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RAPID RESPONSE PAPER

Ocean primary production and available light: further algorithms for remote sensing

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Abstract—In the context of remote sensing of the ocean, the general problem of estimating water column production from surface irradiance and column chlorophyll concentration is examined, and some refinements are made to the linear theory presented by PLATT (1986, *Deep-Sea Research*, **33**, 149–163). Further empirical evidence is presented to show the stability of the relationship between surface light and biomass-normalized primary production of the ocean water column. A theoretical explanation is given for the non-zero intercept often obtained when these two variables are regressed. The systematic errors in the estimation of primary production by remote sensing, due to non-uniformity in the biomass profile, are examined through sensitivity analyses on a generalized biomass profile. The errors are shown to be functions of the parameters of the biomass profile, of the photosynthetic parameters and of the optical properties of the water. The probable random errors in the estimation of water column primary production using remotely sensed data are evaluated. Some general issues related to the collection and assimilation of data on ocean primary production are addressed.

INTRODUCTION

THE notion is becoming generally accepted that satellite remote sensing is one of the principal keys to further progress in basin- and global-scale biological oceanography (REVELLE, 1985). Among the problems that have to be solved before remote sensing can be exploited to the full for ecological research, one of the most challenging is the interpretation of ocean color data in terms of the rate of primary production (PLATT, 1986). Initial approaches to this problem were empirical (PLATT and HERMAN, 1983; SMITH *et al.*, 1982; EPPLEY *et al.*, 1985). More recent work has gone back to physiological first principles to explain the nature of the empirical correlations (LEWIS *et al.*, 1986), and to find results of a more general validity (PLATT, 1986; SATHYENDRANATH, 1986; PLATT and LEWIS, 1987).

The possibility of being able to estimate ocean primary production from a small number of variables accessible to remote sensing is an attractive one. Inevitably, however, the search for such simple results involves sweeping simplifications in the

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theoretical treatment. An earlier analysis (PLATT, 1986) depended on two major assumptions: (i) a linear photosynthesis–light model, and (ii) uniform distribution of photosynthetic biomass with depth. The consequences of the first assumption were explored, and a correction procedure was presented. The implications of the second assumption, however, were not discussed in detail.

In this paper, we examine the consequences, for estimation of primary production from remotely sensed data, of non-uniformity in the vertical distribution of photosynthetic biomass. A generalized photosynthetic biomass profile is introduced to analyse the sensitivity of water column production to changes in the depth distribution of chlorophyll and the consequent bias in the estimation of primary production. We discuss the significance of choice of formalism in the calculation of water column production. We evaluate the exact integral for the relationship between biomass-normalized, water column production and insolation, approximated in PLATT (1986), and show that it is not linear at low light, leading to a potential bias in the estimation of production. We give some further examples, from a variety of habitats, of data sets relating water column production and surface light, including examples showing the stability of the relation between years at the same location. Finally, we discuss the probable errors associated with estimating primary production from remotely sensed data.

SKETCH OF THE EARLIER THEORY

We seek an expression for the water column photosynthesis $\int_z P = \int_0^\infty P(z)\mathrm{d}z$, where $P(z)$ is the instantaneous primary production at depth z. For ease of comparing different stations, we remove the influence of biomass, $B(z)$, by normalizing $\int_z P$ to the photic-zone biomass $\int_0^{z_p} B(z)\mathrm{d}z$, where z_p is the depth of the photic zone. Call this normalized integral production Λ. Under the assumptions of uniform vertical distribution of biomass and a linear photosynthesis–light model, Λ is a linear function of surface light, I_0, with slope ψ (PLATT, 1986). A linear model corresponds well with a large body of field data. It is found that, to within a dimensionless constant, ψ is equal to the biomass-normalized initial slope, α^B, of the photosynthesis–light curve (PLATT, 1986, equation 16), a quantity potentially accessible to remote sensing (TOPLISS and PLATT, 1986).

The errors incurred by taking a linear photosynthesis–light model were evaluated by PLATT (1986) and found to be expressable in terms of the dimensionless light $I_* = I_0/I_k$, where I_k is a derived parameter of the photosynthesis–light curve. The photoadaptation parameter, I_k is equal to P_m^B/α^B, where P_m^B is the assimilation number (e.g. PLATT *et al.*, 1980). The errors were found to be relatively slight and could be calculated given a reasonable estimate for I_k.

The initial treatment for instantaneous production rates $\int_z P$ extends easily to cases where the time dependence is explicit, $\int_z P(t)$, and to time averages (PLATT, 1986).

FURTHER EMPIRICAL EVIDENCE

Examples illustrating the application of the linear theory for estimating water column production, drawn from a variety of oceanographic regimes (estuarine, coastal offshore, oceanic and high latitude), are chosen to illustrate the following points: year-to-year reproducibility of results at the same station; presence of a positive intercept on the ordinate in some of the regressions of Λ on I_0; conservative nature of the magnitude of the regression slope ψ.

Jacques and Minas (1981); *Collos and Slawyk* (1986)

Some 25 stations were sampled between 43°S and 62°S on a transect along 66° 30'E in the Southern Ocean during March 1977 by Jacques and Minas (1981). Optical depths were calculated from direct measurements of underwater irradiance: five such depths were sampled for chlorophyll biomass and primary production. Incubations lasted 24 h under simulated *in situ* conditions, with results given as daily rates integrated to the 1% light depth. The authors have kindly made available to us their data on incoming radiation, allowing calculation of a regression slope $\psi = 0.37$ g (g Chl a)$^{-1}$ m^2(E)$^{-1}$, with 29% of the variance explained.

During March 1980, seven stations were occupied on the same transect by Collos and Slawyk (1986), using methods similar to those of Jacques and Minas (1981). In this case, the data could be described by a regression slope $\psi = 0.38$ g C (g Chl a)$^{-1}$ m^2(E)$^{-1}$, with 79% of the variance explained. As can be seen in Fig. 2 of Collos and Slawyk (1986), the regression did not pass through the origin, but had a positive intercept on the ordinate.

Bruno, Staker and Sharma (1980)

In situ primary production was measured on 15 occasions during a 12-month period in the shallow Peconic Estuary at the easternmost end of Long Island Sound by Bruno *et al.* (1980). Three depths were sampled for chlorophyll biomass and primary production. Incubation period varied from 3 to 5 h. Incident radiation was measured throughout. Extinction coefficients were estimated from Secchi-disc readings. From their Fig. 2, the mean, photic-zone, light energy and the 1% light level can be derived. From these we estimated the mean incident radiation corrected to PAR, and combining with the data extracted from their Figs 5 and 6 (treating late September datum as an outlier), we find a regression slope of $\psi = 0.38$ g C (g Chl a)$^{-1}$ m^2(E)$^{-1}$, with 49% of the variance explained.

Cole and Cloern (1987)

Using data compiled from a large number of estuarine productivity studies, Cole and Cloern (1987) regressed water column production against the composite variable Bz_pI_0, where B is the (average) euphotic zone chlorophyll biomass, z_p is the depth of the photic zone and I_0 is the surface irradiance, as before. This procedure is exactly equivalent to the one followed by Platt (1986) and contains the implicit assumption of uniform distribution of biomass in the vertical. The product Bz_p is simply the euphotic zone biomass, as used in Platt (1986) to normalize water column production. Thus, the regressions of water column production on Cole and Cloern's composite variable are equivalent to regressions of Λ on I_0 as in Platt (1986).

An average of 82% of the variance in water column production could be explained by the composite variable in nine data sets from six estuarine locations in the U.S.A. For the six data sets where Cole and Cloern were able to reduce the optical data to common units, a pooled data set was constructed, representing some 211 experiments in four different estuaries. For the pooled data, again, more than 80% of the variance could be explained by the model. However, the regression slopes obtained with this method are higher than those obtained using the procedure of Platt (1986), for reasons not yet understood.

PLATT and IRWIN (1972)

In situ primary production was measured at a single station in Petpeswick Inlet, Nova Scotia from May 1971 to May 1972. This inlet becomes anoxic below 10 m depth during the autumn. Moreover, it is ice-covered between December and April, such that the model cannot be applied. Therefore the data (PLATT and IRWIN, 1972) from mid-September to mid-April were excluded from the analysis, leaving some 12 data points in the regression. These data gave a regression slope of $\psi = 0.43$ g C (g Chl *a*)$^{-1}$ m^2(E)$^{-1}$ with 84% of the variance explained. The regression line had a positive intercept on the ordinate.

IRWIN, CAVERHILL and PLATT (1986)

In situ primary production was measured on seven occasions at the same nominal station in a 4-day period on the Grand Banks of Newfoundland during April 1984. Water samples were collected at 5 m intervals in the upper 40 m, and incubated for 6, 12 or 24 h. Total surface radiation was measured continuously from the ship. Biomass and production were integrated down to 20 m, the estimated depth of the euphotic zone. Biomass-normalized production was expressed as an hourly rate. Data are available in IRWIN *et al.* (1986). A regression slope of $\psi = 0.35$ g C (g Chl *a*)$^{-1}$ m^2(E)$^{-1}$ was obtained, with 92% of the variance explained.

PLATT and IRWIN (1971)

Primary production and nutrients were measured in Bedford Basin, Nova Scotia during 1970. *In situ* production was integrated to 10 m, the estimated depth of the photic zone. Incoming radiation was measured with a recording pyranometer located 5 km south of the sampling station. The data are available in PLATT and IRWIN (1971; note that this analysis includes only data from April onwards, when the radioactive assay was changed from gas-flow counting to liquid-scintillation counting). A regression slope of $\psi = 0.52$ g C (g Chl *a*)$^{-1}$ m^2(E)$^{-1}$ was obtained, with 75% of the variance explained (four outlying data points excluded). There was a positive intercept on the ordinate.

