

# Estimators of Primary Production for Interpretation of Remotely Sensed Data on Ocean Color

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The theoretical basis is explained for some commonly used estimators of daily primary production in a vertically uniform water column. These models are recast into a canonical form, with dimensionless arguments, to facilitate comparison with each other and with an analytic solution. The limitations of each model are examined. The values of the photoadaptation parameter  $I_k$  observed in the ocean are analyzed, and  $I_k$  is used as a scale to normalize the surface irradiance. The range of this scaled irradiance is presented. An equation is given for estimation of  $I_k$  from recent light history. It is shown how the models for water column production can be adapted for estimation of the production in finite layers. The distinctions between model formulation, model implementation and model evaluation are discussed. Recommendations are given on the choice of algorithm for computation of daily production according to the degree of approximation acceptable in the result.

## 1. INTRODUCTION

By virtue of their broad, synoptic coverage, remotely sensed images of ocean color are seen as important tools for the spatial extrapolation of local data collected from ships in ocean biogeochemical studies. One of the principal applications of the images is the estimation of ocean primary production at large geographical scale. Various methods have been proposed to convert pigment fields derived from ocean color images into maps of primary production. These models differ in complexity and therefore in the computing time and the amount of information required to implement them. It is natural and proper to ask how these models compare with each other, and how the essence of the more complex models can be captured with the least computation time.

Models to compute daily water column primary production as a function of available light and biomass were published more than 35 years ago [Ryther, 1956; Talling, 1957]. Other models have been proposed since then, and new models are still under development. It is often not easy to discern how the various models are related to each other.

Our objectives in this paper are therefore to outline a systematic procedure by which the models available for estimation of primary production can be compared; to analyze the different models using this procedure; to point out important relationships between the models and among the underlying parameters; and to discuss the issues that arise when the models are implemented in a remote sensing context. We deal mainly with nonspectral models for a vertically uniform water column.

The nature of our analysis is such that it leads to robust results without the need to invoke any data. Before embarking on the analysis proper, it will be useful to clarify some fundamental points.

## 2. VARIABLES AND PARAMETERS

It is essential first to distinguish between variables and parameters. Any equation (or "model") may contain variables, parameters and constants. The dependent variable is usually the entity on the

left-hand side of the equation. The independent, or forcing, variables appear on the right, together with constants and parameters. Constants may be quantities such as  $\pi$ , whose value is fixed for all time, or quantities such as the speed of light, which for all practical purposes may be considered as universal.

It is crucial to recognize that when an equation is written out in terms of variables and parameters it describes not just one line on a graph, but an entire family of them. The different members of the family are distinguished from one another by the particular values of their parameter sets. One should not confuse variables and parameters. Although one sees many examples to the contrary, the word "parameters" should only be used to signify the properties that make a curve unique compared to other members of the family of curves with the same general equation in common. As an example, for a circle centered at the origin, the only parameter required is the radius. To specify the radius is sufficient to isolate one particular circle from all the possible circles that could be drawn with their centers at the origin.

Changing the parameter magnitudes does not change the underlying model. The model has a life of its own independent from, and much more fundamental than, the particular parameter set that may be applied to it. The assignment of particular values to the parameters of a given model is an issue of model implementation, not model formulation. The two issues should be kept clearly separate from each other. Use of poorly chosen parameters could lead to spurious conclusions about the performance of a model if this distinction were not maintained.

Models that can be shown to be equivalent to each other, either by transformation of variables or parameters, are not dissimilar from each other. Sometimes, models are written in terms of parameters that are not observables: in such cases, it can be advantageous to recast them. For example, at present the quantum yield of photosynthesis is not a direct observable of the pelagic ecosystem. A model so parameterized may be recast in terms of the initial slope of the photosynthesis–light curve, which is a direct observable in routine field work. But the underlying model will not have changed, any more than the volume of a sphere would change if it were calculated from the diameter rather than the radius.

Finally, one should not overlook the possibility that statistical regression models might be equivalent to existing analytic models. This is especially likely for linear models, where fitting a regression

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model is equivalent to applying an analytic model whose parameters are allowed to float instead of being specified in advance. Regression, linear or otherwise, is a procedure to deduce by inversion the unknown parameters of the underlying model. The advantage of the analytic approach is that it gives life to the parameters that would otherwise be rather sterile (even if useful) quantities. Indeed, looking for the analytic equivalent of regression models is one way to increase the value of regression analyzes and the understanding that might be gained from them.

### 3. STATEMENT OF THE PROBLEM

We will assume that the goal is to estimate daily water column primary production. This is a problem in applied plant physiology and the calculation should be based on the fundamental physiological response, the photosynthesis–light curve [Steemann Nielsen and Hansen, 1961; Winter *et al.*, 1975].

At any depth  $z$  (positive downwards) and time  $t$ , the dependence of biomass-specific, primary production  $P^B(z)$  on photon flux or irradiance  $I$  can be written as

$$P^B(z, t) = p(I(z, t)), \quad (1)$$

where the superscript indicates normalization to the pigment biomass  $B$ , and the function  $p$  represents a family of curves whose general shape is known from experiments. A glossary of the mathematical notation used in this paper appears in the notation section. In the absence of photoinhibition, it is a function that requires no more than two parameters [Platt *et al.*, 1977, 1988], conventionally chosen to be the slope  $\alpha^B$  of  $p(I)$  near the origin (the initial slope), and the height  $P_m^B$  of the plateau (the assimilation number).

For generality, the parameters are also normalized to the pigment biomass, as indicated by the superscripts  $B$ . When an explicit function has been adopted for the family of curves  $p(I)$ , the dependence of photosynthesis on irradiance in any particular set of circumstances is determined once the parameter magnitudes appropriate to the circumstances are specified. Among the various possibilities available for two-parameter, photosynthesis–light curves,  $p(I)$ , the choice is not critical [Platt *et al.*, 1977] provided that the Michaelis-Menten equation is avoided: it saturates too slowly compared to typical data. The equation of Steele [1962] should also be avoided in this context, since, although it is only a two-parameter equation, it is intended to embrace photoinhibition and has no extended plateau of light-saturation.

To the extent that at least two parameters are required to define the photosynthesis–light curve, we expect that at least two parameters will be needed in a minimal description of daily water column primary production.

Let us designate the daily water column production as  $P_{Z,T}$ . To find it we have to evaluate the following double integral:

$$P_{Z,T} = \int_0^D \int_0^\infty B(z) P^B(z, t) dz dt \quad (2)$$

The upper limit of integration over depth is set to infinity, avoiding the need to specify the photic depth: contributions to the integral at this limit will vanish, given the exponential decay of irradiance with depth. The integration over time is through the light day, measured in hours from zero at sunrise to  $D$  at sunset. Our initial objective is to make a dimensional analysis to anticipate the general form of the solution to equation (2).

### 4. SOLUTION BY DIMENSIONAL ANALYSIS

The first-order determinants of primary production are irradiance and pigment concentration. To make the dimensional analysis then,

we suppose that the key variables controlling  $P_{Z,T}$  include a measure of the surface irradiance (say the value at local noon,  $I_0^m$ ), and the average, diffuse attenuation coefficient for photosynthetically active radiation,  $K$ . Together, these are sufficient to specify the irradiance field at all depths. Given irradiance, primary production will be determined by the normalized photosynthesis parameters  $\alpha^B$  and  $P_m^B$  and the autotrophic biomass  $B$ . The effect of second-order factors, such as temperature, nutrient concentration or photoadaptation, may be regarded as acting through their influence, either express or implied, on  $\alpha^B$  and  $P_m^B$ . We do not expect any length scale other than  $K^{-1}$  to appear in the solution: the justification is the same as that for setting the upper limit of integration over depth at infinity. On the other hand, we do expect a time scale to appear, represented by the day length  $D$ , since we are integrating a rate through time.

Thus, we anticipate that the solution to equation (2) will be a function of the variables  $B$ ,  $D$ ,  $I_0^m$ , and the parameters  $\alpha^B$  and  $P_m^B$ . The most general statement of this expectation is

$$P_{Z,T} \sim B^q (\alpha^B)^u (P_m^B)^v D^w (I_0^m)^x K^y, \quad (3)$$

where  $q$ ,  $u$ ,  $v$ ,  $w$ ,  $x$  and  $y$  are exponents that remain to be determined. Let us take the basic dimensional set for the problem to be  $[B]$ ,  $[C]$ ,  $[L]$ ,  $[T]$ , and  $[F]$ , respectively, the mass of pigment, the mass of carbon, length, time and photon flux. For dimensional consistency between the left- and right-hand sides of equation (3) we must then have

$$[CL^{-2}] = [BL^{-3}]^q [CB^{-1}T^{-1}F^{-1}]^u [CB^{-1}T^{-1}]^v [T]^w [F]^x [L^{-1}]^y, \quad (4)$$

or, collecting terms

$$[CL^{-2}] = [B]^{q-u-v} [C]^{u+v} [T]^{w-u-v} [F]^{x-u} [L]^{-3q-x}. \quad (5)$$

Matching exponents on either side of equation (5) leads to the following set of simultaneous equations:

$$\begin{aligned} 1 &= u + v \\ 0 &= q - u - v \\ 0 &= w - u - v \\ 0 &= x - u \\ -2 &= -3q - y. \end{aligned} \quad (6)$$

This set cannot be solved completely as the number of unknowns exceeds the number of equations (by one). If we choose  $x$  to be the indeterminate exponent, equation (6) implies  $q = 1$ ;  $y = -1$ ;  $w = 1$ ;  $u = x$ ; and  $v = 1 - x$ . We conclude therefore that the general form of the solution to equation (2) is

$$P_{Z,T} \sim \frac{B P_m^B D}{K} (I_0^m \alpha^B / P_m^B)^x. \quad (7)$$

The terms in parentheses on the right hand side form a dimensionless group whatever the value of  $x$ . From Buckingham's theorem [Pankhurst, 1964] we are led to expect one such dimensionless group for each undetermined exponent. It is conventional to rewrite statements such as equation (7) in the form

$$P_{Z,T} \sim \frac{B P_m^B D}{K} f(I_0^m \alpha^B / P_m^B), \quad (8)$$

where  $f$  is an undetermined function of the dimensionless group  $(I_0^m \alpha^B / P_m^B)$ .

Equation (8) is instructive. It implies that the quotient  $P_m^B / \alpha^B$  (which has the dimensions of irradiance and is called the photoadaptation parameter,  $I_k$ ) is the natural irradiance scale for the problem

under discussion. That is to say, we may generalize the analysis further by working in terms of a normalized irradiance  $I_*$  obtained by scaling irradiance to  $I_k$ . In other words, we define a dimensionless, surface irradiance at local noon as

$$I_*^m = I_0^m / I_k. \quad (9)$$

Equation (8) is then stated more generally as

$$P_{Z,T} \sim \frac{BP_m^B D}{K} f(I_*^m). \quad (10)$$

The elements  $(BP_m^B D/K)$  and  $f(I_*^m)$  may be regarded as separate parts of the solution to equation (2). The factor  $BP_m^B D/K$  is the scale factor for the solution. It has the same dimensions as daily water column production. The function  $f(I_*^m)$  is dimensionless and accounts for all the variability in  $P_{Z,T}$  due to variation in forcing. It may be tabulated, once and for all, over a suitable range of the normalized variable  $I_*^m$ . Observe that  $f(I_*^m) = P_{Z,T}$  when the scale factor is unity. Equation (10) is the most general and economical way to state the solution of equation (2): finding it is then equivalent to finding the function  $f(I_*^m)$ .

