The Relation of Oceanic Primary Production to Available Photosynthetic Irradiance*

H. R. Jitts, A. Morel and Y. Saijo

^ Division of Fisheries and Oceanography, CSIRO, P.O. Box 21, Cronulla, N.S.W. 2230. Present address: Department of Environment, P.O. Box 1937, Canberra, A.C.T. 2601.
\(^{b}\) Laboratoire d'Oceanographie Physique, Station Marine de Villefranche-sur-mer (Univeristé de Paris et C.N.R.S.), Villefranche-sur-mer, France.
\(^{c}\) Water Research Laboratory, University of Nagoya, Nagoya, Japan.

Abstract

Primary production was measured at 14 stations covering a wide range of oceanic waters. Measurements were made by both the in situ method \((P_s)\) and the simulated in situ method \((P_e)\). Production \(v\) constant irradiance \(\left(E_0(350\text{-}700)\right)\) was also measured. Available photosynthetic irradiance \(\left[E_0(350\text{-}700)\right]\) was calculated from continuous records of total irradiance and measurements of the percentage submarine transmission of irradiance were made with a quantum meter. Using the \(P\) \(v\) \(I\) curves and \(E_0(350\text{-}700)\), primary production at several depths at each station was calculated \((P_e)\). \(P_e\) was shown to be a precise estimate of \(P_s\) at all depths. \(P_e\) was also highly correlated with \(P_s\), but both \(P_e\) and \(P_s\) overestimated \(P_1\) at the surface by 40%. Some experiments at three stations showed that a 2-mm thickness of clear glass placed over surface samples in the measurement of \(P_s\) could increase \(P_s\) by about 50%. This suggested that u.v. irradiance in surface ocean waters decreased \(P_1\) and could explain the overestimates by \(P_e\) and \(P_s\). The results showed the need for precise information of spectral composition of irradiance in studies of primary production but demonstrated the validity of \(E_0(350\text{-}700)\) as an estimate of available photosynthetic irradiance. They also showed that \(P_e\) could estimate \(P_1\) with a high degree of precision, and that such a calculative method could provide a useful way of continuously monitoring the primary production of large bodies of water for extended periods.

Introduction

One of the basic requirements in understanding the processes of oceanic primary production is a knowledge of its relations to submarine irradiance. Primary production has been extensively measured using the \(^{14}\text{C}\) method introduced by Steemann Nielsen (1952), but until recently equipment to measure submarine irradiance in a meaningful way has not been readily available. As re-emphasized by Tyler (1973b), equipment which measured light in foot-candles, lux or lumen was useful only for determining relative levels of irradiance where the spectral characteristics of the irradiance remained constant. Submarine irradiance of course does not meet this condition and therefore any attempt to relate primary production to irradiance under natural conditions was precluded.

A second difficulty was the use of incubators with artificial light sources (such as incandescent or fluorescent lamps) which had spectral characteristics bearing little or no resemblance to submarine irradiance. Moreover, sources of this type produced irradiance fields of such indeterminate geometry that it was impossible to measure the irradiance incident on the plankton with any confidence. The levels of irradiance

* The work reported here formed part of that carried out by IAPSO/SCOR/UNESCO Working Group 15 aboard the USC and GSS Discoverer in May–June 1970.
obtainable in these incubators were usually much lower than those found under natural conditions.

Steemann Nielsen has published several studies on the relations between primary production and irradiance, but was unable to quantify the relations beyond the empirical and relative levels. Sorokin (1961) in his 'indirect' method for measuring primary production used an empirical relationship derived from the response of phytoplankton populations to different levels of irradiance by suspending replicates of a single sample of ocean water at several depths in the ocean. Again, lack of adequate irradiance measurements made it impossible to quantify the relationship.

Very few measurements of primary production as a function of controlled irradiance (P v. I) have been published for natural phytoplankton populations. Most of the earlier studies, such as those of Ichimura (1960) and Ichimura et al. (1962), were made with unsuitable light and photometric units. Some recent measurements of P v. I have appeared but these were not carried out in conjunction with measurements of submarine irradiance.

