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Factors affecting productivity in fertilized salt water*

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Summary—The response of phytoplankton populations to added nutrients was studied by filling large out-of-door concrete tanks with sea water, and adding phosphate and nitrate. In general there was an immediate increase in photosynthesis and in growth of the population. In some cases, but not all, addition of phosphate alone was ineffective.

A large part of the variation in photosynthetic rate over a 40-day period is attributable to variation in the amount of light falling on the tanks, in the chlorophyll content of the phytoplankton, and in the phosphate concentration in the water. Large variations in the qualitative composition of the population had no apparent effect on this relation. The efficiency of the population in using light varied directly with the amount of fertilizer added, but not in proportion to it. Addition of nutrients to the bottles in which measurements of photosynthesis were made permitted evaluation of limiting factors.

The rate of phosphorus absorption, measured either as decrease of phosphate in the water or increase of phosphorus in particulate form, was directly related to the rate of photosynthesis.

INTRODUCTION

THE STUDY of phytoplankton production in fresh and salt waters has been hampered by a paucity of experimental techniques applicable to large bodies of water; it is difficult enough to make the necessary observations. The invention of the suspended bottle method of measuring population growth and photosynthesis (WHIPPLE, 1896, GAARDER and GRAN, 1927) was a long step forward, but it is desirable that techniques be invented and improved to the extent that various population functions can be effectively studied beyond the limits set by observation alone. Knowledge of algal physiology is at present too limited to permit widespread ecological prediction of the detailed behaviour of populations. Enough is known of the complex relations existing in natural habitats to make it clear that there is a need for developing methods of assessment of the condition of natural populations as they occur, and of the operation of environmental factors. Since large bodies of water are difficult to experiment with, save in the crudest way by mass fertilization, the most promising approach seems to involve manipulation of samples of natural populations. For example, HUTCHINSON (1941) was able to demonstrate that both nitrate and phosphate were acting as limiting factors to photosynthesis in Linsley Pond on several occasions by enriching the bottles in which measurements of photosynthesis were being made. NELSON and EDMONDSON (in press) used similar methods with photosynthesis and population growth preliminary to fertilizing a lake. LUND (1949; 1950) was able to evaluate limiting and controlling conditions in lakes in detail by such manipulation.

Furthermore, while the physiological role of chlorophyll has been elaborately studied, more information is needed on the ecological role of chlorophyll. Various studies have shown that, in a variety of aquatic populations, the rate of photosynthesis was closely related to the chlorophyll content of the plankton population, if proper

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allowance was made for light intensity (MANNING and JUDAY, 1941; review by EDMONDSON, in press).

The present paper is a contribution to the study of these matters. It briefly reports some of the main results of an investigation of the effects of added nutrients upon marine phytoplankton populations growing in large, out-of-door concrete tanks. It is based on the results of three experiments, one in 1947, two in 1948, and reference will be made to them by chronological number. Although several aspects of population biology were studied, the present paper is limited to a discussion of the effects of added nutrients upon the rate of photosynthesis, and relations with certain factors known to affect this rate. Since the work was undertaken with particular reference to the effect of fertilization on productivity of small bodies of salt water, high concentrations of nutrients were added. Nevertheless, the general approach is applicable to all aquatic communities including the ocean. The work followed the preliminary experiments by EDMONDSON and EDMONDSON (1947).

This is one of a series of investigations carried out at the Woods Hole Oceanographic Institution, Massachusetts, under the general supervision of Dr. GEORGE L. CLARKE. The author expresses his indebtedness to Dr. CLARKE and to Dr. C. O'D. ISELIN, then Director of the Institution, for making available an institutional fellowship and for support for the work. Thanks are due to Miss ROSEMARY HEWLETT who made all the counts of phytoplankton. Help with the work was received from a number of other persons, particularly Miss JEAN KEEN, Dr. B. H. KETCHUM, Dr. D. M. PRATT, Dr. W. S. VON ARX, Mr. ALBURT ROSENBERG, and my wife, YVETTE H. EDMONDSON. Financial assistance for some of the computation was received from the State of Washington Research Fund in Biology and Medicine (Initiative 171). A grant from the Agnes Anderson Fund of the University of Washington is gratefully acknowledged.

It is a pleasure to dedicate this paper to Professor HENRY B. BIGELOW, founder and former director of the Woods Hole Oceanographic Institution.

PROCEDURE

The tanks and most of the procedure and methods have already been described (EDMONDSON and EDMONDSON, 1947; PRATT, 1950). In the present experiments, one large concrete tank was divided by wooden partitions into four sections, each containing five cubic metres of water. The tanks were shaded by a whitewashed glass roof in order to reduce the inhibitory effect of full sunlight.