For equation (10), we regard  $D$  as a constant (actually, it is a parameter that can be determined exactly, for a given latitude and date, using standard astronomical methods),  $I_0^m$  and  $B$  as independent variables and  $P_m^B$  and  $\alpha^B$  (implicit in  $I_*^m$ ) as parameters. The status of  $K$  is less straightforward. It could be regarded either as a parameter (of Beer's law) to be specified, or as a quantity to be estimated from knowledge of the biomass. Note that two photosynthesis parameters are still required in this formulation, even though only one of them ( $P_m^B$ ) appears explicitly. The other ( $\alpha^B$ ) is buried in  $I_*^m$ .

### 5. ANALYTIC SOLUTION

Within the assumptions of the model (no spectral effects, biomass and photosynthesis parameters independent of depth, sinusoidal variation of surface irradiance through the day), an exact solution for  $f(I_*^m)$  was found by Platt *et al.* [1990] using the equation of Platt *et al.* [1980] for the photosynthesis–light curve  $p(I)$ . For computation, the solution can be expressed most simply as a truncated polynomial:

$$f(I_*^m) = \sum_{r=1}^X \Omega_r (I_*^m)^r. \quad (11)$$

It was found that setting  $X = 5$ , a fifth-order polynomial, was sufficient to ensure that  $f(I_*^m)$  was as good as error-free.

With  $f$  specified as in equation (11), the exact solution for  $P_{Z,T}$  may be represented as

$$P_{Z,T} = A \sum_{r=1}^5 \Omega_r (I_*^m)^r, \quad (12)$$

where the scale factor  $A = (P_m^B DB/K)$  and the weights,  $\Omega_r$  are known [Platt *et al.*, 1990]. (Note that in previous publications we have included a factor  $\pi$  in the denominator of the scale factor  $A$ . In this and future publications, we shall absorb the  $\pi$  into the weights  $\Omega_r$ . The numerical values of the weights will therefore change. The revised weights are given in Appendix A of this paper. We make this change in the definition of  $A$  to emphasize the correspondence between the solution from dimensional considerations and the analytic solution: the initial choice was an arbitrary one, and no material change in the solution is implied by the modification.)

The analytic solution of Platt *et al.* [1990] for  $P_{Z,T}$  and its simple representation, equation (12), may be taken as the benchmark solutions for the purposes of this paper. The weights  $\Omega_r$  need be determined only once for all time. That is, they may be regarded

as constants for the calculation. Notwithstanding that there are five weights, equation (12) is still an equation in only two parameters. In practice,  $f(I_*^m)$  can be tabulated (see Appendix A). Estimation of  $P_{Z,T}$  is then a simple matter of looking up the value of  $f$  for the appropriate value of  $I_*^m$  and multiplying by the appropriate value of the scale factor  $A$ .

The function  $f(I_*^m)$  contains information about the shape of the photosynthesis–light curve and the sinusoidal variation of surface irradiance through the day. It is easily generalized to the case of a water column of finite depth [Platt and Sathyendranath, 1991] and to conditions of photoinhibition [Platt *et al.*, 1990]. That  $f(I_*^m)$  describes a single curve does not contradict our earlier remark that an equation typically depicts a family of curves distinguished from each other by their parameter values: this economy is achieved by the dimensionless or scaled representation.

In the next section we consider a series of estimators for  $P_{Z,T}$ , based either on empiricism or on analysis under simplifying assumptions. We show how these approximators are related to the benchmark solution. We also recover and discuss the assumptions that underlie each of them.

### 6. ESTIMATORS OF $P_{Z,T}$ FOR UNIFORM BIOMASS PROFILES

A number of estimators exist for  $P_{Z,T}$  that apply specifically to the case of a uniform biomass profile. In this section, we describe the properties of these estimators. Further, by expressing them all in the common format

$$P_{Z,T} = A \times f(I_*^m), \quad (13)$$

which we may refer to as the canonical form, we can show how they relate to each other (Table 1) without invoking or accessing any field data. This method makes clear the assumptions, implied or expressed, associated with the use of each of the models. The general approach has its historical roots in Vollenweider [1965] and in Platt *et al.* [1977]. A more recent, useful reference is McBride [1992].

#### 6.1. Ryther [1956]

The method of Ryther [1956] is based on planimetry (for the integration over depth) of plots of daily primary production (calculated) as a function of optical depth ( $Kz$ ). The analogue of  $f(I_*^m)$  is then an empirical curve  $R_s(I_T)$  derived, by Ryther, from calculations on eight different days. Because its abscissa uses absolute irradiance (the total daily irradiance  $I_T$ ), it is less general than  $f(I_*^m)$ , which uses dimensionless irradiance.

Ryther's approach does not use a closed functional form for the dependence of photosynthesis on irradiance: instead, it relies on a graphical representation of photosynthesis, as a function of irradiance, derived from experiments on cultured phytoplankton showing strong photoinhibition (Figure 2 in Ryther's paper). In this plot, photosynthesis is expressed in relative units, from 0 to 1, where the normalisation factor is the observed production at light saturation,  $P_m^B B$ . In any particular application of the curve, it is rescaled using the magnitude of  $P_m^B B$  appropriate for the circumstances. This has the effect of ensuring that, for the hypothetical population described by Ryther,  $I_k$  is always constant, since any rescaling affects  $P_m^B$  and  $\alpha^B$  in the same way, such that their ratio is invariant. The refinement of the approach of Ryther and Yentsch [1957], where  $P_m^B$  is assumed to be a universal constant, therefore has the effect of also making  $\alpha^B$  into a universal constant. These assumptions were consistent enough with information available at that time, but are now known not to be robust.

Ryther calculated the function  $R_s(I_T)$  using the time course of surface irradiance at half-hourly intervals. For each time step, surface primary production can be estimated from the graphical photosynthesis–light curve. Next, the half-hourly estimates of sur-

TABLE 1. Comparison of Estimators for  $P_{Z,T}$  When the Biomass Profile is Uniform

Author	Definition	$f(I_*^m)$
Ryther [1956]	$P_{Z,T} = (P_m^B B/K) f(I_T)$	graphical
Ryther and Yentsch [1957]	$P_{Z,T} = (3.7 B/K) f(I_T)$	graphical
Talling [1957] (i)	$P_{Z,T} = (P_m^B B D/K) (\log_e(2I_*))$	$\log_e(I_*^m)$
Talling [1957] (ii)	$P_{Z,T} = 0.9(P_m^B B D/K) \log_e(2(I_*))$	$0.9 \log_e(4I_*^m/\pi)$
Rodhe [1965]	$P_{Z,T} = 2.3 P_m^B B D/K$	2.3
Platt [1986]	$P_{Z,T} = (4 P_m^B B D/(3\pi K)) I_*^m$	$4I_*^m/(3\pi)$
Platt <i>et al.</i> [1990]	$P_{Z,T} = (P_m^B B D/K) \sum_{x=1}^5 \Omega_x (I_*^m)^x$	$\sum_{x=1}^5 \Omega_x (I_*^m)^x$

For ease of comparison, all estimators are expressed in common form. The dimensionless functions  $f(I_*^m)$  arise in the formalism  $P_{Z,T} = A \times f(I_*^m)$ , where  $A = P_m^B B D/K$ . In the entries for Ryther [1956] and Ryther and Yentsch [1957],  $I_T$  is the total daily irradiance at the surface. The expressions for Talling's equations are as derived by Platt *et al.* [1990]. In the second of his equations, where the average of a logarithm is replaced by the logarithm of an average (easier to calculate for planimetric data), the factor 0.9 is an empirical correction determined by Talling himself. The quantity  $I_*$  is the instantaneous surface irradiance, normalized to  $I_k$ . The angle brackets indicate averaging with respect to time.

face production can be integrated through the day to give daily production. Primary production can also be estimated for any value of the optical depth  $Kz$ . Therefore a vertical profile of daily primary production can be drawn and integrated by planimeter to give daily water column production. The final step is to plot many such estimates of daily production (Ryther used eight) as a function of total daily irradiance to yield an analogue of  $f(I_*^m)$ , which can be used as the keystone of an algorithm to calculate daily production. Ryther called this curve  $R_s$ . It is based entirely on calculation using a universal photosynthesis–light relation: the result is therefore a smooth curve, as shown in Figure 1a (digitized by us from Ryther's paper).

Because the algorithm is based on a graphical construct, and since it uses absolute rather than dimensionless irradiance, it does not convert neatly and immediately into the canonical form, equation (13). However, a conversion is possible, as we now show. First, note that the Ryther protocol to calculate  $P_{Z,T}$  is

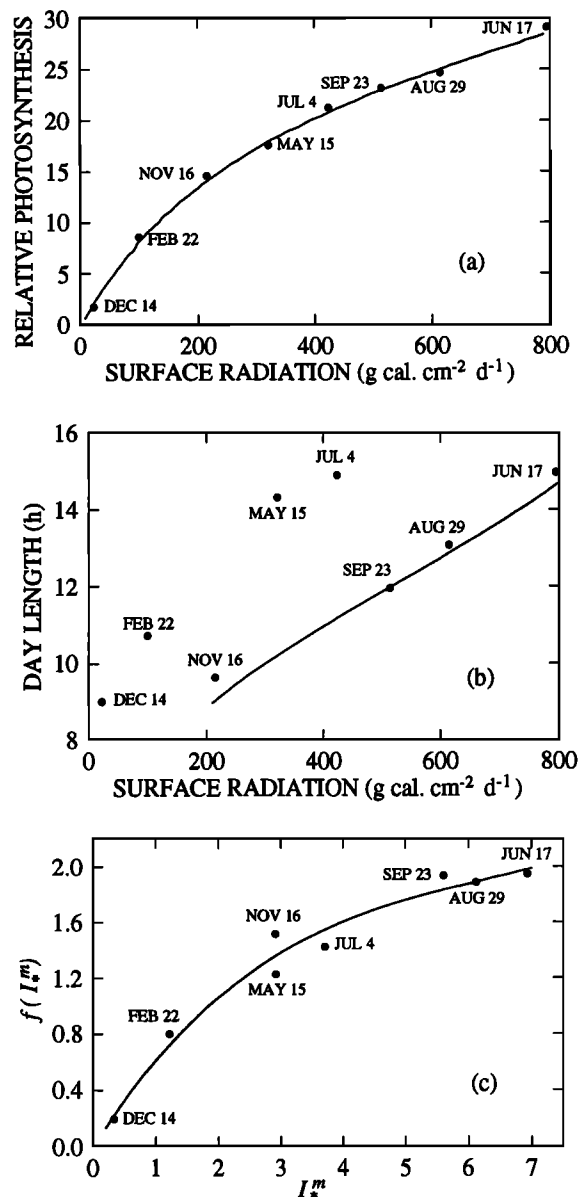
$$P_{Z,T} = (P_m^B B/K) R_s(I_T), \quad (14)$$

where the factor  $K$  arises in the denominator from his use of the dimensionless depth scale  $Kz$ , and where  $R_s$ , a function of the total daily irradiance  $I_T$ , is the daily (relative) photosynthesis for the water column. Here "relative" means that the absolute value is found after multiplication by the scale factor  $P_m^B B/K$ .