Some data are available for P v. I in artificial cultures of some phytoplankton species (e.g. Jitts et al. 1964) but the problems of extrapolating these results to natural populations make them of little value in studies such as the present one.

The establishment by IAPSO/SCOR/UNESCO of Working Group 15 on 'Photosynthetic Radiant Energy' (see Tyler 1964, 1966) has led to the development of equipment and techniques for measuring submarine irradiance in absolute radiometric units and with specified spectral characteristics, e.g. quanta between 350 and 700 nm (Jerlov and Nygård 1969b; Prieur 1970). During a joint cruise of Working Group 15 aboard USC and GSS Discoverer in waters ranging from the Eastern Equatorial Pacific, through the Panama Canal, to the central Atlantic, the opportunity arose for attempting to overcome many of the problems discussed above. Simultaneous measurements were made of the amount of submarine irradiance available for photosynthesis by natural populations of phytoplankton and of the rate of primary production by these populations. A suitable high-pressure Xenon lamp incubator was also available to measure primary production by the populations as a function of irradiance. This paper describes the results of this joint study.

Methods

Irradiance Measurements

(i) Total irradiance

Total irradiance (E_{tot}) was recorded continuously on deck with an Eppley pyranometer, calibrated in W m^{-2} by the manufacturer. These measurements were of the whole irradiance from 300 to 2800 nm and included the infrared. The continuous record was averaged over 5-min periods and the results published in the form of bar graphs (Morel 1973).

(ii) Quantum measurements

Measurements of E_q(350–700), both above the surface and submarine, were made with a quantum meter described by Prieur (1970). This instrument, built and calibrated by the Physical Oceanography Laboratory of the University of Paris, consisted of a cosine collector and measured downward irradiance between 370
(approx.) and 700 nm as quanta m$^{-2}$ s$^{-1}$. However, we refer to the quantity measured as $E_q(350–700)$ as recommended by Working Group 15. The error introduced is very small, less than 1%.

**Calculation of Available Photosynthetic Irradiance**

At the three depths chosen for measurement of primary production (see below) the available photosynthetic irradiance, i.e. $E_q(350–700)$ in quanta m$^{-2}$ s$^{-1}$ as a function of time between noon and sunset, was calculated as follows.

(1) Bar graphs of total irradiance ($E_{tot}$) at each station, taken from Morel (1973), were multiplied by the constant factor $1.175 \times 10^{18}$ arrived at below. This gave bar graphs of $E_q(350–700)$ of the irradiance above the surface at each station.

(2) For the surface sample, nominally taken at 0 m, the bar graphs were multiplied by the arbitrary factor 0.75. The actual depth of sampling and in situ incubation for the surface sample varied between 0.2 and 0.5 m. Because of the erratic nature of irradiance at these depths, it was not possible to make direct measurements. At these depths there is a rapid absorption of the red part of the spectrum, as well as a reduction of irradiance by surface reflection. The factor 0.75 was arrived at by extrapolation of typical curves of submarine irradiance as a function of depth. It is possible that the factor of 0.75 may produce an underestimate of $E_q(350–700)$ at 0.5 m below the surface. However, when a factor of 0.80 was used there was no significant change in the calculations or conclusions.

(3) A mean curve for the percentage of irradiance as a function of depth was calculated from 2–4 curves measured with the attenuation quantum meter at each station (see above). The percentage of irradiance at the required sampling depths was determined and the bar graphs of $E_q(350–700)$ were multiplied by these factors to give bar graphs of irradiance $v$. time at each depth.

An example of the results of these calculations is given in Fig. 4b. These calculations were based on two assumptions. The first was that $E_q(350–700)$ is a constant fraction of $E_{tot}$, and the second was that irradiance at a given depth is a constant fraction of $E_q(350–700)$ above the surface throughout the period from noon to sunset. These assumptions are discussed below.

