Photosynthesis in the Ocean as a Function of Light Intensity

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ABSTRACT

Photosynthesis was measured in 14 species of marine plankton algae in relation to light intensities within the entire range to which natural phytoplankton populations may be exposed. A mean curve was constructed showing relative photosynthesis in marine phytoplankton as related to light intensity. From this curve and surface radiation data, relative values for photosynthesis were determined throughout the day at the surface and at depths in the ocean at which the surface intensity is reduced by given amounts. Integration of these values over the entire day gave values for daily relative photosynthesis at each depth considered, and integration of the daily values with depth resulted in a single figure for daily relative photosynthesis beneath a unit of sea surface.

An empirically derived relationship was discovered between daily surface radiation and daily relative photosynthesis within the water column. From this relationship the effect of light intensity upon photosynthesis throughout the year at a temperate latitude was demonstrated.

A preliminary method is described for estimating absolute daily photosynthesis beneath a square meter of sea surface from measurement of (1) photosynthesis of a sample of the population at light saturation, (2) the extinction coefficient of light in the water, and (3) the daily surface radiation.

From an estimate of the ratio of photosynthesis to respiration at light saturation, the daily ratio \( P:R \) for the entire population is calculated. It is shown that phytoplankton populations cannot photosynthesize sufficiently to compensate for their own respiration during periods of low solar radiation, as may occur in the winter months at temperate or northern latitudes.

INTRODUCTION

Although light is the most important limiting factor to photosynthesis in the ocean, the effects of light intensity upon the photosynthetic rate of the principal group of marine plants, the plankton algae, has never been adequately investigated. Laboratory studies appear to be confined to some experiments by Barker (1935) with the diatoms *Nitzschia closterium* and *N. palea* in which both light intensity and photosynthesis are expressed in relative units. In the field, Jenkin (1937) measured simultaneously light intensity and photosynthesis by the diatom *Coscinodiscus excentricus* at various depths in the English Channel, producing what has persisted as the only quantitatively useful information on the subject with respect to marine phytoplankton.

There exists a large literature dealing with the relationship between light intensity and photosynthesis in terrestrial plants, aquatic phanerogams, and a few freshwater algae, notably *Chlorella*. This has been reviewed by Rabinowitch (1951, chap. 28), showing the same general trend in every case of a linear increase of photosynthesis with light intensity up to a saturation point, beyond which higher intensities do not increase photosynthesis but eventually result in an inhibition, the physiology of which is discussed by Steemann Nielsen (1952). The majority of laboratory studies with terrestrial or freshwater plants have not been concerned with the high intensities at which this inhibition occurs, but the phenomenon has been clearly demonstrated in all measurements of photosynthesis in natural waters by a marked depression at or near the surface where the organisms are exposed to nearly full incident solar radiation (Marshall and Orr 1928, Jenkin 1937, Steemann Nielsen 1951, 1952).

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The following report will describe some experiments in which the relationship between photosynthesis and light intensity has been investigated in 14 species of marine plankton algae within the wide range of light intensities to which they may be exposed in nature. On the basis of these experiments an attempt will be made to construct a general photosynthesis-light curve for marine phytoplankton, which in turn will serve as a basis for some speculation on the effect of light upon total photosynthesis and the ratio of photosynthesis to respiration within the euphotic layer of the ocean.

**Experimental Methods**

Photosynthesis measurements were made on the roof of the Woods Hole Oceanographic Institution during June and July, 1955, using solar radiation as a light source. Incident light measurements were made with a calibrated Weston Model 594RR photoelectric cell and are reported in foot-candles. Experiments were conducted for four-hour periods consisting of the two hours before and after noon, and were confined to bright sunny days with no appreciable cloud cover. The incident solar intensity increased during the first half and decreased during the latter half of the experiments, but did not vary from the mean intensity within the four-hour period by more than 8%.

Photosynthesis was measured in 20-ml glass-stoppered bottles which were placed in a light-tight box divided into 9 compartments. Each compartment held three bottles so that three experiments could be conducted simultaneously. The compartments were then covered with a graded series of neutral density filters prepared from exposed photographic plates. The absorptive indices of the filters were determined by photometric measurements made within each compartment, which thereby also took into account influences of the container itself upon the radiation.

