RAPID RESPONSE PAPER

Primary production of the ocean water column as a function of surface light intensity: algorithms for remote sensing

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Abstract—Empirically, the phytoplankton production per unit area of sea surface, normalised to total pigment biomass in the water column, is a linear function of the surface insolation. The slope ψ varies by only a factor of two in samples from a variety of environments. A theory is developed that describes the empirical results. A simplifying assumption of the theory, that photosynthesis is a linear function of available light, leads to a bias (overestimate) that can be calculated as a function of a measureable dimensionless parameter. With the bias corrected, ψ is shown to be equal, to within a dimensionless constant, to the initial slope α of the photosynthesis–light curve. The theory can be applied to the calculation of primary production from satellite surveys of ocean colour or from survey data collected by ship.

INTRODUCTION

ONE OF the major tasks facing biological oceanography today is the quantification of the mean and variance of primary production over the world's oceans. The information is required not just for its traditional application in marine food chain studies (MOISEEV, 1971), but also for more contemporary calculations concerning the biogeochemical cycling of elements such as carbon and oxygen (NATIONAL ACADEMY OF SCIENCES, 1984; MALONE and ROEDERER, 1985). It has become clear that reconciliation of conflicting reports (SHULENBERGER and REID, 1981; JENKINS, 1982; PLATT, 1984; JENKINS and GOLDMAN, 1985; REID and SHULENBERGER, 1986) about the magnitude of the biogenic fluxes of carbon and oxygen in the ocean depends on the understanding of the significance of their variances (PLATT and HARRISON, 1985, 1986). All of these considerations bear on the question of the response of the autotrophic ocean biota to increasing concentrations of CO_2 in the atmosphere and hence on the prediction of future trends in the climate of the earth.

Even the most rapid of conventional methods for measuring primary production (LEWIS and SMITH, 1983) is not suitable for mapping on the regional or global scale. Supplementary data, collected in synoptic survey, will have to be supplied. To fill the gap, one looks, naturally to data remotely sensed from satellites (REVELLE, 1985). It is

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well accepted (PLATT et al., 1981; FASHAM, 1984) that ecological problems require information on fluxes as well as biomass for their resolution. On the other hand, although remote sensing has achieved moderate success (GORDON et al., 1980; HOVIS et al., 1980; SMITH, 1981; SMITH and BAKER, 1982; BROWN et al., 1985) in the mapping of phyto-plankton pigments (biomass), no method has emerged for calculation of phytoplankton production from the electromagnetic signals detectable by satellite (but see TOPLISS and PLATT, in press). The procedures used so far (SMITH et al., 1982; PLATT and HERMAN, 1983) therefore have been based on empirical correlation, and have ignored, for the most part, the accumulated knowledge on phytoplankton physiology (but see SMITH and BAKER, 1978).

In this paper I present a new, analytic relationship between the primary production of the oceanic water column and the sunlight available at the sea surface. From data collected by members of this laboratory, and from data collected by other workers, it appears that the relationship is remarkably stable. Furthermore, the magnitude of the slope of the relationship may be rationalised in terms of known phytoplankton physio-logy. The independent variable (surface light) is assumed known, or measurable from satellite data (GAUTIER et al., 1980; GAUTIER, 1982; GAUTIER and KATSAROS, 1984). The slope is controlled by properties potentially accessible to remote sensing. The approach should be useful in estimating phytoplankton production over large tracts of the ocean from remotely sensed data.

BACKGROUND

For at least 15 years (LARRANCE, 1971), workers have noticed (or it is implicit in their data) that fluctuations between days in surface light intensity account for a high proportion of the variance in water column primary production normalised to water column pigment concentration (MALONE, 1976; FALKOWSKI, 1981; HARRISON et al., 1982; JORDAN and JOINT, 1984). Because of the diverse systems of units and presentation of data employed by different authors, any quantitative similarity between these indepen-dent reports has largely escaped notice (but see JORDAN and JOINT, 1984). During analysis of data on primary production in the Canadian high arctic (PLATT, unpublished data) it was remarked that these various studies were, in fact, remarkably coherent. This observation led to the following analysis.