The tanks were filled by pumping sea water through two layers of #10 bolting silk to strain out the larger animals. After varying periods, sodium nitrate or dibasic potassium phosphate or both were added as concentrated tap water solutions, while the tanks were vigorously stirred with an oar. Subsequently, almost daily determinations were made of phytoplankton population, phosphate, oxygen, chlorophyll, light income, rates of photosynthesis and phosphate assimilation. Before each sampling, usually made between 7 and 9 a.m., the tanks were stirred. The morning temperature of the tanks was found to vary little over the entire period of time, and most of the temperatures were between 20 and 22°.

Usually there was no attempt to dislodge material from the sides. It was realized that periphyton would grow, but felt that, to achieve interpretable results, most of the work should be limited to the organisms which naturally would be found free in the water, rather than a heterogeneous mixture of plankton and dislodged periphytic organisms. In Experiment 3, the sides of one of the tanks were scraped down daily prior to sampling. This procedure dislodged sessile organisms, and had a profound effect on the phosphorus metabolism of the tank, as described by PRATT (1950).

Since the details of the fertilization are important, the schedule of additions of nutrients is shown (Table I). It will be noticed that in some cases phosphate was added before nitrate, and various time intervals elapsed between additions. The only method used not adequately described in existing publications is that used for measuring light.

An integrating photometer was used. The instrument was designed by Dr. W. S. von Arx and built by Mr. Robert Walden. It consists essentially of a photo-tube mounted under a flat sheet of flashed opal glass and fed by a constant-voltage power supply. The output, which varies linearly with the incident light, is fed into a condenser. The condenser, upon reaching a pre-determined voltage, is discharged by a thyratron tube, actuating a relay which operates a counter. The phototube used is RCS ♯926, which has its maximum sensitivity at 425 mμ and is relatively insensitive to red. The condenser was chosen to have a capacity such that the discharge interval is slightly less than one second in the brightest sunlight encountered in Woods Hole during the summer.

The instrument was calibrated in 1947 by comparison with an Eppley pyrheliometer mounted on the roof of the Oceanographic Institution at Woods Hole, and early in the summer of 1948 by similar comparison at the Blue Hill Meteorological Observatory. I am indebted to Mr. I. F. Hand for making the latter comparison possible, and Messrs. von Arx, Andrew Bunker, and Kenneth McCasland for the former. Values are given as visible light on the basis that one half the value given by the Eppley pyrheliometer is visible (see Edmondson, in press, for further discussion).

Reference will be made in this paper to the rate of photosynthesis; what was actually measured is the rates of oxygen change in illuminated and covered bottles suspended in the tanks for two-day periods.

Table I

Schedule of fertilization in the three experiments. Quantities of nitrogen and phosphorus are given as microgram atoms per litre

Date	*Tank* 1	*Tank* 2	*Tank* 3	*Tank* 4
1947 *Experiment* 1				
July 1	Tanks filled			
July 2	0	5P	10P	160N
July 3	0	80N	160N	10P
August 11	0	1P, 16N	0	1P, 16N
August 18	5P	0	0	0
August 25	0	0	5P	0
1948 *Experiment* 2				
June 28	Tanks filled			
July 2	5P	5P	5P	5P
July 6	80N	80N	80N	80N
1948 *Experiment* 3				
August 6	5P	5P	5P, 80N	5P, 80N*
August 23	80N	80N	0	0

* Walls of tank 4 were scraped daily.

EFFECT OF FERTILIZATION ON PHOTOSYNTHESIS

Bottles were filled and set out for the measurement of photosynthesis just before and just after addition of fertilizer. The two sets of bottles were therefore exposed to almost identical conditions, the only difference being in the amount of nutrient. As already reported (1947) the addition of such nutrients to natural populations increases the rate of photosynthesis greatly, as determined in four-day runs. In the present work, large increases in oxygen production were observed, up to an increase by a factor of as much as 5 (Fig. 1). It is interesting that the difference in order of addition of nitrogen and phosphorus in Tanks 3 and 4 in Experiment 1 appears to have made a difference in the subsequent behaviour of the populations. Addition of the large amount of phosphate in Tank 3 was not followed by an increase, whereas in Tank 2, a smaller amount of phosphate had doubled the rate. In Tank 4, nitrogen was added first and the subsequent addition of phosphorus had a further effect. The refertilization of Tank 3 on August 25 was followed by an increase in photosynthesis.