**Approximations in Optical Calculations**

(i) Relation of $E_q(350–700)$ to $E_{tot}$

On 67 separate occasions, surface irradiance was measured simultaneously with both a quantum meter, for $E_q(350–700)$, and a pyranometer, for $E_{tot}$ (see above). These measurements were made under a variety of conditions. The sky varied from clear through hazy to completely overcast. Solar elevation varied from 80 to 17° and $E_{tot}$ varied from 80 to 1100 W m$^{-2}$. The results, given in Fig. 1, show the two measurements to be linearly related by the equation $E_q(350–700) = 1.176 \times 10^{18} E_{tot}$, with a highly significant correlation coefficient of $r = 0.99$. Using this relation and the values of $E_{tot}$, values for $E_q(350–700)$ were calculated. For sun and sky radiation reaching the sea surface Morel and Smith (1974) have shown that the averages of quanta per unit energy are $2.77 (\pm 0.02) \times 10^{18}$ and $2.72 (\pm 0.02) \times 10^{18}$ quanta s$^{-1}$ W$^{-1}$ respectively for the wavelength regions 400–700 and 350–700 nm. These values hold for a wide range of sun altitudes and meteorological conditions. The
ratio $1.176/2.77$ leads to the commonly found value of 0.425 for the ratio of the energy in the band 400–700 nm to total energy.

This calculation of $E_q$ from $E_{tot}$ is similar to the method described by Jerlov (1974). The constant derived from the above measurements is very close to that proposed by Jerlov.

![Fig. 1. The relationship of 67 on-deck measurements of $E_q(350-700)$ to simultaneous measurements of $E_{tot}$ made with a quantum meter (Prieur 1970) and an Eppley pyranometer respectively.](image)

(ii) **Solar elevation and submarine irradiance**

Considering measurements of submarine irradiance made on different occasions during the day at each station, no systematic variation with solar elevation was found. Such variations have been reported in some cases (Jerlov and Nygård 1969a), but not in others (Bethoux and Ivanoff 1970). More recent experiments (Højerslev 1974) have shown the effect of solar elevation to be small. The validity of the assumption used in the calculation can be briefly examined as follows.

Assuming the hypothesis of a sun in a black sky, and a non-scattering sea with a perfect flat surface, the ratio $r(i)$ of the irradiance $E_z$ at a given depth $z$ to the irradiance above the surface, $E_0$, varies with $i$, $i$ being the sun-zenith distance, according to the equation

$$r(i) = \frac{E_z}{E_0} = (r_0)^{1/\cos i} \left[(1 - \rho_0)/(1 - \rho_i)\right],$$

where $r_0$ is the initial value when the sun is at the zenith ($i = j = 0$), $j$ is the angle of refraction corresponding to $i$, and $\rho_0$ and $\rho_i$ are the Fresnel values of reflectance respectively for the angles of incidence 0 and $i$. The dashed lines in Fig. 2 show the variations of $r(i)$ for three initial values of $r_0 = 75, 36, \text{ and } 17\%$.

If the skylight is now taken into account, and if $m$ and $n$ (with $m + n = 1$) are the parts of irradiance due to direct sun and to the diffuse sky respectively, the ratio becomes $r'(i)$, with

$$r'(i) = m r_s(i) + n r_D,$$

where the subscript $S$ stands for the sun and $r_s(i)$ is equal to $r(i)$, as expressed above and the subscript $D$ stands for the diffuse light from the sky and $r_D$ can be assumed
to remain constant with respect to $i$. Values of $m$ and $n$ with varying solar elevation were taken from Sauberer and Ruttner (1941) by averaging the values given for 431 and 535 nm, as the major part of submarine radiation is found between these wavelengths. For low sun, the increasing part of diffuse light from the sky enhances the influence of the constant term $r_0$ and reduces the variations. This is demonstrated in Fig. 2 where the variations of $r'$ with $i$ are shown as solid lines. The maximum deviations from the initial values $r_0$ occur at solar elevation less than 20°.

