On models of growth and photosynthesis in phytoplankton

John J. Cullen[*]

Abstract—A model of the growth of a marine diatom (Sakshaug *et al.*, 1989, *Limnology and Oceanography*, **34**, 198–205) is examined. One equation describes the relationship between chemical composition and growth rate as a function of irradiance and daylength. It is valid for both nutrient-limited and nutrient-saturated growth. The model equation is rearranged to describe photosynthesis normalized to chlorophyll. The new equation is essentially the same as several other models. Its mechanistic basis is the variation of quantum yield as a function of the number of excess photons absorbed by a photosynthetic unit during the time it takes to process one photon. The mechanistic interpretation of the model could be deceptive because the general equation describes a composite response and does not represent any one growth state. Nonetheless, the reformulated equation is important because it shows that at a given temperature, the *adapted* rate of photosynthesis normalized to chlorophyll is a function solely of growth irradiance. The equation can be used to describe primary production in the sea as a function of insolation and chlorophyll in the water column. For comparison, the model of Ryther and Yentsch (1957, *Limnology and Oceanography*, **2**, 281–286) is modified and found to fit observations as well or better than other formulations. Some data sets are not at all consistent with general models, however. Discrepancies may be due to taxonomic differences, temperature and vertical structure of phytoplankton biomass. It is also possible that changes in the photosynthesis–irradiance relationship associated with unbalanced growth are extremely important in determining primary production in perturbed environments.

INTRODUCTION

More than 30 years ago, Ryther (1956) used experimental data to describe the photosynthesis of phytoplankton as a function of irradiance. His generalized model was used to develop a method for estimating primary production in the ocean from the chlorophyll content of the water, incident solar radiation, and the extinction coefficient of visible light in the water column (Ryther and Yentsch, 1957). Subsequently, numerous studies demonstrated that the photosynthetic characteristics of phytoplankton could vary greatly by depth, region, season and with growth conditions (e.g. Curl and Small, 1965; Glover, 1980; Falkowski, 1981; Welschmeyer and Lorenzen, 1981; Richardson *et al.*, 1983; Harrison *et al.*, 1985; Kana and Glibert, 1987b). It was therefore easy to conclude that a general model of photosynthesis for marine phytoplankton was too much of an oversimplification to be useful. More precise but less general experimental methods are now used to estimate productivity from observed distributions of chlorophyll and light (Harrison *et al.*, 1985).

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[*] Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, ME 04575, U.S.A.

Recent developments in remote sensing have stimulated renewed interest in models of productivity as a function of irradiance and chlorophyll. Empirical (e.g. EPPLEY et al., 1985) and theoretical (e.g. COLLINS et al., 1986; PLATT, 1986) models have been developed, and refinements are being made continually (PLATT et al., 1988; PLATT and SATHYENDRA-NATH, 1988; BALCH et al., 1989). In this paper, I examine new experimental data (SAKSHAUG et al., 1989) in the context of general models of photosynthesis for phytoplankton. The data show that at a given temperature, the *adapted* rate of photosynthesis normalized to chlorophyll is a function solely of growth irradiance. General models of photosynthesis as a function of irradiance should therefore be valid if phytoplankton in the ocean are well adapted to conditions at the depth of sampling. As an example, the general model of RYTHER and YENTSCH (1957) is revived and modified. It compares well with recent efforts to describe primary productivity in the sea. In some environments, though, such simple models explain little of the variability in primary productivity.

BACKGROUND: A MODEL OF PHYTOPLANKTON GROWTH

SAKSHAUG et al. (1989) modeled the growth of a marine diatom with an equation that encompassed variable daylength as well as irradiance. It was intended to describe nutrient-limited as well as nutrient-saturated growth. An extensive set of data on growth rates at 15°C under different light and nutrient regimes was used for validation. Growth rate is related to cellular light absorption as follows:

$$(\mu + r) = \frac{Chl}{C} \cdot D \cdot I_o \cdot a_p \cdot \phi_{max} \cdot \frac{1 - e^{(-\sigma\tau I_o)}}{\sigma\tau I_o}. \tag{1}$$