ANALYSIS

It may be noticed first that the empirical evidence refers to quantities expressed per unit area of sea surface. Let I_0 be the flux of photosynthetically active radiation (PAR) available at the surface. Following PLATT et al. (1984), let S be the rate of absorption of energy by photosynthetic pigments per unit area per unit time:

$$S = \int_0^\infty Q(z) \, dz, \tag{1}$$

where $Q(z)$ is the rate of absorption by pigments per unit volume at depth z. The limits of integration are 0 and ∞: in fact the non-trivial contributions to the integral, by definition, come only from the euphotic zone.

The magnitude of Q depends on $I(z)$, the light available at z, and on the total

absorption cross-section of pigments in the unit volume around z:

$$Q(z) = kB(z) \, I(z), \qquad (2)$$

where k is the pigment-specific attenuation coefficient and $B(z)$ is the pigment biomass. In turn, $I(z)$ depends in part on the product $kB(z)$:

$$I(z) = I_0 e^{-\xi z - \chi z - k\int_0^z B(z')dz'}, \qquad (3)$$

where ξ is the attenuation coefficient of the water itself and χ is that due to suspensoids other than pigmented phytoplankton cells (PLATT *et al.*, 1977). In equation (3) the implicit assumption is that χ and k do not vary with depth in the interval $(0, z)$.

We can now evaluate the integral in equation (1). It is convenient to make the simplifying assumption that the pigment biomass is distributed uniformly with depth, $B(z) = B$, constant. This leads to the result

$$S = \left(\frac{kB}{\xi + \chi + kB} \right) I_0. \qquad (4)$$

We assume also that the realised water column production will be a linear function of the light absorbed:

$$\int P dz = \eta S, \qquad (5)$$

where η is an efficiency factor to be determined. These assumptions, particularly the latter, will be discussed at length below.

We now define the quantity Λ

$$\Lambda \equiv \int P dz / \int B dz, \qquad (6)$$

where the pigments are integrated through the photic zone. Under the assumption of uniform pigment distribution we have,

$$\int_0^{Z_p} B dz = B Z_p, \qquad (7)$$

where Z_p is the thickness of the photic zone, leading to the simple result

$$\Lambda = \frac{\eta S}{B Z_p}. \qquad (8)$$

Writing out equation (8) explicitly for Λ we find

$$\Lambda = \frac{k I_0 \eta}{Z_p(\xi + \chi + kB)}. \qquad (9)$$

Thus we conclude that a plot of Λ vs I_0 should be a straight line with slope ψ (notation of FALKOWSKI, 1981), where

$$\psi = \frac{k\eta}{Z_p(\xi + \chi + kB)}. \qquad (10)$$

ESTIMATING THE MAGNITUDE OF ψ

Consider the case that I_0 is given as a photon flux in units of Einsteins (E) m^{-2} h^{-1}. The efficiency factor η depends on maximum quantum yield of photosynthesis (ϕ) and some thermodynamic efficiency factor θ

$$\eta = \theta\phi. \tag{11}$$

We take the quantum requirement of photosynthesis to be 10 (ϕ = 0.1 mol C $(E)^{-1}$) and θ to be 10%. Then $\eta \approx 10^{-2}$ mol C $(E)^{-1}$ or 1.2×10^{-1}g C $(E)^{-1}$.

For the rest of the quantities in equation (10) we refer to Table 1 in JORDAN and JOINT (1984). There we estimate, roughly, $Z_p \approx 40$ m; $B \approx 1$ mg Chl a m^{-3}; the quantity $(\xi + \chi) \approx 0.1$ m^{-1}. We take $k = 0.016$ m^2 (mg Chl $a)^{-1}$, following BANNISTER (1974). Then $\psi \approx 4 \times 10^{-3}\eta$ mol C m^2 (mg Chl $a)^{-1}$ E^{-1}. Converting to gC and substituting for η we find $\psi \approx 4 \times 10^{-3} \times 12 \times 10^3 \times 10^{-2}$ or $\psi \approx 0.5$ g C (g Chl $a)^{-1}$ m^2 $(E)^{-1}$. This is entirely consistent with the empirical slope of 0.48 g C (g Chl $a)^{-1}$ m^2 E^{-1} found by JORDAN and JOINT (1984) for the primary production experiments corresponding to the background data in their Table 1.