PLATT, IRWIN and SUBBA RAO (1973)

In situ primary production was measured on 10 occasions during the spring phytoplankton bloom in Bedford Basin, Nova Scotia in March 1971. Total incident radiation was measured directly at the Bedford Institute. Data are available in PLATT *et al.* (1973). Heavy rains led to strong discoloration of surface water, rendering data from two sampling dates (17 and 19 March) unusable. The remaining eight data points gave a regression slope of $\psi = 0.43$ g C (g Chl *a*)$^{-1}$ m^2(E)$^{-1}$, with 68% of the variance explained. There was a positive intercept on the ordinate.

PLATT (unpublished data)

In situ primary production was measured on 22 occasions between January and April 1986 (covering the period of the spring phytoplankton bloom), in the Bedford Basin, Nova Scotia. All incubations lasted 24 h, using samples from 1, 5 and 10 m. Total incident radiation was measured at the Bedford Institute of Oceanography. These data gave a regression slope of $\psi = 0.29$ g C (g Chl *a*)$^{-1}$ m^2(E)$^{-1}$, with 59% of the variance explained. The regression slope for 22 data points collected at the same location during the same part of the year in 1985 was 0.31 g C (g Chl *a*)$^{-1}$ m^2(E)$^{-1}$ (PLATT, 1986).

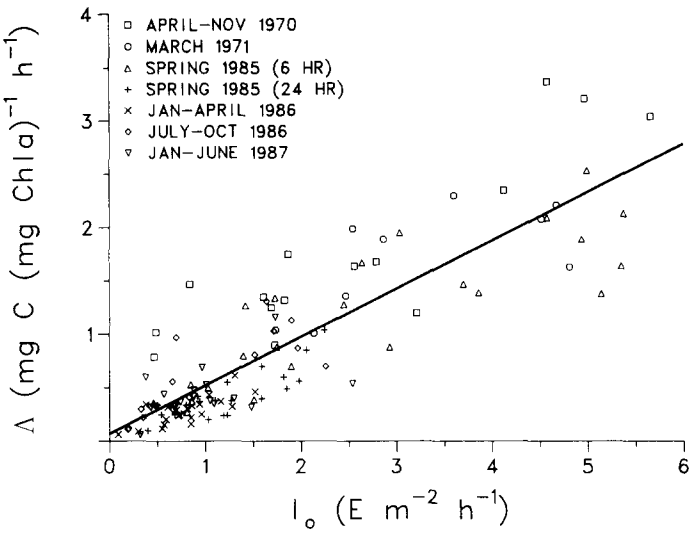

Fig. 1. Biomass-normalized water column production vs surface light intensity. Pooled data for Bedford Basin, spanning a period of 17 y (1970–1987) collected under the supervision of the same personnel (PLATT and IRWIN). Linear regression yields Λ (mg C (mg Chl *a*)$^{-1}$ h^{-1}) = 0.069 + 0.45 I_0 (E m^{-2} h^{-1}) with n = 125 and r^2 = 0.75.

Pooled Bedford Basin data

Data on primary production and insolation for the Bedford Basin, measured under supervision of the same personnel, are available for the 17-y period from 1970 to 1987. Blocs of these data are discussed above and in PLATT (1986). The data from the entire period (n = 125) lie on the same regression of Λ on I_0 with slope 0.45 g C (g Chl *a*)$^{-1}$ m^2(E)$^{-1}$ and 75% of the variance in Λ explained (Fig. 1).

MALONE (1976); *FALKOWSKI* (1981)

In PLATT (1986), a spurious inconsistency was noted between the irradiance data of MALONE (1976) and those of FALKOWSKI (1981), both referring to seasonal studies in the New York Bight. In fact, the irradiance data published by MALONE (1976) did not refer to surface values but to average values for the photic zone (see also MALONE, 1987). It is a straightforward matter to calculate the mean irradiance for the photic zone in terms of I_0. In fact, the mean irradiance for the euphotic zone, $<I_z>$ is given by:

$$<I_z> = \frac{1}{z_p}\int_0^{z_p} I_0 \exp(-Kz)dz$$

$$\approx \frac{1}{z_p}\int_0^{\infty} I_0 \exp(-Kz)dz$$

$$= 0.22\, I_0,$$

with $z_p = 4.6/K$ (compare, for example, the empirical result of MALONE, 1987: $<I_z> = 0.195I_0$). Indeed, the linear theory could be formulated just as well in terms of this average irradiance. If Malone's average irradiances are recast in terms of I_0, then,

the slope for his data is $\psi = 0.50$ g C (g Chl a)$^{-1}$ m^2(E)$^{-1}$, which is not significantly different from the slope of 0.43 reported by FALKOWSKI (1981), at 95% confidence level. Note also that both data sets have a positive intercept on the ordinate.

DEPARTURE FROM LINEARITY AT LOW LIGHT

We have seen in several examples of field data that linear regression of biomass normalized water column production (Λ in the notation of PLATT, 1986) on surface light (I_0) can yield a positive intercept on the ordinate. This implies positive production at zero light, which is clearly inadmissible. The explanation lies in the fact that the earlier theory for Λ (I_0) given in PLATT (1986) forces an inherently non-linear relationship (the photosynthesis–light curve) to be linear. Paradoxically, it can lead to errors at low light, where the photosynthesis–light curve itself is indeed linear.

To see these points more clearly, we first calculate the exact integral for water column production ($\int_z P$) when the photosynthesis–light curve is non-linear. For example, using Smith's equation for $P(I)$ (SMITH, 1936), we find (cf. PLATT, 1986, equation 22):

$$\int_z P = (P_m/K) \ln[I_* + \sqrt{1 + I_*^2}], \tag{1}$$

where K is the attenuation coefficient for downwelling irradiance. Note that in this equation, P_m is not normalized to B. This function is sketched in Fig. 2. To see how it would respond in linear regression, we calculate the slope of the tangent:

$$\frac{\partial}{\partial I_*}\left(\int_z P\right) = \frac{P_m}{K}\frac{\partial}{\partial I_*}\left[\ln(I_* + \sqrt{1 + I_*^2})\right]$$

or

$$\frac{\partial}{\partial I_*}\left(\int_z P\right) = \frac{P_m}{K}\frac{1}{\sqrt{1 + I_*^2}}. \tag{2}$$

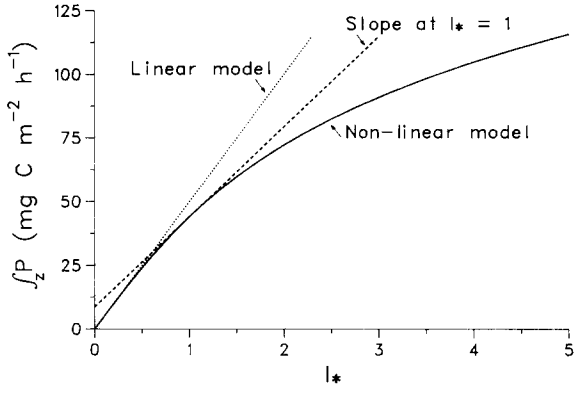

Fig. 2. Depth-integrated production ($\int_z P$) as a function of the dimensionless parameter I_*, for the non-linear and linear models (uniform distribution of biomass in the water column is assumed). The non-linear model uses equation (1), based on SMITH (1936). The slope of the curve at $I_* = 1$ is also drawn. In the examples presented here, we have assumed $P_m^B = 5$ mg C (mg Chl a)$^{-1}$ h^{-1} and $K = 0.1$ m^{-1}. Note that the linear model for integrated production passes through the origin. The exact integral deviates from the linear approximation for high values of I_*, and when fitted as if it were a straight line, it extrapolates back to give a postive intercept on the ordinate.

When $I_0 = I_k$, $I_* = 1$ and equation (2) has the simple form

$$\frac{\partial}{\partial I_*}\left(\int_z P\right)\Big|_{I_*=1} = \frac{P_m}{K\sqrt{2}},$$

which may be taken as the bench mark value for the slope of equation (1).

Equation (2) is sketched in Fig. 2, for $I_* = 1$. It is easy to see that if data are available on Λ and I_0, the value of the regression slope deduced from them will depend on the range of I_0 in the data. Extrapolation of the regression as a predictor outside the empirical range of I_0 will lead to a bias, in particular to a positive intercept on the ordinate, because equation (2) is a decreasing function of I_* (Fig. 2). The rate of change of $\partial(\int_z P)/\partial I_*$ tends to decrease at higher values of I_*, but it does not fall off less rapidly than I_*^{-1}.

The magnitude of the intercept on the ordinate can be calculated as follows. Let $T(I_*)$ be the equation of the tangent to $\int_z P(I_*)$. Then $T(I_*)$ will have the general form:

$$T(I_*) = T_0 + \frac{P_m}{K}\frac{I_*}{\sqrt{1 + I_*^2}}, \tag{3}$$

where T_0 is the intercept and the slope has been substituted from equation (2). If the tangent is taken at the point $I_* = I'_*$, we have:

$$T_0 = \frac{P_m}{K}\left[\ln\left(I'_* + \sqrt{1 + I'^2_*}\right) - \frac{I'_*}{\sqrt{1 + I'^2_*}}\right]. \tag{4}$$

In the particular case $I'_* = 1$,

$$T_0 = \frac{P_m}{K}\left[\ln(1 + \sqrt{2}) - 1/\sqrt{2}\right] = 0.174\,\frac{P_m}{K}. \tag{5}$$

The intercept will be larger as P_m becomes larger or K becomes smaller. Generally speaking, these two trends can be expected to be self-cancelling.