Comparing (13) and (14), we determine, after substitution for  $A$ ,

$$f(I_*^m) \sim D^{-1} R_s(I_T). \quad (15)$$

Fig. 1. The model of Ryther [1956] for estimating daily, water column production, and the transformation of the model to the canonical form. (a) The function  $R_s$  (relative photosynthesis), as a function of  $I_T$  (total, daily, shortwave radiation), and the eight data points on which the function is based. The curve, representing function  $R_s$ , and the data points are digitized from Figure 6 of Ryther's paper. (b) Plot of day length, computed for the same 8 days, as a function of the surface radiation ( $I_T$ ). The smooth curve is the clear-sky solution to daily, total, shortwave radiation at the sea surface, using the approach described by Platt *et al.* [1990]. Note that, for four out of eight data points, the observed radiation is less than the clear-sky computations, indicating the influence of clouds on these days. (c) The plot of Ryther's model in the canonical form, after transformation from Figure 1a, using information on day length, and with  $I_k = 55 \text{ W m}^{-2}$ . The initial estimates  $\hat{f}(I_*^m)$  corresponding to the same 8 days, as well as the third-order polynomial fitted to the data ( $f(I_*^m)$ ) are shown. The scatter in the data points is explained by breakdown of the simple sinusoidal model for variation of irradiance through the day when the cloud cover is not constant.



Before we can exploit this equivalence,  $f(I_*)$  and  $R_s(I_T)$  must both be expressed in terms of the same argument. Hence we adjust the argument of  $R_s$  to produce a new function  $R'_s(I_*)$ . Then  $\hat{f}(I_*)$ , the preliminary estimates of  $f(I_*)$ , are obtained from

$$\hat{f}(I_*) = D^{-1} R'_s(I_*). \quad (16)$$

To make the transformation, we note that, for a sinusoidal variation of surface irradiance through the day, the daily irradiance  $I_T = (2D/\pi)I_0^m$ . Therefore, if we multiply the irradiance scale of Figure 1a by the factor  $\pi/(2DI_k)$ , it will be expressed in terms of  $I_*$ . To implement the transformation, we must know the day length  $D$  that applies to each point in Figure 1a, and the value of  $I_k$ , assumed to be a universal constant. We must also ensure that  $I_0^m$  and  $I_k$  are in the same units. A final caution to users of Ryther's paper is that, although in one part of the paper he corrects the irradiance data for the photosynthetically active wave band, the abscissa in his Figure 6 clearly refers to total, shortwave irradiance, uncorrected for the visible part: the values are simply too high to be read as photosynthetically active radiation (Figure 1b; see also Table 2).

Because the photosynthesis–light curve is a graphical construct rather than an explicit formula,  $I_k$  cannot be found by an exact, objective procedure. Cullen [1990] determined it by inspection of Ryther's Figure 2 to be some 1400 foot candles of solar irradiance (units no longer in favor, but converted by Ryther on the assumption that  $1 \text{ g-cal cm}^{-2} \text{ min}^{-1} = 15500 \text{ foot candles}$ ). In our treatment of Ryther's model, we have used Cullen's value for  $I_k$ , equivalent to about  $55 \text{ W m}^{-2}$  in the units used here.

With  $I_k$  set at  $55 \text{ W m}^{-2}$  and  $P_m^B$  set at  $3.7 \text{ mg C (mg Chl)}^{-1} \text{ h}^{-1}$ , as by Ryther and Yentsch [1957], the corresponding value of  $\alpha^B$  is  $0.067 \text{ mg C (mg Chl)}^{-1} (\text{W m}^{-2})^{-1} \text{ h}^{-1}$ . Cullen [1990] observed that improved methodology for pigment determination since 1957 indicates that Ryther's pigment values should be decreased by some 30%. Thus both  $P_m^B$  and  $\alpha^B$  would be increased by 30%. Of course, the magnitude of  $I_k$  would remain unchanged.

We can find  $D$  by standard methods. Here, another complication arises. In the data presented by Ryther,  $I_T$  and  $D$ , contrary to expectation, are rather poorly correlated (Figure 1b). The reason is that Ryther used direct observations of  $I_0(t)$  rather than clear-sky calculations of it. On some of the days, the results will reflect the incidence of clouds, whereas other days will have been cloud-free. The effect of this difference is not seen in Figure 1a, which depicts total daily irradiance and the estimations of production calculated from it: the curve is therefore smooth.

However, when Figure 1a is recast in terms of  $I_*$ , the effect of clouds is seen (Figure 1c). When cloud cover is variable throughout the day, a simple, sinusoidal conversion between noon irradiance and total daily irradiance is no longer fully justified. Then the individual data points for  $f(I_*)$  do not lie on a smooth curve as they do in Figure 1a. But we can find the corresponding smooth curve by regression. We fitted a third-order polynomial with the following result (Figure 1c):

$$f(I_*) = 0.701I_*^m - 0.00954(I_*^m)^2 + 0.00512(I_*^m)^3. \quad (17)$$

This equation is plotted in Figure 2. Observe that it is not possible to draw the curve for values of  $I_*^m \gtrsim 7$ . This would require extending the relation given in equation (17) outside the range of its validity (see also Figure 1c). With a constant value of  $I_k$ , the upper limit of  $I_*^m$  that can be accommodated in  $f(I_*)$  is limited. Within the range for which it can be used, the Ryther curve is a reasonably good approximation to equation (11), the benchmark solution for  $f(I_*)$ , though not nearly as good as the approximation of Talling, to be discussed next. Indeed, it must be said that the representation of Ryther's method in Figure

TABLE 2. Construction of  $f(I_*^m)$  From Figure 6 of Ryther [1956]

$d$	$D$	$I_T$	$R_s$	$I_*^m$	$\hat{f}(I_*^m)$	$f(I_*^m)$
348	9.0	22.9	1.752	0.331	0.194	0.222
53	10.7	100	8.552	1.218	0.798	0.722
320	9.6	215	14.60	2.913	1.515	1.359
135	14.3	321	17.57	2.921	1.227	1.361
185	14.9	424	21.23	3.713	1.426	1.549
266	12.0	514	23.13	5.611	1.935	1.834
241	13.1	614	24.65	6.128	1.885	1.891
168	15.0	796	29.15	6.936	1.948	1.981

Ryther computed for eight different dates through the year, shown here as day numbers  $d$ . The corresponding day lengths  $D$ , in hours, are calculated from latitude ( $41.5^\circ \text{ N}$ ) and day number according to equations (14) and (15) of Platt *et al.* [1990]. The total daily radiation  $I_T$ , in  $\text{g cal cm}^{-2} \text{ d}^{-1}$ , was calculated by Ryther from planimetry of pyranometer records. The quantity  $R_s$  is Ryther's daily relative photosynthesis: it is dimensionless, but contains an implicit factor to convert the units from hourly rates to daily rates. The values of  $I_T$  and  $R_s$  in this table are digitized from Figure 6 of Ryther's paper. To obtain  $I_*^m$  from  $I_T$  we first multiplied by 0.45 to give the photosynthetically active radiation. Next, we converted the units to  $\text{W m}^{-2}$ . Then we assumed the usual sinusoidal variation of surface irradiance through the day [Platt *et al.*, 1990], such that  $I_0^m = \pi I_T / (2D)$ . Finally,  $I_*^m$  is computed through division of  $I_0^m$  by  $I_k$ , which was taken to be  $55 \text{ W m}^{-2}$ , as obtained by Cullen [1990] based on Figure 2 of Ryther's paper. To find  $\hat{f}(I_*^m)$ , the first estimate of  $f(I_*^m)$ , we used equation (16). The final values of  $f(I_*^m)$  were found by fitting a cubic equation (17) to the raw estimates  $\hat{f}(I_*^m)$ . Both  $\hat{f}(I_*^m)$  and  $f(I_*^m)$  are plotted in Figure 1c.

2 puts the method in its best possible light: recasting the model in terms of the dimensionless irradiance  $I_*^m$  overcomes the fundamental limitation of the original method, that it does not admit independent variation in the parameters of the photosynthesis–light curve.

We have examined Ryther's method at some length, motivated by a belief that it is often misunderstood. The steps by which it is converted to canonical form are summarized in Table 2.

## 6.2. Talling [1957]

Like that of Ryther, the method of Talling [1957] is also based on planimetry, but in this case the underlying photosynthesis–light curve is free from photoinhibition. Its relation to equation (12) was derived exactly in Platt *et al.* [1990, p. 105]. It is written in terms of  $I_*$ , the instantaneous surface irradiance, scaled to  $I_k$ . Clearly, this scaled irradiance is a variable, not a parameter.

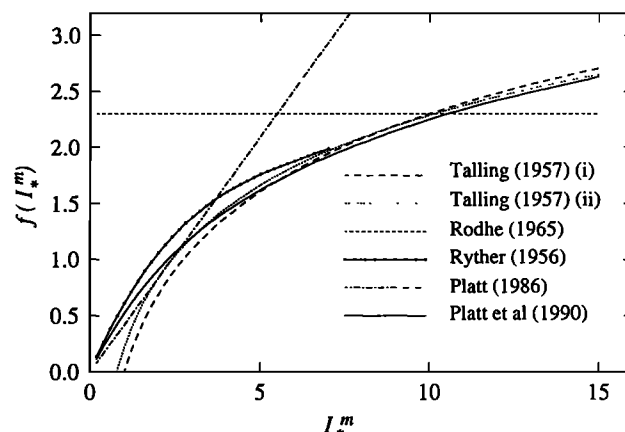


Fig. 2. Comparison of the five approximate solutions for daily, water column production, with the exact solution given by Platt *et al.* [1990]. The models of Ryther [1956], Talling [1957], Rodhe [1965] and Platt [1986] are shown. Note that the model of Ryther [1956] cannot be computed for  $I_*^m > 7$ . See also Table 1.

Talling's model can be stated as

$$P_{Z,T} = (P_m^B BD/K) \langle \log_e(2I_*) \rangle. \quad (18)$$

Here, and elsewhere in this paper, angle brackets denote the time average of the quantity inside them. Equation (18) implies [Platt *et al.*, 1990]

$$f(I_*^m) = \log_e(I_*^m). \quad (19)$$

To avoid the difficulty of averaging the logarithm of planimetric data in equation (18), Talling worked with the logarithm of the average irradiance and determined (empirically, by planimetry) a correction factor of 0.9 to compensate for the resultant bias. Platt *et al.* [1990] showed that this approach implied

$$f(I_*^m) = 0.9 \log_e(4I_*^m/\pi). \quad (20)$$

Note that the difficulty motivating this empirical correction disappears when equation (18) is expressed in canonical form with  $f(I_*^m)$  given by equation (19). Both equation (19) and equation (20) are plotted in Figure 2. They are in excellent agreement with the exact solution, except for very low values of  $I_*^m$ .

Talling worked with the attenuation coefficient for the most penetrating wavelength ( $K_{min}$ ). He recommended an empirical correction factor of 1.33 to be applied to  $K_{min}$ , to obtain  $K$ , the attenuation coefficient representative of total photosynthetically active radiation ( $K = 1.33 K_{min}$ ). Note that application of this factor 1.33 is unnecessary, and in fact is incorrect, if one is working with  $K$  estimated directly or indirectly from the distribution of visible light with depth.

### 6.3. Rodhe [1965]

The method of Rodhe [1965] is adapted directly from Talling [1957]. That is, its origins are in the planimetry of primary production profiles. It is based on the further assumption, for which he had some empirical evidence in his field data (from lakes), that the depth at which irradiance is  $I_k/2$  is found at the 10% light level [Rodhe, 1965]. The model was later applied by Bannister [1974], Smith and Baker [1978], Eppey *et al.* [1985] and Banse and Yong [1990].