It is also instructive to estimate Λ from the typical magnitude of α^B, the initial slope of the photosynthesis–light curve for phytoplankton. The pertinent quantity here is the efficiency η. A characteristic value of α^B is ≈ 0.05 mg C (mg Chl $a)^{-1}$ h^{-1} (W $m^{-2})^{-1}$ (e.g. PLATT et al., 1980, 1982). It is important to note that α^B is based on the light available, not the light absorbed,

$$\alpha^B = \frac{1}{B} \cdot \left.\frac{\partial P}{\partial I}\right|_{I \to 0} . \tag{12}$$

An alternative definition for η is then similar to that for α^B, but based on the light *absorbed*

$$\eta = \frac{1}{kB} \cdot \left.\frac{\partial P}{\partial I}\right|_{I \to 0} = \frac{\alpha^B}{k} . \tag{13}$$

Noting that 1 W $m^{-2} \approx 1.5 \times 10^{-2}$ E m^{-2} h^{-1}, we can then estimate η as

$$\eta \approx \frac{0.05}{1.5} \times 10^2 \times \frac{1}{0.016} \times 10^{-3} \text{ g C } (E)^{-1} \approx 2.0 \times 10^{-1} \text{ g C } (E)^{-1},$$

or roughly the same order of magnitude as before, leading to a similar estimate for ψ. We can thus proceed with the reassurance that the analysis and the empirical results relating water column production to surface light are securely consistent with what has been learned from independent experiments on phytoplankton physiology.

STABILITY OF ψ

It may now be considered whether ψ can be expected to remain constant to any useful degree. The question is best approached through examination of equation (10). Only a relatively small number of quantities is involved. The value of Z_p itself will depend on the magnitude of the bracket $(\xi + \chi + kB)$. In particular, if all contributions to optical

attenuation are uniform with depth, and if Z_p is defined (conventionally) as the depth at which light is reduced to 1% of its surface value, we have simply

$$Z_p = \frac{4.6}{\xi + \chi + kB} \cdot \tag{14}$$

In this case equation (10) reduces to

$$\psi = \frac{k\eta}{4.6} \cdot \tag{15}$$

An even simpler result emerges if we substitute for η according to equation (13)

$$\psi = \frac{\alpha^B}{4.6} \cdot \tag{16}$$

Hence ψ can be considered constant to the extent that α^B is uniform with depth and that α^B is constant with respect to time and station.

THE EMPIRICAL EVIDENCE

The principal problem encountered in assembling the empirical data is knowing the averaging time to which the primary production measurements refer. Taking equation (16) literally, the time scale does not occur, since ψ is more in the nature of an efficiency than a rate; but one is not always sure that the irradiance data are calculated for the same time period over which the average primary production rates are quoted. The duration of the incubation affects the interpretation of the ^{14}C results (MARRA et al., 1981; DRING and JEWSON, 1982; SMITH, 1982; SMITH and PLATT, 1984).

Another problem is the interconversion between different sets of irradiance units, which cannot be done exactly if the spectral composition of the light is not known. The integrals over depth for P and B may not be precise if only a few depths are sampled (a problem that becomes less serious the more uniform the distribution of properties with depth). The integral over depth for P may be inaccurate if a simulated in situ procedure is used and the light levels have been improperly matched. In other words one expects a certain amount of inconsistency between data sets collected by different workers just from the differences in methodology and sampling.

LARRANCE (1971)

Primary production data collected during the period 1966–1968 in the mid-subarctic Pacific (south of the Aleutians) were published by LARRANCE (1971). Samples were collected at five relative light depths and incubated on deck in a simulated in situ format. Sampling depths were calculated from Secchi disc readings. Incubation lasted for one half the daylight period, but results were quoted as daily rates. Some 56 data points were reported. Incoming radiation was quoted as a daily rate, not corrected for PAR.

Some one-tenth of Larrance's data came from south of 46°N and therefore in the Transitional Domain between the subarctic and subtropical water masses. If these stations were excluded, an excellent regression of Λ on I_0 was obtained by Larrance. The

intercept is not significantly different from zero. In the units used in this paper, the slope $\psi = 0.66$ g C (Chl $a)^{-1}$ m^2 (E)$^{-1}$, where a factor of 0.5 has been used to correct for PAR. The data points from the transitional water appeared to have a steeper regression slope (LARRANCE, 1971, Fig. 3).