![Figure 2. Theoretical variations of the percentage of surface irradiance ($r$ and $r'$) with sun-zenith angle $i$ at three depths where the initial percentages (i.e. when the sun is at the zenith) are 75, 36, and 17% respectively. $r$ (- - -) assumes a sun in a black sky. $r'(-----)$ assumes a sun plus sky light.](image)

It must be noted that this simple approach is pessimistic and overestimates these deviations. Without entering into the details of the radiative transfer, it can be said that the effects of scattering in the submarine light field and of the roughness of the sea surface contribute to reduce the above computed variations. Moreover, the error, if significant, could only occur when the energy level and consequently the primary production become very low (see Fig. 4c).

*Determination of Sampling Depths*

The depths from which samples were collected at each station for the measurement of primary production were determined as follows.

1. Transmission of blue-glass filters used in the incubator for measuring primary production by the simulated *in situ* technique (see below) was measured with a quantum meter (Jerlov and Nygaard 1969b). The quantum meter was placed in a gimballed water bath on deck and the percentage transmission of solar irradiance (in quanta, 350–700 nm) by each of the six sets of filters was determined in succession. This determination was repeated only when the blue-glass filters were changed.

2. The percentage transmission of submarine irradiance was measured at about 1030 h at each station with the instrument described above. Irradiance was measured (in quanta, 350–700 nm) as a function of depth and replotted as percentage of the surface irradiance.

3. The sampling depths were selected from the percentage transmission curves obtained in (2) as those depths at which the same six percentages were found as for the sets of blue-glass filters in (1).
Measurement of Primary Production

(i) Sampling and $^{14}$C techniques

Using a twin 6-litre plastic sampler (Jitts 1964), samples were taken at about 1100 h at each station from the six depths determined above. These six samples were subsampled into 50-ml Pyrex bottles and 10 $\mu$Ci of $^{14}$C added to each subsample. These replicates were then incubated under one of the three conditions described below.

After incubation, all subsamples were filtered through 0.45-\mu m membrane filters (Millipore, type HA) and their Geiger activity was measured. The primary production for the period of incubation was calculated by isotope dilution. The column primary production (i.e. production under 1 m$^2$ of sea surface) at each station was calculated by arithmetic integration of the primary production of the six depths. Details are given in Jitts (1973).

(ii) Incubation methods

In situ primary production ($P_i$) was measured by suspending subsamples for the period from noon to sunset from a free-floating buoy at the six depths from which they were taken (Saijo 1973).

![Spectral compositions of irradiance in the Xenon incubator. Curves are for the maximum irradiance to which samples are exposed when those samples are from depths where submarine irradiances are about 75 (surface), 36, and 17% of surface irradiance.](image)

For measuring simulated in situ primary production ($P_s$), replicate subsamples from the six depths determined as above were placed in a deck incubator through which surface seawater was continuously pumped. This incubator was similar to those described in Jitts (1963) having six compartments with clear glass covering one and increasing thicknesses of a blue-glass filter over the other five; together with sunlight these gave irradiance conditions similar to six depths in the ocean. This incubator differed from earlier models in that it was gimbaled, the samples were in 50-ml bottles held with their round bottoms facing upwards, and the compartments and filters were circular.

Primary production as a function of irradiance ($P_s$) was measured with replicates of samples taken for measuring $P_i$ and $P_s$ at the surface and the next two depths below the surface. From each depth six replicate subsamples were incubated for 4 h from 1230 to 1630 h in a controlled-temperature bath illuminated by a high-pressure Xenon lamp (Jitts and Scott 1976). Surface subsamples were incubated under white
light of $20-850 \times 10^{18}$ quanta m$^{-2}$ s$^{-1}$. Subsamples from the next two depths were incubated under one and two thicknesses respectively of the same filters as used in measuring $P_r$, irradiance levels being 7–300, and $4-150 \times 10^{18}$ quanta m$^{-2}$ s$^{-1}$.

The spectral compositions of the irradiances used in the incubator for samples from the three depths are given in Fig. 3. These spectral curves were determined with an ISCO Spectroradiometer. The irradiance to which each subsample was exposed in the Xenon incubator was calculated by integration of the spectral curve between 350 and 700 nm.

