Available, usable, and stored radiant energy in relation to marine photosynthesis

ANDRÉ MOREL*

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Abstract—At 32 stations covering a wide variety of phytoplankton biomass, results have been obtained for in situ production, daily irradiation, photosynthetically available radiation (PAR), and spectral composition of submarine radiant energy. PAR is compared to the photosynthetically stored radiant energy (PSR), and a dimensionless quantity, $\varepsilon$, describing the efficiency of the energy storage, is calculated. $\varepsilon$ varies from less than 0.01% to about 0.1% between the surface and the base of the euphotic layer in oligotrophic waters (Sargasso Sea). The corresponding values for productive waters (Mauritanian upwelling area) range between 0.1 and 0.8%. On average, for the whole productive column, about 3% ($\pm 1.5\%$) of the total incident energy (including infra-red) is stored by photosynthesis per unit area of ocean per unit of chlorophyll (1 g Chl-a m$^{-2}$), despite the variability of biomass (0.003 to 0.3 g Chl-a m$^{-2}$).

The photosynthetically usable radiant energy (PUR), i.e. the part of PAR that can be absorbed by algae, is evaluated. Comparison of PSR and PUR allows the estimation of the quantum yield $\phi$ and its variation with depth. The exact calculation of PUR requires the introduction of an effective absorption coefficient, $a_{\text{eff}}$, for the living phytoplankton in its actual environment. The coefficient $a_{\text{eff}}$ must take into account both the algal absorption and the spectral composition of the remnant light. Low values obtained for PUR and the consequent excessive values for $\phi$ emphasize the necessity for chromatic adaptation, especially for an increase in accessory pigments absorbing green-yellow light.

INTRODUCTION

The SCOR/UNESCO/IAPSO Working Group 15 on Photosynthetic Radiant Energy recommended that oceanic primary production be studied in conjunction with adequate irradiance measurements, i.e. with measurements of the total photosynthetic available radiation, PAR. PAR is defined as the amount of radiant energy, preferably expressed as quantum units, available at a particular depth, within the approximate spectral range, 350 to 700 nm (Tylor, 1966).

This definition does not prejudice the possible usefulness of this energy for phytoplankton because all photons, regardless of wavelength, within the defined spectral band must be counted. To be efficient in the photosynthetic process, these photons must be absorbed by the algal pigments. Thus one can define the photosynthetically usable radiation, PUR, as the fraction of radiant energy of such wavelength that it can be absorbed by the algae. PUR depends on the pigment composition of the algal population as well as on the spectral composition of the submarine radiant energy.

Lastly, only a fraction of the absorbed energy is really used in the photosynthetic process. The transformation of absorbed energy into chemical energy is carried out with variable yields. A quantum yield, $\phi$, has been defined by plant physiologists as the number of CO$_2$ molecules transformed (i.e. reduced to carbohydrate), per quantum

* Laboratoire de Physique et Chimie Marines, Station Marine de Villefranche-sur-Mer, 06230 Villefranche sur Mer, France.
absorbed, or the number of CO₂ moles per Einstein absorbed. The photo- synthetically stored radiation, PSR, can be defined as the amount of radiant energy converted into and stored as chemical energy, in the form of organic matter created through photosynthesis. There exists an obvious relation among these three quantities:

\[ \text{PSR} < \text{PUR} < \text{PAR}. \]

Comparison of the extreme terms, PSR and PAR, leads to the concept of efficiency of utilization of radiant energy entering the water, by the phytoplankton. This efficiency is described by a dimensionless parameter, introduced below. This pure number, \( \varepsilon \), is characteristic both of the water mass and of its algal content. PSR and PAR are measurable and \( \varepsilon \) can be calculated for all depths.

The comparison of PSR and PUR allows the evaluation of \( \phi \), the quantum yield. Unlike \( \varepsilon \), \( \phi \) is independent of the optical properties of the seawater, and hence depicts uniquely the physiological response of the algal cells. PUR is not directly measurable, but has to be computed from the values of the spectral irradiance measured at different depths, in conjunction with the \textit{in vivo} spectral absorption of the living phytoplankton. The latter is not generally known in routine work.

The first aim of this work is to study, in the euphotic layer, the variations of the quantities PAR, PUR, and PSR for diverse oceanic situations with respect to algal biomass and production. The second aim is to estimate the values of \( \varepsilon \) and \( \phi \), efficiency and quantum yield, for natural populations of phytoplankton in their actual environment. Finally the question of chromatic adaptation is examined in relation to the spectral diversity of submarine light field.