INTEGRAL FORM OF PHOTOSYNTHESIS–LIGHT MODELS: GENERAL PROPERTIES

Some general remarks on computation of primary production for unit area of sea surface will be useful at this point. First, the choice of equation to describe the dependence of photosynthesis on light is of relatively little significance for the results. As pointed out in PLATT *et al.* (1977, p. 820), the integrals over depth of all such equations known in the literature (including light saturation but not necessarily photoinhibition, and assuming vertically uniform water column properties) can be expressed in the same general form:

$$\int_z P = \frac{P_m}{K} f\left(\frac{\alpha I_0}{P_m}\right) \tag{6}$$

or

$$\int_z P = \frac{P_m}{K} f(I_*) \tag{7}$$

in the notation used here. Note that the argument I_* does not contain an independent parameter, but only the derived parameter $I_k = P_m/\alpha$. Therefore the dependence of integrated photosynthesis on available light can be specified by no more than two photosynthesis parameters and the optical extinction coefficient K of the water column. Any formulation that contains more parameters would be over-specified. Integrals of existing photosynthesis–light models are virtually indistinguishable for $I_* < 1$ and vary by no more than ±8% of the mean for $I_* = 8$ (PLATT *et al.*, 1977, p. 821).

Second, recall that photosynthesis–light models are usually formulated in terms of light *available* rather than light *absorbed*. Then, the parameter α represents efficiency of photosynthesis at low light, normalized to the incident light. Expressed in this way, α depends on both the efficiency of photosynthesis itself, normalized to the light absorbed (the quantum yield ϕ), and the efficiency of photon capture (PLATT and JASSBY, 1976). In practice, these two elements are difficult to separate. The formal correspondence between α and the quantum yield is (PLATT and JASSBY, 1976; PLATT, 1986):

$$\alpha^B = \phi_m k_c. \tag{8}$$

The ϕ_m used in equation (8) is not the *absolute* maximum quantum yield that can be deduced from the biophysics of photosynthesis: it is rather the maximum, *realized* quantum yield (in the sense that quantum yield tends to a maximum as irradiance tends to zero) attained by a given sample at a given time. If we treat the chlorophyll-specific attenuation coefficient k_c as a constant, α^B and ϕ_m are equal, to within a numerical factor. In fact, the problem is more complicated, because k_c is not a constant (TAMIYA *et al.*, 1953; DUYSENS, 1956; KIRK, 1975; PLATT and JASSBY, 1976; PLATT *et al.*, 1977). In recent years, it has become common to refer to this phenomenon as the "package effect" (KIRK, 1983), although packing is but one of the possible causes of impaired photon capture. For example, SATHYENDRANATH *et al.* (1987) have pointed out the effect of changing pigment composition. Furthermore, the wavelength-averaged k_c should be weighted according to the spectral composition of available light (MOREL, 1978) which, far from being constant, will be a strong function of depth and of the pigment content of the water column.

The formal equivalence between α^B and ϕ_m expressed in equation (8) suggests that formulations of the photosynthesis–light relationship in terms of ϕ will be equivalent to those in α. Using ϕ rather than α would not advance the case, since we have no direct way to measure it. Nor would it decrease the number of parameters required for a description, since the photosynthesis–light relationship is an inherently two-parameter function. Only at the lowest light levels does a single parameter function suffice, and of course the satellite does not detect the biomass existing deep in the waters where such low light levels occur.

To see more clearly the equivalence between ϕ and α models of primary production, consider the model of KIEFER and MITCHELL (1983). The basic equation is:

$$\mu = k_c \rho I \phi, \tag{9}$$

where μ is the carbon-specific growth rate (assuming no respiration) and ρ is the chlorophyll to carbon ratio (KIEFER and MITCHELL, 1983, equation 1b). The function ϕ expresses the well known decrease in quantum yield as light level increases:

$$\phi = \frac{\phi_m K_\phi}{K_\phi + I}, \tag{10}$$

where K_ϕ is a parameter (KIEFER and MITCHELL, 1983, equation 2).

Combining equations (9) and (10) we find:

$$\mu = \frac{1}{C}\frac{dC}{dt} = \frac{k_c \phi_m \rho K_\phi I}{K_\phi + I}, \tag{11}$$

where C is the concentration of photosynthetically active carbon. Writing $P = dC/dt$ and replacing the product ρC by the chlorophyll biomass B gives:

$$P = \frac{\alpha^B B K_\phi I}{K_\phi + I} \tag{12}$$

where we have used equation (8) to substitute for $k_c\phi_m$. Noting that $\alpha^B B = \alpha$, it can now be seen that equation (12) is just a Michaelis–Menton expression for P with parameters $P_{max} = \alpha K_\phi$ and half-saturation constant K_ϕ. The correspondence of the scale factor P_{max} ($\equiv P_m$ in the notation used in this paper) with the product αK_ϕ immediately identifies K_ϕ with the light-adaptation parameter $I_k (\equiv P_m/\alpha)$. Thus the Kiefer and Mitchell model reduces to the form:

$$P = \frac{P_m I}{I_k + I}. \tag{13}$$

That the second parameter for this formalism of the photosynthesis–light curve is indeed I_k was proved in PLATT *et al.* (1977, equation 11). The general form $\int_z P = (P_m/K)\, f(\alpha I_0/P_m)$ of equation (6) will therefore be preserved also for formulations in terms of ϕ. In fact, the solution $\int_z P = (P_m/K)\ln(1 + I_*)$ is given in PLATT *et al.* (1977, equation 21).

We therefore can conclude that formulations of the relationship between plankton photosynthesis and available light in terms of quantum yield are entirely equivalent to those in terms of α, both for the rates at discrete depths and for the integrals over depth.

ERROR IN ESTIMATION OF AREAL PRODUCTION ARISING FROM NON-UNIFORM BIOMASS PROFILE

The earlier treatment of the relationship between Λ and I_0 (PLATT, 1986) was based on the assumption of uniform distribution of phytoplankton biomass with depth. We know, however, that a deep chlorophyll maximum (DCM) is a common feature of pigment profiles (e.g. CULLEN, 1982), expecially in the open ocean (e.g. HERBLAND *et al.*, 1983). In this section, therefore, we examine the effect on $\Lambda(I_0)$ of departures from the simple case $B(z)$ = constant

First, it will be convenient to introduce a generalized pigment profile (Fig. 3) with the following form (cf. LEWIS *et al.*, 1983):

$$B(z) = B_0 + \frac{h}{\sigma\sqrt{2\pi}} \exp\left[-\frac{(z - z_m)^2}{2\sigma^2}\right]. \tag{14}$$

The second term on the right-hand side of equation (14) is a Gaussian curve (to represent the chlorophyll maximum) superimposed on a constant background B_0. The three Gaussian parameters can be varied to represent the range of shapes of DCM likely to be encountered in the field (Fig. 4). Thus h controls the total biomass above the baseline B_0; z_m is the depth of the maximum; and σ controls the thickness of the DCM layer. Because of the properties of the Gaussian curve, the parameter σ is not identically

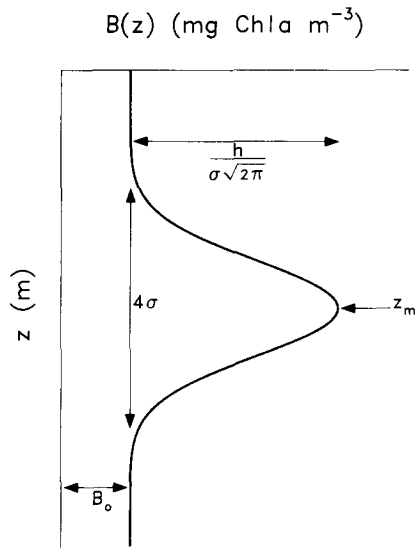

Fig. 3. Idealized deep chlorophyll maximum, represented by a Gaussian curve superimposed on a constant background. Parameters, B_0 = background biomass (mg m^{-3}), z_m = depth of chlorophyll maximum (m), σ = standard deviation (m) and h = total biomass above the background (mg m^{-2}). The peak height above the baseline is given by $h/(\sigma\sqrt{2\pi})$.

equal to the thickness, which is of order 4σ (in the sense that 95% of the integral biomass in the peak will lie within $\pm 2\sigma$ of z_m) or 2σ (in the sense that 68% of the biomass in the peak lies within $\pm\sigma$ of z_m). The amplitude of the DCM above the background concentration is $h/(\sqrt{2\pi}\sigma)$. The total biomass above the baseline is equal to h when the integration is carried out from $-\infty$ to $+\infty$. However, we are interested only in the biomass within the photic zone, and the integral within the limits 0 and z_p (where z_p is the depth of the photic zone) may be substantially less than h when (i) z_m approaches the surface; (ii) z_m is near or below z_p; or (iii) $4\sigma > z_p$.

With the generalized biomass profile $B(z)$ established in this way, we can proceed to a sensitivity analysis of the effect of non-uniform distribution of pigment with depth on the form of $\Lambda(I_0)$. As a point of reference, the parameters of equation (14) can be estimated by non-linear fitting to field data (Fig. 4) for stations with a well-developed, non-uniform, chlorophyll profile (note that the case where there is no DCM, but an accumulation of biomass at the surface, can be accomodated easily by setting $z_m = 0$). The equation is sufficiently versatile to mimic a large variety of profiles from coastal, upwelling, open ocean and Arctic waters, as long as the profiles contain only a single peak.

The general approach for the sensitivity analysis is as follows:

(i) Assign a parameter set to produce a pigment profile $B(z)$ according to equation (14).