![Graphs](image)

**Fig. 4.** Example of calculation of $P_e$ for three depths (0, 11, and 15 m) from station 14. (a) $P_r$ as a function of irradiance in the Xenon incubator. $\bullet$ 0 m. $\triangle$ 11 mm. $\times$ 15 m. (b) $E_r$ as a function of solar time, as calculated from $E_{tot}$. I, 0 m, 75% of surface irradiance. II, 11 m, 28.5% of surface irradiance. III, 15 m, 19.5% of surface irradiance. (c) $P_i$ as a function of solar time, obtained by taking values for primary production from Fig. 4a corresponding to irradiance values in Fig. 4b and plotting the former as a function of the solar time at which the latter occurred. $P_e$ was obtained by integrating the curves in Fig. 4c by the equation $P_e = 2 \int_{1200}^{1800} P_r$, 0 m, $P_e = 9.09$ mg C m$^{-3}$ day$^{-1}$. 11 m, $P_e = 9.87$ mg C m$^{-3}$ day$^{-1}$. 15 m, $P_e = 8.15$ mg C m$^{-3}$ day$^{-1}$.

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**Calculation of Primary Production ($P_e$) from Irradiance and $P_v$ vs I Curves**

Having measured the relation of primary production to irradiance ($P_e$) for a given sample of phytoplankton from the ocean, and having estimated the photosynthetic quanta [$E_r(350-700)$] available to that sample as a function of time, it was possible to calculate primary production for that sample as a function of time. The method of calculation is shown in the example given in Fig. 4. In this example samples were taken from three depths (0, 11, and 15 m) where 75, 28.5% and 19.5% of surface...
irradiance was found respectively. Using the Xenon incubator, curves were established for $P_e$ (Fig. 4a). From a continuous record of irradiance on deck and the percentage submarine transmission of irradiance, irradiance as a function of time ($E_t$) at each depth was plotted (Fig. 4b). From the curves of $P_e$ and $E_t$ at each depth, primary production as a function of time ($P_t$) was plotted (Fig. 4c). From the curves of $P_t$, primary production at each depth during the day was calculated ($P_τ$) by integrating the curve for $P_t$ from noon to sunset and multiplying the result by 2.

**Results**

Simultaneous measurements of primary production (measured as both in situ and simulated in situ), production v. irradiance, and available submarine irradiance were made at the 14 stations shown in Fig. 5. The raw data were published in the ‘Data Report SCOR Discoverer Expedition’ (Tyler 1973a), in situ production by Saijo, simulated in situ production and production v. irradiance by Jitts, and solar irradiance and submarine quanta by Morel. The results obtained at each station are summarized in columns 1–9 in Table 1.

![Fig. 5. Track of Discoverer SCOR Working Group 15 cruise, May 1970, showing positions of stations 7–21.](image)

Due to errors in measuring the transmission of the blue-glass filters in the simulated in situ incubator, only surface values were available from stations 7–10. At stations 11–21 data were obtained from three depths, except at stations 15 and 19 where data from only two depths were obtained. The data given in column 5 (Table 1) are for column primary productions calculated from in situ measurements on samples from six depths at each station from the surface to the bottom of the euphotic layer (see Saijo 1973).

The in situ column production (column 5, Table 1) showed that production at the stations studied varied from moderately productive oceanic waters of the eastern equatorial Pacific (0·15–0·40 g C m$^{-2}$ day$^{-1}$) at stations 8–14, to highly productive coastal waters (0·6 g C m$^{-2}$ day$^{-1}$) off Panama at station 16, to very poor waters (0·07 g C m$^{-2}$ day$^{-1}$) in the Sargasso Sea. This range of values encompasses those
reported for most of the world ocean. The half-day surface irradiances given in column 4 (Table 1) showed that a wide range of sun and cloud conditions was included in this study (3·4–14·4 × 10^6 J m^{-2}).