MALONE (1976)

Seasonal data from the New York Bight area were reported by MALONE (1976). Samples were collected at five relative light depths (as determined by Secchi disc) and incubated on deck by the simulated *in situ* method for 24 h. The results were quoted as daily rates. Incoming radiation was quoted as a daily rate, corrected for PAR. Some 30 data points were collected. For these data, Malone found an excellent regression with slope, converted to the units used in this paper, $\psi = 2.5$ g C (g Chl $a)^{-1}$ m^2 (E)$^{-1}$. Some 80% of the variance in Λ could be ascribed to variations in I_0. The slope is roughly five times the average of the slopes found in the other studies reported here, including one for the New York Bight itself (FALKOWSKI, 1981), and one may suspect a systematic error in the data, perhaps in the solar radiation figures, which seem low (MALONE, 1976, Fig. 11).

MOREL (1978)

Some 32 stations in the subtropical North Atlantic and the eastern tropical Pacific were reported by MOREL (1978). A variety of trophic regimes was sampled, from the less productive Sargasso Sea to the Mauritanian upwelling. Although the water column biomass varied by a factor of 10^2 between stations, the photosynthetically stored energy was a much less variable proportion of the available PAR, roughly $7 \pm 3\%$. In the units used here this is equivalent to a slope $\psi = 0.44$ g C (g Chl $a)^{-1}$ m^2 (E)$^{-1}$.

FALKOWSKI (1981)

A further seasonal study of the New York Bight area was reported by FALKOWSKI (1981). Some 37 data points were collected. For these data FALKOWSKI (1981, Fig. 6) could explain 86% of the variance in Λ by a regression on I_0 for which the slope was $\psi = 0.43$ g C (g Chl $a)^{-1}$ m^2 (E)$^{-1}$ (units incorrectly written in original paper). Comparing the abscissa in FALKOWSKI (1981, Fig. 6) with that in MALONE (1976, Fig. 11) for the same region, one sees after converting the units, that the irradiance scale is low by a factor of about 5 in Malone's data compared to Falkowski's. Correcting for this discrepancy would bring Malone's data into line with those of the rest of the studies discussed here.

HARRISON et al. (1982)

Data from 14 stations made during the summer of 1978 off the coast of northeast Baffin Island and in the open waters of Baffin Bay were published by HARRISON *et al.* (1982). Sampling was at five relative light depths chosen with the aid of the Secchi disc. The samples were incubated for 24 h on deck by the simulated *in situ* method. Incident radiation was measured directly on the ship and adjusted for PAR. Note that the conversion factor between W m^{-2} and Langleys h^{-1} was incorrectly printed in the original paper.

These data could be described very well (HARRISON *et al.*, 1982, Fig. 9) by a regression (59% variance explained) of slope $\psi = 0.33$ g C (g Chl $a)^{-1}$ m^2 (E)$^{-1}$ in the units used here and after correcting the error referred to in the previous paragraph. It is worth

noting that these stations (September, latitude $\approx$ 70°N) represent conditions of almost continuous daylight.

JORDAN and JOINT (1984)

Primary production measurements made at various stations in the western English Channel during 1980 and 1981 were published by JORDAN and JOINT (1984). The results of some 13 *in situ* experiments were tabulated. Samples were collected at six fixed depths and incubated apparently for from 4 to 6 h (text not clear). Results were quoted as hourly rates. Insolation was recorded continuously during the incubations. The depth-averaged diffuse attenuation coefficient was calculated from submarine photometer readings. A regression slope of 0.43 g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$ was obtained by Jordan and Joint for these data (units incorrectly stated in original paper).

The extent to which the assumption of uniform distribution of properties is justified can be judged from Fig. 5 of JORDAN and JOINT (1984) which shows profiles for chlorophyll and primary production on two different sampling dates. The assumption would be a good one for the 5 May data but less so for the 5 August data.

