeded the estimated total consumption. Moreover, the values in the last column of Table II for April and May are of the same order of magnitude as the estimate made by Harvey and his associates (1935) for one day's consumption at the height of the diatom flowering, while the estimates for other months are similar to the minimum requirements for one day determined by Marshall, Nicholls and Orr (1935) from a study of the respiration of *Calanus finmarchicus.*

In this connection it can be seen in Table II that between the April and May cruises, when the zooplankton was increasing most rapidly, the mean phytoplankton crop decreased about 50 g. per m^2, although experiments on Georges Bank plankton (Riley, 1941) showed that the photosynthetic rate was increasing rather than decreasing during this period. The total difference between the experimentally estimated phytoplankton production and the observed crop was about 80 g. per m^2, most of which probably was due to grazing, although perhaps some of it can be ascribed to death by other causes. Therefore, the total consumption may have been more than ten times as great as the increase in the phytoplankton-zooplankton correlation during the same period would indicate. Thus it is desirable to attempt to evaluate the grazing rate more carefully by considering all the factors involved and by trying to decide whether there is good reason for the discrepancy that appears to exist.

Other Factors Involved in the Grazing Phenomenon. The maximum grazing rate can be estimated by methods similar to those described by Fleming (1939), who suggested the equation

$$\frac{\Delta P}{\Delta t} = P\,[a - (b + ct)]\,, \tag{1}$$

in which the change in the diatom population in respect to time is dependent on a, the rate of multiplication of the population, b, the initial grazing rate, and c, the change in the grazing rate due to changes in zooplankton population. The validity of the equation depends on the assumptions that the rate of multiplication of phytoplankton is constant, that an animal grazes a fixed proportion of the diatoms (filters a unit volume of water) per day, that there is no loss other than by grazing, and that the effects of turbulent mixing are negligible. The equation can be applied to the present study by introducing a term a_1, which represents the change in the multiplication rate with time, which is required according to the evidence from experiments on the photosynthesis of diatom populations on Georges Bank. The resulting equation is

$$\frac{\Delta P}{\Delta t} = a + a_1 t - (b + ct)\,, \tag{2}$$

and integrating,

$$P_t = P_0 e^{t[a + \frac{1}{2} a_1 t - (b + \frac{1}{2} ct)]}\,, \tag{3}$$

in which P_0 is the initial population, and P_t is the population at time t. Using the equation to express the change in phytoplankton between the April and May cruises, with the experiments on photosynthesis as the basis for estimates of a and a_1, and with c expressed in terms of the change in zooplankton population,

$$\ln 870 - \ln 2300 = 20\,(.023) + 200\,(.0065) - 20b - 200\,(.115b)$$
$$b = .064.$$

Thus, it is estimated that the April grazing rate was 6.4% of the phytoplankton population per day, or 25% of the weight of zooplankton. In May the consumption can be shown to be 17% of the animals' weight per day. These figures are very dependent on the assumption that there was no loss of phytoplankton by any cause other than grazing. Harvey and his associates (1935) believed that in the English Channel loss of diatoms by sinking or natural death was negligible. It is not yet certain whether this conclusion is also applicable to Georges Bank. Therefore the calculated values should be regarded as maximum estimates of grazing.

But the various calculations, rough as they may be, do not leave very much doubt that the correlation represents only a part of the grazing phenomenon, and perhaps a relatively small part. Furthermore, the most obvious explanation of the situation is that the continual tendency of grazing to produce such a correlation was inhibited to a greater or lesser degree by turbulent mixing, which tended to redistribute the populations more uniformly.

Georges Bank is an area dominated by strong winds during most of the winter and spring. It has rotary tidal currents typical of offshore banks, which attain a maximum velocity of three or four knots at the surface. Much of the bank water is homogeneous in respect to temperature and salinity, as is shown in diagrams by Clarke, Pierce and Bumpus (1943). However, mixing is seldom rapid or complete enough to destroy completely the last vestiges of vertical stratification of biologically active materials (Riley, 1941). With this general picture of the hydrography of the bank, it is to be expected that there might be enough turbulent mixing to interfere with the development of plankton patchiness due to grazing.

Therefore, the examination of the data with the idea of determining how mixing would affect the distribution of the plant and animal populations is in order. In the first place it is clear that although mixing tends to level the populations, growth by geometrical progression has the opposite effect. For example, during the rapid period of increase of animals between April and May, the average population rose from 24 to 106 thousand animals per m^2, a growth rate of 5.9% per day. In April 70 thousand animals was a moderately large population (the mean plus the standard deviation). If this latter population increased at the same rate, it would number 232 thousand in May. Obviously this is a much larger numerical difference between the large and average populations, although the ratio remains constant. Actually, however, in May 183 thousand animals was a large population, judged by the same criteria. In other words, there was a large numerical increase but a reduction in the ratio. Moreover, this reduction in the ratio can be used as an index of dilution of the population by mixing, provided the growth rates were relatively uniform. According to the figures given above, mixing caused a rate of reduction of the percentage difference between a large and an average population of 2.4% per day.