We can present the basic argument as follows. With  $I_k/2 = 0.1 I_0$ , we have  $I_* = I_0/I_k = 5$ . Substitution into (18) yields

$$P_{Z,T} = (P_m^B BD/K) \langle \log_e(2 \times 5) \rangle = 2.3 P_m^B BD/K. \quad (21)$$

In this case,  $f$  is equivalent to a constant, 2.3. Rodhe's solution is also plotted in Figure 2.

A fundamental problem with Rodhe's method is that it treats  $I_k$  as a relative rather than an absolute quantity. This is the reason that the final result is independent of irradiance, dimensionless or otherwise. Rodhe realized this limitation of his method and cautioned against its use when  $I_k/2$  is not found at the 10% light level [Rodhe, 1965, p. 378].

### 6.4. Platt [1986]; Platt *et al.* [1988]

In an attempt to explain a large body of field data in which water column production, normalized to euphotic zone biomass, was found to be an apparent linear function of daily surface irradiance, Platt [1986] discussed an approximation to equation (8) based on the assumption of a linear photosynthesis–light curve. In this case the instantaneous water column production  $P_Z$  is given by (his equation (20))

$$P_Z = P_m I_*/K, \quad (22)$$

where  $I_*$  is the instantaneous surface irradiance normalized to  $I_k$  and  $P_m = B \times P_m^B$ . To convert to a daily rate, a forcing equal to

the average surface irradiance for the day was assumed. Then the solution for  $P_{Z,T}$  was found to be (his equation (28))

$$P_{Z,T} = 4 P_m^B DB I_*^m / (3 K \pi), \quad (23)$$

where the factor  $4/(3\pi) = 0.42$  arises from averaging a cubic-sine dependence for the variation of surface irradiance through the day. With this approximation (Figure 2), we have  $f = 4I_*^m/(3\pi)$ . A later analysis of alternative formulations for the time-dependence of surface irradiance [Platt *et al.*, 1990] indicated that a simple sine function was to be preferred. In this case the factor 0.42 would be replaced by  $2/\pi = 0.63$ . (Note that in the work by Platt *et al.* [1990] there is a misprint on p. 105 that should read  $2(I_*) = 1.27 I_*^m$  for the sine curve.) That is,

$$P_{Z,T} = 2 P_m^B DB I_*^m / (K \pi). \quad (24)$$

Hence for this approximation  $f$  is equivalent to  $2I_*^m/\pi$ . The model of Lewis *et al.* [1986] is identical in every respect to equations (23) and (24), except that it is not explicit about how to specify average daily irradiance.

Recognizing that a linear function was but a crude approximation to the photosynthesis–light curve, Platt [1986] calculated, in the same paper, the bias between equation (23) and the exact result computed using a nonlinear curve. The bias was a function of  $I_*^m$ . It is an indication of the extent to which  $0.42 I_*^m$  deviates from  $f(I_*^m)$ .

The problem still remained, however, to explain why so many field studies showed a linear relation between  $\Delta$ , daily water column production normalized to photic zone biomass, and daily irradiance. Platt *et al.* [1988] examined the analytic approximation further, showing how, at moderate to high irradiances, the weakly curvilinear variation of daily water column production as a function of dimensionless irradiance could be mistakenly interpreted as a linear variation with lower slope than predicted by equation (23). The interpretation also explained the often observed  $y$  intercept in such plots. We shall return to this theme later in the paper.

To summarize this section, two broad groups of approximations to equation (10) have been discussed. They are all based on the assumption that the autotrophic biomass is distributed uniformly with depth. One group is based on planimetry and has  $f$  approximated by various devices from a constant [Rodhe, 1965] through an empirical function of  $I_*$  [Talling, 1957] to a graphical construct [Ryther, 1956; Ryther and Yentsch, 1957]. These devices replace information about the curvilinear dependence of photosynthesis on light and the variation of irradiance throughout the day. A limitation of planimetric models is that it is not clear how one should proceed to adjust them when the observations do not fit the model. The other group [Platt, 1986; Lewis *et al.*, 1986; Platt *et al.*, 1988] is based on analysis and treats  $f$  as a linear function of  $I_*^m$ . Note that equation (17) of Platt [1986] is entirely equivalent to equation (23) above. All the solutions are shown together in Figure 2 for comparison with each other.

## 7. THE OBSERVED RANGE OF $I_*^m$

Implementation of any of the models discussed here requires that we calculate  $f(I_*^m)$ . Rodhe's model treats water column primary production as independent of day-to-day changes in surface light, and  $f(I_*^m)$  is constant. For the other models, we must know the value of  $I_*^m = I_0^m/I_k$ . In this section we examine the observed variability in surface irradiance and  $I_k$  to establish the range of variation of  $I_*^m$ . Unless stated otherwise, by "range" we mean the interval between the fifth and ninety-fifth percentiles of the data sets.

Beginning with  $I_k$ , we have examined the results of some 974 light-saturation experiments conducted in the North Atlantic, from the High Arctic to the oligotrophic central gyre (unpublished summary

of data collected on our own cruises). The range in  $I_k$  for individual experiments is from 7.7 to 89  $\text{W m}^{-2}$ . The median value is 35  $\text{W m}^{-2}$ , and there is a tendency for  $I_k$  to decrease as sample depth increases. If we consider only the surface layer, say from surface to 40 m, the range shifts to slightly higher values with a new median of 38  $\text{W m}^{-2}$ . The (full) range of the mean values for individual cruises is from 11 to 72  $\text{W m}^{-2}$ ; there is a general tendency for  $I_k$  to decrease with increasing latitude. That the realized range is narrow is partly to be accounted for by the observed tendency for  $\alpha^B$  and  $P_m^B$  to be positively correlated within cruises.

Dealing next with observed values of  $I_0^m$ , the numerator of  $I_*^m$ , it is clearly dependent upon latitude and season. In the data set under review,  $I_0^m$  (photosynthetically active radiation) is distributed in the range from 48 to 480  $\text{W m}^{-2}$ , close to the maximum expected value under a clear sky for any latitude and season, with a median of 365  $\text{W m}^{-2}$ .

The observed range of  $I_*^m$  is much less than would be expected from the ranges of its numerator and denominator. For individual samples, the range of  $I_*^m$  is from 3.4 to 27, with a median of 7.2, or, for the upper 40 m only, from 3.3 to 19, with a median of 7.6. If, instead of using the values of  $I_k$  at particular depths, we normalize  $I_0^m$  to the depth-averaged (surface to 40 m) value of  $I_k$  for the day in question, the range of  $I_*^m$  is further reduced (from 3.2 to 15) with a new median of 5.7.

Compression in the range of  $I_*^m$  is accounted for by a positive correlation between  $I_k$  and  $I_0^m$ . Indeed,  $I_k$  is known as the photoadaptation parameter, to indicate a belief that it is related to the light history of the phytoplankton. Using as a measure of light history the average of noon irradiance for the 3 days up to and including the day of the experiment, we have tested this belief for the results of some 122 light-saturation experiments over the same range of oceanographic regimes. For a given sampling day, we used the value of  $I_k$  averaged for samples taken from the top 40 m of the water column (Figure 3). It is clear that much of the variance in  $I_k$  (in fact, some 50%), can be explained by variations in surface light. The intercept is not significantly different from zero.

This empirical observation should be of considerable convenience for application of the algorithms for primary production: the numerator and the denominator of the dimensionless irradiance  $I_*^m$  are correlated. We can exploit the empirical relation between  $I_k$  and  $I_0^m$  to determine a nominal value for  $I_*^m$ . For this we use the 3-day average of  $I_0^m$ , rather than the value of  $I_0^m$  for the day in question, as the numerator for  $I_*^m$ . Then, with the slope of  $I_k$  on  $I_0^m = 0.176$  (Figure 3), we find  $I_*^m = 1/0.176 = 5.7$ , equal to the median value of  $I_*^m$  calculated from the depth-averaged values of  $I_k$ . Note that the single figure estimated for  $I_*^m$  by this method does not imply that  $I_*^m$  is a universal constant. Only 50% of the variance in  $I_k$  was explained by the three-day average of surface irradiance: considerably less of the variance (23%) in  $I_k$  is explained by the noon irradiance on the same day.

To summarize this section, we find that observations of  $I_*^m$  anywhere in the interval from 3 to 20 are possible, and that the typical value of  $I_*^m$  lies in the interval from 5 to 8. When applying any of the models discussed above, in a remote sensing context, for example, one should ensure the validity of the model for the required range of  $I_*^m$  (Figure 2). Clearly, linear models passing through the origin would be heavily biased over much of the range  $5 \leq I_*^m \leq 8$ , and the Ryther model is not defined at the high end of the range.

## 8. LINEAR APPROXIMATIONS TO THE EXACT SOLUTION

We have seen that the more realistic models of daily water column production are nonlinear functions of (scaled) surface irradiance. On the other hand, it has often been observed that field data on daily

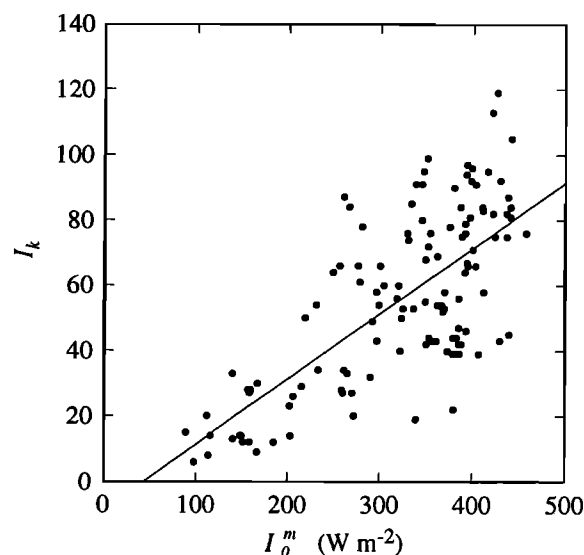


Fig. 3. Dependence of  $I_k$  on light history. The  $I_0^m$  values plotted are the 3-day averages for surface irradiance at local noon. The  $I_k$  values plotted are daily averages for the top 40 m. Compilation of data from Biological Oceanography Division, Bedford Institute of Oceanography.

production appear to show a linear dependence on surface light. In this section, we consider how these two statements can be reconciled. We begin with further analysis of the exact solution, equation (11), for the daily primary production of a uniformly mixed water column under broad-band illumination. The point of departure is that  $f(I_*^m)$  is only weakly curvilinear, especially in the range of  $I_*^m$  of expected ecological interest, as identified in the previous section. Most of the curvature in  $f(I_*^m)$  is near the origin, say in the range  $0 < I_*^m < 5$ . Beyond this range,  $f(I_*^m)$  is quasi-linear.

We propose to look for linear approximations to the exact solution, first for the extended range of  $I_*^m$  from 3 to 20, then for the restricted range from 5 to 8. We use an expanded version of the tabulation of  $f(I_*^m)$  by Platt *et al.* [1990], corrected for the factor  $\pi$ , which no longer appears in the definition of  $A$ , as mentioned above.

### 8.1. Extended range of $I_*^m$

For the wider range in observed values of  $I_*^m$ , the linear equivalent of the analytic solution to  $f(I_*^m)$  is

$$f(I_*^m) = 1.23 + 0.0910 I_*^m, \quad 3 \leq I_*^m \leq 20. \quad (25)$$

The error between this approximation and the exact solution for  $f(I_*^m)$  is shown in Figure 4a. In the interval  $5 \leq I_*^m \leq 19$ , the linear approximation is within 5% of the exact solution. Outside of this interval, however, the linear form departs rapidly from the exact solution, especially on the low side of the interval: it is in error by 25% at  $I_*^m = 3$ .