PLATT (unpublished data)

In situ primary production data were collected at seven stations during August and September 1983 in Jones Sound (at $\approx$ 76°N), eastern Canadian Arctic. Samples were taken at five fixed depths and incubated for 6 or 24 h nominal incubation times. Results are reported as daily rates. Incident radiation was measured directly on the ship and corrected for PAR. Conditions were open pack ice and almost 24 h continuous sunlight. Variations between days in insolation were considerable due to the sporadic incidence of thick fog.

These data could be described by a regression of slope $\psi = 0.36$ g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$.

PLATT (unpublished data)

In situ primary production measurements were made on 22 occasions during the spring bloom of 1985 in Bedford Basin, Nova Scotia. Both 6 and 24 h incubations were done at 1, 5 and 10 m. Incident radiation was measured directly at the Bedford Institute and converted to PAR. The 6 h incubations could be described by a regression slope $\psi = 0.34$ g C (g Chl a)$^{-1}$ m^2(E)$^{-1}$ with 70% of the variance explained. The 24 h data could be described by a regression slope $\psi = 0.31$ g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$ with 59% of the variance explained.

DISCUSSION

The slope of the regression of Λ on I_0 varies remarkably little in the studies collected here (range 0.31–0.66 g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$). The theoretical analysis shows that, to the extent that properties can be assumed uniformly distributed throughout the photic zone, the slope ψ in the equation

$$\Lambda = \psi I_0 \tag{17}$$

is given to within a dimensionless constant by the value of the initial slope of the

photosynthesis–light curve (α^B). This is a particularly simple result, and we now examine the underlying assumptions.

Assumption that photosynthesis is linear in absorbed light

The assumption, stated in equation (5), that photosynthesis is linear in the absorbed light deserves considerable discussion. It will lead to bias to the extent that part of the water column lies outside the range of light-limited photosynthesis. The bias is likely to be negligible in turbid waters, but may be significant at transparent ocean stations. In general also, the agreement should be better in higher latitudes than low, and for the same reason.

The appropriate index for the light-limited region is the adaptation parameter $I_k \equiv P_m^B/\alpha^B$, where P_m^B is the assimilation number (PLATT and JASSBY, 1976). Data on the typical magnitude and variability of I_k on a range of time and space scales may be found in MacCAULL and PLATT (1977); HARRISON and PLATT (1980, 1981, 1986); CÔTÉ and PLATT (1983); SUBBA RAO and PLATT (1984). The light-limited range of photosynthesis may be described very roughly as the interval $0 < I(z) \leqslant I_k$.

The dimensionless quantity $I_* \equiv I_0/I_k$ is then the relevant scale for judging the potential bias introduced by the linear approximation. The practical problem in applying it, however, is that I_0 changes throughout the day. For further discussion, it is therefore essential to distinguish between the following quantities: (a) I_0'', the maximum instantaneous value of I_0 as encountered at local noon; (b) $I_0(t)$, the instantaneous value of I_0 measured at any time t; and (c) I_0, as used in equations (3), (4), (9) and (17), with the implication of averaging or integrating over some period of time $\leqslant 1$ day. Of course, I_0 and $I_0(t)$ become indistinguishable if the integration time is sufficiently short, and I_0 may be used instead of $I_0(t)$ where it is not essential to retain the explicit time dependence. Similar distinctions can be made for other quantities used in this paper, such as ψ, I_*, Λ and S.

We consider first the bias introduced for the instantaneous integral $\int P(z)\mathrm{d}z$. Let us call this integral P_Z. It will be a function of time, $P_Z(t)$. For the *linear* model,

$$P_Z = \alpha I_0 \int_0^\infty e^{-\kappa z}\mathrm{d}z, \tag{18}$$

where $\kappa \equiv (\xi + \chi + kB)$ is the total attenuation coefficient and the lack of superscript on α indicates no normalisation to pigment. Equation (18) reduces

$$P_Z = \frac{\alpha I_0}{\kappa}. \tag{19}$$

Substituting for α, we find

$$P_Z = \frac{P_m}{\kappa} \cdot \frac{I_0}{I_k} = I_* \frac{P_m}{\kappa}, \tag{20}$$

where the lack of superscript in P_m again implies no normalisation to pigment.