Studying the effect of mixing on the diatom population is more complicated because of the number of factors involved. It is necessary to use an equation of type (3) as a basis and to elaborate it by introducing factors representing the change caused by mixing. Thus in the equation

$$P_t = P_\circ e^{[t(a-b) + \frac{1}{2}t^2(a_1 - c)]\,[1 - t\,(d + \frac{1}{2}\,d_1\,t)]}, \qquad (4)$$

d is the initial rate of dilution of the population by mixing, and d_1 is the change in the rate with time. This is not quite the same as the procedure described for zooplankton mixing rates, but it can easily be transformed into comparable terms.

In dealing with a population of average size, it is assumed that d and d_1 are negligibly small. They have a finite value when the population is larger or smaller than average. A moderately large population, defined as the mean plus the standard deviation, was 3120 thousands of units of plant pigments in April and 1393 in May. Because of the negative phytoplankton-zooplankton correlation, the larger plant populations were accompanied by smaller animal populations, the number as determined by the regression equations being 23 thousand per m^2 in April and 67 thousand in May. It is assumed that the initial grazing rate was correspondingly less than the value previously determined for the average population, or $b = 23/32 \times .064 = .046$. It is also assumed that the grazing rate increased proportionally to the increase in population; that is, $c = (67 - 23)\,b/23t = .096b$. Then

$$\begin{aligned} ln\ 1393 - ln\ 3120 = {} & \{20\,(.023 - .046) + 200\,[.0065 - .096\,(.046)]\} \\ & \{(1 - 20\,(d + 10d_1)\}\quad d + 10d_1 = .082. \end{aligned}$$

Thus the average rate of dilution of a moderately large plant population by mixing was 8.2% per day during the April–May period. In order to compare this figure with the previously determined rate of dilution of zooplankton by mixing, it is necessary to determine the ratio between the large and average populations, reduce it by the amount indicated for zooplankton mixing, and transcribe this figure back into terms of plant pigments. When this is done, the calculated values of d and d_1, based on the zooplankton dilution rate, are 0.0022 and 0.00014 respectively. It is apparent that there is a wide discrepancy in the two estimates. The rate of mixing of phytoplankton populations appears to be 23 times as great as that of zooplankton.

The calculations suggest alternative conclusions. (1) The importance of the grazing phenomenon may be exaggerated. If part of the decrease in phytoplankton were caused by other factors, the estimate of mixing would be altered. (2) There may actually be more or less difference in the rate of mixing of plant and animal populations. Such a difference could occur only by partial segregation of the populations, but diurnal migration provides a means by which this might be effected. The alternative conclusions will be examined in turn, although, as will be seen, it is speculatory to attempt to choose between them.

Grazing Effect versus Loss of Phytoplankton by Natural Death. Experiments with laboratory cultures of diatoms (Riley, 1943) showed that after the development of a maximum population there followed a period of decrease which appeared to be a logarithmic function of the number of cells in the culture, and which appeared to be initiated by exhaustion of available nutrients. During this period of rapid natural death a large part of the population looked debilitated and was in a state of depressed physiological activity as evidenced by a low photosynthetic rate.

Comparison of these results with the natural plankton associations of Georges Bank revealed some similarities and some differences. Many of the May diatoms appeared senile, yet the photosynthetic rate was higher than in April. Counts made on individual species after three or four days' growth in experimental bottles showed increases in some species and decreases in others. It seemed likely that each species went through a growth cycle somewhat similar to that of laboratory cultures but at different times, so that at no time was the whole plankton association in a state of decay. Nor was there any time when such nutrients as phosphate or nitrate approached exhaustion.

It seems likely therefore, that a certain amount, although probably not a major part, of the decrease in population previously ascribed to grazing was actually caused by natural death. In attempting to establish its quantitative aspects it seems reasonable to assume that the death rate was a logarithmic function of the population, as in the case of laboratory cultures. Therefore, as the simplest example of such a relationship a factor s will be introduced into equation (4), which represents the death of a fixed percentage of the population each day. At the same time it will be assumed that the rate of dilution of the phytoplankton by mixing is the same as that previously determined for zooplankton. The values for d and d_1 are, as previously stated, .0022 and .00014 respectively. Then in respect to the average population, which is not affected by mixing,

$$\ln 870 - \ln 2300 = 20\,(.023) + 200\,(.0065) - 20b - 200\,(.115b) - 20s$$
$$43b + 20s = 2.731.$$