The gross growth rate $(\mu + r)$ is the sum of specific growth rate and the specific rate of respiration (s^{-1}). For validation of the model, the rate of respiration is assumed to be 12% of the observed growth rate. The ratio of cellular chlorophyll to carbon [mol Chl (mol C)$^{-1}$], the specific absorption coefficient of chlorophyll a [a_p, m^2 (mol Chl)$^{-1}$], and ϕ_{max}, the maximum quantum yield [mol C (mol photons)$^{-1}$] are common terms in earlier models. Daylength, D, is the illuminated period as a fraction of the day (dimensionless) and I_o is quantum scalar irradiance (mol m^{-2} s^{-1}), assumed to be constant over the light period (Sakshaug et al. used the symbol E_o). The mean absorption cross-section of the photosynthetic unit (PSU) is σ [m^2 (mol PSU)$^{-1}$]. The minimum turnover time of the rate-limiting photosystem is τ (s). The model considers only photosynthetically active radiation. The units presented here (Table 1) differ slightly from the original presentation so that parameters from different models can be compared.

The model is an energy budget (GEIDER et al., 1986) modified from that of KIEFER and MITCHELL (1983) by incorporating variation in daylength and by using a theoretically justifiable term for quantum yield. It includes features of the models of BANNISTER and LAWS (1980) and DUBINSKY et al. (1986) and is very similar to equations presented by GEIDER et al. (1986). The model of Sakshaug et al. is more general than earlier formulations (e.g. SHUTER, 1979; LAWS and BANNISTER, 1980; KIEFER and MITCHELL, 1983; LAWS et al., 1985) because it describes in one equation nitrogen-limited and nitrogen-saturated growth as a function of daylength and irradiance. Nutrition is not explicit in the model: essentially, the supply of nitrogen limits growth rate by restricting the synthesis of chlorophyll (i.e. light-harvesting systems; cf. PRÉZELIN and MATLICK, 1983) rather than by

influencing the efficiency of light absorption or photosynthesis. The daylength term in equation (1) is particularly important because it allows photosynthetic efficiency to be a function of instantaneous irradiance whereas growth rate is largely determined by total irradiance over the day. It can be argued that the model is valid at other temperatures (KIEFER and ENNS, 1976), but regardless, temperature effects can be assessed (LANGDON, 1988; BALCH et al., 1989).

The model has a mechanistic interpretation. The product of Chl/C and a_p is equal to the absorption cross-section of cellular carbon [m^2 (mol C)$^{-1}$] (cf. FALKOWSKI et al., 1985). The quantum yield for absorbed light is described as the maximum quantum yield, ϕ_{max} [mol C (mol photons)$^{-1}$], times the proportion of absorbed photons that will first strike a PSU during its turnover time:

$$\frac{\text{first strikes during turnover time}}{\text{photons absorbed during turnover time}} = \frac{1 - e^{(-\sigma\tau I_o)}}{\sigma\tau I_o}. \tag{2}$$

The product $\sigma\tau I_o$ is the mean number of photons absorbed by the PSU during its turnover time and $[1 - e^{(-\sigma\tau I_o)}]$ is the Poisson probability of one or more strikes per PSU during that period [i.e. $e^{(-\sigma\tau I_o)}$ is the Poisson probability of zero strikes during time τ]. This term corrects for fruitless absorption of excess photons by a PSU during the time it takes to process one absorbed photon. It is firmly based on studies of the kinetics of photosynthesis (KOHN, 1936; MYERS and GRAHAM, 1971; FALKOWSKI, 1981; LEY and MAUZERALL, 1982; DUBINSKY et al., 1986; PETERSON et al., 1987; EILERS and PEETERS, 1988).