**MATERIAL AND METHODS**

(1) \textit{Optical and biological data}

The data were obtained during two oceanographic expeditions. The first, in May 1970, was aboard the \textit{Discoverer} (SCOR/UNESCO/IAPSO Working Group 15 cruise) and the other, in March to April 1974, was aboard the \textit{Jean Charcot} (CINECA—Charcot 5 cruise).* Complete measurements were made at 32 stations during the two cruises. The first expedition (Fig. 1a) took place in oligotrophic waters of the Sargasso Sea and in moderately productive waters of the eastern equatorial Pacific. The level where \( E_q \), the downwelling quantum irradiance, is reduced to 1% of its value at the surface varied from 155 to 37 m (Fig. 2a). The column primary production varied from 0.06 to 0.63 g C m\(^{-2}\) day\(^{-1}\) and the phytoplanktonic biomass, expressed in terms of chlorophyll-\( a \) content, varied from 3 to 22 mg Chl-\( a \) m\(^{-2}\) (Table 1a).

The second expedition was in the eutrophic waters of the Mauritanian upwelling zone (Fig. 1b). The 1% level was between 20 and 25 m (Fig. 2b). Production was in the range 1.1 to 4.7 g C m\(^{-2}\) day\(^{-1}\) and biomass was in the range of 75 to 321 mg Chl-\( a \) m\(^{-2}\) (Table 1b). The 32 stations covered a wide range of primary production. Irradiation conditions, however, were similar as all these stations are in tropical or sub-tropical zones, the studies were confined to a single time of year, and apart from a few occasions, the cloud cover was light or absent.

* Meaning the fifth cruise of the Charcot, which was a part of the Cooperative Investigations of the Northern part of the East Central Atlantic (CINECA). The goal of this cooperative effort was recently presented (Barber, 1977).
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Fig. 1. Position of stations where optical and primary production measurements were carried out (a) during the WG 15—Discoverer cruise (May 1970) and (b) during the CINECA 5—Charcot cruise (March to April 1974).

WG 15—Discoverer cruise

![Graph](image)

Station No.

Fig. 2. The depths (in meters) where $E_a$ is reduced to 10, 1, 0.1, and 0.01% of its value above the surface are graphically represented for each station. These depths are averaged over several (two to four) determinations. (a) WG 15—Discoverer cruise, (b) CINECA 5—Charcot cruise.

CINECA 5—Charcot cruise

![Graph](image)

Station No.

Primary production was determined by the in situ $^{14}$C method by SAIJO (1973) for the WG 15 cruise and by MINAS (1976) for the CINECA 5 cruise. Chlorophyll-$a$ and phaeophytin-$a$ were determined by BAIRD (1973) for WG 15 and by JACQUES, PANOUSE and GOSTAN (1976) for CINECA 5. Optical measurements were carried out by MOREL (1973) for WG 15 and by MOREL and PIERRE (1976) for CINECA 5. These references discuss the methods and accuracy.
Table 1(a).  WG 15—Discoverer cruise.

<table>
<thead>
<tr>
<th>Station</th>
<th>Chl a</th>
<th>$\lambda_{\text{max}}$ at depth</th>
<th>Lu</th>
<th>column primary efficiency</th>
<th>Global $\varepsilon/\text{Chl a}$</th>
</tr>
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<tr>
<td></td>
<td>(ng m$^{-2}$)</td>
<td>(nm)</td>
<td>(m)</td>
<td>gc m$^{-2}$ day$^{-1}$</td>
<td>%</td>
</tr>
<tr>
<td>2</td>
<td>2.29</td>
<td>477</td>
<td>(100)</td>
<td>0.056</td>
<td>0.0086</td>
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<td>502</td>
<td>(47)</td>
<td>(0.530)</td>
<td>(0.0905)</td>
</tr>
<tr>
<td>7</td>
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<td>491</td>
<td>(48)</td>
<td>0.136</td>
<td>0.0782</td>
</tr>
<tr>
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<td>(50)</td>
<td>0.229</td>
<td>0.0630</td>
</tr>
<tr>
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<td>21.97</td>
<td>495</td>
<td>(44)</td>
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<tr>
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<td>(75)</td>
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<td>0.0290</td>
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<tr>
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<td>(98)</td>
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<td>(100)</td>
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<td>21</td>
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<td>469</td>
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<td>0.071</td>
<td>0.0096</td>
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</table>

* Station 6 excluded (experiments not extended to the bottom of the euphotic layer).

$\mu$mean * 3.21

standard deviation 1.21

Table 1(b).  CINECA 5—Charcot cruise.