### 8.2. Restricted range of $I_*^m$

For the more commonly encountered range of  $I_*^m$ , the linear equivalent of the exact solution to  $f(I_*^m)$  is

$$f(I_*^m) = 0.940 + 0.0.139 I_*^m, \quad 5 \leq I_*^m \leq 8. \quad (26)$$

As Figure 4b shows, this approximation is never more than 1% in error anywhere in the restricted range of  $I_*^m$ .

### 8.3. Comparison with observations

The excellence of the linear approximation in the restricted range of  $I_*^m$  (Figure 4b), and the tolerable quality of the linear equivalent in the extended range of  $I_*^m$  (Figure 4a), help to explain the well-known

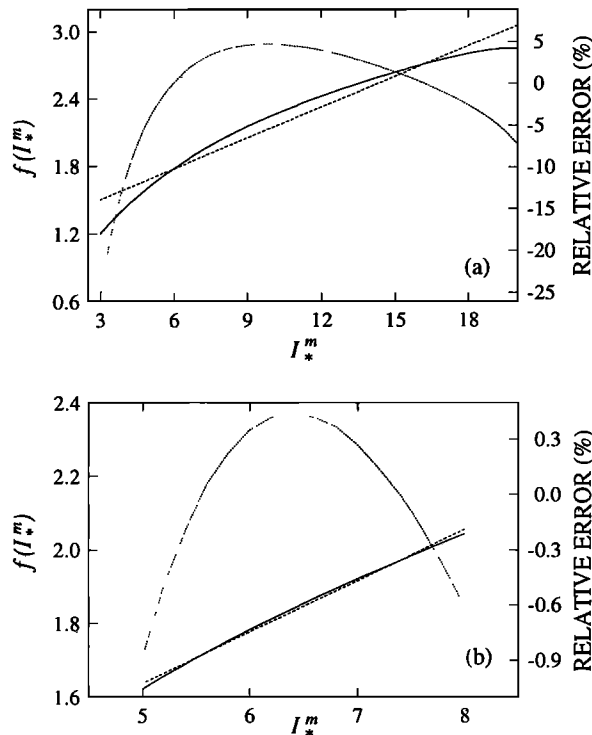


Fig. 4. Linear fits to the exact solution (a) for the range  $3 \leq I_*^m \leq 20$  and (b) for the more restricted range  $5 \leq I_*^m \leq 8$ . The fitted linear approximations are in dashed lines, the exact solution [Platt *et al.*, 1990] in solid curve, and the relative errors (percent) in broken curves. The solution of Talling (equation (20)) is also shown, in dots and dashes.

result that daily, water column, primary production normalized by photic zone biomass ( $\Lambda$ ), is a quasi-linear function of daily irradiance [Platt, 1986; Platt *et al.*, 1988, and references therein]. In such a plot, the commonly observed, positive intercept on the ordinate (which, taken at face value, would imply production at zero irradiance) is seen as a natural consequence of the linear approximation [Platt *et al.*, 1988].

We now show how this empirical result can be deduced from, and related to, equations (25) and (26). Moreover, we show that the coefficients of the linear regression of normalized daily production on daily irradiance can be used to estimate nominal values of  $\alpha^B$  and  $P_m^B$ , assumed to be constant across the data set under consideration.

In linear equations such as (25) and (26), approximations to the exact solution for  $f(I_*^m)$ , let  $c$  be the intercept and  $m$  be the slope. That is

$$f(I_*^m) = c + m I_*^m. \quad (27)$$

Now, use equation (13) to rewrite the left-hand side as  $P_{Z,T}/A$  and multiply both sides by  $I_k$  to give

$$P_{Z,T} P_m^B / (A \alpha^B) = c I_k + m I_0^m. \quad (28)$$

Next, substitute for  $A$  and multiply by  $\alpha^B$  to yield, quite generally,

$$K P_{Z,T} / (BD) = c P_m^B + m \alpha^B I_0^m. \quad (29)$$

We remark that a linear regression of  $K P_{Z,T} / (BD)$  on  $I_0^m$  would have slope  $m \alpha^B$  and intercept  $c P_m^B$ .

We now construct an expression for daily production normalized to photic zone biomass ( $\Lambda$ ), as a function of total daily irradiance. Taking photic depth to be  $4.6/K$ , the photic zone biomass is  $4.6B/K$ , and the normalized daily production is therefore  $\Lambda = P_{Z,T} K / (4.6B)$ .

We can recover this term through multiplication of equation (29) by the factor  $D/4.6$ . Thus

$$\Lambda = \frac{P_{Z,T} K}{4.6B} = \frac{c D P_m^B}{4.6} + \frac{m \alpha^B \pi}{2 \times 4.6} \left( \frac{2D}{\pi} \right) I_0^m, \quad (30)$$

where we have multiplied and divided the second term on the right by  $\pi$ , and where the factor  $(2D/\pi) I_0^m$  can be identified as the total daily irradiance, assuming sinusoidal variation through the day.

Therefore, in its linear range, a plot of daily production, normalized to photic zone biomass, against total daily irradiance, will have intercept  $c D P_m^B / 4.6$  and slope  $m \alpha^B \pi / 9.2$ . These are sufficient to estimate nominal values of the photosynthesis parameters, assumed to be constant across the data set. Note that the initial plot could just as well be made against  $I_0^m$ , perhaps more readily available than total daily irradiance. In this case the slope is  $m D \alpha^B / 4.6$ . Or, one could divide equation (30) by  $D$  throughout, and work in terms of average hourly rates instead of daily rates.

To follow this approach to estimation of the photosynthesis parameters, one would require measurements of daily production from dawn-to-dusk incubations. One would use values of  $c$  and  $m$  appropriate to the range of  $I_*^m$  covered by the data. This is essential as the procedure is sensitive to the magnitudes of  $c$  and  $m$  used, and they do vary with the range of  $I_*^m$ . Hence an iterative solution for  $\alpha^B$  and  $P_m^B$  may be necessary. Note that  $c$  and  $m$  depend only on the range of  $I_*^m$  prescribed.

There is overwhelming observational evidence that the slope of biomass-specific daily water column primary production to daily irradiance available at the surface ( $\psi = P_{Z,T} K / (4.6 B I_T) = \Lambda / I_T$ ) is stable over a broad range of  $I_*^m$  (many references given by Platt [1986] and Platt *et al.* [1988]; see also Cullen [1990]). In the compilation of Balch *et al.* [1992], the linear model of Platt [1986], presented by Balch *et al.* as the Lewis *et al.* [1986] model (recall that  $P_m^B = \alpha^B I_k$ ), accounts for 30% of the variance in measured primary production at 1171 stations. The theoretical support for this strong empirical evidence is the weak curvature of the exact solution for  $f(I_*^m)$ , as explained here [see also Platt *et al.*, 1988]. When this integral relationship appears to break down, as in Campbell and O'Reilly [1988] and Balch *et al.* [1989], it would be fruitful to investigate whether the basic assumptions of the model hold for the data set. For example, one would expect that the slope  $\psi$  would not be stable if the  $P - I$  parameters were not constant for the entire data set, or if the water column were not homogeneous.

If one decides to explore the relation between production and light at particular depths, it is important to bear in mind that none of the models discussed above would apply: they are designed to represent water column integrals. For discrete depths, one should revert to photosynthesis-light models, integrated over time if necessary, but not over depth.

The main objective of this section was to reconcile theoretical results with observational evidence that appears to support linear models for daily production. Given the simplicity of the exact, non-linear solutions now available, it could be argued that linear models have outlived their usefulness. Although there is some merit in this view, it ignores the requirement for knowledge of the photosynthesis parameters before the analytic solutions can be implemented. On the other hand, regression models such as equation (30), once established for a particular region, may be useful in the absence of explicit, empirical knowledge of the photosynthesis parameters.

## 9. MODELS FOR WATER COLUMN OF FINITE DEPTH

The models we have treated so far dealt with an infinitely deep water column, a mathematical device to ensure that the entire photic



zone was covered. It is often required to integrate primary production over a layer that is shallower than the photic depth. For example we frequently need production integrated through the surface mixed layer (depth  $Z_m$ , say). The integral to be evaluated is then the following

$$P_{Z,T} = \int_0^D \int_0^{Z_m} B(z) P^B(z, t) dz dt. \quad (31)$$

In this section we discuss how the basic models are affected by this change in the upper limit on the integration over depth.

### 9.1. Dimensional analysis

The dimensional analysis is more complex than for the infinite water column because another length scale is introduced, namely the thickness of the layer concerned,  $Z_m$ . Equation (3) should then be rewritten as

$$P_{Z,T} \sim B^q (\alpha^B)^u (P_m^B)^v D^w (I_0^m)^x K^s (Z_m)^s, \quad (32)$$

where  $s$  is a new exponent to be determined. Proceeding as before, the dimensional equation corresponding to equation (32) is

$$[CL^{-2}] = [B]^{q-u-v} [C]^{u+v} [T]^{w-u-v} [F]^{x-u} [L]^{-3q-1+s}. \quad (33)$$

The requirement of dimensional consistency leads to a set of simultaneous equations in the exponents

$$\begin{aligned} 1 &= u + v \\ 0 &= q - u - v \\ 0 &= w - u - v \\ 0 &= x - u \\ -2 &= -3q - y + s. \end{aligned} \quad (34)$$

We now have two fewer equations than we have unknowns, such that two of the exponents will remain undetermined. We choose one of these to be  $x$ , as before, and the other to be the new exponent  $s$ . The solutions are then  $q = 1$ ;  $y = s - 1$ ;  $w = 1$ ;  $u = x$ ; and  $v = 1 - x$ . Our general solution to equation (31) is therefore of the form

$$P_{Z,T} \sim \frac{B P_m^B D}{K} (I_0^m \alpha^B / P_m^B)^x (K Z_m)^s. \quad (35)$$

The product  $K Z_m$  is the second dimensionless group that we expect, from Buckingham's theorem, given the additional undetermined exponent. Products of depth and attenuation coefficient are known as optical depths:  $K Z_m$  is the optical depth of the mixed layer.

We can rewrite equation (35) in final form analogous to that of equation (10):

$$P_{Z,T} \sim A \times f(I_*^m) \times g(K Z_m), \quad (36)$$

where  $A$  is the same scale factor as before, carrying all the dimensions,  $f$  is the same function of  $I_*^m$  and  $g$  is a new function (of the mixed layer optical depth) to be determined.

### 9.2. General properties of analytic solutions

There is a clear relation between the analytic solutions for finite and infinite layers. One way to find this relation is to solve for a finite layer depth  $Z_m$  and then allow  $Z_m$  to tend to infinity. Another way is through the identity

$$\begin{aligned} P_{Z,T} &= \int_0^D \int_0^\infty P(z, t) dz dt \\ &= \int_0^D \int_0^{Z_m} P(z, t) dz dt + \int_0^D \int_{Z_m}^\infty P(z, t) dz dt. \end{aligned} \quad (37)$$

We can easily recover the solution for daily production  $P_{Z_m,T}$  in

the layer from surface to  $Z_m$ :

$$\begin{aligned} P_{Z_m,T} &= \int_0^D \int_0^{Z_m} P(z, t) dz dt \\ &= \int_0^D \int_0^\infty P(z, t) dz dt - \int_0^D \int_{Z_m}^\infty P(z, t) dz dt. \end{aligned} \quad (38)$$

Equation (38) may be interpreted as follows. To find the production in a layer from surface to  $Z_m$  we subtract, from the production in an infinite column forced with the surface irradiance, the production in another infinite column forced with an irradiance smaller by a factor  $e^{-K Z_m}$  than that at the surface (that is to say, forced with the irradiance at the top of a layer extending downwards from  $Z_m$ ).