The bottles were suspended on wire rods above a flat, black surface so that reflected light was negligible. The bottom of the compartments were open to the air but shielded from the light by a system of baffles. The temperature in the entire series of experiments ranged from 18–23°C but did not vary between bottles in any one experiment by more than 1°C.

Photosynthesis was measured by the uptake of C\textsuperscript{14}O\textsubscript{2} using essentially the same technique described by Steemann Nielsen (1952). However, to permit comparison of the different species, photosynthesis at each intensity (\(P_i\)), as determined by the activity of the organisms after exposure, is reported relative to the maximum photosynthesis (\(P_{\text{max}}\)) observed in the same experiment (\(P_i/P_{\text{max}}\)).

The cultures used for the experiments were routinely grown at 20°C under 1000 foot-candles of illumination provided by daylight fluorescent lamps. They were approximately one week old when used, at which time they were diluted with enriched Millipore-filtered seawater to such a density that no appreciable absorption of light could be detected through the thickness of the experimental vessel (3.2 cm). In order to eliminate any short-term effects of suddenly exposing the organisms to light intensities different from those at which they had grown, the bottles containing the algal suspensions were placed in their appropriate compartments in the experimental box and exposed to the sun for approximately two hours before the start of the experiment at which time the C\textsuperscript{14} was added with a hypodermic syringe.

In addition to 28 experiments with organisms grown in the manner described above, three additional experiments were made with cultures which were grown on the roof of the building and hence exposed to full sunlight.

Finally a third type of experiment consisted of measuring photosynthesis by the same method as described above and during the same four-hour, mid-day period, at various depths in Woods Hole Harbor. The simultaneous measurements of incident radiation and the extinction coefficient of the water permitted the calculation of the light intensity at each depth at which photosynthesis was measured. These experi-
ments were made with the green flagellate, *Dunaliella euchlora*, which had been grown in the laboratory at light intensities of 350 and 1200 foot-candles.

A total of 14 species of phytoplankton were used in these experiments including seven green algae, three diatoms, and four dinoflagellates. The species are listed in Figure 1. *Gymnodinium splendidens* was obtained from Dr. Beatrice Sweeney, *Gyrodinium* sp. and *Exuviaella* sp. from Dr. Luigi Provasoli, and *Amphidinium Klebsii* and *Dunaliella euchlora* from Dr. R. R. L. Guillard. The remaining organisms were isolated by the author from marine or brackish water near Woods Hole.

**INTERPRETATION OF THE DATA**

The uptake of C\(^{14}\) measures only photosynthesis above compensation, or photosynthesis minus respiration (Ryther 1954). Thus the point of zero apparent photosynthesis occurs at the compensation intensity, or somewhere between 50 and 100 foot-candles, and the resulting curve shows the relationship between light intensity and net photosynthesis. However, since respiration is constant, the curve for total photosynthesis lies parallel to the net photosynthesis curve and passes through the origin. The curves relating intensity and total photosynthesis which will be described below were
constructed on the basis of this relationship from net photosynthesis measurements.

Although there is evidence that photosynthesis below the compensation intensity proceeds with twice the efficiency as that above that point (Kok 1951), the increase is shown here as being linear from zero light intensity to saturation. However, the error resulting from this assumption is negligible and photosynthesis below 50 foot-candles has been considered as insignificant for the purposes of this report.

RESULTS

There was a remarkable similarity in the behavior of the organisms within each of the three taxonomic groups (green algae, diatoms, and dinoflagellates) and a rather striking difference between those of different groups. For this reason the data for each group are shown separately (Fig. 1). Within each group, the scatter of data in different experiments with the same species was as great as that between different species, so the results for the individual species are not shown.

Saturation intensity was reached for the Chlorophyta at 500–750 foot-candles, for the dinoflagellates at 2500–3000 foot-candles, and at intermediate intensities for the diatoms. Inhibition of photosynthesis became apparent in all three groups within about 1000 foot-candles of saturation. At intensities of 8000–10000 foot-candles, comparable to full noon sunlight, photosynthesis in the Chlorophyta and diatoms was only 5–10% of that at saturation, while photosynthetic activity in the dinoflagellates was reduced somewhat less to 20–30% of maximum.