Table 1. Symbols and units

Description	Symbol	Units	Conversion
Chlorophyll a	Chl	mol Chl	mg Chl · 1.119 × 10^{-6}
Cellular carbon	C	mol C	
Daylength	D	dimensionless	h/24 h
Irradiance	I, I_u	mol m^{-2} s^{-1}	(mol m^{-2} d^{-1}) · 1.157 × 10^{-4}
		mol m^{-2} d^{-1}	(ly d^{-1}) · 0.174
		μmol m^{-2} s^{-1}	W m^{-2} · 4.15*
Quantum yield	ϕ_{max}	mol C (mol photons)$^{-1}$	
Absorption coefficient	a_p	m^2 (mol Chl)$^{-1}$	(m^2 (mg Chl)$^{-1}$) · 8.93 × 10^5
Photosynthetic unit	PSU		
Absorption cross-section of PSU	σ	m^2 (mol PSU)$^{-1}$	
PSU size	U	mol Chl (mol PSU)$^{-1}$	
Turnover time of PSU	τ	s	
Growth rate	μ	s^{-1}	d^{-1} · 1.157 × 10^{-4}
Respiration rate	r	s^{-1}	d^{-1} · 1.157 × 10^{-4}
Photosynthesis (biomass specific)	P^B	g C (g Chl)$^{-1}$ h^{-1}	
Photosynthetic efficiency	α	g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$	
Photoinhibition term	β	g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$	
Integrated production	IP	g C m^{-2} d^{-1}	
Integrated biomass	IB	g Chl m^{-2}	
Light utilization index	Ψ	g C (g Chl)$^{-1}$ m^2 (mol photons)$^{-1}$	

* Conversion for natural waters from MOREL and SMITH (1974).

The gross specific growth rate is equal to the product of incidence irradiance, daylength, absorption cross-section of cellular carbon, and quantum yield.

Measurements of growth rates and Chl/C for nutrient- and light-limited cultures of the marine diatom, *Skeletonema costatum*, were fit to equation (1) by least-squares regression with good results. The best fit yielded two composite "constants" in equation (1),

$$\sigma\tau = 4320 \text{ m}^2 \text{ s (mol PSU)}^{-1}, \tag{3}$$

and

$$a_p \cdot \phi_{max} = 554 \text{ mol C m}^2 \text{ (mol photons)}^{-1} \text{ (mol Chl)}^{-1}. \tag{4}$$

Predicted growth rate deviated from observed with a standard deviation of $\pm 0.1 \text{ d}^{-1}$.

The "constants" are products of two parameters and thus the value of any one variable cannot be specified (cf. FASHAM and PLATT, 1983). Nonetheless, the products in equations (3) and (4) compare favorably with direct measurements of the four component parameters (SAKSHAUG et al., 1989). Turnover times (τ) for photosynthetic oxygen evolution vary at least from about 0.002 to 0.04 s (FALKOWSKI, 1981; FALKOWSKI et al., 1985). The absorption cross-section (σ) for oxygen evolution in *Chlorella vulgaris* has been determined to range from 0.38 to 1.10 nm^2 (LEY and MAUZERALL, 1982). A typical value for $\sigma\tau$ might be 3600 m^2 s (mol PSU)$^{-1}$, quite consistent with the fit of the model (equation 3). Because PSU size and turnover time can be inversely related to growth irradiance (MYERS and GRAHAM, 1971), the product $\sigma\tau$ may vary substantially. The quantum requirement for photosynthetic oxygen evolution has been found to be 10 ± 1 photons absorbed per oxygen molecule evolved (LEY and MAUZERALL, 1982; but see DUBINSKY et al., 1986). An assimilation quotient of 0.74 mol CO_2 absorbed per mol O_2 produced should be used to relate fluxes of oxygen to carbon during growth on nitrate (MYERS, 1949, in MORRIS, 1981; see also LANGDON, 1988). Thus ϕ_{max} would be 0.074 mol C (mol photons)$^{-1}$. The inferred value for a_p from equation (4) is then 7486 m^2 (mol Chl)$^{-1}$, or in more commonly used units, 0.0084 m^2 (mg Chl)$^{-1}$, on the lower end of a range of estimates for specific absorption coefficient (KIRK, 1983), but extremely close to the average for 13 species of cultured phytoplankton reviewed by LANGDON (1988).