In canonical form, this interpretation can be written, following equation (13) as

$$P_{Z_m,T} = A \times f(I_*^m) - A \times f(I_*^m e^{-K Z_m}). \quad (39)$$

In these terms, it is easy to see how equation (12) should be modified for a surface mixed layer [Platt and Sathyendranath, 1991]:

$$P_{Z_m,T} = A \sum_{r=1}^5 \Omega_r (I_*^m)^r - A \sum_{r=1}^5 \Omega_r (I_*^m e^{-K Z_m})^r. \quad (40)$$

The scale factor  $A$  remains unchanged as do the weights  $\Omega_r$ .

Neat as this procedure is for analytic solutions, it is potentially unworkable for some solutions based on planimetry. For example, in the second term on the right of equation (39) with Talling's model, it could easily happen that the forcing irradiance was sufficiently low that the integral would be undefined (see Figure 2 and see Platt *et al.* [1990]). When applied to Rodhe's model it will always return a zero answer, which clearly has no biological meaning. There is no difficulty to follow this approach with Ryther's model.

### 9.3. Evans and Parslow [1985]

In an attempt to find an analytic solution to the double integration for daily production in the mixed layer, Evans and Parslow [1985] simplified the time variation of surface irradiance through the day: rather than a sinusoid they adopted a triangular function (linear increase from sunrise to local noon, followed by a symmetrical decrease towards sunset). This approximation had been used earlier by Steele [1962].

Platt and Sathyendranath [1991] showed that a triangular irradiance function, with amplitude  $I_*^m$ , would always lead to an underestimate of daily production compared to the result obtained with a sinusoid. The bias could be up to 20%, decreasing with  $I_*^m$ .

However, Evans and Parslow [1985] made the further assumption that matching total daily irradiance was more important than matching the instantaneous irradiance. Hence they adjusted the maximum noon irradiance (upwards) such that the area under the triangle equalled the total daily irradiance, which was determined independently through standard astronomical calculations. In the notation used in this paper, the assumption is equivalent to scaling  $I_0^m$  by a factor  $4/\pi$ , an increase of some 27%. Let us call this adjusted noon irradiance  $J_*^m$ .

Evans and Parslow [1985] used the equation of Smith [1936] to represent the photosynthesis–light curve. Here, however, we illustrate their approach using the same photosynthesis–light curve that we employed to find the solution for the case of sinusoidal variation of irradiance, equation (40). With this form of the light response, the mixed layer daily production  $P_{Z_m,T}$  takes the form [Platt and Sathyendranath, 1991]:

$$P_{Z_m,T} = A \sum_{n=1}^{\infty} \frac{(-1)^{n+1}}{n(n+1)(n)!} (J_*^m)^n (1 - e^{-n K Z_m}). \quad (41)$$

Now we substitute for the adjusted noon irradiance  $J_*^m = 4I_*^m/\pi$  to conserve total daily irradiance for the simplifying case of a triangular variation of  $I_0(t)$  throughout the day. The daily production for the mixed layer under the assumptions of Evans and Parslow is then, in the notation of our paper,

$$P_{Z_m, T} = A \sum_{n=1}^{\infty} \frac{(-1)^{n+1}}{n(n+1)(n)!} \left(\frac{4}{\pi}\right)^n (I_*^m)^n (1 - e^{-nKZ_m}). \quad (42)$$

Observe that this solution is also useful for infinitely deep water columns if we let  $Z_m \rightarrow \infty$ , such that the exponential term on the right-hand side of equation (42) vanishes. Hence for the Evans and Parslow model applied to an infinite water column, we have

$$f(I_*^m) = \sum_{n=1}^{\infty} \frac{(-1)^{n+1}}{n(n+1)(n)!} \left(\frac{4}{\pi}\right)^n (I_*^m)^n. \quad (43)$$

This expression for  $f(I_*^m)$  is within about 2% of the solution given by Platt *et al.* [1990] throughout the range of  $I_*^m$ . Thus, adjusting  $I_*^m$  upwards to compensate for the smaller area of a right triangle compared with a sinusoid of the same amplitude is a successful device, and the underlying assumptions of Steele [1962] and Evans and Parslow [1985] are justified for the case of a triangular variation of irradiance through the day. However, it should not be assumed that any arbitrary function will suffice for the time variation of irradiance so long as the area under it is conserved. For example, a rectangular variation, equivalent to constant forcing with the daily averaged irradiance, leads to errors of about 7% for an infinite water column, and nearly 12% for shallow, finite layers [Platt *et al.*, 1991a].

One motivation for illustrating the Evans and Parslow method using the photosynthesis–light curve of Platt *et al.* [1980] is that it provides an opportunity to test the choice of function to describe time variation of irradiance without the added complication of alternative forms for the light-saturation curve. We have also compared the results from Evans and Parslow [1985] with those computed from equation (43), that is with two different photosynthesis–light curves each forced with an adjusted noon irradiance and a triangular variation of light through the day. We find that the two sets of results are within 5% of each other for most of the range of  $I_*^m$ , but that the difference increases to about 8% for  $I_*^m = 1$ .

#### 9.4. Daily production in an arbitrary, finite layer

It may be required to estimate the daily production in a layer that begins below the surface (say at some depth  $Z_1$ ) and ends shallower than the photic depth (say at some depth  $Z_2$ ).

A dimensional analysis will lead to the general result

$$P_{Z_1, Z_2, T} \sim A \times f(I_*^m) \times g(KZ_1) \times h(KZ_2), \quad (44)$$

where  $h(KZ_2)$  is a new dimensionless function to be determined. To find the exact solution, we proceed as before, noting that  $\int_{Z_1}^{Z_2} = \int_0^\infty - \int_0^{Z_1} - \int_{Z_2}^\infty$ . Using equation (39) to substitute for the integral from surface to  $Z_1$ , we find

$$P_{Z_1, Z_2, T} = A \times f(I_*^m e^{-K_1 Z_1}) - A \times f(I_*^m e^{-K_2 Z_2}), \quad (45)$$

where  $K_1$  and  $K_2$  are the attenuation coefficients for the first and second layers respectively. Observe that equation (45) would remain valid even if the magnitude of the scale factor  $A$  were different in the three layers. The value of  $A$  to be used in equation (45) is that value characteristic of the (middle) layer from  $Z_1$  to  $Z_2$ .

#### 9.5. Comparison of models: biomass profile uniform

It should be emphasized that all the models in Table 1 are predicated on the explicit assumption that the vertical distributions of pigment

biomass and other properties are homogeneous. Hence to avoid needless complication and misleading conclusions, it makes sense, in the first instance, to apply them to a set of data for which this condition is believed to be respected. Only when the models have been tested under the restrictions for which they were designed is it fair and useful to look into how they fail when these restrictions are relaxed. However, for the reasons given in the next subsection, when the models are applied to nonuniform profiles, we expect them all to fail in a strictly consistent way: the models stand in a constant and known relation to each other.

Among the models listed in Table 1, that of Rodhe [1965] contains no functional dependence of daily production on light. As can be seen in Figure 2, the only way that this model could work (and Rodhe acknowledged this) would be if  $I_*^m$  always took the constant value 10. We have shown that this is not the case. If we consider the typical ecological range of  $I_*^m$  to be from 3 to 20, and if we take the exact result as a yardstick, we find that the relative error in the Rodhe approximation is about 100% (overestimation) at  $I_*^m = 3$ , 42% at  $I_*^m = 5$ , 12% at  $I_*^m = 8$  and about 20% (underestimation) at  $I_*^m = 20$ .

The model Ryther [1956] cannot be recommended for interpretation of field data, as it employs a graphical construct developed from experiments with cultured phytoplankton. It is based on absolute irradiance rather than dimensionless irradiance, thereby losing in generality. It is based on a strongly photoinhibited photosynthesis–light curve. Using the methods presented here, it can be applied also to water columns of finite depth. In the original model,  $I_k$  is constrained always to take the same value. One consequence is that it can give no result for  $I_*^m \gtrsim 7$ . The related algorithm of Ryther and Yentsch [1957] suffers from the additional limitation that  $P_m^B$  is assumed to be a universal constant, which, since  $I_k$  is constant, implies that  $\alpha^B$  is also constant. The assumption of universal photosynthesis parameters is now known to be at variance with the facts. These comments are not intended to detract from the historical importance of Ryther's work: as expressed here in its most general, dimensionless form, and as discussed by Cullen [1990], it is a good estimator of daily production in the range of  $I_*^m$  for which it is valid.

Within the assumptions of the paper, the model of Platt *et al.* [1990] is exact. The approximate result of Platt [1986] is a tolerable approximation to it at low  $I_*^m$  (Figure 1), but not otherwise. This is because it uses a linear photosynthesis–light model passing through the origin: the resulting bias is a known and simple function of  $I_*^m$  [Platt, 1986]. Conversely, the models of Talling [1957] are excellent approximations to the exact result, except at very low  $I_*^m$  (Figure 2). As far as we know at present, the region of very low  $I_*^m$  is of minimal ecological interest (except for computation of primary production in a finite water column). Talling's models do not admit photoinhibition, and do not adapt well to cases where the depth of the water column is less than the photic depth.

To summarize this part, when compared against the benchmark, analytic solution, equation (12), the Talling model, is superior to (and less restrictive than) the Ryther model, which in turn is superior to (and less restrictive than) the Rodhe model. These conclusions are diametrically opposed to those given by Balch *et al.* [1992].

#### 9.6. Nonuniform biomass profiles and spectral effects

All of the models considered so far are based on the explicit assumption that biomass and other phytoplankton properties are uniform with depth. It is well known that seasonally, in many parts of the ocean, the assumption of uniform biomass profile does not accord with the facts. Platt *et al.* [1988] adopted a Gaussian, superimposed on a constant background, as a standardized biomass profile. Four parameters are required to specify it, or only three if the surface

biomass is prescribed from satellite data. This representation is capable of describing a wide variety of biomass profiles as observed in the field. With the standardized profile, it has not yet been possible to find an analytic solution for daily water column production. The problem of comparing estimators for nonuniform profiles is therefore more difficult. However, *Platt et al.* [1988] calculated the bias in  $P_{Z,T}$ , compared with the result for a uniform profile, as a function of dimensionless combinations of the parameters of the standardized profile.

As well as treating the biomass distribution as vertically uniform, the models discussed here also assume that the photosynthesis parameters are constant with depth. It is well known that, in a stratified water column, the photosynthesis parameters may become differentiated by depth according to the light history of the cells [*Harrison et al.*, 1982; *Platt et al.*, 1982; *Gallegos et al.*, 1983]. Conversely, where wind mixing acts to destroy stratification, photoadaptation by depth tends to break down [*Lewis et al.*, 1984]. To what extent can we use the photosynthesis parameters measured at discrete depths as representative of the entire water column, for the purposes of computing daily water column production?