Cultures of one species of each group—the green flagellate, Dunaliella euchlora, the diatom Skeletonema costatum, and the dinoflagellate, Amphidinium Klebsi—were grown on the roof of the laboratory where they were exposed to full incident radiation. During their growth period of one week there were one rainy day, two overcast days, and four bright, clear days. The cultures grew slowly and showed marked chlorosis, but both flagellates remained motile and all were later successfully subcultured under normal laboratory conditions.

Photosynthesis-light intensity experiments similar to those discussed above were made with these cultures at the end of seven days. Although their uptake of C\textsuperscript{14} was low, the relative rates at different light intensities were essentially the same as that of the same organisms grown in the laboratory under 1000 foot-candles (see Fig. 1). There was no indication of adaptation to the high intensities to which they had been exposed.

Photosynthesis of the flagellate, Dunaliella euchlora, was also measured at depths of 0, 1, 2.5, 5, 7.5 and 10 meters in Woods Hole Harbor. The extinction coefficient was obtained by lowering a submarine photometer (a Weston Model 594RR photoelectric cell) and measuring the reduction of light. The water was homogeneous with respect to light extinction within the upper 10 meters with a coefficient \((k)\) of 0.40. No significant loss of radiation through reflection at the surface could be detected. Incident radiation was measured as before with a recording Weston photoelectric cell.

Cultures were used which had grown for two weeks in the laboratory at light intensities of 350 and 1200 foot-candles. Those which were grown at the lower light intensity contained 4.3 times as much chlorophyll a per cell, and their photosynthetic rate per cell was 3–4 times that of the cells grown at light saturation. But the relative response of the two cultures to different light intensities was essentially identical and comparable to that found in the roof experiments with neutral density filters and with cultures grown at 1000 fc (Fig. 1: Chlorophyta).

Figure 1 also shows for comparison some of Jenkin’s data for the diatom, Coscinodiscus excentricus. The data were taken from her Figure 9 (p. 333) showing oxygen production per hour plotted against average energy per hour. The July 25 measurements were chosen for the comparison since on that day “the sea was calm, the light was very bright, and conditions were relatively constant throughout the exposure”.

Light values, which were originally
measured in photometric units and converted to energy units by Jenkin, were reconverted to foot-candles to permit comparison with the present data, using the same conversion factors employed by Jenkin. A reasonably good fit of Jenkin’s data to the author’s diatom curve is obvious.

Despite the variability of the photosynthetic response to light intensity of the different taxonomic groups, an attempt has been made to construct a general photosynthesis-light intensity curve for marine phytoplankton. This has been done by averaging the relative photosynthesis values at each light intensity for the three groups of algae as given by the curves in Figure 1. Because the Chlorophyta are relatively unimportant in the marine phytoplankton, they have been weighted only one-half as heavily as the other organisms in obtaining the average. The resultant curve is given in Figure 2.

RELATIVE DAILY PHOTOSYNTHESIS IN THE OCEAN AS A FUNCTION OF LIGHT INTENSITY

If one knows the incident radiation falling on the surface of the ocean throughout the day and the extinction coefficient \((k)\) of the water, it is possible to calculate from this information and the data in Figure 2 the daily relative photosynthetic rate at any depth in a water column in which the phytoplankton is distributed homogeneously.

A continuous record of incident radiation as measured by a 50-junction Epply pyrheliometer is kept by the Epply Laboratories of Newport, Rhode Island and was made available to the author through the kindness of Mr. Hedley Greer of that organization. According to Forsythe (1954) 50.4–52.3% of solar radiation falls within the range of 4000–7700 Å, while according to List (1951) 42.5–45.25% falls within the range 4000–7000 Å. The present author has followed Edmondson (1955) in considering 50% of the total incident solar radiation as photosynthetically active.

Pyrheliometer values are expressed in energy units as gram calories per cm². These have been converted to units of luminosity using Jenkin’s figures of 240 lumens per watt as suggested to her by Poole and Atkins, and results in the relationship 1 gram calorie per cm² per min (photosynthetically active radiation) = 15500 foot-candles.