<table>
<thead>
<tr>
<th>Station</th>
<th>Chl a</th>
<th>$\lambda_{\text{max}}$ at depth</th>
<th>Lu</th>
<th>column primary efficiency</th>
<th>Global $\varepsilon/\text{Chl a}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(ng m$^{-2}$)</td>
<td>(nm)</td>
<td>(m)</td>
<td>gc m$^{-2}$ day$^{-1}$</td>
<td>%</td>
</tr>
<tr>
<td>21</td>
<td>219.5</td>
<td>563</td>
<td>(19)</td>
<td>4.45</td>
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<td>307.7</td>
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<tr>
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<td>(18)</td>
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<td>559</td>
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<td>1.88</td>
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<td>39</td>
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<td>(24)</td>
<td>1.14</td>
<td>0.179</td>
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<td>(25)</td>
<td>1.67</td>
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<td>(20)</td>
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<td>(24)</td>
<td>2.98</td>
<td>0.402</td>
</tr>
<tr>
<td>76</td>
<td>(19.2)</td>
<td>(0.66)</td>
<td>(0.094)</td>
<td>(4.90)</td>
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<tr>
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<td>559</td>
<td>(18)</td>
<td>2.54</td>
<td>0.357</td>
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<tr>
<td>87</td>
<td>110.0</td>
<td>558</td>
<td>(28)</td>
<td>3.21</td>
<td>0.480</td>
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<tr>
<td>92</td>
<td>321.5</td>
<td>564</td>
<td>(15)</td>
<td>4.74</td>
<td>0.685</td>
</tr>
</tbody>
</table>

* Station 76 excluded (bottom at 15 m).

The optical measurements included:
(1) A continuous record of on-deck total irradiance, $E_{\text{tot}}$ (W m$^{-2}$), obtained with a calibrated Eppeley pyranometer. Integrating over the period of the entire day yields the total irradiation (J m$^{-2}$ day$^{-1}$) for the spectral range 300 to 2800 nm.
(2) At various depths, $z$, the downwelling quantum irradiance, $E_q(z)$, was measured for the 370- to 700-nm spectral region. $E_q(z)$ is expressed as quanta m$^{-2}$ s$^{-1}$, or as per cent of $E_q (0^+)$ determined above the surface ($z = 0^+$).
(3) At the same depths simultaneous spectral analysis of the downwelling radiant flux was carried out between the wavelengths 400 and 700 nm. These spectral irradiance values, $dE/d\lambda$, are expressed as W m$^{-2}$ nm$^{-1}$.

The wavelength for which $dE/d\lambda$ has a maximum value, $\lambda_{\text{max}}$, can be used as an index of water color. It has been shown that $\lambda_{\text{max}}$ is strongly related to the pigment concentration, at least in the case of offshore waters (MOREL and SMITH, 1974). The $\lambda_{\text{max}}$ values
listed in Tables 1(a) and (b) are those observed at the depth, Z, that approximately corresponds to the 1% quanta level. During the Discoverer cruise, deep-blue (λ_{max} \approx 470 to 480 nm) and blue-green waters (λ_{max} \approx 490 to 500 nm) were encountered. Green waters (λ_{max} \approx 560 nm) prevailed during the Charcot cruise with a few exceptions (Stas. 33, 35, and 63) in silty waters near the coast, leading to a λ_{max} value near 500 nm.

(2) Evaluation of PAR, Photosynthetic Available Radiation, for the full incubation period

E_{q}(z) represents the value of PAR at the time of the experiment. It is necessary to estimate PAR for the duration of the in situ incubation (half day or whole day) for each different level where the production was measured.

PAR, expressed as quanta m^{-2} day^{-1}, can be calculated as described by Jitts, Morel and Saito (1976) using the optical data mentioned above. Briefly, the total irradiation (J m^{-2} day^{-1}), multiplied by the factor 1.175 \times 10^{18} gives PAR (0^{+}) in quanta m^{-2} day^{-1} above the surface. Then PAR (z), at the depth z, is deduced from PAR (0^{+}) by assuming that the value of E_{q}(z)/E_{q}(0^{+}), averaged from several measurements during the day, remains valid throughout the day. For the subsurface sample (z = 0^{-}), the actual depth cannot be rigorously zero and practically varies by several tens of centimetres. When computing PAR (0^{-}), it is assumed that E_{q}(0^{-})/E_{q}(0^{+}) is constant and its value is assumed to equal 0.75. The various approximations and hypotheses associated with this calculation are discussed in the article cited. They are sufficient for the problems considered here.