The range of growth conditions studied by SAKSHAUG et al. (1989) was very broad. A fit to any kind of general model is a noteworthy accomplishment. Because growth has been described with a mechanistic model, the work deserves special attention. Further examination uncovers interesting features.

ANALYSIS OF THE MODEL: PHOTOSYNTHESIS AS A FUNCTION OF IRRADIANCE

Knowledge of the growth rates of phytoplankton in the sea is of central importance in biological oceanography, but routine estimation of growth rates and testing of predictions is particularly problematic (EPPLEY, 1980). It is relatively easy to measure primary productivity and Chl a, however. The ratio of the two, P^B [g C (g Chl)$^{-1}$ h^{-1}], relates pigment biomass to primary productivity (e.g. HARRISON and PLATT, 1980; FALKOWSKI, 1981). Models of P^B vs irradiance (I) are essential elements of algorithms for remote sensing of primary production (EPPLEY et al., 1985; PLATT, 1986; CAMPBELL and O'REILLY, 1988). I discuss here the model of SAKSHAUG et al. (1989) as a special case of a P^B vs I model.

Equation (1) can be rearranged to describe P^B as a function of irradiance:

$$P^B = \frac{(\mu + r)}{D} \cdot \frac{C}{Chl} = \frac{a_p \cdot \phi_{max}}{\sigma\tau} \cdot (1 - e^{(-\sigma\tau I_o)}). \tag{5}$$

Here, the units of P^B are mol C (mol Chl)$^{-1}$ s^{-1}. Using values for $a_p \cdot \phi_{max}$ and $\sigma\tau$ from the best-fit of the model (equations 3 and 4), expressing I_o as μmol m^{-2} s^{-1}, and converting P^B to familiar units [g C (g Chl)$^{-1}$ h^{-1}]:

$$P^B = 6.20(1 - e^{-0.00432 \cdot I_o}). \tag{6}$$

The relationship described in equations (5) and (6) follows the formulation for P^B vs I presented by WEBB et al. (1974). It is also comparable to an equation proposed by PLATT et al. (1980): $P^B = P^B_s \cdot (1 - e^{(-aI/P^B_s)}) \cdot (e^{(-\beta I/P^B_s)})$, where P^B is the instantaneous rate of photosynthesis normalized to chlorophyll at irradiance I [g C (g Chl)$^{-1}$ h^{-1}], P^B_s is the maximum rate of photosynthesis if there were no photoinhibition [g C (g Chl)$^{-1}$ h^{-1}], a is the initial slope of the P^B vs I curve [g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$] and β is the parameter chosen to characterize photoinhibition [g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$]. In the absence of photoinhibition ($\beta = 0$), the equation of PLATT et al. (1980) is the same as equations (5) and (6). The formulation dates back to ARNOLD (1932) and KOHN (1936) and has recently been presented by DUBINSKY et al. (1986) and, scaled to maximum photosynthesis, by PETERSON et al. (1987). The data of SAKSHAUG et al. (1989) therefore can be legitimately presented and statistically analysed as a P^B vs I curve according to the equation

$$P^B = P^B_s \cdot (1 - e^{(-aI/P^B_s)}). \tag{7}$$
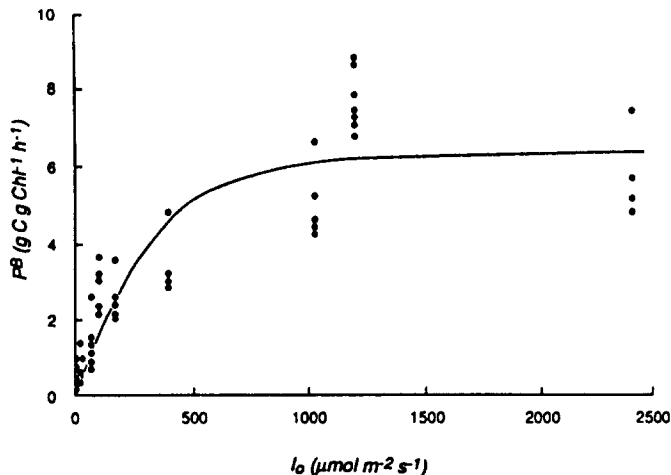
The result is presented in Fig. 1.