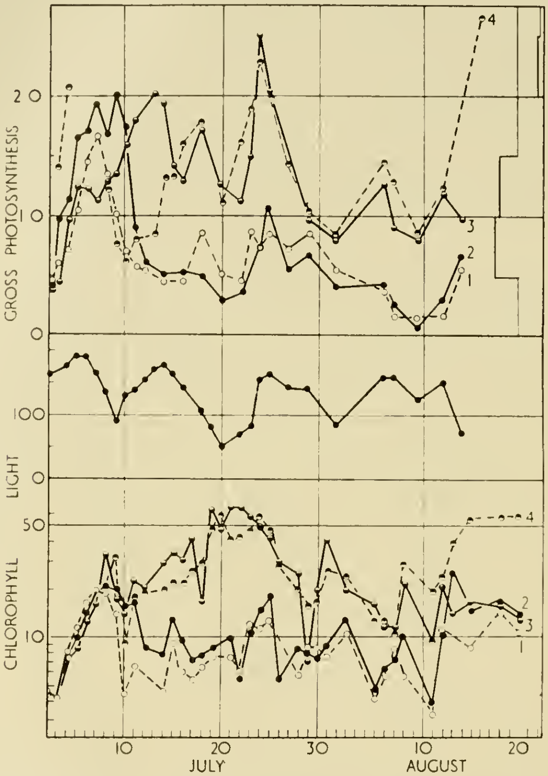

Fig. 1. Gross photosynthesis, incident light and chlorophyll in the four tanks. Photosynthesis as mg/l/day of oxygen produced, light as cal/cm²/day of visible light, and chlorophyll as μg/l. Note that chlorophyll is plotted on a logarithmic scale. The first two sets of points in the top panel are for bottles filled on July 2 before and after the first fertilization. The histogram at the right of the top panel gives the relative frequency of the rates in the ranges shown.

It was necessary to know whether removal of the population from the open water to the tanks would have an effect aside from the effects of added nutrients. For that reason, in Experiment 2, fertilization with phosphorus was delayed for four days after filling, and addition of nitrogen delayed another four days. Population density and photosynthesis did not change significantly until after the second fertilization.

Fertilization was usually followed by an increase in population, but at first the increase was not as great as that in rate of photosynthesis, suggesting that lack of nutrients had been inhibiting the photosynthesis of the individual organisms.

After the initial increase in the rate of photosynthesis following fertilization, there were large changes in the rate in all four tanks. The changes will be discussed in detail only in Experiment 1. During this experiment, the values varied greatly, from a low of 0·07 mg/l/day of oxygen to a high of 2·50, mean 1·07, standard deviation 0·55 (Fig. 1). The mean values for the tanks separately for the period ending just before the fertilization of August 11 were 0·74, 0·90, 1·30 and 1·29 in order. The difference between Tank 2 and Tank 3 is significant to the 5% level of probability, but that between Tank 1 and Tank 2 is not quite significant. Tank 1 had been intended as a control, but failure of the caulking between Tanks 1 and 2 permitted some exchange of water. The increase of phosphorus in Tank 1 was 0·69 μg at/l.

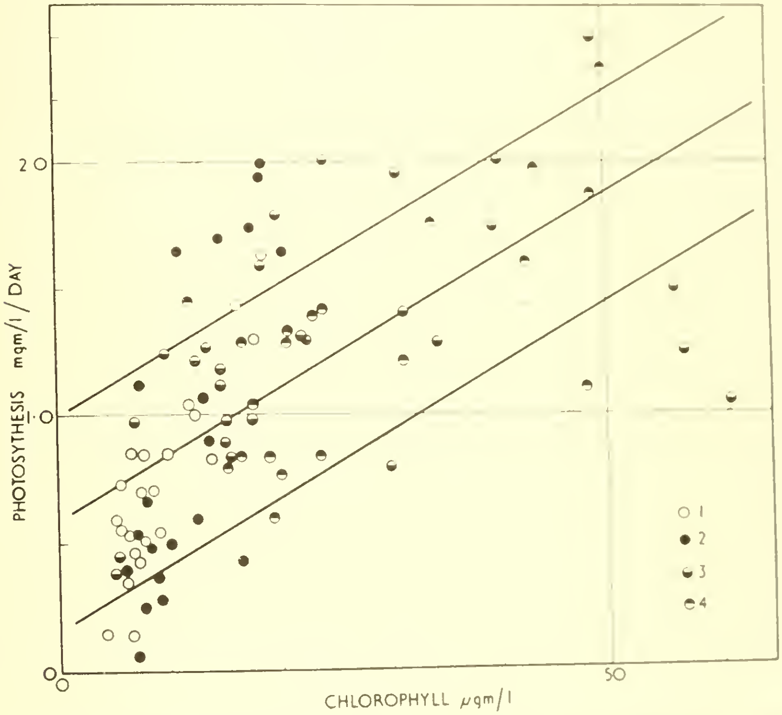

Fig. 2. Gross photosynthesis in the four tanks as a function of chlorophyll concentration. The centre line is the linear regression line and the others represent the standard error of estimate.