The reflection of light from the surface of the water varies with cloud cover, surface roughness, and the altitude of the sun, but is normally rather small (Powell and Clarke 1936, Harvey 1955). For present considerations the light just penetrating the water has been taken as 95% of that incident to the surface. This is obviously an oversimplification and results in some overestimation of submarine light intensity, particularly in the early morning and late afternoon.

Figure 3 shows the light intensity in the surface layers of the ocean at the same latitude and under similar weather conditions which prevailed at Newport, Rhode Island, on June 17 and December 14, 1954, which were respectively the brightest and darkest days of the year. Mean intensities are given for half-hour intervals throughout

Fig. 2. Mean curve from Figure 1 showing relationship between photosynthesis and light intensity in marine phytoplankton.

Fig. 3. Daily incident surface radiation at Newport, Rhode Island, on June 17 and December 14, 1954.
the day. Figure 4 shows relative photosynthesis also plotted at half-hour intervals at the surface and at the depths where the surface intensity is reduced to 50%, 25%, 10% and 1% of its initial value for the same two days, as obtained from Figures 2 and 3. Relative photosynthesis values may now be integrated over the entire day thereby giving daily relative photosynthesis at each depth considered (Fig. 5). The depth scale is given here as a function of the extinction coefficient of the water (km) as derived from the expression:

\[ I_m = I_0 e^{-km} \]

where \( I_0 \) is the surface intensity and \( I_m \) the intensity at depth \( m \). The curves in Figure 5 may, in turn, be integrated giving total daily relative photosynthesis within the entire euphotic zone.\(^2\) These relative values, for the same value of \( k \), are 29.2 and 1.8 for June 17 and December 14, respectively.

A COMPARISON BETWEEN THEORETICAL AND MEASURED DAILY PHOTOSYNTHESIS CURVES IN THE OCEAN

In December, 1950, Steemann Nielsen measured C\(^{14}\) uptake in water collected from 10 meters and suspended at various depths in the Benguela Current of Luando, Angola, S. W. Africa (see Steemann Nielsen 1952: 129). The experiment was carried out on a bright, sunny day. According to Kimball (1928) the total daily radiation on a cloudless day at that time and latitude is 720 g.cal/cm\(^2\). The length of the day was 12 hours and the altitude of the zenith sun 67°.

On June 17, 1954, at Newport, Rhode
Island, the total radiation was 802 g.cal/cm², the length of the day about 15 hours, and the sun's altitude also 67°. The two days were thus quite similar with respect to radiation, with the exception of the somewhat longer period of daylight at Newport.

Since Steemann Nielsen was dealing with a homogeneously distributed population (i.e. in using water collected from a single depth) it is possible to compare his curve of daily photosynthesis with the theoretical curve for June 17 at Newport. To do this, the depth scales must be equilibrated, which may be done by superimposing the points of maximum photosynthesis of the two curves. Thus maximum photosynthesis in the Benguela Current (at 10 meters) is arbitrarily assumed to occur where \( km = 1.15 \), \( k \) then becomes 0.115, and the remaining points may be plotted on Figure 5 using the same depth scale.

Photosynthesis is expressed in relative units. The rather good fit of Steemann Nielsen's data to the theoretical curve, considering that radiation in the two cases was not identical, lends some support to the preceding theoretical treatment and suggests that the response of the phytoplankton to light intensity was similar in the two cases.

THE RELATIONSHIP BETWEEN DAILY INCIDENT SURFACE RADIATION AND RELATIVE PHOTOSYNTHESIS WITHIN THE WATER COLUMN

In addition to the two days considered above (June 17 and December 14) the daily relative photosynthesis within the euphotic zone was calculated by the same method for 6 additional days in 1954. The 8 days chosen for this purpose were characterized by total incident radiation ranging at more-or-less even intervals from the darkest to the brightest day of the year. Relative photosynthesis was then plotted against total daily incident surface radiation for the 8 days (Fig. 6). The resulting smooth curve which may be drawn through the 8 points clearly indicates an empirically derived relationship between the two variables.