A large population, as previously defined, takes the form

$$\ln 1393 - \ln 3120 = [20\,(.023) + 200\,(.0065) - 20\,b_1 - 200\,(.096b_1) - 20s]\,[1 - 20\,(.0022) - 200\,(.0014)]$$
$$39b_1 + 20s = 2.633.$$

The term b_1 in the second equation points out the fact that the grazing rates of the two populations differ by the ratios of the populations, or 32 : 23; therefore the equation may be rewritten $28b + 20s = 2.633$. Subtracting this from the equation for the average population, $b = .0065$. Thus the grazing rate in April is estimated to be about 0.5% of the diatoms per day, or 2.5% of the weight of the zooplankton. This is less than the increase in the weight of the zooplankton crop, and is therefore impossibly small. If the death rate were not constant, but accelerated or decelerated with time, it would not make any difference in the apparent value of the grazing rate. The latter would be changed only if the death rate of the large population were different from that of the average population. This seems unlikely, although there is no definite evidence on the subject. Lacking such evidence, any conclusion is speculatory. However, it seems rather likely that while some small part of the observed decrease in phytoplankton may be ascribed to natural death, no reasonable assumption about the death rate can avoid the necessity of postulating also a phytoplankton mixing rate larger than that of the zooplankton.

Diurnal Migration and Grazing. The currents on Georges Bank are of two kinds: rotary tidal currents and a residual drift. In either case the frictional effect of the bottom is such that the currents are expected to have their greatest velocity near the surface. In the case of tidal currents, not only does the velocity generally diminish toward the bottom, but also the direction of the current deviates toward the right. This is described in a paper by Sverdrup (1927). Therefore the plankton at any particular depth has a different history of past movements from the plankton above and below, and if the plankton patches are sufficiently small, it also has a different history of past associations with other populations. This, combined with vertical turbulence, facilitates the mixing of populations. The mixing effect, moreover, will be more pronounced in the case of phytoplankton, which is passively scattered through the entire water column, but less in zooplankton, which tends by vertical migration to swarm at a particular depth range and therefore to be transported by horizontal currents that are more nearly uniform in velocity and direction. Thus it is possible to conceive that zooplankton swarms might be scattered less than the diatoms by turbulent mixing, and also that the association of a group of animals with any one phytoplankton population might be relatively transitory.

This would adequately explain the evidence that the observed negative correlation between plants and animals represents only part of the total grazing effect. It might be noted also that the theory resembles Hardy's theory of animal exclusion insofar as it postulates that diurnal migration is an essential part of the plant-animal relationship. Like his hypothesis, it is applicable in any place where, within the depth range of diurnal migration, current velocity varies with depth. There the resemblance ends, since the negative correlation is postulated as a result of transitory but intensive grazing of any population encountered at random rather than an avoidance of dense patches of phytoplankton.

Unfortunately, however, the theory must remain in qualitative terms for the present. More complete data on both the currents of Georges Bank and the horizontal distribution of plankton will be required before it will be possible to attempt a final solution of grazing, mixing, and phytoplankton death rates. Further work is also required to test some of the assumptions on which the equations are based, which, although they appear reasonable at the moment, are not necessarily true. It does not seem inappropriate, however, to approach the subject in this way if by doing so the unsolved problems of plankton biology can be stated more clearly.

SUMMARY

1. There is a significant inverse relationship between the horizontal distribution of Georges Bank phytoplankton and zooplankton at the time when the latter is increasing most rapidly. This is true not only of the total zooplankton but also of several individual species and genera that were examined. The evidence points to grazing as the cause of the inverse relationship.

2. Quantitative estimates of the amount of grazing required to develop the observed negative correlation between plant and animals are of the order of 35% of the weight of the animals in May, when the most rapid increase in the animal population occurred. This, however,

did not represent the total amount of grazing that occurred during the spring period, because the increase in weight of the zooplankton was considerably larger. It is suggested that turbulent mixing tended to redistribute the populations so that the correlation was not as fully developed as it would be otherwise.

3. An attempt is made on theoretical grounds to determine rates of grazing. The maximum amount of grazing that could occur (judged by the difference between the phytoplankton production rate and the rate of change of the standing crop) was about 25% of the animals' weight per day in April and 17% in May.

4. It is estimated that the effect of turbulent mixing on zooplankton amounted to a daily reduction of about 2.4% of the percentage difference between a given population and the average population. The effect of mixing on phytoplankton appears to be very much greater.

5. The reason for the apparent difference in mixing rates cannot be absolutely established, but it appears likely that diurnal migration is involved. It is reasonable to suppose that on Georges Bank the velocity and direction of the currents vary with depth. In such a case turbulent mixing should be more effective in levelling the phytoplankton populations, which are scattered through the entire water column, than zooplankton, which tends to aggregate at particular depths.

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