(ii) Calculate integral production, $\int_z P$, for this $B(z)$ as a function of I_0 using a non-linear, photosynthesis–light model. Normalize $\int_z P$ to the integral biomass to give Λ.

(iii) Using the same photosynthesis–light model, calculate $\int_z P$ now for the case $B(z)$ = constant, where the constant value of $B(z)$ is chosen such that the photic-zone biomass $\int_0^{z_p} B(z)dz$ is equal to that in step (ii). Normalize $\int_z P$ to this integral

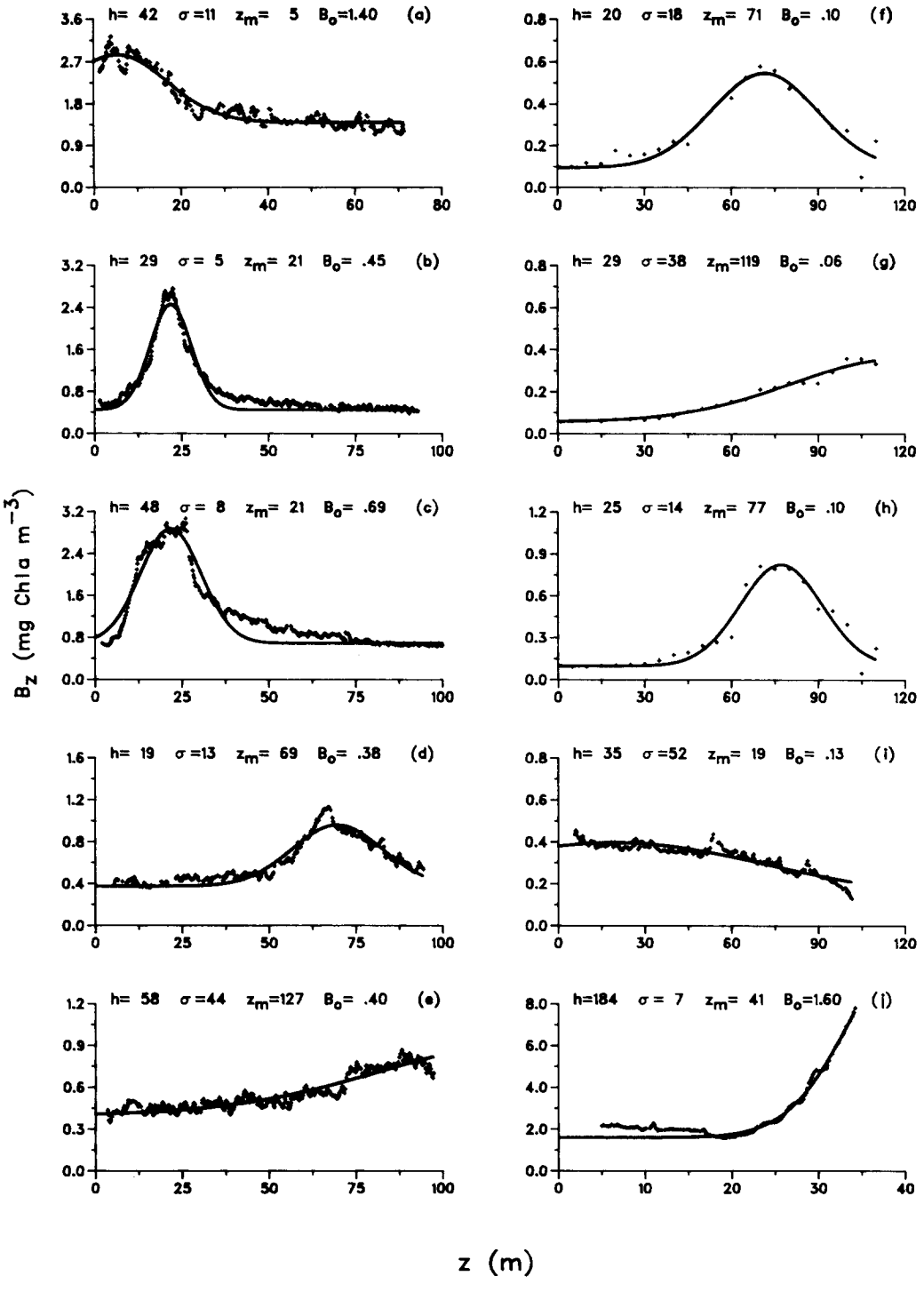

Fig. 4. Some examples of fitting the generalized biomass profile (equation 9) to field data on the vertical distribution of chlorophyll. The examples (a) to (e) are drawn from temperate coastal waters (the Georges Bank); (f) to (h) from tropical oligotrophic waters (Central Atlantic); and (i) to (j) from tropical waters (the Caribbean Sea). Discontinuous line: observed profile. Continuous line: fitted curve. The profile parameters for the best fit are also given for each curve.

biomass to give a new value of Λ, say Λ_u, where the subscript u implies "uniform". Note that Λ and Λ_u have a common normalization factor.

(iv) Calculate the relative error, $\Delta = (\Lambda_u - \Lambda)/\Lambda$ as a function of I_0 for this parameter set.

(v) Vary the parameter set in a systematic manner over the range likely to be encountered in typical field stations.

The following parameter values were selected to generate a mean $B(z)$ profile for the sensitivity analysis: $h = 18.8$ (mg Chl a m^{-2}) and $\sigma = 5$ m (which gave a peak height = 1.5 mg Chl a m^{-3} above the baseline); $z_m = 42.5$ m; and $B_0 = 0.1$ mg Chl a m^{-3}. By comparison with the parameter sets in Fig. 4, it may be seen that the selected set is such that the non-uniformity is accentuated, but not so much as to be wholly unrealistic. The parameters of the photosynthesis–light curve, P_m^B and α^B, are assumed to be 5 mg C (mg Chl a)$^{-1}$ h^{-1} and 0.1 mg C (mg Chl a)$^{-1}h^{-1}$ (W m^{-2})$^{-1}$, respectively. The attenuation coefficients used to compute I_z, the light intensity at depth z, are: $k_c = 0.04$ m^{-1} (mg Chl a m^{-3})$^{-1}$ (MOREL and BRICAUD, 1981), where k_c is the specific attenuation due to phytoplankton, per unit concentration of Chl a; $K_w = 0.027$ m^{-1} (SMITH and BAKER, 1978), where K_w is the clear seawater attenuation; and $K_x = 0.015$ m^{-1}, where K_x is the attenuation due to particulate and dissolved material uncorrelated with Chl a [vertical diffuse attenuation coefficient at depth z, $K(z)$ (m^{-1}) = $K_w + K_x + B(z)k_c$]. With these attenuation values, the euphotic depth is 85 m, and therefore $z_m = z_p/2$.

The relative error in estimated production, Δ, for this chlorophyll profile is presented in Fig. 5 as a function of the dimensionless independent variable I_*. The error curve is easily understood if we also examine Fig. 6, in which the production profiles at various light intensities are plotted, for both the non-uniform and the uniform cases. At low light intensities, the P–I curve is linear. When I_* is very small, the assumption of uniform chlorophyll distribution leads to an over estimate in production (positive Δ), since this implies redistributing the biomass in the DCM in such a way as to bring more biomass to the surface waters where more light is available. An initial increase in I_0 (or I_*, in this case, since I_k is held constant here) has the effect of making more light available to activate the DCM, and Λ increases more rapidly than Λ_u, with a corresponding decrease

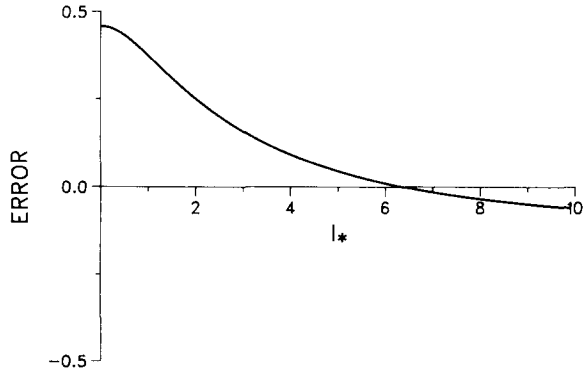

Fig. 5. The relative error in estimated production (positive sign implies an overestimate in production) as a function of I_*, for the typical biomass profile selected for the sensitivity analysis.

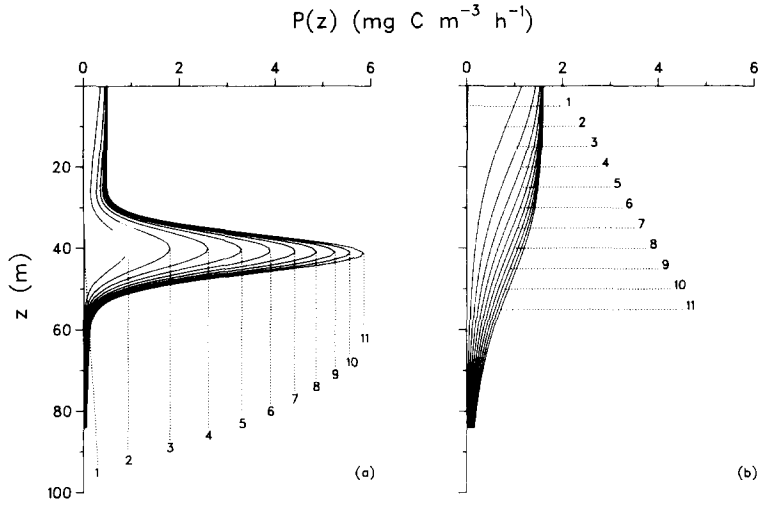

Fig. 6. The production profiles at various surface light intensities for the typical biomass profile used in the sensitivity analysis (a), and for the uniform case with the same amount of total chlorophyll in the euphotic zone (b). Numbers 1 to 11 indicate surface irradiance values ranging from 1 to 500 W m^{-2}, in equal increments.

in error. When I_* becomes >1, saturation of production sets in, and initially this extends to a greater depth in the non-uniform case than in the uniform (because of lower optical attenuation near the surface, in the non-uniform case). Consequently, there is a fall-off in the rate of decrease of Δ. At $I_* \approx 6$, the error becomes negative and decreases very slowly with further increase in I_*.