RESULTS AND DISCUSSION

(1) Production and photosynthetic available radiation

At the 32 stations in question, the phytoplanktonic biomass was extremely variable, as reflected by the chlorophyll-a concentration, which ranged from 0.02 to 10 mg m^{-3}. To compare the results, we will use the production per unit of biomass, P_{B}, which is the ratio of carbon fixed to the concentration of chlorophyll-a, expressed as mg C day^{-1} (mg Chl-a)^{-1}. The values of P_{B} obtained at various depths are shown as a function of the corresponding values of PAR in Figs. 3(a) and (b) for two expeditions.*

* The deepest production values (when PAR is less than 0.2% of its values at the surface), have been excluded as being too much inaccurate.
The curves obtained are related to conventional $P$ versus $I$ curves but differ from them in that irradiance is not constant and in that PAR is integrated over the whole day. The shape of the $P_B$ versus PAR curves is similar for the two expeditions. From one station to another, during both cruises, $P_B$ varied approximately in a ratio 10:1, at a given value of PAR. It is noteworthy that this variation of $P_B$ remained within the same limits for the two cruises, in spite of quite different levels of biomass and production.

Values of PAR ranging from $3 \times 10^{24}$ to $10^{25}$ quanta m$^{-2}$ day$^{-1}$ constitute optimal radiative conditions for photosynthesis by these tropical algae and maximal values lie between 15 and 90 mg C day$^{-1}$ (mg Chl-a)$^{-1}$. The inhibitory effect of an excess of irradiance was virtually systematic for subsurface samples (PAR $>10^{25}$ quanta m$^{-2}$ day$^{-1}$) and is reflected in diminishing values of $P_B$. In the range of irradiation between $3 \times 10^{24}$ and $3 \times 10^{22}$ quanta m$^{-2}$ day$^{-1}$, $P_B$ decreases systematically. This decrease, which results from limiting light conditions, appears to be irregular and not linearly related to the decrease of PAR, because the mean slope of the bilogarithmic representation often differs from unity.

It is well known that the photosynthetic yield increases with decreasing irradiation, and this fact is clearly demonstrated by plotting the yield, $Y$, defined as the ratio of $P_B$ to PAR, as a function of PAR (Fig. 4a and b). In spite of the diversity and irregularity of the curves, the general trend is indeed an increase of $Y$ when the available radiation diminishes. At most of the stations the conversion of radiant energy into chemical energy through photosyntheses is more efficient at the bottom of the euphotic layer, where PAR lies in the range 0.3 to 1% of its value above the surface.

(2) Radiation utilization by photosynthesis

Radiation utilization can be characterized by the coefficient $k_s$, defined as the ratio of PSR to PAR, where PSR is the photosynthetically stored radiation. This coefficient, $k_s$, is simply the yield $Y$ after having converted the production to its equivalent in energy (see Appendix I). Between $Y$ and $k_s$, the numerical correspondence is:

for $Y = 1 \times 10^{-23}$ (mg C m$^{-3}$ day$^{-1}$) (mg Chl-a m$^{-3}$)$^{-1}$ (quanta m$^{-2}$ day$^{-1}$)$^{-1}$ one has:

$k_s = 1 \times 10^{-3}$ m$^{-1}$ (mg Chl-a m$^{-3}$)$^{-1}$;

then the second ordinate scales of Fig. 4(a) and (b) are constructed by using this equivalence. It is observed that the values of $k_s$ near the surface are minimal and are included between 0.1 and $0.4 \times 10^{-3}$ m$^{-1}$ (mg Chl-a m$^{-3}$)$^{-1}$. They can be 10 times higher at low energy levels.
(3) **Utilization efficiency**

The radiation utilization coefficient, $k_s$, defined for the chlorophyll-$a$ concentration unit, is related to the biological extinction coefficient, $k_b$, introduced by Platt (1969), because $k_b = k_s [\text{Chl-}a]$, where $[\text{Chl-}a]$ is the chlorophyll-$a$ concentration. Platt stated in his introduction that it would be useful to define a utilization efficiency, especially for the comparison of production in various locations and at different times. In addition, he stated judiciously that this quantity must be dimensionless. The coefficient $k_b$, which has the dimensions of $(\text{length})^{-1}$, does not satisfy this condition. A satisfactory definition could be proposed as the ratio $\varepsilon$ of $k_b$ to $K$, where $K$ is the diffuse attenuation coefficient for the downwelling quantum irradiance $E_{\text{d}}$, as measured by a quantum meter. At a given point, $\varepsilon$ is an expression of the ratio of the energy chemically stored, to the energy removed from the submarine radiative field by all the physical and chemical processes. The efficiency calculated by Dubinsky and Berman (1976) is apparently defined differently, but in fact their definition can be reduced to the ratio mentioned above.