Records maintained at the Epply Laboratories include weekly averages of the total daily radiation at Newport, Rhode Island. These figures may be converted to photosynthesis values from the curve in Figure 6 to illustrate the effect of the seasonal variation of light intensity upon photosynthesis (Fig. 7). It should be emphasized here that this treatment considers only the factor of light and applies only to a hypothetical phytoplankton population which remains constant with respect to both time and depth within the euphotic zone. The actual magnitude of photosynthesis throughout the year varies as well with fluctuations in the population size, nutrient concentrations, and other limiting factors.

THE DETERMINATION OF ABSOLUTE PHOTOSYNTHESIS IN THE OCEAN

An absolute value for total photosynthesis \((P)\), in mg of carbon assimilated per day beneath a square meter of sea surface, may now be obtained for a homogeneously distributed population from the expression:

\[
P = \frac{R_s}{k} \times P_{\text{sat}}
\]

where \( R_s \) = total relative photosynthesis within the euphotic zone for the appropriate value for total daily surface radiation \((S)\), from Figure 6

\[
k = \text{extinction coefficient per meter, as measured}
\]

\[
P_{\text{sat}} = \text{measured total or "gross" photosynthesis at light satu-}
\]
ration of a sample of the population, expressed as mg carbon/m²/hour.

The value for (S) may be determined by measurement on the day in question, or may be taken from the published tables of Kimball (1928). The latter not only eliminates the necessity for measuring radiation, but also provides a mean value for the particular time and place under consideration. For purposes of a general survey of marine productivity, this is generally more significant than direct measurements on any single day, which cannot make allowance for the day-to-day variations in radiation resulting from local meteorological conditions.

The procedure outlined above may be used only under highly restricted conditions and is presented at this time merely to illustrate the ultimate applicability of the methods described herein. Procedures for estimating both total and net photosynthesis under varying natural conditions, based upon the same general approach as developed in this paper, will be described in a subsequent publication.

**THE RATIO OF PHOTOSYNTHESIS TO RESPIRATION**

At light saturation the ratio $P:R$ varies depending upon the state of nutrition of the algae. During exponential growth of *Dunaliella euchlora* a maximum ratio of 12.1:1 was observed which decreased to about unity in cultures highly deficient in nitrogen and phosphorus (Ryther 1954). Kok (1952) found ratios in *Chlorella* as high as 20:1, but under "bad conditions" reported values as low as 1.4:1. In short term manometric measurements of photosynthesis, ratios of 20:1 or higher are commonly encountered, but the behavior of organisms under the highly artificial and idealized conditions of such experiments cannot be assumed to prevail over extended periods of growth.

It is not possible to measure the ratio directly in natural populations, since the respiration of the plants cannot be separated from that of the associated non-photosynthetic forms. At best it probably falls somewhat short of that observed under ideal conditions in laboratory experiments. Let us consider for the present a hypothetical situation in which the ratio of photosynthesis to respiration is 10:1 at light saturation. Respiration then assumes a value of 0.1 relative to maximum photosynthesis.

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3 Reported in that publication as *Chlamydomonas* sp. and correctly identified by Dr. Ralph Lewin.
Since respiration is essentially independent of light (Brown 1952) it remains constant throughout the day. Furthermore we are considering a population which is distributed homogeneously throughout the water column, so that $R$ also remains constant with depth if we may disregard the effects of temperature. Except under conditions of extreme thermal stratification, which will be discussed below, temperature does not normally vary by more than a few degrees within the euphotic zone.

Daily respiration throughout the euphotic zone is then $0.1 \times 24 \times 4.6 = 11.04$ relative units, and this remains constant as long as the ratio $P:R$ at light saturation does not change. While absolute values for $P$ and $R$ are dependent upon the size of the population, their values relative to each other are independent of this factor.

In Figure 5, which shows the vertical distribution of daily relative photosynthesis within the euphotic zone on June 17 and December 14, the straight vertical line represents respiration. The point at which the curves for photosynthesis and respiration cross is the daily compensation depth. On June 17, this occurred at 3.83/($k$ meters, which in clear oceanic water ($k \sim 0.04$) is about 95 meters and in coastal water ($k \sim 0.1$) is about 38 meters. On December 6 the curves never cross indicating that the plants could not compensate even at the surface. The daily ratio of $P:R$ for the euphotic zone was roughly 2.6:1 on June 17 and 0.2:1 on December 14, even though $P:R$ at light saturation was 10:1 in both cases.