| (1) Station No. | (2) Date  | (3) Position | (4) ½-Day surface irradiation (MJ m^{-2}) | (5) In situ column primary production (g C m^{-2} day^{-1}) | (6) Sample depth (m) | (7) Submarine irradiance (350–750 nm) (% surface) | (8) Primary production (mg C m^{-3} day^{-1}) P_i | (9) P_s | (10) P_c |
|-----------------|-----------|--------------|------------------------------------------|-------------------------------------------------|-----------------|---------------------------------------------|-----------------------------|------|-------|------|
| 7               | 10 May    | 4°49'N, 81°46'W | 3·44                                      | 0·14                                            | 0                | 75                                          | 3·9                         | 5·9  | 7·2   |
| 8               | 12 May    | 3°10'S, 84°42'W | 7·09                                      | 0·23                                            | 0                | 75                                          | 6·1                         | 9·9  | 7·6   |
| 9               | 13 May    | 3°55'S, 84°44'W | 7·54                                      | 0·38                                            | 0                | 75                                          | 11·4                        | 14·6 | 15·0  |
| 10              | 14 May    | 5°20'S, 87°17'W | 6·30                                      | 0·24                                            | 0                | 75                                          | 4·6                         | 7·0  | 6·1   |
| 11              | 15 May    | 7°52'S, 90°15'W | 8·02                                      | 0·14                                            | 0                | 75                                          | 3·0                         | 5·7  | 5·7   |
| 12              | 16 May    | 5°37'S, 87°45'W | 10·85                                     | 0·21                                            | 0                | 75                                          | 2·8                         | 4·4  | 4·7   |
| 13              | 17 May    | 3°03'S, 85°25'W | 9·91                                      | 0·13                                            | 0                | 75                                          | 2·7                         | 3·2  | 6·6   |
| 14              | 18 May    | 3°05'S, 84°48'W | 9·25                                      | 0·24                                            | 0                | 75                                          | 5·0                         | 12·1 | 9·1   |
| 15              | 20 May    | 4°30'N, 82°54'W | 9·11                                      | 0·30                                            | 0                | 75                                          | 4·2                         | 9·0  | 8·6   |
| 16              | 21 May    | 6°35'N, 79°57'W | 11·58                                     | 0·63                                            | 0                | 75                                          | 13·9                        | 19·9 | 20·7  |
| 17              | 28 May    | 16°52'N, 76°04'W | 12·48                                     | 0·18                                            | 0                | 75                                          | 1·50                        | 1·13 | 1·50  |
| 18              | 29 May    | 19°21'N, 73°47'W | 12·12                                     | 0·16                                            | 0                | 75                                          | 0·58                        | 0·86 | 0·93  |
| 19              | 30 May    | 20°20'N, 70°57'W | 13·26                                     | 0·12                                            | 0                | 75                                          | 0·89                        | 1·10 | 1·01  |
| 21              | 1 June    | 25°45'N, 65°38'W | 14·35                                     | 0·07                                            | 0                | 75                                          | 0·25                        | 0·82 | 0·67  |
|                |           |               |                                          |                                                 | 11               | 42                                          | 0·18                        | 0·52 | 0·69  |
|                |           |               |                                          |                                                 | 33               | 17                                          | 0·32                        | 0·40 | 1·13  |

Using the method described previously, primary production was calculated \( P_c \) for all 32 samples from the 14 stations at which simultaneous measurements were obtained of \( P_i \) and \( P_s \). The results for \( P_i, P_s, \) and \( P_c \) are given in columns 8, 9 and 10 respectively in Table 1.
The relation between \( P_c \) and \( P_s \) is shown in Fig. 6a. The results showed that \( P_c \) and \( P_s \) were linearly related with a very high correlation coefficient \( r = 0.98 \), giving the equation

\[
P_c = 1.039 \, P_s - 0.25.
\]

This highly correlated 1:1 ratio unequivocally demonstrated that \( P_c \) was an accurate estimate of \( P_s \).

![Graphs showing the relation between \( P_c \) and \( P_s \)](image)

Fig. 6. Primary production of 32 samples and their calculated linear regressions. + Samples from the surface (14) and their regression (--.--). ● Samples from below the surface (18). —— Regression of all samples. (a) \( P_c \) v. \( P_s \). (b) \( P_c \) v. \( P_i \). (c) \( P_s \) v. \( P_i \).