The efficiency $\varepsilon$ has been computed for the depths at which production experiments were made. In Fig. 5, $\varepsilon$ is plotted not versus the geometrical depth $z$, but versus PAR ($z$) to allow a meaningful comparison of the different stations. The $\varepsilon$ curves are similar in shape, with a similar slope between the top and the bottom of the euphotic layer. But the absolute $\varepsilon$ values are widely spaced and their distribution is mainly determined by the abundance

![Graph](image-url)

**Fig. 5.** Dimensionless quantity, $\varepsilon$, radiation utilization efficiency, plotted versus PAR ($z$) for all experiments. Both scales are logarithmic. ⋮ ⋮ ⋮, CINECA 5—Charcot stations; ⋮ ⋮ ⋮, WG 15 stations.
of phytoplankton. The oligotrophic waters of the Sargasso Sea and the Caribbean Sea present the lowest values, where $\varepsilon$ varies with depth from less than 0.01 to 0.1%. In the Gulf of Panama and near the Galapagos Islands, $\varepsilon$ reaches 1% at low light level. Higher values were obtained at all depths in the productive waters off the Mauritanian coast. Values as high as 7 or 8% are sometimes reached at the base of the productive layer, in the case of high biomasses ($> 200 \text{mg Chl-a m}^{-2}$).

The respective positions of the $\varepsilon$ curves are not solely determined by the photosynthetic activity and by the biomass of algae. If abundant particulate and dissolved detrital material is intermingled with the algal cells, $K$ will be increased and $\varepsilon$ will be decreased, assuming a constant value of $k_a$. Certain coastal waters of high turbidity exemplify this situation. Moreover, in this case the photosynthetic capacity of the algae seems reduced as observed by Huntsman and Barber (1977) in the same Mauritanian area. It should be pointed out that $\varepsilon$ depends on the optical properties of the water (by $K$), on the biomass (by Chl-a), and finally on the photosynthetic activity (by $k_a$). Thus $\varepsilon$ describes the water body together with its phytoplankton content and could be considered as an oceanographic parameter, especially useful for time and space comparisons.

By a suitable integration of $a(z)$ with respect to $z$, an averaged or global efficiency, $\bar{\varepsilon}$, can be obtained characterizing the whole productive water column. More easily, $\bar{\varepsilon}$ can also be computed, as was done by Patten (1961), by converting the column production into its energetic equivalent and then dividing the result by the incident irradiation. The $\bar{\varepsilon}$ values given in Tables 1(a) and (b) have been calculated in reference to the total incident energy, including infra-red.*

For the Discoverer stations the global efficiency, $\bar{\varepsilon}$, lies within the range 0.01 to 0.10%. In the Mauritanian upwelling area, $\bar{\varepsilon}$ values ranging from 0.16 to 0.69% are obtained; these are comparable to those found by Patten (1961) for Raritan Bay. The influence of the biomass upon the $\bar{\varepsilon}$ value can be eliminated by dividing $\bar{\varepsilon}$ by the chlorophyll-a content of the euphotic layer. The variation of this ratio, from one place to another, reflects primarily the chlorophyll activity, but it also depends on the vertical distribution of plankton and turbidity, as seen above (moreover, as turbidity increases the thickness of the euphotic layer is reduced). The values of $\bar{\varepsilon}$, expressed as % (g Chl-a m$^{-2}$)$^{-1}$ are listed in Tables 1(a) and (b). They remain within a rather narrow interval when considering the variety of situations. It can be concluded that, on average, approximately 3% of the incident radiant energy is stored by photosynthesis in the production column per each gram of Chl-a per unit area (m$^2$) of ocean.

(4) In situ values of the quantum yield $\phi$

To calculate the quantum yield, it is first necessary to evaluate the photosynthetically usable radiation, PUR. A first approach is to multiply PAR by the in vivo phytoplankton absorption coefficient, $\bar{a}_{ph}$. More precisely, $\bar{a}_{ph}$ is the average absorption coefficient in the 350- (or 400-) to 700-nm range, per unit of phytoplankton concentration, where the latter is expressed as concentration of chlorophyll-a in the water. Lorenzen (1972) obtained a value of $\bar{a}_{ph} = 0.0138 \text{m}^{-1} (\text{mg Chl-a m}^{-3})^{-1}$. The spectral values $a_{ph}(\lambda)$ presented by Morel and Prieur (1977) give, by averaging for the whole spectrum, the value