The results of sensitivity analysis in this typical case are presented in Figs 7–10. The main consequences of changing the four parameters of the $B(z)$ profile and the two parameters of the P–I curve are as follows:

Change in h

When h is decreased, the biomass in the peak decreases with respect to the background biomass (in other words, the non-uniform distribution approaches the uniform distribution), and as a result, the error decreases (see Fig. 7a). When h is increased, the peak height increases, with a consequent increase in error. However, increasing h also results in a decrease in euphotic depth, and when h becomes so high that $z_m > z_p$, the error begins to decrease. Maximum errors (>100%) are found at low I_* values, for very sharp peaks lying close to the euphotic depth.

Change in σ

As long as the entire peak remains within the euphotic zone, changing σ does not change either the total biomass in the euphotic zone, or the depth of the euphotic zone. Increasing σ leads to a decrease in the ratio of peak height to background, as well as an increase in chlorophyll values near the surface, with a resultant flattening of the error curve (see Fig. 7b).

Change in z_m

As in the case of σ, changing z_m does not change either biomass or z_p, provided that the whole peak is contained in the photic zone. Moving the peak closer to the surface

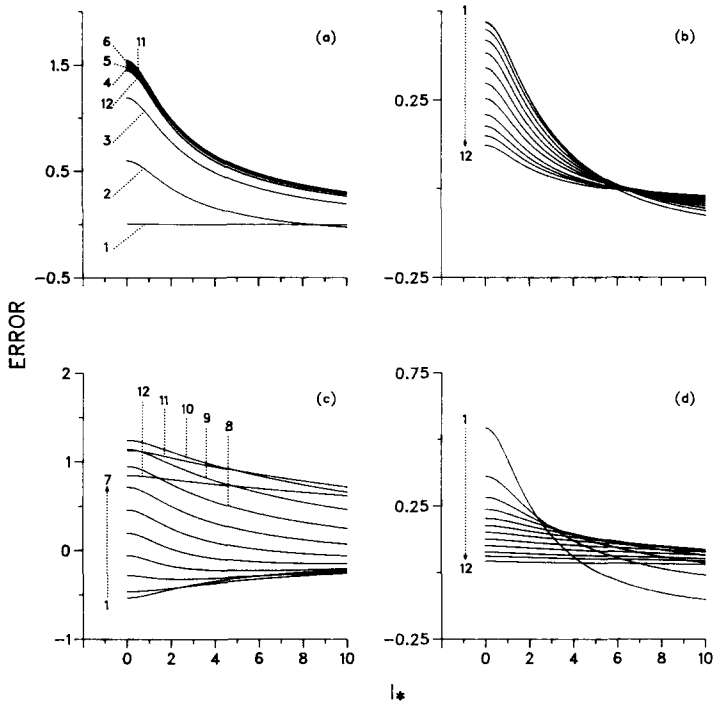

Fig. 7. Analysis of sensitivity of error to changes in the profile parameters. In each of the plots, one of the parameters is changed systematically, in equal increments over a range of probable values. The curves are numbered in the increasing order of parameter values: (a) h ranging from 0.1 to 275 (mg Chl a m^{-2}). (b) σ, range 2–24 m. (c) z_m from 0 to 93.5 m. For curve 11, $z_m = z_p$. (d) B_0 from 0.05 to 1.65 (mg Chl a m^{-3}). For curve 11, $B_0 = 1.5$ (mg Chl a m^{-3}), which is equal to the peak height above the baseline.

leads to an increase in negative error, while moving it downward toward z_p leads to an increase in positive error (Fig. 7c). Moving z_m below z_p leads, of course, to a decrease in error. Note that when either $z_m = 0$ or $z_m = z_p$, the biomass in the water column is reduced by half, compared to the case where the whole peak is in the euphotic zone. This would account for the fact that the curves corresponding to these two cases cross the curves for the intermediate z_m values. The error is always negative when z_m is close to zero and always positive when z_m is close to (but not below) z_p, the magnitude of the error being maximal at low light intensities. For intermediate values of z_m, the error may be positive or negative depending on I_*, and the error curve may reach its maximum for higher values of I_*. Maximum positive errors (>100%) are found at low intensities, for $z_m \approx z_p$. The magnitude of this error is considerably greater than that of the negative error maximum, also at low light, for a similar peak lying close to the surface.

Change in B_0

Increasing B_0 implies a decrease in the ratio of peak biomass to background biomass. The increase in total biomass also reduces the euphotic depth, leading to an increase in the ratio of z_m to z_p. The result is a decrease in relative error (Fig. 7d). The error becomes zero when $B_0 \approx 2h/\sigma\sqrt{2\pi}$.

Change in P_m^B *and* α^B

Both P_m^B and α^B influence relative error through changes in I_k. Thus, the plots of relative error as a function of I_* are unchanged when either P_m^B or α^B is changed. Their effects do, however, show up in plots of relative error vs I_0 (see Fig. 8). Increasing α^B or decreasing P_m^B results in a decrease in I_k. When I_k becomes smaller, the error curve peaks for lower values of I_0 (Fig. 8). Similarly, for extremely low values of I_k, the error tends towards zero with increasing I_0, reflecting light-saturated production over increasing portions of the euphotic zone.

Change in biomass and optical parameters

Even though the integral production values examined in this study are normalized to unit biomass, the effect of biomass is not totally eliminated, because it intervenes in the light attenuation term K. To study the effect of biomass, we multiplied both the terms on the right-hand side of equation (14) by constant factors (thereby conserving the h/B_0 ratio). Because a change in the biomass altered the euphotic depth z_p, the z_m values were scaled in each case to the z_p values that would obtain if the whole peak were contained within the photic zone.

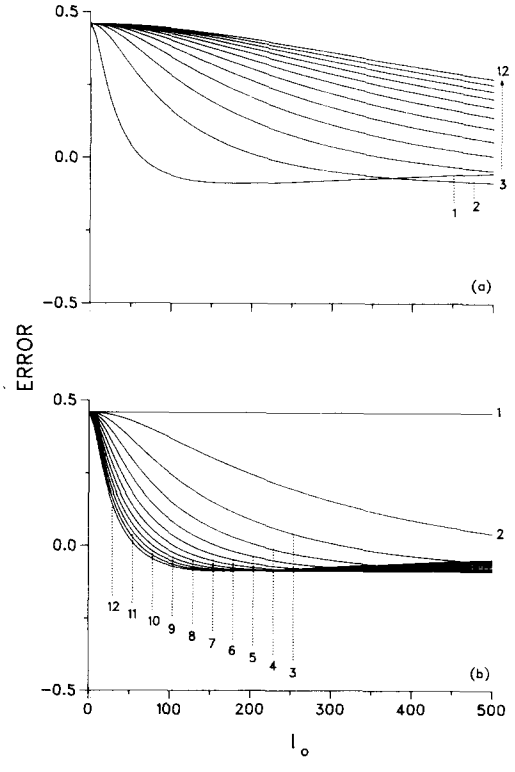

Fig. 8. Analysis of sensitivity of error to changes in the photosynthetic parameters P_m^B (a) and α^B (b). Errors are plotted here as a function of surface light intensity (I_0) (W m^{-2}). Range of P_m^B is from 1 to 27.4 [mg C (mg Chl *a*)$^{-1}$ h^{-1}] and of α^B, from 0.001 to 0.55 [mg C (mg Chl *a*)$^{-1}$ h^{-1} (W m^{-2})$^{-1}$].

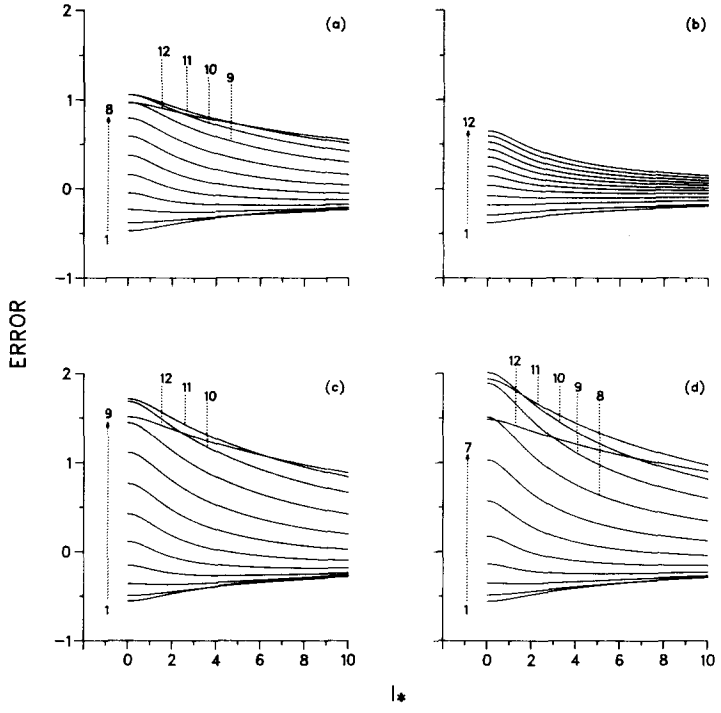

Fig. 9. Analysis of sensitivity of error to changes in the optical parameters $(K_w + K_x)$ and $B(z)k_c$: (a) $B(z)$ multiplied by 2. (b) $B(z)$ multiplied by 4. (c) $(K_w + K_x) = 0.07$ (m^{-1}). (d) $(K_w + K_x) = 0.1$ (m^{-1}). The profile parameter being varied in each plot is z_m. The curves are numbered from 1 to 11 to indicate increasing z_m values from surface to the base of the euphotic zone, in equal increments. Number 12 indicates one increment below the euphotic depth.