The maximum rate of photosynthesis was reached in five to twelve days after fertilization, and the rate then fluctuated with a general tendency to decrease. The two more heavily-fertilized tanks remained at a much higher level after the initial maximum was achieved.

VARIATIONS IN PHOTOSYNTHESIS

The large variations in photosynthesis may be attributed to variations in both population and environment. The relationship between rate of photosynthesis and some of the factors known to affect it was analyzed; much of the variation in photosynthesis turned out to be attributable to variations in chlorophyll, light, and phosphate concentration in the water. The details now follow.

During the time of the 1947 experiment, there were four periods during which relatively large levels of light were reached. The periods of greater photosynthesis tended to coincide with periods of high illumination; nevertheless, the coincidence is not perfect, and many variations in photosynthesis are not related to light (Fig. 1).

Obviously, the size of the population must be taken into account, since it showed large variations. The rate of photosynthesis per unit volume of water is the product of the population and the rate per unit of population. Even more pertinent to an explanation of the changes in photosynthesis is the amount of chlorophyll in the population (Fig. 1). After fertilization the population of phytoplankton increased greatly, and with it, chlorophyll. It is seen that the large amount of chlorophyll present in Tanks 3 and 4 during the period of time centred around July 20 partly compensated for the much lower light intensity relative to the period around July 13. The generally higher level of photosynthesis in Tanks 3 and 4 is matched by generally higher concentration of chlorophyll. The chlorophyll concentration in Tank 2 achieved a value only slightly more than that obtained in the 1946 experiment with the same amount of fertilizer in an unshaded tank, (erroneously recorded as mg/l in the 1947 paper).

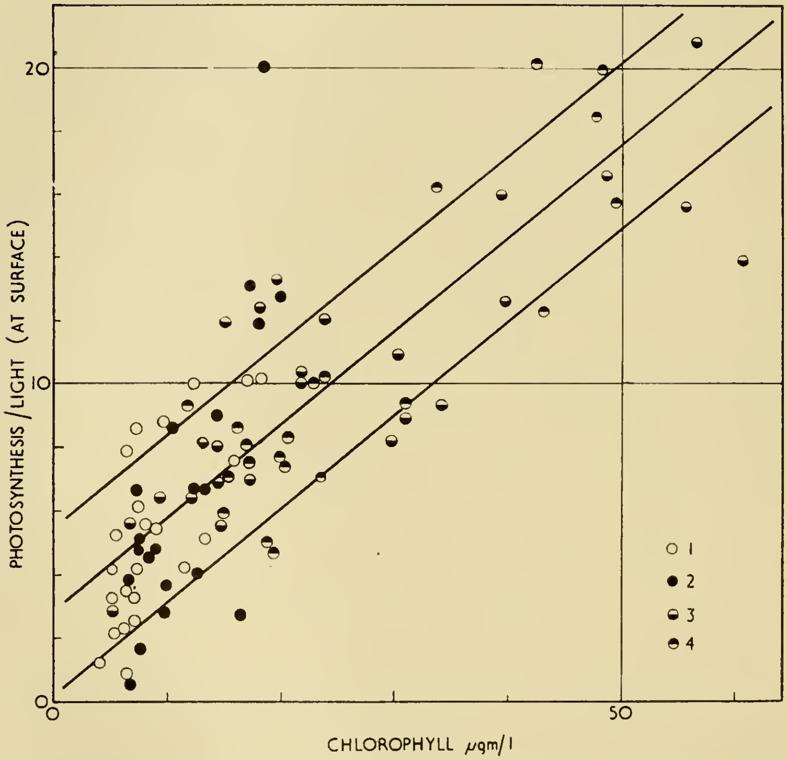

Fig. 3. Photosynthesis per unit of light as a function of chlorophyll concentration. The rates of photosynthesis shown in Fig. 2 have been divided by the mean light income (cal/cm^2/day) during the period of measurement, and the values multiplied by 1000.

The relationships just discussed are more clearly visualized if reference is made to correlation graphs (Figs. 2, 3, 4), in which consideration is limited to the 90 measurements made in the period before the re-fertilization on August 11. In the discussion which follows, the conventional correlation coefficient is designated as r_{AB}.