* They would be approximately 2.4 times higher if calculated in reference to only photosynthetic irradiation or if calculated by integration of $\varepsilon (Z)$, because on average 42% of the impinging solar energy is in the visible part of the spectrum.
\( \bar{a}_{ph} = 0.0142 \) (Fig. 6). Bannister (1974) proposed 0.016 as being the mean of several recent estimates by different authors. If the value \( \bar{a}_{ph} = 0.015 \text{ m}^{-1} \) (mg Chl-a m\(^{-3}\))\(^{-1} \) is adopted, the ordinate scale of Fig. 4(a) and (b) can be transformed into the \( \phi \) scale as follows: if \( 10^{23} \) quanta m\(^{-2}\) are available, \( 0.015 \times 10^{23} \) quanta m\(^{-3}\) are absorbed when the chlorophyll-a concentration is \( 1 \text{ mg m}^{-3} \) (or 0.00249 Einstein absorbed m\(^{-3}\)). On the other hand, \( 1 \text{ mg C} = 0.0833 \times 10^{-3} \) mole, so when \( Y = 1 \times 10^{-23} \text{ mg C m}^{-3} \text{ day}^{-1} \) (mg Chl-a m\(^{-3}\))\(^{-1} \) (quanta m\(^{-2}\) day\(^{-1}\))\(^{-1} \), the corresponding value of \( \phi \) is

\[
\phi = 0.0833 \times 10^{-3} / 0.00249 = 0.033 \text{ moles C per Einstein absorbed.}
\]

On the basis of this equivalence, the \( \phi \) scale can be established.

It is now currently thought (e.g. see Rabinowitch and Godvindjee, 1969) that the maximal value for \( \phi \) is 0.125 (shown as dashed lines in Figs. 3 and 4). In other words the minimum quantum requirement, 1/\( \phi \), is 8. This means that under the most favourable conditions, when the maximal yield is reached, between 20 and 34% of the radiant energy absorbed is converted into chemical energy for blue light (400 nm) and red light (700 nm) respectively. In the marine environment, where radiant energy is mainly in the 450- to 580-nm band, the mean optimal conversion is around 25%.

The differences in \( \phi \) values among the stations are supposedly related to the natures of the algal populations as well as their nutritional and physiological state. Irradiance adaptation of cells in stratified situations or misadaptation when vertical mixing occurs inside the euphotic layer are also partly responsible for the diversity of \( \phi \) values. These intricate influences are outside the scope of the present discussion, which is restricted to the light dependence of \( \phi \) and to the problems involved in its correct evaluation.

As a rule, \( \phi \) increases with decreasing available energy. The \( \phi \) values observed in the case of blue or blue-green waters (Fig. 3a) are on average lower than those in green eutrophic waters (Fig. 3b). Moreover, the highest values for the Discoverer cruise were observed for the greenest waters (Stas. 6 and 16, in the Gulf of Panama). In several cases, at the bottom of the euphotic layer, the optimal conversion yield seemed to be approached (\( \phi = 0.125 \)).

The values obtained by Tyler (1975) for seven stations during the same WG 15 expedition are lower than those presented here. One reason for the difference is that the absorption used to calculate \( \phi \) was higher than the value adopted here (0.0415 instead of
0.015 m\(^{-1}\)), and in addition, his evaluation of PAR does not seem correct. In Lake Kinneret, Dubinsky and Berman (1976) observed an increasing quantum yield with depth, and estimated a maximum value of 0.07 at the lowest level, where PAR is reduced to 0.03% of its surface value. Average \(\phi\) values ranging from 0.064 to 0.048 were recently presented by Platt and Jassby (1976) for coastal marine plankton. The values presented here, particularly those of deep layers in green waters, are often above 0.06. They may appear uncomfortably high, especially when considering that 0.06 could be a more realistic maximum value in natural and time averaged conditions (Bannister, 1974). In the evaluation of \(\phi\), the adoption of a constant value for the in situ absorption by phytoplankton can only be an approximation, which will be discussed below.
Fig. 7. Spectral downwelling irradiance in three typical situations. For each depth the curve is normalized by its maximum. The actual depths of measurements are given on the figures. The notation $0^+$ stands for the daylight spectrum obtained above the surface.

(5) Spectral variability in the underwater light field. Consequence on the quantum yield evaluation

If the spectral absorption curves of Fig. 6 are compared to the curves of spectral irradiance for different depths, at three typical stations (Fig. 7), it is clear that the possibilities of absorption are very variable. In blue waters (Sn 21 Discoverer in the Sargasso Sea), available energy becomes concentrated with depth increasing in a spectral band (450 to 480 nm), which is approximately that of the absorption maximum by the algae. Conversely, for green waters where plankton is abundant (e.g. Sn 28 Charcot), the radiations are centred around 560 nm, wavelength of minimal absorption by algal pigments. Turbid and milky waters (Sn 35 Charcot) constitute an intermediate situation for the in-water spectral composition, and hence for the algal absorption.