*Harrison et al.* [1985] compared in situ estimates of primary production with those derived from calculation and concluded that the assumption of uniform parameters through the photic zone was adequate at most stations examined. Similar conclusions were reached by *Herman and Platt* [1986], who fitted vertical profiles of primary production based on both in situ and simulated in situ measurements to find the values of the photosynthesis parameters most representative of the water column as a whole.

Another approach, which has its roots in the work of *Sakshaug et al.* [1989] and *Cullen* [1990] is based on the proposition that if a photosynthesis–light curve were constructed from measurements made on phytoplankton assemblages, each one of which would be incubated at its respective growth irradiance, the resulting curve would be universal in form. We could consider this to be a photosynthesis–light curve for fully photoadaptive cells. This is a provocative idea that remains to be fully explored. However, if it proves to be robust, it will be of considerable importance as a basis for further developments in this field.

The models that have been discussed so far also ignore any effects due to the wavelength of the incident light, even though these are known to be of considerable importance in some circumstances. All other things being equal, a fully spectral calculation is to be preferred. But spectral computations are more time consuming than nonspectral ones, and the information required to do them may not always be available. Other advantages of using nonspectral calculations include the existence of analytic solutions and the insight that can be gained from them.

If one decides in favor of nonspectral calculations, however, it is as well to be aware of the potential errors involved. This issue has been treated by *Sathyendranath et al.* [1989], *Platt et al.* [1991b] and *Kyewalyanga et al.* [1992]. The general problems of minimizing the error in estimates of primary production arising from spectral effects, and of reducing the computation time for spectral calculations are treated by *Platt and Sathyendranath* [1991] and in *Anderson* [1993]. A detailed discussion is outside the scope of this paper.

#### 9.7. Random and systematic errors

When the algorithms for primary production of a uniform water column are written in canonical form (Table 1), we can see that they differ from each other in a predictable, systematic way. The relation of one to another can be expressed in closed form. We know exactly how the predictions of one will compare with those of another. Moreover, because they are expressed in terms of a dimensionless

variable, we know how the comparison will turn out even before we apply them to any data. Provided that the same parameters values, and the same values of the forcing variables, are used in each case (surely a prerequisite for any such comparison), it is automatic that the predictions of the various models will be in a fixed and known relation to each other. When the models are compared in the context of their application to data, provided that the same data are used in each case (surely another prerequisite for a useful comparison), the same relationships should be preserved. From the results of a test of one model, we ought to be able to tell how the other models would behave with the same bloc of data.

But a great deal can be learned without data. There is a sense in which it is both superfluous and premature to invoke any data set in the initial comparison of the models. It is an unnecessary complication that, by introducing random errors, obscures the absolute, systematic relationships between the different models. The conclusions reached in this paper concerning the relative performance of the uniform biomass models are quite opposed to those reached by *Balch et al.* [1992]. We believe that this difference arises from random measurement errors in the data base used by *Balch et al.* [1992], compounded by systematic errors due to uncritical pooling of many blocs of data without regard to their oceanographic provenance.

#### 9.8. The question of scale

The issue of scale also requires comment. Parameterizations intended for use in remote sensing should be developed in the context of the scale implied by the application. Thus the remotely sensed biomass has an intrinsic horizontal scale of, say 1 km, whereas the sea-truth biomass is typically measured at a single point. If these two measurements, made at two different scales, were used to test the biomass-retrieval algorithm, the results would be inconclusive, as it would be impossible to separate systematic errors in the algorithm from sampling errors due to spatial variability. Ideally, the ocean-color biomass and the sea-truth biomass should be measured at the same scale. Similar considerations apply to the testing of primary production algorithms. More specifically, if an algorithm has several elements, such as a submodel for surface irradiance, another for biomass, another for light penetration and another for photosynthesis, each with its own characteristic scale, the rigorous way to evaluate the uncertainty of the overall algorithm would be to test each at its own intrinsic scale, determine the associated error, then compound the errors according to a formal procedure.

#### 9.9. Implementation and testing of models

Implementation of the models discussed in this paper requires that we specify two photosynthesis parameters and the surface light field. We have shown that they can all be expressed in the same canonical form with the same parameters, demonstrating that they share the same level of complexity. The simple model of *Platt* [1986] and the ultrasimple one of *Rodhe* [1965] require less information to be input, but we have shown that their utility is limited.

To implement any model, it should be supplied with the best parameter estimates possible in the circumstances. One should not conclude that the models are inadequate if the problem lies with the allocation of the parameters. We have stated our views on this subject in a discussion of the extension of equation (12) to the case of a mixed layer of finite depth [*Platt and Sathyendranath*, 1991, p. 2591]:

...the reliability of the solutions themselves does not depend on how the parameters are specified. It is immaterial to the correctness or otherwise of these equations whether the photosynthesis parameters are assigned on the basis of a partition of the ocean into biogeochem-

ical provinces or on any other basis: this is altogether a different issue — that of *implementation*.

For example, it may be desired, or required, to calculate primary production on the basis of received wisdom concerning its dependence on environmental variables such as temperature. When we first introduced our formalism for description of the photosynthesis–light curve [Platt and Jassby 1976], a formalism which is now widely used, we stated our point of view (p. 422) that ‘... the effects [on primary production] of temperature, nutrients, [photo]adaptation and diurnal rhythms could be expressed through their influence on the parameters  $\alpha$ ,  $P_m^B$  and [respiration]  $R^B$ ’. We still adhere to this point of view. Nothing in the approach followed in the present paper would preclude its implementation. Specifically, if one believed that a universal function existed to compute assimilation number from temperature, the appropriate way to apply our solutions would be first, to use the temperature function to estimate  $P_m^B$ , then to use this value of  $P_m^B$  to calculate the scale factor  $A$ .

Given that one knows in advance how the results of different models should relate to one another when they are all applied to the same data sets, there is a lesson to be learned if the results do not unfold as expected. For example, if the Rodhe model appears to explain more of the variance in the observations than the Talling model, whereas the Talling model is so clearly the superior of the two, it is a strong indication either that the data have been incorrectly pooled or that the parameters have been incorrectly assigned to the models, or both.

Indeed, provided that the models are applied in conditions for which they were designed, their performance should be a good guide to how large blocs of data should be stratified. But this insight will not be achieved, for example, if models designed for deep ocean conditions are applied indiscriminately to coastal water, or if vertically uniform models are used without thought for nonuniform profiles.

Implementation of nonuniform models calls for additional inputs over and above those required for uniform models: the biomass should be specified as a function of depth either by direct measurements or in terms of the parameters that define the vertical structure in the biomass field. On the other hand, in the implementation of Platt and Sathyendranath [1988], a spectral model can be implemented using the same inputs as those needed for a nonspectral model. Since the shape of the action spectrum is assumed to be invariable, only nonspectral photosynthetic parameters are needed for the spectral model. Similarly, the shape of the absorption spectrum is held constant, permitting a spectral light attenuation to be computed from biomass  $B$ . From this point of view, a minimal spectral model is no more difficult to implement (requires no more inputs) than a nonspectral model.

Within oceanic regimes, or provinces, we can expect that any of the models will show both systematic and random errors with respect to the data even if the data have been perfectly pooled. When data from different provinces are combined for a joint test of goodness of fit, neither the systematic errors nor the parameters will be homogeneous through the data set under test. The performance of the model will inevitably be degraded and a spurious conclusion will be reached about its value. Thus useful models may be rejected for unsound reasons, or inadequate models may be unjustly preferred. Large data sets have much to teach us about the way the ocean should be partitioned for analysis and how the relevant processes should be parameterized. But they can lead to misunderstanding, rather than enlightenment, if they are not handled with care.

## 10. RECOMMENDATIONS

It is recommended, for maximum generality, to work in terms of the dimensionless irradiance  $I_*^m$ . It may be the case that, instead of the noon irradiance  $I_0^m$  being computed, the total daily irradiance  $I_T$  is prescribed from satellite data, for example, according to the procedure of Bishop and Rossow [1991]. Then it is a simple matter to convert between them using the identity  $I_0^m = \pi I_T / (2D)$ .

A hierarchy of algorithms exists for computation of primary production according to the level of detail required and the computation time that can be spared. Of the empirical estimators of daily primary production in a vertically uniform water column, the best is that of Talling [1957]. However, the analytic solution [Platt et al., 1990] is just as efficient to compute and generalizes easily to cover photoinhibition and shallow water columns: it is recommended.

At the next level of complexity, spectral effects have to be taken into account. Specific recommendations on computationally-efficient ways to treat spectral effects are given by Platt and Sathyendranath [1991] and by Anderson [1993]. No exact solution has yet been found for the primary production of a nonuniform water column. Numerical solutions according to the procedure of Platt and Sathyendranath [1988] are recommended if computation time is not a limitation. Otherwise the short cuts presented by Platt and Sathyendranath [1991] or Anderson [1993] are advised.

It is important to distinguish at all times between model structure and model parameterization. Large data bases, such as that compiled by Balch et al. [1992] are more suited to testing methods of assigning parameters to models than to comparing the models themselves, which can often be achieved more readily without data or with fabricated data. When testing different ways of assigning parameters, it is essential to use the same set of data for all sides of the test.

For future field work in support of ocean color applications to primary production, as much, or more, effort should be directed at measuring the parameters controlling the flux of interest than the flux itself [Platt et al., 1992]. Emphasizing the central role of the parameters can lead to the development of useful relations, such as the one between  $I_k$  and the 3-day average of  $I_0^m$  presented above, that will facilitate implementation of the remote sensing algorithms. Progress in remote sensing of primary production is limited not by lack of measurements of primary production but by our knowledge of the distribution, over regions and seasons, of the principal parameters that control production.

## APPENDIX A: TABULATION OF $f(I_*^m)$

The values of  $f(I_*^m)$  from the analytic solution to equation (2) were tabulated by Platt et al. [1990] for the range  $0.2 \leq I_*^m \leq 15$ . In this appendix, we retabulate the function, first to cover a wider interval for the argument  $0.2 \leq I_*^m \leq 20$ , consistent with the findings above on the range of  $I_*^m$  observed in the field; and second because the values have changed as a consequence of the new definition of the scale factor  $A$  (see equation (12)): the new values are lower by a factor  $\pi$  than the old ones. The revised values of  $f(I_*^m)$  are given in Table A1.

Because of the change in the magnitudes of  $f(I_*^m)$ , we must also recompute the weights  $\Omega_x$  in equation (11). Because they are the coefficients of a truncated polynomial approximation, they also depend on the range of the argument  $I_*^m$  over which they are computed. Table A2 shows the new weights for the range  $0.2 \leq I_*^m \leq 20$ .