The relation of \( P_c \) to \( P_i \) is shown in Fig. 6b. \( P_c \) was linearly related to \( P_i \) with \( r = 0.95 \) and gave the equation

\[
P_c = 0.95 \, P_i + 1.67.
\]

Whilst \( P_c \) was again shown to be highly correlated to \( P_i \), the magnitude of the constant factor 1.67 in the equation showed that \( P_c \) was an accurate estimate of \( P_i \) only at higher values. To study this deterioration in the relation of \( P_c \) to \( P_i \), when compared to the relation of \( P_c \) to \( P_s \), the results obtained from the 14 surface samples only were examined. The results from the surface (Fig. 6b) gave the equation

\[
P_c = 1.39 \, P_i + 0.74, \quad r = 0.98.
\]

These results showed that \( P_c \) was overestimating \( P_i \) at the surface by about 40%. When the relation of \( P_s \) to \( P_i \) was examined (Fig. 6c) the results were practically
identical to those found for the relation of \( P_e \) to \( P_i \), the 32 samples giving the equation

\[
P_s = 0.98 P_i + 1.53, \quad r = 0.94.
\]

The results from the surface (Fig. 6c) gave the equation

\[
P_s = 1.39 P_i + 0.73, \quad r = 0.96.
\]

These results showed that \( P_s \) was overestimating \( P_i \) by about 40% at the surface.

In an effort to determine the cause of this overestimate of \( P_i \) at the surface by both \( P_e \) and \( P_s \), an experiment was carried out at stations 18, 19, and 21, where six replicate samples of surface waters were incubated in the simulated in situ incubator on deck.

### Table 2. Results of experiments at three stations showing the effects on the measurement of \( P_s \) for replicate samples taken from the sea surface and exposed with and without a 2-mm thick clear-glass covering

<table>
<thead>
<tr>
<th>Station No.</th>
<th>Date</th>
<th>Position</th>
<th>Sample No.</th>
<th>Primary production (mg C m(^{-3}) day(^{-1}))</th>
<th>Ratio with/without</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>With glass</td>
<td>Mean</td>
</tr>
<tr>
<td>18</td>
<td>29 May</td>
<td>19°21'N.</td>
<td>1</td>
<td>0.81</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td>73°47'W.</td>
<td>2</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>30 May</td>
<td>20°20'N.</td>
<td>1</td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>70°57'W.</td>
<td>2</td>
<td>0.074</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>0.78</td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>1 June</td>
<td>25°45'N.</td>
<td>1</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>65°38'W.</td>
<td>2</td>
<td>1.07</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>1.06</td>
<td></td>
</tr>
</tbody>
</table>

Three replicates were incubated in the normal way, i.e. under a 2-mm thickness of clear glass. For the other three replicates the clear glass was omitted. The results are given in Table 2, and show that the ratio of ‘with glass’ to ‘without glass’ was 1.70, 1.68, and 1.22 respectively at the three stations with an average of 1.55. The results showed that a 2-mm sheet of clear glass over the samples could increase the primary production by about 50%.