If the spectrum $a_{ph}(\lambda)$ (solid line in Fig. 6) is regarded as representative, on average, of in vivo algal absorption, the exact value of PUR for each depth is obtained according to:

$$\text{PUR}(z) = \int_{400}^{700} A(\lambda) \frac{dE(\lambda)}{d\lambda} \, d\lambda,$$

where $A(\lambda)$ is $a_{ph}(\lambda)$ normalized at its maximum [$A(\lambda) = 1$, for $\lambda = 440$ nm], and $dE(\lambda)/d\lambda$ are the experimental values of spectral downwelling irradiance at depth $z$.

The values of PUR calculated for all depths and for all stations are shown in Fig. 8 as a function of PAR, the two quantities being expressed as the percentage of their values above the surface. At the level where the available energy is reduced to 1% of its surface value, it appears that the absorbable energy can vary in a ratio of about 3:1, depending on the optical water types. If the level of the compensation point were fixed in reference to the absorbable energy (PUR = 1%) instead of in reference to available energy, it is seen
that at this level, PAR varies from 0.5 to 1.4%, depending, respectively, on whether desert-blue waters or productive green waters are under consideration. Another way to demonstrate this effect is to study the values of the actual, or effective, absorption coefficient, which would take into account the spectral variability within the submarine light field. This coefficient, $a_{\text{eff}}$, is consequently defined as the following ratio:

$$a_{\text{eff}} = \frac{\int_{400}^{700} a_{\text{ph}}(\lambda) \frac{dE(\lambda)}{d\lambda} d\lambda}{\int_{400}^{700} \frac{dE(\lambda)}{d\lambda} d\lambda}.$$ 

Above the surface $a_{\text{eff}}(0^+)\text{ appears to differ slightly from } a_{\text{ph}}\text{ because daylight is not pure white, in that } \frac{dE(\lambda)}{d\lambda}\text{ is not constant throughout the spectrum. So, for the experiments presented here, the value of } a_{\text{eff}}(0^+)\text{ range from 0.0143 to 0.0151, instead of 0.0142 m}^{-1}\text{ (mg Chl-a m}^{-3})^{-1}\text{ for } a_{\text{ph}}.\text{ At other depths, } a_{\text{eff}}(z)\text{ departs from } a_{\text{eff}}(0^+).\text{ Some typical cases have been selected and presented for clarity (Fig. 9). The ratio } a_{\text{eff}}(z)/a_{\text{eff}}(0^+)\text{ is plotted versus decreasing PAR (i.e. a quantity that can be regarded as increasing optical depth). Compared to its value at the surface the effective absorption coefficient}
increases by as much as 50% with depth in the case of blue waters, and conversely it decreases by 20 or 30% in green waters.

In the case of blue waters the absorbed energy has probably been underestimated by using the hypothesis of a constant potential absorption and $\phi$ has been overestimated. The contrary holds for green productive waters where $\phi$ could be underestimated by a factor reaching 1.4. The already high values obtained in this case are also increased if, as must be, $a_{\text{eff}}$ is used in the computation instead of $a_{\text{ph}}$. Thus for the CINECA cruise, apart from three stations, all the $\phi$ values for the deep experiments would exceed 0.07, and even 0.125 for some of them. This inconsistency leads to the conclusion that the spectrum $a_{\text{ph}}(\lambda)$, used in the computations, does not represent the in vivo absorption by deep phytoplankton, either quantitatively or qualitatively (see Appendix II).

**CONCLUSION**

It is well known that the presence of high levels of algal biomass (and consequently also detrital material) reduces light penetration and thus the euphotic layer thickness. They also drastically change the spectral composition. In the deep layer of productive waters, the light becomes green or even yellow-green and can be expected to be poorly absorbable. The contrary is also true, because production remains high and partly unexplainable with the assumed algal absorption. It must be assumed that the actual absorption (for unit concentration of Chl-a) is appreciably higher, particularly in the 520 to 580-nm domain (at least two times higher if the $\phi_{\max}$ value estimated by Bannister is adopted).