As discussed in Platt et al. [1990], the relative residual errors associated with the truncated polynomial approximation were highest near the origin. Therefore we have also computed the weights for the restricted range  $1.6 \leq I_*^m \leq 20$ . This range includes the interval of most ecological interest, at the same time excluding the interval

TABLE A1. Tabulation of the Dimensionless Function  $f(I_m^*)$ 

$I_m^*$	$f(I_m^*)$
0.2	0.123
0.4	0.236
0.6	0.342
0.8	0.440
1.0	0.532
1.2	0.618
1.4	0.699
1.6	0.774
1.8	0.846
2.0	0.914
2.2	0.978
2.4	1.038
2.6	1.096
2.8	1.151
3.0	1.204
3.2	1.254
3.4	1.301
3.6	1.347
3.8	1.391
4.0	1.434
4.2	1.474
4.4	1.513
4.6	1.551
4.8	1.588
5.0	1.623
5.2	1.657
5.4	1.690
5.6	1.722
5.8	1.753
6.0	1.783
6.2	1.812
6.4	1.841
6.6	1.868
6.8	1.895
7.0	1.922
7.2	1.947
7.4	1.972
7.6	1.997
7.8	2.020
8.0	2.044
8.2	2.066
8.4	2.088
8.6	2.110
8.8	2.132
9.0	2.152
9.2	2.173
9.4	2.193
9.6	2.212
9.8	2.232
10.0	2.251
10.2	2.269
10.4	2.287
10.6	2.305
10.8	2.323
11.0	2.340
11.2	2.357
11.4	2.374
11.6	2.390
11.8	2.406
12.0	2.422
12.2	2.438
12.4	2.453
12.6	2.468
12.8	2.483
13.0	2.498
13.2	2.513
13.4	2.527
13.6	2.541

TABLE A1. (continued)

$I_m^*$	$f(I_m^*)$
13.8	2.555
14.0	2.569
14.2	2.582
14.4	2.596
14.6	2.609
14.8	2.622
15.0	2.635
15.2	2.647
15.4	2.660
15.6	2.672
15.8	2.684
16.0	2.696
16.2	2.708
16.4	2.720
16.6	2.732
16.8	2.743
17.0	2.755
17.2	2.766
17.4	2.777
17.6	2.788
17.8	2.799
18.0	2.810
18.2	2.821
18.4	2.831
18.6	2.841
18.8	2.852
19.0	2.862
19.2	2.872
19.4	2.882
19.6	2.892
19.8	2.902
20.0	2.912

Note that daily production can be computed from  $P_{Z,T} = Af(I_m^*)$ , where  $A = BP_m^B D/K$ .

TABLE A2. Coefficients and Relative Error for Polynomial Approximations to Analytic Solution for  $P_{Z,T}$ 

$x$	$\Omega_x$ for $0.2 \leq I_m^* \leq 20$	$\Omega_x$ for $1.6 \leq I_m^* \leq 20$
1	$6.1035 \times 10^{-1}$	$5.8661 \times 10^{-1}$
2	$-8.9251 \times 10^{-2}$	$-7.8647 \times 10^{-2}$
3	$8.1477 \times 10^{-3}$	$6.6063 \times 10^{-3}$
4	$-3.7427 \times 10^{-4}$	$-2.8402 \times 10^{-4}$
5	$6.6103 \times 10^{-6}$	$4.7670 \times 10^{-6}$
Relative error	$3.2186 \times 10^{-2}$	$1.5491 \times 10^{-2}$

Note that  $P_{Z,T} \approx A \sum_{x=1}^5 \Omega_x (I_m^*)^x$ . Relative error is the maximum over the specified interval. Coefficients are from weighted least-squares regression on the intervals  $0.2 \leq I_m^* \leq 20$  and  $1.6 \leq I_m^* \leq 20$ .

of largest residual variance, and gives an estimator for  $f(I_m^*)$  with very low error throughout the range. These weights are also given in Table A2. The distribution of residual errors for the polynomial approximations is shown in Figure A1.

The user can decide which is the more appropriate set of weights to choose for any particular application. We recommend that, in general, the weights for the range  $1.6 \leq I_m^* \leq 20$  be used, but that in cases where extremely low surface light is encountered the weights for the wider range  $0.2 \leq I_m^* \leq 20$  be used. Examples of such applications would be in high latitudes during winter, or in cases where the production for a finite layer is to be found by subtraction of integrals as in equations (39) and (45).

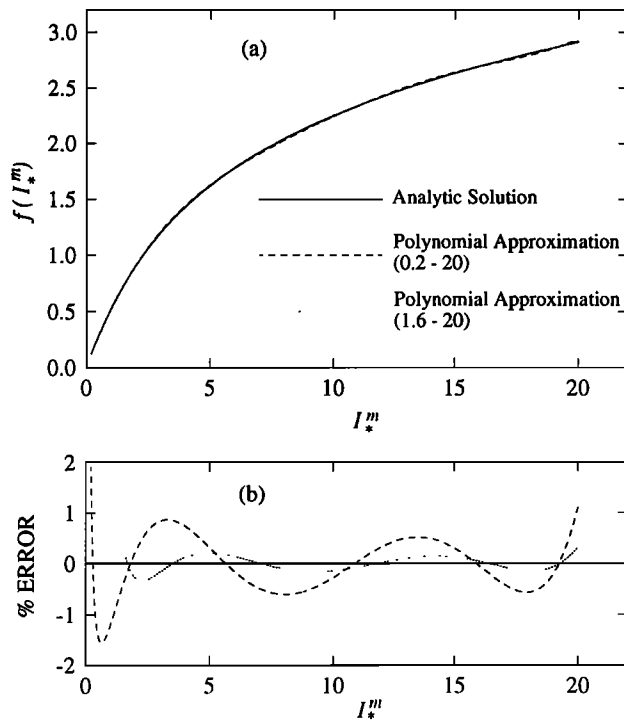


Fig. A1. (a) The function  $f(I_*^m)$  calculated from the analytic solution for the range  $0.2 \leq I_*^m \leq 20$ , and the fifth-order polynomial approximations for the full range of  $I_*^m$  and for the restricted range  $1.6 \leq I_*^m \leq 20$ . Note that  $P_{Z,T} = f(I_*^m)$  when  $A = 1$ . (b) Distribution of relative errors as function of  $I_*^m$  for the polynomial approximators shown in Figure A1a.

#### NOTATION

- $\alpha$  initial slope of  $P$ - $I$  curve, defined as  $\partial P / \partial I|_{I \rightarrow 0}$ ,  $\text{mg C h}^{-1} (\text{W m}^{-2})^{-1}$ .
- $\alpha^B$  initial slope of  $P^B$ - $I$  curve, defined as  $\partial P^B / \partial I|_{I \rightarrow 0}$ ,  $\text{mg C (mg Chl)}^{-1} \text{h}^{-1} (\text{W m}^{-2})^{-1}$ .
- $\Lambda$  daily, water column production normalized to photic zone biomass,  $\text{mg C (mg Chl)}^{-1}$ .
- $\psi$  the quotient  $\psi = \Lambda / I_T$ ,  $\text{mg C (mg Chl)}^{-1} \text{d}^{-1} (\text{W m}^{-2})^{-1}$ .
- $\Omega_T$  weights of polynomial approximation to compute  $P_{Z,T}$ , see equation (12), dimensionless.
- $A$  scale factor,  $A \equiv (B D P_m^B) / K$ , see equation (12),  $\text{mg C m}^{-2}$ .
- $B$  biomass, as concentration of chlorophyll  $a$ ,  $\text{mg Chl m}^{-3}$ .
- [B] dimension of pigment biomass, independent of units.
- $c$  intercept of linear approximation to  $f(I_*^m)$ , see equation (27), dimensionless.
- [C] dimension of carbon biomass, independent of units.
- $D$  day length, hours.
- $f$  function of  $I_*^m$  arising in dimensional analysis and in canonical form, of solution for daily primary production, dimensionless.
- $\hat{f}$  preliminary estimate of  $f$ , before smoothing, as inferred from Ryther's data, dimensionless.
- [F] dimension of photon flux, independent of units.
- $g$  function of  $KZ_m$  or  $KZ_1$  arising in dimensional analysis for finite layer, dimensionless.

- $h$  function of  $KZ_2$  arising in dimensional analysis for finite layer, dimensionless.
- $I$  irradiance in the photosynthetically active range (PAR),  $\text{W m}^{-2}$ .
- $I_*$  dimensionless surface irradiance,  $I_*(t) \equiv I_0(t) / I_k$ .
- $\langle I_* \rangle$  dimensionless irradiance at surface averaged over light day.
- $I_*^m$  dimensionless irradiance at local noon,  $I_*^m \equiv I_0^m / I_k$ .
- $I_0$  irradiance at the surface ( $z = 0$ ),  $\text{W m}^{-2}$ .
- $I_0(t)$  time variation of surface irradiance through the day,  $\text{W m}^{-2}$ .
- $I_0^m$  maximum surface irradiance at local noon,  $\text{W m}^{-2}$ .
- $I_k$  adaptation parameter of the  $P$ - $I$  curve,  $I_k \equiv P_m^B / \alpha^B \equiv P_m / \alpha$ ,  $\text{W m}^{-2}$ .
- $I_T$  total daily irradiance at the surface,  $\text{W m}^{-2}$ .
- $J_*^m$  the adjusted, dimensionless, noon irradiance when a triangular variation is assumed for  $I_0(t)$  and when the area under the triangle is adjusted to match  $I_T$ .
- $K$  vertical attenuation coefficient for irradiance,  $K = -I^{-1}(dI/dz)$ ,  $\text{m}^{-1}$ .
- $K_{min}$  vertical attenuation coefficient for the most penetrating wavelength in the irradiance field,  $\text{m}^{-1}$ .
- [L] dimension of length, independent of units.
- $m$  slope of the linear approximation to  $f(I_*^m)$ , see equation (27), dimensionless.
- $p(I)$  generic functional form of the photosynthesis-light curve,  $\text{mg C m}^{-3} \text{h}^{-1}$ .
- $P$  primary production rate per unit volume,  $\text{mg C m}^{-3} \text{h}^{-1}$ .
- $P^B$  primary production rate normalized to biomass,  $P^B \equiv P / B$ ,  $\text{mg C (mg Chl)}^{-1} \text{h}^{-1}$ .
- $P_m^B$  assimilation number, specific production at saturating light, in the absence of photoinhibition,  $P_m^B = P^B|_{I \rightarrow \infty}$ ,  $\text{mg C (mg Chl)}^{-1} \text{h}^{-1}$ .
- $P_m$  primary production (maximum) at saturating light,  $P_m \equiv B P_m^B$ ,  $\text{mg C m}^{-3} \text{h}^{-1}$ .
- $P_{Z,T}$  daily primary production for the water column,  $\text{mg C m}^{-2}$ .
- $P_{Z_m,T}$  daily primary production for the mixed layer,  $\text{mg C m}^{-2}$ .
- $P_{Z_1,Z_2,T}$  daily primary production for a layer between  $Z_1$  and  $Z_2$ ,  $\text{mg C m}^{-2}$ .
- $q$  exponent to be determined in dimensional analysis, dimensionless.
- $R_s(I_T)$  daily, relative photosynthesis for the water column, as computed by Ryther, dimensionless.
- $R'_s(I_*^m)$   $R_s(I_T)$ , with argument transformed to dimensionless irradiance.
- $s$  exponent to be determined in dimensional analysis, dimensionless.
- $t$  time, hours.
- [T] dimension of time, independent of units.
- $u$  exponent to be determined in dimensional analysis, dimensionless.
- $v$  exponent to be determined in dimensional analysis, dimensionless.

- $w$  exponent to be determined in dimensional analysis, dimensionless.
- $x$  exponent to be determined in dimensional analysis, dimensionless.
- $y$  exponent to be determined in dimensional analysis, dimensionless.
- $z$  depth, m.
- $Z_1$  an arbitrary depth, m.
- $Z_2$  an arbitrary depth,  $Z_2 > Z_1$ , m.
- $Z_m$  depth of the mixed layer, m.

Note that any quantity (such as primary production) described as a rate will contain the dimension  $[T^{-1}]$ . However, when the same quantity is qualified by the adjective "daily", it will not contain the dimension  $[T^{-1}]$  because the rate has been integrated through time to get the daily total. When the term "daily rate" is encountered, care should be taken to see what dimensions are implied by the author.

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