The following symbols will be used:

P	Gross rate of photosynthesis, as mg/l/day of oxygen
C	Chlorophyll concentration, as μg/l
L	Light at surface of tanks, cal/cm^2/min of visible light
L'	Light at mid-depth of tanks, same units
F	Phosphate concentration, μg at/l
P'	P/L
P''	P/L'
R	Rate of respiration of the population, mgm/l/day of oxygen
N	Net rate of photosynthesis, $P-R$

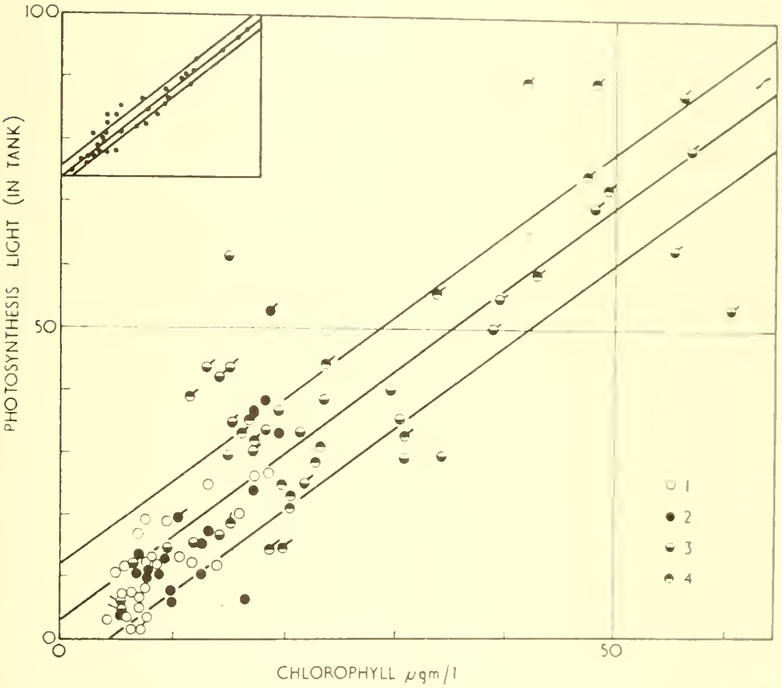

Fig. 4. As in Fig. 3, but the values of light used are those at a depth of 50 cm in the water. The points marked by lines are for periods when diatoms made up less than half the photosynthetic population by volume. The insert at the upper left is a copy of FLEISCHER's Fig. 7 (see text).

The simple relationship between photosynthesis and chlorophyll (Fig. 2) is seen to be rather low with a wide range of rate existing at all levels of chlorophyll concentration ($r_{PC} = 0{\cdot}64$). When each value of photosynthetic rate is divided by the corresponding light income, the degree of scatter is considerably reduced (Fig. 3) and the field of points is more nearly linear ($r_{P'C} = 0{\cdot}81$).

These coefficients show that, under the existing circumstances, a large part of the variation in photosynthesis is closely correlated with variations in but two factors known to have influence, chlorophyll and light, and suggest that chlorophyll was controlling more often than was light.

To give the results in a more complete numerically descriptive form, several linear regression equations were calculated. Of particular use in these equations is the standard error of estimate (S.E.E.) which, following SNEDECOR (1946, p. 117), can be used as a measure of dispersion of the points from the line of best fit, entirely analagous to the standard deviation in a frequency distribution.

It will be of interest to compare the standard errors of estimate of the regression equations with the standard deviation of the rate of photosynthesis, 0·545.

When photosynthesis is taken as a function of chlorophyll concentration alone (Fig. 2), the standard error of estimate is 0·420. When surface light intensity is added as a second independent variable, the standard error of estimate is reduced to 0·382 (Fig. 3). The equation relating these variables is $P = 0{\cdot}0172\text{C} - 0{\cdot}0056\text{L} - 0{\cdot}273$. Taking further account of the volume of plankton does not decrease variability, but taking account of phosphate concentration reduces the standard error of estimate still further to 0·283. In this analysis, phosphate concentration gives better results than does the rate of phosphate assimilation.

Thus, a large fraction of the deviation from the regression line can be accounted for statistically by variations in chlorophyll, light, and phosphate concentration. (Compare with RILEY, STOMMEL and BUMPUS, 1949.) The regression equation which relates these four variables is:

$P = 0{\cdot}0304\text{C} + 0{\cdot}0052\text{L} + 0{\cdot}0275\text{F} - 0{\cdot}239$ (S.E.E. 0·28). This equation describes the relationships which existed among the variables during the course of the experiment; but, on the basis of the known physical mechanisms involved, we can regard it additionally as a statement of relative effect of controlling factors.

The massive doses of phosphate which were added to the tanks do not represent usual concentrations available in natural conditions. Examination of the data shows that a positive relation with phosphate concentration existed only when the entire range of concentration was considered. Within the small range of variation of phosphate concentration usually met in natural waters, no correlation existed. Each tank behaved somewhat differently from the rest, and the relationships with phosphate concentration in the water are too complex for further discussion in this paper.