We now calculate P_Z for a *non-linear* representation of the photosynthesis–light curve. Alternative representations have been discussed by JASSBY and PLATT (1976) and by PLATT *et al.* (1977). As a standard (LEDERMAN and TETT, 1981), we may take Smith's equation (SMITH, 1936).

We now calculate P_Z when $P(z)$ is given by Smith's equation:

$$P(z) = \frac{P_m I_k^{-1} I(z)}{[1 + (I_k^{-1} I(z))^2]^{1/2}}. \tag{21}$$

In this case

$$P_Z = \frac{P_m}{\kappa} \log_e (I_* + \sqrt{1 + I_*^2}). \tag{22}$$

To find the relative error ε incurred by the linear approximation we subtract equation (22) from (20) and divide by (22)

$$\varepsilon = \frac{I_* - \log_e (I_* + \sqrt{1 + I_*^2})}{\log_e (I_* + \sqrt{1 + I_*^2})} . \tag{23}$$

The result is plotted in Fig. 1. We see that the relative error of the linear approximation is 13% at $I_* = 1$, rising to 65% at $I_* = 3$. These are the magnitude of errors that might be expected for instantaneous evaluations of water column integrals using the linear approximation.

The next step is to take into account the time variation in I_0. A standard representation (IKUSHIMA, 1967) is

$$I_0(t) = I_0^m \operatorname{Sin}^3 \left(\frac{\pi t}{D}\right), \tag{24}$$

where D is the daylength. The average light intensity throughout the day, $\langle I_0 \rangle$, can then be calculated as

$$\langle I_0 \rangle = \frac{1}{D} \int_0^D I_0^m \operatorname{Sin}^3 \left(\frac{\pi t}{D}\right) dt \tag{25}$$
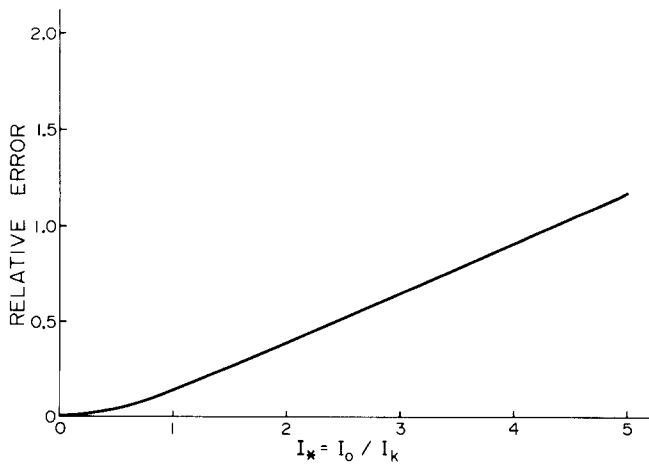

Fig. 1.   Relative error ε (overestimate), as function of dimensionless parameter I_*, of linear approximation compared to Smith's equation for computing instantaneous water column integrals of primary production.

or

$$\langle I_0 \rangle = 0.42\, I_0^m. \tag{26}$$

The factor 0.42 gives a crude indication of the reduction in the relative error on P_Z from working with the average surface light rather than the maximum (for which the error is maximal). For example, if the instantaneous relative error is ε^m at I_*^m, the average error $\langle \varepsilon \rangle$ for the day would be roughly $0.42\, \varepsilon^m$, or the error when $I_* = \langle I_* \rangle$.

Because the underlying relationships are nonlinear, evaluation of the average error for the day requires, more strictly, a complete double integration over depth and time. This is the problem we address next. We calculate $P_{Z,T}$, where

$$P_{Z,T} = \int_0^D \int_0^\infty P(z,t)\, dz,\, dt \tag{27}$$

with $P(z,t)$ and $I_0(t)$ specified as before.