Sensitivity analysis on these profiles shows that the errors decrease with increasing biomass (Fig. 9a,b). This may be attributed to the fact that, when the term $B(z)\ k_c$ increases, the fraction of incident light absorbed by phytoplankton increases, approaching the limiting case where almost all the light is absorbed by phytoplankton occurring in extremely high concentrations at the surface. The difference in production between uniform and non-uniform biomass profiles tends to vanish in such instances. Increasing the phytoplankton specific absorption coefficient k_c would have a similar effect. By analogy, it may be expected that increasing the background absorption (the $K_w + K_x$ term) would have the inverse effect of increasing the errors for similar cases, which is in fact borne out by Fig. 9c,d.

Daily integrated production

In all the examples we have seen, the relative errors arising from structure in the biomass profile are maximal for very small values of I_*. That is, the relative errors are maximum for the times when the magnitude of the actual production is very low, because of low light. This means that when daily integrated production is computed, the errors may be expected to be maximal in high latitudes in winter and on overcast days, and minimal at low latitudes on sunny days. This expectation may be checked as more data become available, particularly from low latitudes.

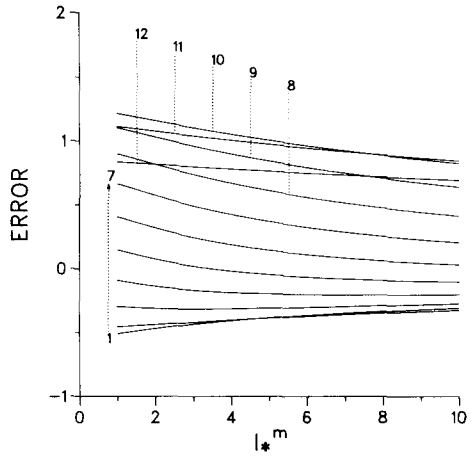

Fig. 10. Error curves for daily integrated production as a function of I_*^m. The variable parameter is z_m, as in Fig. 9.

As in PLATT (1986) the errors in daily integrals were computed, using the following expression of IKUSHIMA (1967) to estimate the I_0 as a function of time t:

$$I_0(t) = I_0^m \sin^3\left(\frac{\pi t}{D}\right), \tag{15}$$

where I_*^m is the maximum irradiance at noon, D is the daylength. The results of sensitivity analyses on daily integrals are presented in Fig. 10.

Error curves for field data

Error curves were also computed for the typical profiles presented in Fig. 4. For ease of computation, the fitted curves were used rather than the actual observed profiles. The results (Fig. 11) indicate clearly that the errors incurred in real situations may often be far less than those computed for some of the extreme cases discussed (for the sake of completeness) in earlier sections.

Summary of sensitivity analysis

Some generalizations can now be made. The critical dimensionless factors that determine the error are:

(i) The depth of the DCM relative to the euphotic depth, z_m/z_p.
(ii) The width of the peak relative to the euphotic depth, σ/z_p.
(iii) The ratio of peak height to background, $h/(\sigma B_0)$.
(iv) The ratio of background to phytoplankton absorption, $(K_w + K_z)/(k_c < B >)$, where $< B >$ is the mean biomass for the water column.

Maximal negative errors can be expected at low intensities, for a sharp chlorophyll maximum near the euphotic depth, and maximal positive errors for a similar peak near the surface. Flatter biomass curves generate flatter error curves, with decreasing dependence on I_*. Higher background chlorophyll and lower peaks lead to lower errors.

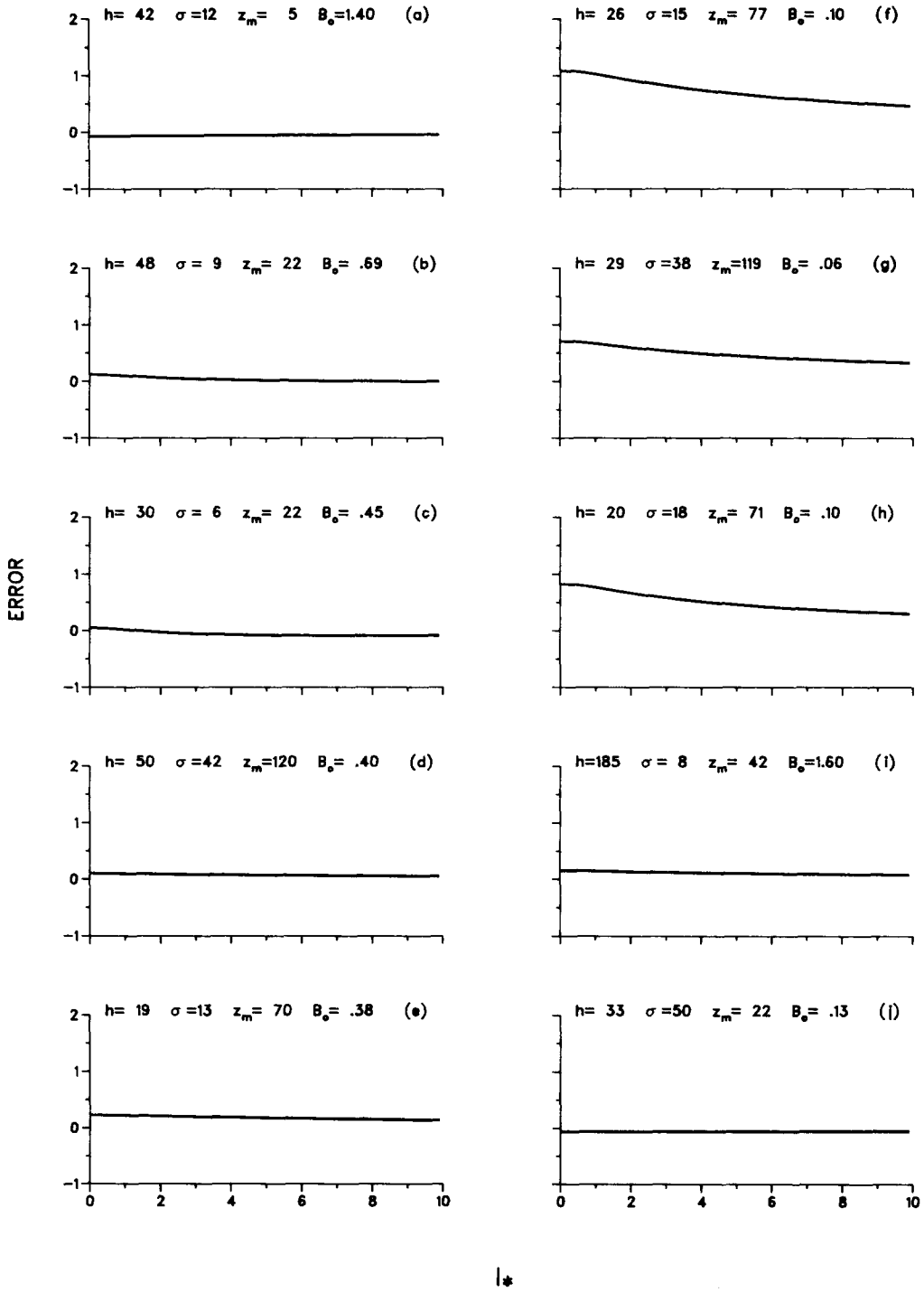

Fig. 11. Error curves for the profiles fitted to field data, as presented in Fig. 4.

All other factors being equal, the errors decrease when the phytoplankton absorption increases relative to the background absorption.

RANDOM ERRORS IN ESTIMATION OF WATER COLUMN PRODUCTION BY REMOTE SENSING

One protocol for estimating water column production by remote sensing using the theory outlined here and in PLATT (1986) would be:

(i) Estimate $\Lambda = \psi I_0 = (\alpha^B/4.6)I_0$.
(ii) Estimate $\int_0^z B(z)dz$ from weighted surface-layer value, B_s, given by satellite-borne ocean-color sensor.
(iii) Estimate $\int P(z)dz = \Lambda \int B(z)dz = (\alpha^B/4.6)I_0 \int B(z)dz$.

We examine the minimum random errors that would be associated with this protocol. Assuming first that the photosynthesis parameters are known as well as possible for the station in question, the measurement technique usually cannot do better than $P_m^B \pm 5\%$ and $\alpha^B \pm 20\%$ (e.g. PLATT *et al.*, 1980). Surface light can be estimated within 10% from satellite data (GAUTIER and KATSAROS, 1984). The precision of estimation of surface chlorophyll from the CZCS is ~35% (GORDON *et al.*, 1983). Given exact values for the surface chlorophyll, water column chlorophyll can be estimated with a precision of about 10% (PLATT and HERMAN, 1983) under ideal circumstances: the 35% error associated with the satellite algorithm will dominate that associated with extrapolation to water column values, and we can therefore assign a lower limit to the precision of estimating areal biomass of 35%.