### Discussion

The almost perfect 1:1 ratio obtained for \( P_e \) v. \( P_s \) in Fig. 6 for samples from a wide range of oceanic water leads to several conclusions. (1) It shows that by using equipment presently available it is possible to measure available photosynthetic irradiance with a high degree of reliability. (2) It gives strong support for the validity of the recommendation made by Working Group 15 for using the number of quanta in the spectral range of 350-700 nm as a measure of available photosynthetic irradiance. (3) Knowing the available photosynthetic irradiance and the relation of \( P \) v. \( I \) for a given phytoplankton population, it is possible to calculate the primary production of that population.
The last conclusion must be qualified by the results obtained for $P_0$ vs. $P_i$ and for $P_s$ vs. $P_i$ in Figs 7 and 8. This evidence that $P_s$ can overestimate $P_i$ for surface samples by some 40% was not found in earlier studies (Jitts 1963). The experiments reported in Table 2, showing that a single 2-mm sheet of clear glass could explain the discrepancy, cannot be regarded as conclusive as they were results from only three stations in a single part of the world ocean (the central Atlantic). However, they do suggest that u.v. irradiance, present in the surface waters in the ocean but stopped in the simulated *in situ* incubator by the sheet of glass, can significantly reduce primary production by phytoplankton in these shallow layers. This phenomenon has been described earlier by Steemann Nielsen (1964) but its significance in the measurement of oceanic primary production has been neglected. The 50-ml round-bottomed bottles used throughout the present study for incubation of the samples were made of very thin Pyrex glass. The bottles used in earlier studies by Jitts (1963) were simple Pyrex B.O.D. bottles with very much thicker walls. As most workers have used similar thick-walled bottles, this leads to the possibility that most of the reported results for primary production in surface waters are overestimates by some 40%. It can also be speculated that this u.v. suppression of primary production explains why supersaturation is commonly found at high irradiance in $P$ vs. $I$ curves (see Fig. 4a), and surface production in oceanic waters is usually lower than that of subsurface layers (e.g. see $P_i$ in column 8, Table 1).

Though $P_0$ estimated $P_s$ perfectly, it did not give an adequate estimate of $P_i$ for surface waters. This was probably due to the reduced amount of u.v. irradiance in the Xenon lamp incubator when compared to that of surface waters. No measurements of u.v. irradiance were made in the present studies, but the spectral curve for irradiance used for surface samples in the incubator, given in Fig. 3, shows that at 350 nm the irradiance was reduced to about 25% of that at other wavelengths. Jerlov (1968, Table XX p. 120) reports a reduction to about 90% at 1 m for most oceanic waters at the same wavelength. As solar irradiance at 350 nm is about 50% of that at other wavelengths, this suggests that the u.v. irradiance in the incubator is probably less than 50% of that in surface waters. These results demonstrate the need for precise information on the spectral composition of irradiance in studies of primary production.

One of the assumptions made in the calculation of primary production ($P_0$) is that the curve $P$ vs. $I$ remains constant throughout the period from noon to sunset. The known diurnal variation of photosynthesis under constant irradiance (Doty and Oguri 1957) suggests that $P$ vs. $I$ is likely to undergo a similar variation. However the 1:1 ratio found for $P_0$ to $P_s$ suggests that this effect was not significant. This may simply be due to $P$ vs. $I$ having been determined by incubation between 1230 and 1630 h, thus giving an adequate mean curve for the period from noon to sunset.

In spite of the problems discussed above, it has been demonstrated that primary production can be calculated with a high degree of accuracy from a knowledge of the $P$ vs. $I$ curve of a natural phytoplankton population and the available photosynthetic irradiance. The use of this calculation as a method for studying oceanic primary production has several advantages over direct measurements by the *in situ* or simulated *in situ* methods:

1. It is a comparatively simple task to determine the available photosynthetic irradiance for very large areas of the ocean with a quantum meter and to continuously monitor its variations with a pyranometer over long periods.
The transmission characteristics of ocean waters can change only over long periods, apart from exceptional circumstances such as seasonal plankton blooms.

(2) Large areas of the ocean can be shown to have similar populations of phytoplankton. The characteristic $P v. I$ curves determined for a given population will change only slowly with changes in the population or its metabolic state.

(3) Using the characteristic $P v. I$ curves and the continuously monitored irradiance, it is possible to calculate the continuous variation of production of large areas of the ocean.

(4) Integration of the calculated variation of production gives estimates of production over long periods which will be more accurate and certainly much more easily obtainable than by direct measurements at discontinuous intervals.

Ryther (1956) proposed the calculation of primary production from measurements of light and chlorophyll. This method has been extensively examined (e.g. Ichimura et al. 1962), but has suffered from the intrinsic unreliability of chlorophyll as an estimate of photosynthetic ability, from the past lack of suitable methods for measuring submarine irradiance, and from the empirical nature of the equations used. Recently, Fee (1973) has described a method for calculating production that is basically similar to the principle of the method described in this study. Although the verification of this method was inadequately based on two in situ experiments, he demonstrated the advantage of the calculative method.

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