In general, integrals of the form equation (27), where $P(z)$ is nonlinear will be closer to their linear approximations than the instantaneous integrals evaluated at $I_*(t) = I_*^m$ because $I_*(t) < I_*^m$ for all times except noon. When P_Z is given by the simple *linear* approximation (equation 18), it is easy to show from equation (27) that

$$P_{Z,T} = 0.42\, I_*^m\, D\, \frac{P_m}{\kappa}. \tag{28}$$

Equation (27) may be evaluated by numerical integration when $P(I)$ is *nonlinear*. We can then calculate the relative error, ε, as before. As an example, we have computed equation (27) with $P(z)$ specified by the standard Smith's equation and then the relative error between it and equation (28). This function $\varepsilon(I_*^m)$ is plotted in Fig. 2. There we see that a linear approximation is in error by only 16% at $I_*^m = 2$ and by 36% at $I_*^m = 4$.
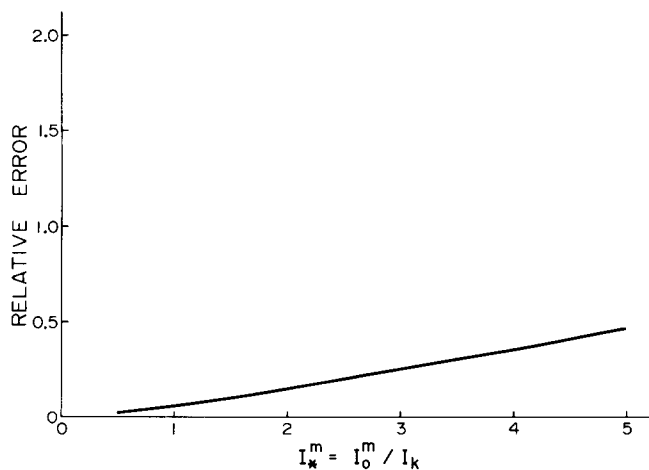

Fig. 2. Relative error ε (overestimate), as function of dimensionless parameter I_*^m, of linear approximation compared to Smith's equation for computing daily water column integrals of primary production.

We can summarise the arguments in this section as follows. The instantaneous water column integrals for primary production may be evaluated using various functional forms for the photosynthesis–light curve. The relative error $\varepsilon(I_*)$ between any of these integrals and that for the approximation of linear (non-saturating) photosynthesis can be computed as a function of the dimensionless parameter $I_* \equiv I_0/I_k$. Taking the Smith equation as standard, it is found that the linear approximation of the instantaneous column integral is within 50% of the correct answer for $I_* \le 2.5$. When the time dependence of I_0 is taken into account, a similar calculation shows that the linear approximation of the daily column integral is within 20% of the correct answer for $I_*^m \le 2.5$. Furthermore the extent of the bias (overestimate) is given as I_*^m changes.

The dependence of ψ on α^B

The data from Bedford Basin afford an opportunity to test equation (16) connecting ψ and α^B, since independent measures of the photosynthesis–light curves were made using shipboard incubators. The average value of α^B for samples taken at both 1 and 10 m on 22 occasions (different days) during the sampling period was 0.053 mg C (mg Chl a)$^{-1}$ h^{-1} (W m^{-2})$^{-1}$. This is equivalent, from equation (16) to $\psi = 0.77$ g C (g Chl a)$^{-1}$m^2 (E)$^{-1}$. The empirical result for the *in situ* incubations was $\psi \approx 0.33$ g C (g Chl a)$^{-1}$m^2 (E)$^{-1}$.

We know from equation (23) that the linear approximation embodied in equation (16) should overestimate ψ, and by an amount depending on the ratio of I_0 to I_k. The mean value of the derived photosynthetic parameter I_k for the Bedford Basin experiments was 62 W m^{-2}. During the same period, the average value of I_0^m was 300 W m^{-2}. Thus, a representative value of I_*^m for the sampling period is $I_*^m \approx 5$. From Fig. 2, we therefore expect that ψ estimated from equation (16) will be 47% too high, just from the bias introduced by the linear assumption. The bias may be removed through multiplication by the factor 1/1.47, giving $\psi = 0.52$ g C (g Chl a)$^{-1}$m^2 (E)$^{-1}$, to compare with $\psi \approx 0.33$ g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$ calculated from the *in situ* incubations.

The test of consistency in this one case is most satisfactory. In practice we know that things will not be so simple because the assumption of uniform distribution of properties with depth will not always be respected. In those cases where the depth of the mixed layer exceeds the photic depth, however, equation (16) should be more robust.