Compounding the errors according to TOPPING (1962) we find the relative error on water column production to be $\sqrt{(0.2)^2 + (0.1)^2 + (0.35)^2} = 42\%$, with the error in the biomass dominating the result. The bias introduced through the use of the linear photosynthesis–light model can be calculated as a function of $I_* = I_0/I_k$, where $I_k = P_m^B/\alpha^B$. The relative error in α^B is four times that in P_m^B and will dominate error in I_k, which cannot be known to better than 20%. Adding in the error associated with I_0 makes I_* uncertain to within 22%. The bias in integral production is a fairly linear function of I_*, certainly for $I_* > 1$ (PLATT, 1986, Fig. 1), such that the uncertainty in I_* propagates to an uncertainty of 22% in the bias. When the bias is removed, its uncertainty will combine with the 42% uncertainty in the unbiased integral production to give an uncertainty in the corrected figure ~60% $[\sqrt{(0.22)^2 + (0.42)^2}/(1 - 0.22)]$.

This estimate of error does not include systematic errors nor the effect of spatial variance in photosynthetic parameters, that is, of not knowing the values of α^B and P_m^B applying to the particular station in question. Nor does it include the further error that would arise if α were estimated from fluourescence line height. It is possible that an empirical regression model could be found for a given region for which the error of an estimate of primary production might be lower than that of the physiological model. But it is unlikely that such a model would be equally valid for all regions of the world's oceans. It seems that we are obliged to live with a fundamental limitation of over 50% on the precision of estimating primary production from remote sensing.

Systematic errors associated with non-uniformity in the biomass profile would further increase the uncertainty in estimation of integral production. These are evaluated below in the explicit context of remote sensing.

An alternative way of applying the protocol would be to avoid explicit use of the parameter α and use instead the relation $\int P(z)\mathrm{d}z = \psi I_0 \int B(z)\mathrm{d}z$. The uncertainty in α^B is now replaced, in a sense, by the standard error in ψ, which will reflect the scatter in the regression from which it was derived. Note that since ψ is established by regressing data from real stations, its standard error will already incorporate some variance arising from non-uniformity in the biomass profile. Hence the systematic errors as calculated here, between the uniform and non-uniform cases, may not add in a simple way to the random errors associated with the parameters themselves.

SYSTEMATIC ERRORS IN ESTIMATION OF PRIMARY PRODUCTION USING SATELLITE-WEIGHTED CHLOROPHYLL CONCENTRATION

In a previous section we calculated the bias on the computation of water column production (using a non-linear physiological model) arising from non-uniformity in the biomass profile. The biomass was calculated against a uniform profile with the same photic zone biomass integral as the non-uniform profile. Because this normalization factor $\int_z B$ was the same in both cases, the conclusions about bias apply equally well to chlorophyll-normalized water column production as to un-normalized production. The results are relevant to the general problem of estimating water column production from surface light.

Structure in the biomass profile is a potential source of systematic error in the estimation of primary production by remote sensing, and we now consider how best to evaluate the systematic error *in this context*.

The protocol outlined above (in the section on random errors) for calculation of primary production (which we may call Method I) involves the determination of the water column chlorophyll concentration from the satellite-determined surface chlorophyll concentration, using an empirical relationship of the type proposed by PLATT and HERMAN (1983). This is not without its difficulties, since the relationship between surface and water column chlorophyll varies with region and season, and the conversion factors are not known for all localities.

An alternate procedure (Method II), which we now evaluate, would be to estimate production directly from the satellite-determined chlorophyll concentration, skipping the intermediate step of evaluating water column chlorophyll concentration. The procedure is as follows: For a given chlorophyll biomass profile, the weighted, surface chlorophyll concentration (B_s, the "effective concentration") that would be estimated by a satellite is evaluated, using the following relationship (GORDON and CLARK, 1980):

$$B_s = \frac{\int_0^{1/K} B(z)\, f(z)\mathrm{d}z}{\int_0^{1/K} f(z)\mathrm{d}z}, \tag{16}$$

where

$$f(z) = \exp\left[-\int_0^z 2K(z')\mathrm{d}z'\right].$$

GORDON and MCCLUNEY (1975) have shown that 90% of the signal comes from the first attenuation length. Integration should extend deeper to cover the other 10%. In this work, we have integrated to 2.3 attenuation lengths, i.e. to half the euphotic depth

[note that integrals over z in PLATT and HERMAN (1983) should read $\int_0^{2k^{-1}}$ and not $\int^{(2k)^{-1}}$ as printed].

The water column production is then computed, as it would be if the effective concentration extended uniformly throughout the entire photic zone. The errors are calculated between production for the uniform profile and the non-uniform profile, relative to the production for the true (non-uniform) profile. There is no normalization to the biomass profile.

The results of sensitivity analyses on the biomass profile parameters for Method II, carried out using the standard generalized profile used earlier, are presented in Fig. 12. Sensitivity of the errors to changes in photosynthetic and optical parameters was calculated (figures not shown). As in Method I, increasing h leads to an increase in relative error, and increasing σ and B_0 lead to a decrease in error. The dimensionless factor $(K_w + K_x)/(<B> k_c)$ and the photosynthetic parameters P_m and α affect the errors in a similar way to Method I. However, the error curves for Method II (Fig. 12) do show some features that are markedly different from those of Method I. The important points to note are:

(i) The errors generally have opposite signs when compared to those for Method I. For example, a DCM leads to an underestimate in production, since the satellite would not have detected its presence. On the other hand, a near-surface chlorophyll maximum leads to over-estimated production, since the method

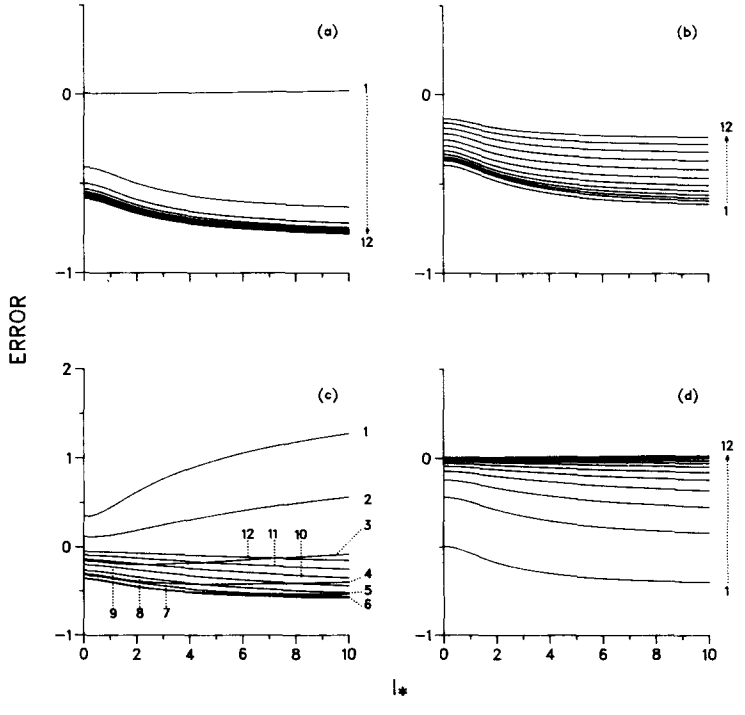

Fig. 12. Error curves for sensitivity analysis according to Method II. The parameter values for each curve correspond to those of Fig. 7.

adopted here would assign the same high chlorophyll concentration right through the water column.

(ii) The magnitudes of the maximum errors are considerably less than in Method I. They are generally <100%, except in the case of a surface chlorophyll maximum with high surface irradiance. The reason for the low errors is that the satellite estimate of chlorophyll is strongly weighted to the surface, where the production per unit chlorophyll is maximum (disregarding the possibility of photoinhibition). A related point is that the photosynthesis per unit pigment is an exponentially decreasing function of depth, as is the weighting function for satellite-derived pigment, which also helps to minimize the errors. In case of the 10 observed profiles presented in Fig. 4, the maximum error (at high light intensities) is <45% (figure not shown).

(iii) The errors are not as strongly dependent on the surface light intensity, as in Method I (except in the case of chlorophyll peaks near the surface). The general trend is towards increasing error with increasing light. This means that when daily integrated production is computed, larger errors may be anticipated at low latitudes and on clear days, than at high latitudes and on overcast days. It remains to be seen whether this expectation will be borne out when more data from low latitudes become available.

(iv) Maximum negative errors are not found for $z_m \approx z_p$, but rather when $z_m \approx z_p/2$. Increasing z_m further causes the errors to decrease. This is a consequence of the fact that deeper chlorophyll peaks make a relatively smaller contribution to water column production.

From these results, it appears that, in the context of remote sensing, Method II is a better protocol than Method I for computation of water column production, because of the likelihood of a smaller systematic error arising from non-uniform biomass distribution. Also, it avoids the necessity of computing water column chlorophyll from surface chlorophyll, thereby eliminating one source of random error.

CONCLUDING REMARKS

The new data sets discussed here reinforce the conclusion of PLATT (1986) that the range of variation in ψ is small. The values of ψ presented in this paper all lie in the interval from 0.29 to 0.52 g C (g Chl a)$^{-1}$ m^2(E)$^{-1}$, notwithstanding the diversity of oceanic regimes from which they were drawn. And if the magnitude of ψ is conservative between regions, the variation between years for the same areas is no less so, as illustrated by the data from the Antarctic, from the New York Bight and from the Bedford Basin. It is true that the model is still untested for many regions of the world's oceans. Caution is therefore recommended in its application in such areas.

One of the limitations in applying the linear theory of ocean production, the potential artefact of a positive intercept at zero light, has been explained. The problem could be avoided by passing to a non-linear model, using the exact solution of equation (2). The disadvantage, apart from the loss of simplicity, would be that it would be necessary to specify P_m as well as α.