The light intensity to which reference has been made above is that at the surface of the water. Since the transparency of the water changed with the size of the population, the intensity to which the bottles were exposed is different, and not by a constant ratio. The intensity at a depth of 50 cm was calculated from measurements of transparency made by Mr. C. M. WEISS, and used in computing the points shown in Fig. 4, derived from Fig. 3. It is seen that, by taking account of the transparency of the water, the field of points is made more nearly linear and the regression line comes closer to the origin than in Fig. 3. The correlation coefficient $r_{P''C}$ is 0·86. While the difference from $r_{P'C}$ is not significant statistically, it is distinctly larger. The equation shown in the figure is:

$$P'' = 0{\cdot}735\text{C} + 3{\cdot}057 \text{ (S.E.E. } 10{\cdot}72)$$

This treatment of the light data is something of an over-simplification, since it implies that there is a direct and linear correlation between rate of photosynthesis and light intensity. While the tanks were shaded to prevent inhibition by bright light, the sun was able to shine in during a small part of the day, and a simple proportionality is not to be expected. However, deviation is not serious, and a more detailed analysis of the available data is not justified. Nevertheless it should be realized that a more elaborate treatment of light might result in considerable reduction in the standard error of estimate. The relation of photosynthesis to light in natural aquatic populations has been reviewed in some detail by EDMONDSON (in press).

Because of considerations just discussed, and because certain influential factors were not measured, calculations were made to ascertain how much of the variation might have been eliminated by more rigorous control of conditions. Data published by FLEISCHER (1935) permit evaluation of variation when measurements of photosynthesis of pure cultures of *Chlorella sp.* were taken as a function of chlorophyll concentration under uniform environmental conditions. The amount of chlorophyll in the population was varied by raising the cells in media deficient in one of the nutrients; thus, in the example selected, the past history of the various cultures differed only in the concentration of iron in the medium in which the cells had grown. Otherwise, conditions were uniform, the cells of fairly uniform age being suspended in a standard medium for the measurement of photosynthesis under constant illumination and temperature. Despite the carefully controlled environment, and the presence of only one species, there was variation in the amount of photosynthesis accomplished by a given amount of chlorophyll. Some of FLEISCHER's series were somewhat less variable. Measurements made from FLEISCHER's Fig. 7 shows that the coefficient of correlation is 0·97. His data are plotted in the insert of Fig. 4, with which they may be directly compared. It has been shown that differences in the age of cultures of *Chlorella* make a difference in the effectiveness of chlorophyll, as do differences in the culture conditions. (EMERSON, GREEN and WEBB, 1940; WINOKUR, 1949; SARGENT, 1940). Thus, with material and conditions very much more uniform than in the tanks, there was a variability which was a relatively large part of that found in the tanks.

EFFECT OF TAXONOMIC COMPOSITION OF POPULATION

The analysis made above takes no account of the qualitative changes in the taxonomic composition of the populations. It might be expected that, as the specific composition of the plankton changed, there would be consequent changes in the photosynthetic rate for given amounts of chlorophyll and light. If so, there are two possibilities to discuss.

If the appearance or disappearance of particular forms were to make a large difference in the relationships under discussion, it might be argued that the largest differences would be made by changes in the representation of major taxonomic groups on the basis that, for example, any dinoflagellate is likely to be more like another dinoflagellate in its ecological requirements than a diatom.

There is a second possibility; that is, within each major taxonomic group there may be a wide variation in photosynthetic efficiency or ecological requirements from one species to the next. Thus, particular species of diatoms may be ecologically almost equivalent to particular species of dinoflagellates and different from other diatoms as far as photosynthetic effectiveness goes. Thus, replacement of a particular diatom by a dinoflagellate might not result in a measurable change in the relationships discussed, but replacement of the same diatom by another might result in a large change. Such adaptive radiation within the major groups is very probable, but data apparently do not exist to permit this question to be decided. There seem to be no comparative studies of the genera which were prominent in the tank populations comparable to WINOKUR'S (1948, 1949) work on eight species of *Chlorella*, and that stops short of a study of comparative nutrition.

Considerable effort was expended in trying to discern such qualitative sources of variation in the present data. As one approach, the fraction of the volume of phytoplankton material made up by diatoms was computed. This fraction varied from less than 1% to 97% by volume, with the other organisms being a great variety of kinds including dinoflagellates and *Chlorella*, but there was no discernible tendency for periods of large diatom content to be low or high in the amount of photosynthesis per unit light and chlorophyll. The periods during which the population was composed of less than 50% diatoms are indicated by lines attached to the points of Fig. 3. Thus, large variations in the representation of diatoms did not alter the relationships discussed. Likewise there was no relation with the fraction of the population made up by non-photosynthetic protista. This is not to say that many aspects of population biology will not be altered by taxonomic changes of this kind, or that such phenomena did not exist during the tank experiments, but merely that the relation of photosynthesis to chlorophyll and light depended more on the sheer quantity of chlorophyll than on the way the chlorophyll was distributed among the major taxonomic groups present.