In Figure 7, showing the seasonal pattern of photosynthesis, the horizontal lines represent respiration where $P:R$ at light saturation is respectively 5:1, 10:1, 15:1 and 20:1. This illustrates the fact that if a maximum ratio of 10:1 is reasonable, phytoplankton populations living at a latitude and under weather conditions comparable to Newport, Rhode Island, are unable to do more than compensate for their own respiration within the euphotic zone during the winter months. This, then, may account for the winter minimum of plankton algae in temperate and northern ocean waters.

**DISCUSSION**

We have discussed above the relationship between light and the ability of phytoplankton populations to maintain themselves or produce excess cellular material. Losses to the population by predation or sinking are not included in the scope of this report. Such permanent losses remove individuals from the population and hence affect the magnitude of photosynthesis and respiration, but not their relative rates with respect to each other.

For the purposes of this discussion the phytoplankton population must be considered to consist of those individuals which, through vertical mixing, spend at least some time in the euphotic zone. But the population, so defined, may extend considerably below the depth at which any photosynthesis can occur. In the open ocean this depth is of the order of 100–150 meters, in coastal waters 25–50 meters. The so-called “mixed layer” of surface water (i.e. water of the same density) may be and usually is considerably greater than these depths except in summer when thermal stratification occurs.

If one considers the entire population, as defined above, rather than that within an arbitrary depth, it is obvious that the $P:R$ ratio is even smaller than indicated above, at least during the late fall, winter and early spring when the mixed layer extends below the euphotic zone.

In summer the surface layers may be thermally stratified and mixing greatly reduced. Under these conditions the photosynthetically active population may not extend below the euphotic zone. But the reduction of mixing also prevents the homogeneous distribution of organisms in the upper layers and, due to the negative buoyancy of the cells, the population density increases with depth to a maximum somewhere below the depth of maximum photosynthesis (see Riley et al 1949: 73). This, too, will have the effect of increasing respiration relative to photosynthesis for the population as a whole. However, the effect here may be somewhat counteracted by the temperature gradient which results in lower respiratory rates near the bottom of the euphotic zone as compared
with that near the surface, whereas photosynthesis at the low light intensities found at these levels is essentially independent of temperature.

From these considerations it would appear that the \( P:R \) ratio for the population may be considerably lower than indicated in the preceding calculations in which only the euphotic zone was considered. This leads to a reconsideration of the choice of a \( P:R \) ratio at light saturation of 10:1. Since there are always some plankton algae in the surface layer of the ocean as well as animals which are dependent upon them for food, it would seem unlikely that there would be any extended period of the year in which no net photosynthesis can occur. Thus the \( P:R \) ratio at light saturation is probably somewhat greater than 10:1. For reasons stated above, it is probably not consistently as great as 20:1, and a mean value probably lies somewhere between these limits. In Figure 7 the relative curve for annual respiration is shown where \( P:R \) at light saturation is 15:1. If this curve is somewhat low for the entire population, as indicated above, the population would approach or reach compensation perhaps only in extreme conditions in mid-winter.

We have thus attributed the winter minimum of phytoplankton in temperate or northern latitudes to the limitation of light. In the normal course of events, this is followed by a spring maximum and a secondary fall peak interspersed by a mid-summer low. The latter has been attributed, at least in part, to nutrient depletion of the surface waters.

As soon as the limiting nutrient concentrations fall to the level at which exponential growth of the organisms can no longer occur at optimum light intensity, the rate of photosynthesis decreases and the ratio \( P:R \) falls to 5:1 or less (Ryther 1954). Under these conditions photosynthesis by the entire population is able to compensate for its respiration only on days of the highest incident radiation, as is indicated in Figure 7. Thus light is always limiting to the photosynthesis of natural plankton populations and the effect of nutrient deficiency is at most additive to the light factor.

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