Such high absorption capabilities exist in some groups (dinoflagellates) as measured by DUNTLEY, WILSON and EDGERTON (1974). The remaining problem is to demonstrate that deep-living phytoplankton, owing to an ecological or physiological chromatic adaptation, have an adequate absorption ability. SHIMURA and ICHIMURA (1973) looked for such an adaptation in situ without clear success, but their experiments were carried out in rather
clear (and not green) waters, where the necessity for a change in pigment composition is not strong. However, in the green productive waters off Peru, Koblenz-Mishke, Pelevin and Semenova (1975) found a significant increase in carotenoids compared to the total pigments. Nevertheless, it does not seem that the resulting higher absorption (mainly around 480 nm but extending to 520 nm) could completely account for the production they observed, because according to their results the energy absorbed in deep layers would be used with yields reaching 100%. This value leads to a minimum quantum requirement of two, instead of eight, which is the lower limit now accepted.

The correct evaluation of the quantum yield, as well as an improved understanding of the mechanism of energy uptake, especially in the productive area, require a better knowledge of pigment composition and in vivo absorption properties of algae. This holds true also in the production modelling because the models, as a rule, rest upon the assumption of a constant potential absorption (per unit of phytoplankton biomass), regardless of the optical water type and depth. Variations of the effective absorption emphasize the uncertainty resulting from this simplifying assumption.

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References


APPENDIX I

The conversion is effected by adopting the minimal value of 112 kcal mole\(^{-1}\), which corresponds to the transformation of 1 mole of CO\(_2\) into carbohydrate (CH\(_2\)O). Thus the fixation of 1 mg of carbon is equivalent to an energy storage of 39 joules. To compute \(k_s\), PAR must also be converted into joules m\(^{-2}\) day\(^{-1}\). It has been shown (MOREL and SMITH, 1974) that in spite of the spectral variability that exists in the underwater light field, the conversion of quanta into energy can be made using the equivalence 1 joule = 2.5 \times 10^{18} quanta for the domain 350 to 700 nm (or 40 joules = 10^{26} quanta), this approximation being valid with an accuracy better than 10%.

So the numerical correspondence between \(Y\) and \(k_s\) is simply:

\[
Y = 1 \times 10^{-23} \text{ (mg C m}^{-3} \text{ day}^{-1}) (\text{mg Chl}\text{-a m}^{-3})^{-1} (\text{quanta m}^{-2} \text{ day}^{-1})^{-1},
\]

we obtain:

\[
k_s = \frac{3 \times 10^{-3}}{40} \approx 1 \times 10^{-3} \text{ m}^{-1} (\text{mg Chl}\text{-a m}^{-3})^{-1}.
\]

Note that \(k_s\) has the dimensions of an extinction coefficient per unit of Chl-a concentration.

APPENDIX II

The computed usable energy, PUR, i.e. the product PAR (\(z\)) \(a_{eq}(z)\) appears to be too low because \(\phi\) would exceed its upper limit. In the above discussion, this underevaluation is attributed solely to the choice of too low values for \(a_{ph}(\lambda)\) in the wavelength range considered. An objection concerning a possible error in evaluation of available energy has to be examined.

The algal cells, more or less randomly oriented, can probably collect and absorb photons arriving from all directions. Thus the most suitable measurement of available radiation would be a measurement (in quanta) of the scalar irradiance \(E_0\) [see e.g. JERLOV (1976) for the definitions]. Because of technical problems involved in such a measurement, at least for routine work, the quantity commonly determined (and recommended by WG 15) is \(E_d\), downwelling irradiance. PAR is here obtained on the basis of \(E_d\) measurements. \(E_d\) is always inferior to \(E_0\) (or at the most equal, but not in natural light conditions). The ratio \(E/E_0\) (where \(E\) the vector irradiance is \(E = E_d - E_u\) and \(E_u\) is the upwelling irradiance), which represents the ratio of cosine collection to equal collection, is called the average cosine, \(\bar{\mu}\). \(E_u\) represents only few per cent of \(E_d\) (excepted near a reflecting bottom)
and can be neglected with respect to $E_d$, so $E_d/E_0 \approx \mu$ and the relative under-estimation by using $E_d$ instead of $E_0$ is thus equal to $(1 - \bar{\mu})$.

Experimental values of $\bar{\mu}$ were published by Høyerslev (1974, 1975). They range between 0.7 and 0.9, increasing with solar elevation and depending also on water type and wavelength. From theoretical values presented by Prieur (1976) and by averaging with respect to wavelength, solar elevation, and diurnal variation of incident energy, it is possible to estimate that the factor $(1 - \bar{\mu})$ would not exceed 15 or 20% in the case of the present experiments. This systematic error cannot account for the much more important underestimate discussed in the conclusion, which must be attributed to the insufficient absorption adopted.