It seems that the precision of an estimate of water column primary production at large horizontal scale from remotely sensed data will not be better than about 100% because of fundamental limitations on the intrinsic precision of the essential parameters. The error

that dominates is that on the determination of biomass by remote sensing. Note that none of the available algorithms for extracting information on biomass from satellite data pretend to recover the structure of the biomass profile $B(z)$. It would therefore be premature, at the least, to attempt to recover the production profile $P(z)$. The additional error introduced into the estimation of water column production through non-uniformity in the biomass profile can seem large when the full range of variation of the relevant parameters is explored, as in this paper, but in real cases we have shown that the error is much less forbidding. Knowledge of the shape of the biomass profile is the single most useful supplemental information for the interpretation of ocean color data in particular cases. Not that errors associated with structure in the biomass profile decrease with increasing surface light, whereas those arising from the linear approximation increase with increasing surface light. Note also that because of the compounding of several non-linear processes, and in particular the effect on photic depth of change in biomass profile, the results of the sensitivity analyses cannot be anticipated by intuition.

It is possible that, in given areas, an empirical regression could be found to estimate water column production from satellite chlorophyll that would give an apparently higher precision than the physiological model. This would be misleading, however, because, as we have seen, the error in the biomass dominates the error in the estimate of production. A local regression of production on surface irradiance should be superior to one developed at larger scale, since it will contain information about the local biomass profile, a source of error that must otherwise be added to those arising from uncertainty in the parameters of the physiological model and from the limitations of the model itself. A complete, non-linear model with non-uniform biomass would require that we specify four parameters for the biomass profile in addition to two photosynthesis parameters.

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REFERENCES

BRUNO S. F., R. D. STAKER and G. M. SHARMA (1980) Dynamics of phytoplankton productivity in the Peconic Bay Estuary, Long Island. *Estuarine and Coastal Marine Science*, **10**, 247–263.

COLE B. E. and J. E. CLOERN (1987) An empirical model for estimating phytoplankton productivity in estuaries. *Marine Ecology—Progress Series*, **36**, 299–305.

COLLOS Y. and G. SLAWYK (1986) ^{13}C and ^{15}N uptake by marine phytoplankton—IV. Uptake ratios and the contribution of nitrate to the productivity of Antarctic waters (Indian Ocean sector). *Deep-Sea Research*, **33**, 1039–1051.

CULLEN J. J. (1982) The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 791–803.

DUYSENS L. N. M. (1956) The flattening of the absorption spectrum of suspensions as compared to that of solutions. *Biochimica et Biophysica Acta*, **19**, 1–12.

EPPLEY R. W., STEWART, M. R. ABBOT and U. HEYMAN (1985) Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. *Journal of Plankton Research*, **7**, 57–70.

FALKOWSKI P. G. (1981) Light–shade adaptation and assimilaton numbers. *Journal of Plankton Research*, **3**, 203–216.

GORDON H. R. and W. R. MCCLUNEY (1975) Estimation of depth of sunlight penetration in the sea for remote sensing. *Applied Optics*, **14**, 413–416.

GORDON H. R. and D. K. CLARKE (1980) Remote sensing of optical properties of a stratified ocean: an improved interpretation. *Applied Optics*, **19**, 3428–3430.

GORDON H. R., D. K. CLARK, J. W. BROWN, O. B. BROWN, R. H. EVANS and W. W. BROENKOW (1983) Phytoplankton pigment concentrations in the Middle Atlantic Bight: comparison between ship determination and Coastal Zone Color Scanner estimates. *Applied Optics*, **22**, 20–36.

GAUTIER C. and K. B. KATSAROS (1984) Insolation during STREX: comparisons between surface measurements and satellite estimates. *Journal of Geophysical Research*, **89**, 11,779–11,788.

HERBLAND A., R. LE BORGNE, A. LE BOUTEILLER and B. VOITURIEZ (1983) Structure hydrologique et production primaire dans l'Atlantique tropical oriental. *Oceanographie Tropicale*, **18**, 249–293.

IKUSHIMA I. (1967) Ecological studies on the productivity of aquatic plant communities. III. Effect of depth on daily photosynthesis in submerged macrophytes. *Botanical Magazine, Tokyo*, **80**, 57–67.

IRWIN B., C. CAVERHILL and T. PLATT (1986) Primary production on the Grand Banks of Newfoundland in April 1984. *Canadian Data Report of Fisheries and Aquatic Sciences* 579, 49 pp.

JACQUES G. and M. MINAS (1981) Production primaire dans le secteur indien de l'océan Antarctique en fin d'été. *Oceanological Acta*, **4**, 33–41.

KIEFER D. A. and B. G. MITCHELL (1983) A simple, steady state description of phytoplankton growth based on absorption cross section and quantum efficiency. *Limnology and Oceanography*, **28**, 770–776.

KIRK J. T. O. (1975) A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. I. General treatment of suspensions of pigmented cells. *New Phytology*, **75**, 11–20.

KIRK J. T. O. (1983) *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press, Cambridge, 401 pp.

LEWIS M. R., J. J. CULLEN and T. PLATT (1983) Phytoplankton and thermal structure in the upper ocean: consequences of nonuniformity in chlorophyll profile. *Journal of Geophysical Research*, **88**, 2565–2570.

LEWIS M. R., R. E. WARNOCK and T. PLATT (1986) Photosynthetic response of marine picoplankton at low photon flux. In: *Photosynthetic picoplankton*, T. PLATT and W. K. W. LI, editors, *Canadian Bulletin of Fisheries and Aquatic Sciences*, **214**, 235–250.

MALONE T. C. (1976) Phytoplankton productivity in the apex of the New York Bight: environmental regulation of productivity-chlorophyll *a*. In: *The Middle Atlantic Continental Shelf and New York Bight*, M. G. GROSS, editor, *Limnology and Oceanography Special Symposium*, **2**, 260–272.

MALONE T. C. (1987) Primary production of the ocean water column as a function of surface light intensity. *Deep-Sea Research*, **34**, 139.

MOREL A. (1978) Available, usable, and stored radiant energy in relation to marine photosynthesis. *Deep-Sea Research*, **25**, 673–688.

MOREL A. and A. BRICAUD (1981) Theoretical results concerning light absorption in a discrete medium and application to the specific absorption of phytoplankton. *Deep-Sea Research*, **28**, 1357–1393.

PLATT T. (1986) Primary production of the ocean water column as a function of surface light intensity: algorithms for remote sensing. *Deep-Sea Research*, **33**, 149–163.

PLATT T. and B. IRWIN (1971) Phytoplankton production and nutrients in Bedford Basin, 1969–1970. *Fisheries Research Board of Canada Technical Report* 247, 172 pp.

PLATT T. and B. IRWIN (1972) Phytoplankton productivity and nutrient measurements in Petpepswick Inlet, 1971–1072. *Fisheries Research Board of Canada Technical Report* 314, 112 pp.

PLATT T. and A. D. JASSBY (1976) The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *Journal of Phycology*, **12**, 421–430.

PLATT T. and A. W. HERMAN (1983) Remote sensing of phytoplankton in the sea: surface layer chlorophyll as an estimate of water column chlorophyll and primary production. *International Journal of Remote Sensing*, **4**, 343–351.

PLATT T. and M. R. LEWIS (1987) Estimation of phytoplankton production by remote sensing. *Advances in Space Research*, **7**, 131–135.

PLATT T., B. IRWIN and D. V. SUBBA RAO (1973) Primary production and nutrient measurements on the spring phytoplankton bloom in Bedford Basin 1971. *Fisheries Research Board of Canada Technical Report* 423, 42 pp.

PLATT T., K. L. DENMAN and A. D. JASSBY (1977) Modelling the productivity of phytoplankton. In: *The sea: ideas and observations on progress in the study of the seas*, Vol. 6, E. D. GOLDBERG *et al.*, editors, Wiley, New York, pp. 807–856.

PLATT T., C. L. GALLEGOS and W. G. HARRISON (1980) Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research*, **38**, 687–701.

REVELLE R. (1985) Oceanography from space. *Science*, **228**, 133.

SATHYENDRANATH S. (1986) Remote sensing of phytoplankton: a review with special reference to picoplankton. In: *Photosynthetic picoplankton*, T. PLATT and W. K. W. LI, editors, *Canadian Bulletin of Fisheries and Aquatic Sciences* 214, pp. 561–583.

SATHYENDRANATH S., L. LAZZARA and L. PRIEUR (1987) Variations in the spectral values of specific absorption of phytoplankton. *Limnology and Oceanography*, **32**, 403–415.

SMITH E. L. (1936) Photosynthesis in relation to light and carbon dioxide. *Proceedings of the National Academy of Sciences*, **22**, 504–511.

SMITH R. C. and K. S. BAKER (1978) The bio-optical state of ocean waters and remote sensing. *Limnology and Oceanography*, **23**, 247–259.

SMITH R. C., R. W. EPPLEY and K. S. BAKER (1982) Correlation of primary production as measured aboard ship in southern California coastal waters and as estimated from satellite images. *Marine Biology*, **66**, 1–8.

TAMIYA H., E. HASE, K. SHIBATA, A. MITUYA, T. IWAMURA, T. NIHEI and T. SASA (1953) Kinetics of growth of *Chlorella*, with special reference to its dependence on quantity of available light and temperature. In: *Algal culture from laboratory to pilot plant*, J. S. BURLEW, editor, Carnegie Institution of Washington Publication 600, Washington D.C., pp. 204–232.

TOPLISS B. J. and T. PLATT (1986) Passive fluorescence and photosynthesis in the ocean: implications for remote sensing. *Deep-Sea Research*, **33**, 849–864.

TOPPING J. (1962) *Errors of observation and their treatment.* Chapman and Hall, London, 119 pp.