PHOTOSYNTHETIC POPULATION EFFICIENCY

Having measurements of the rate of energy input into the tanks and the gross rate of photosynthesis, we can calculate the gross population efficiency, or fraction of energy used in photosynthesis. In Experiment 1, gross efficiency for the four tanks together was 0·34% when computed on the basis of surface intensity of visible light, and 0·95% on the basis of the intensity of the depth of the bottle. The figures for each tank are in order, for surface intensity, 0·23, 0·31, 0·41. and 0·43%. For intensity at the depth of the bottles, the corresponding figures are 0·51, 0·67, 1·29, and 1·56%.

Since these figures are based on the intensity of visible light, they should be multiplied by 2 before comparing them with figures in the literature which are based on total radiation. Efficiencies of natural, unfertilized populations have been reported between 0·02 and 0·40%. NELSON and EDMONDSON (in press) discuss a lake the efficiency of which was greatly increased by fertilization. That the heavily fertilized tanks are not much more efficient relative to natural populations may be surprising, but is easily explained by the fact that the tanks were so shallow that much of the avaliable light must have been wasted by absorption into the sides and bottom and by reflection back out of the water. That fertilization increased efficiency can best be seen by comparing each tank with Tank 1, bearing in mind that Tank 1 was inadvertently fertilized lightly.

ASSESSMENT OF CONDITION BY ENRICHMENT

As shown in previous sections, the responsiveness of different populations to fertilization was different, and varied with the amount of fertilizer. For full interpretation of events in natural populations, it is necessary to obtain information on responsiveness in order to identify limiting and controlling factors. The work of LUND on lakes is the most successful to date, basing interpretation of seasonal events on laboratory analysis of the physiological condition of the population and its response to changed conditions (1949, 1950).

In the present work, a number of enrichments were made with nutrients added to the bottles, not the whole tanks, in order to determine the degree to which these substances might be limiting photosynthesis.

For example, on July 29 the population of Tank 2 was highly responsive to enrichment with phosphate and nitrate, while that of Tank 4 showed no response (Table II). The results are interpretable on the basis that Tank 4 had previously been more heavily fertilized, relative to Tank 2, and the population of the former tank was not inhibited by lack of nutrients. The phosphate concentration in the two tanks before enrichment was 0·13 and 0·46 μg at/l of P, respectively.

Table II

Results of enrichment with nutrients, July 29–31 1947. *The rate of photosynthesis is tabulated for bottles enriched with phosphate, nitrate, both, and nothing*

	Photosynthesis in	
Added:	*Tank* 2	*Tank* 4
O (control)	0·6 mg/l/day	0·9
P (0·5 μg/l)	0·7	0·9
N (80 μg/l)	1·1	0·9
P and N	1·3	0·9

PHOTOSYNTHESIS AND PHOSPHATE ASSIMILATION

Previously, it was demonstrated that there was a close correlation between amount of oxygen produced by a population and amount of phosphate removed from the water (Edmondson and Edmondson, 1947). This relation was investigated further in the present work. In Experiment 3, phosphate assimilation was measured in a manner analogous to that by which photosynthesis was measured, by measuring the phosphate concentration in suspended bottles. In most series, phosphate increased in the dark bottle and decreased in the light bottle. By subtracting the change in the dark bottle from that in the light bottle, one obtains a gross phosphate assimilation which, in most cases, is a negative number, indicating decrease of concentration in the water. Similarly, the changes in particulate phosphorus were measured. The data on phosphorus were taken by Dr. David M. Pratt, who made a detailed study of the phosphorus cycle in Experiment 3 (Pratt, 1950); his paper should be consulted in connection with this section. It is of interest to compare assimilation of phosphorus with the measurements of photosynthesis.

The phosphate which appears as net change in the dark bottle is most likely released by bacteria and animals, not by intact algae. It would seem, therefore, that in addition to comparing the gross changes in phosphorus with gross photosynthesis, it would be meaningful also to study the relation between gross phosphate assimilation and net photosynthesis, where the latter is the rate of change of oxygen in the light bottle, and is equivalent to the quantity (gross photosynthesis–respiration). That it is reasonable to study this relation is shown by considering the fact that carbon dioxide but not phosphate is freely released by algae in the dark bottle. Unfortunately, with present techniques, a true measurement of net photosynthesis is not obtained, since a large population of bacteria develops on the glass surface of the bottle. Thus, the rate of respiration and presumably phosphorus metabolism is higher in the bottle than in the relatively unconfined population of the tank. Nevertheless, under the circumstances which existed, the bacterial population is probably similar in the two bottles. Plate counts differed little. Thus, the difference between the bottle population and the tank population is that the former had a higher proportion of bacteria. Any relation which would depend upon the ratio of bacteria to other organisms would be modified. (See RYTHER, 1954).