Another complication is that when vertical mixing is relatively weak, vertical differences in α^B can be expected to develop through photoadaptation (LEWIS *et al.*, 1984). The differences will be more pronounced when the photic depth exceeds the depth of the mixed layer (PLATT *et al.*, 1982; GALLEGOS and PLATT, 1982, 1985; GALLEGOS *et al.*, 1983). Note that it is the response of the water column as a whole that is in question, not the response at discrete depths. Thus, in the study reported by MOREL (1978), the fraction of available PAR that was stored in photosynthesis varied by a factor of 10 between surface and base of euphotic zone but the utilisation of PAR per unit area of surface varied by only a factor of three between stations.

One should also be aware of the effect of wavelength on α^B. It has recently become possible to measure the action spectrum for phytoplankton at sea (LEWIS *et al.*, 1985a,b). It is found that the wavelength dependence is strong. As more field data of this kind are collected, one should be able to construct appropriate weighting functions involving products of the form $\alpha^B(\lambda) \cdot I_0(\lambda)/k(\lambda)$, where λ is the wavelength.

The general variability of α^B on a variety of time and space scales has been discussed in a number of papers from this laboratory (HARRISON and PLATT, 1980, 1981, 1986;

MacCaull and Platt, 1977; Côté and Platt, 1983, 1984; Therriault and Platt, 1978; Therriault et al., 1978). Taken together, they provide a good background for judging the utility of equation (16), and also (10) in those cases where explicit data on α^B are lacking.

With regard to trophic status, the papers of Morel (1978, 1982) give some idea of the variability in ψ to be expected between regions. Thus, for oligotrophic and mesotrophic stations $\psi = 0.47 \pm 0.18$ g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$ (Morel, 1978, Table 1a) whereas for the more eutrophic stations $\psi = 0.35 \pm 0.14$ g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$ (Morel, 1978, Table 1b). A somewhat different regime exists at the Guinea Dome ($\approx 13°$N). Here there is a well-developed, deep chlorophyll maximum at ≈ 50 m, with little chlorophyll elsewhere. In other words, the vertical distribution of pigment is very far from uniform. In this case, Morel (1982) found $\psi = 0.58 \pm 0.28$ g C (g Chl a)$^{-1}$ m^2 (E)$^{-1}$.

One further implication of the analysis is that annual water column productivity should be acutely sensitive to variations between years in insolation. It is known that these can be significant (Ryther and Menzel, 1961; Platt, 1971).

CONCLUSIONS

Recently a method has been proposed (Topliss and Platt, in press) for estimation of α^B from the fluorescence yield of the solar-stimulated or passive fluorescence response of chlorophyll pigments. This signal is detectable by optical profiling from a ship (Topliss, 1985) as well as by remote sensing from aircraft (Neville and Gower, 1977). Its deployment in satellites is foreseen (Gower and Borstad, 1981). The possibility then arises that Λ could be indexed routinely and synoptically in standard surveys. The water column productivity $\int P(z)dz$ follows immediately from equation (6) if an estimate of biomass is available, for example, from Coastal Zone Colour Scanner Imagery (Hovis et al., 1980; Gordon et al., 1980). A surface layer estimate would be adequate here since the theory assumes $B(z)$ constant throughout the photic zone and since it has been shown that surface values are good predictors of the water column integrals (Platt and Herman, 1983). For ship surveys, vertical profiles of pigment biomass can be developed in minutes on station (Herman et al., 1984) or continuously under way (Herman and Denman, 1977).

Remotely sensed information refers to the upper layers of the ocean where photosynthesis is less likely to be light-limited. The fact that ψ is shown to depend on α^B, a characteristic of the light-limited part of the photosynthesis–light curve, does not, however, invalidate the exploitation of their interrelationship in remote sensing. The explanation lies partly in the points made in the preceding paragraph and partly in that, for the primary production of the water column as a whole, α^B is the characteristic photosynthesis parameter. It is the production per unit of sea surface for the photic zone that is in question, not the production of any smaller depth interval, whether it be light-limited or light-saturated.

The formalism developed in this paper therefore appears to offer a secure framework for organisation of major programs of mapping the primary production of the ocean over large regions of space and with high frequency in time (National Academy of Sciences, 1984; Malone and Roederer, 1985). It has the advantage of being an approach that takes into account what is known about the physiological ecology of natural assemblages of marine phytoplankton.

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