Both the rate of disappearance of phosphate from the water and the rate of increase of phosphorus in particulate form (organisms) showed a rather close relation with net photosynthesis and with gross photosynthesis. In the latter measurements, there were three pairs of points which diverged greatly from the general pattern, because of a high rate of photosynthesis not matched by the high rate of phosphorus uptake (Fig. 5). The reason for the divergence of the aberrant points is not evident. The data are for determinations made toward the end of the period of investigation, and the rate of respiration was unusually high. It is possible that photosynthesis was able to proceed rapidly, without a corresponding uptake of phosphate, because of phosphorus stored in the cells (KETCHUM, 1939).

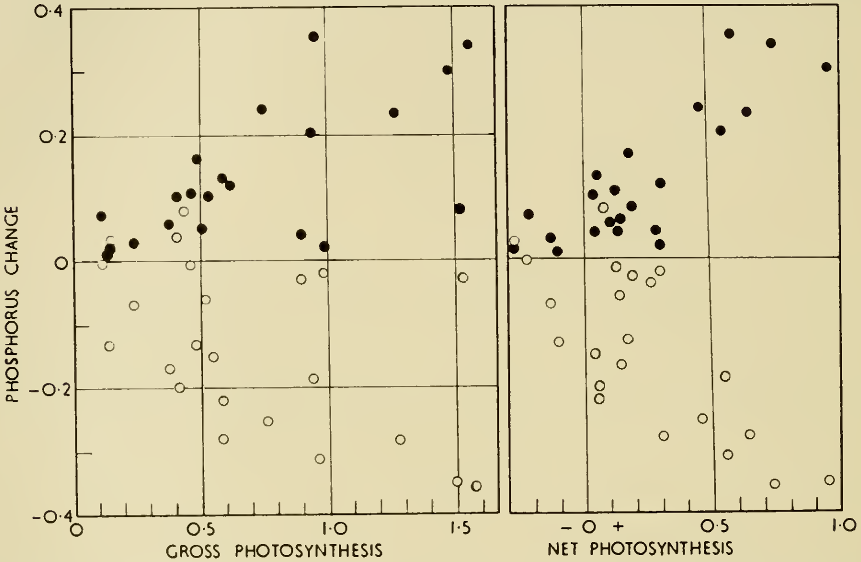

Fig. 5. Rate of change of phosphorus as a function of gross photosynthesis (left) and net photosynthesis (right) in Experiment 3. Particulate phosphorus is shown by filled circles and phosphate phosphorus by open circles. The rate of change of phosphorus is given as µgm at/l/day., photosynthesis as before.

In both cases, the rate of increase of particulate phosphorus very closely matches the rate of decrease of phosphate in the water. Individual pairs may not match well because phosphorus can be lost from the particulate fraction without immediately appearing as phosphate, but the fields of points do match.

DISCUSSION

The investigation partially summarized in this paper was intended primarily to explore certain problems of aquatic productivity. The ideas discussed concern freshwater as well as marine populations. Extrapolation from pure culture work to natural populations is complicated by the existence of many phenomena which do not operate in one-phase, single-species cultures, and which may be exceedingly difficult to duplicate in ordinary laboratory conditions. While the large outdoor tanks do not provide the elegance of complete environmental control available in the laboratory, they permit some control, as well as a degree of simplification not available in natural shallow habitats, in which the mud-water interface makes complications. They proved to be very useful in providing a large, manipulable environment, intermediate between laboratory cultures and natural bodies of water, from which large samples could be withdrawn without seriously depleting the population. They may profitably be used in the problem of interpreting natural situations, and in designing efficient programs of experiments with controlled conditions.

One of the pressing problems is to establish relationships among the various population functions which are involved in biological production. Of these, the relation of photosynthetic rate to amount of chlorophyll present, and the degree to which this relation may be modified by various environmental conditions, has been discussed at length. The ecological position of chlorophyll is obvious, but critical studies must be continued before much useful prediction from measurements of chlorophyll can be made. A second problem of interest is that of the interrelations among photosynthesis, population growth, and nutrient uptake. It must be expected that in general these functions will be related, and measurements of one will give information about others which may in some situations not be measurable directly. Finally, further development of methods of evaluating the extent to which various factors are limiting production at any moment should lead to greater understanding of the general problem of productivity.

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