Fig. 1. *Skeletonema costatum*: adapted rate of photosynthesis as a function of growth irradiance for the data presented by SAKSHAUG et al. (1989), calculated according to the left side of equation (5). The line is a nonlinear least-squares fit to equation (7). The best-fit values ± S.E., were: $P^B_s = 6.23 \pm 0.27$ g C (g Chl)$^{-1}$ h^{-1}, $a = 0.0202 \pm 0.002$ g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$. These values differ slightly from those obtained using equations (8) and (9) and the best-fit estimates of $a_p \cdot \phi_{max}$ and $\sigma\tau$ from the original model of Sakshaug et al. ($P^B_s = 6.20$ g C (g Chl)$^{-1}$ h^{-1}, $a = 0.027$ g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$).

It must be recognized that the model of SAKSHAUG *et al.* (1989) as presented in equation (7) is a composite of *adapted* rates of photosynthesis at numerous steady states, whereas a conventional P^B vs I curve as commonly described by similar equations shows the photosynthetic response to perturbations from growth conditions and will differ in shape according to light history (FALKOWSKI, 1980, 1981; PERRY *et al.*, 1981; RICHARDSON *et al.*, 1983; KANA and GLIBERT, 1987b) and nutrition (WELSCHMEYER and LORENZEN, 1981; OSBORNE and GEIDER, 1986; PRÉZELIN and MATLICK, 1986; KOLBER *et al.*, 1988). Figure 2 shows how *adapted* rates of photosynthesis can fit a P^B vs I model even though the P^B vs I relationship is strongly a function of growth irradiance.

It is very instructive to examine the mechanistic basis of the P^B vs I model. By comparing equations (5) and (7), it can be seen that

$$P^B_s = \frac{a_p \cdot \phi_{max}}{\sigma \tau},$$
(8)

and

$$\alpha = a_p \cdot \phi_{max}.$$
(9)

The parameter of light saturation, I_k (μmol m^{-2} s^{-1}; TALLING, 1957; PLATT *et al.*, 1980), equals P^B_s/α, that is:

$$I_k = \frac{1}{\sigma \tau}.$$
(10)

Equations much the same as these have been presented before (e.g. FALKOWSKI, 1980; GALLEGOS *et al.*, 1981; DUBINSKY *et al.*, 1986; SUKENIK *et al.*, 1987): they are consistent with physiological interpretations of photosynthesis and are useful for examining the utilization of light by phytoplankton.

The parameters of the exponential model of P^B vs I (equations 8–10; PLATT *et al.*, 1980) can also be described in terms of the specific absorption of chlorophyll, PSU size and PSU turnover time. Let U equal the number of chlorophyll a molecules per photosynthetic unit [mol Chl (mol PSU)$^{-1}$]. The absorption cross-section can then be expressed as $\sigma = U \cdot a_p$. Substitution into equations (5), (8) and (10) makes it fairly easy to assess the effects on photosynthesis of changes in PSU size and number (FALKOWSKI, 1980; PRÉZELIN, 1981; KANA and GILBERT, 1987b) and to resolve uncertainties about predictions of different models of photoadaptation (RICHARDSON *et al.*, 1983). The implication is that the rate of photosynthesis is determined by light absorption and the probability of multiple strikes of a photosynthetic unit during its turnover time. Such an explanation is reasonable for photosynthesis in flashing light (MYERS and GRAHAM, 1971) and has been extended to describe photosynthesis in continuous light (DUBINSKY *et al.*, 1986; PETERSON *et al.*, 1987; EILERS and PEETERS, 1988).

From the model of SAKSHAUG *et al.* (1989) reformulated to describe P^B (equation 7, Fig. 1), the best-fit parameter estimates for adapted rates of P^B vs I over a wide range of growth conditions are $P^B_s = 6.23$ g C (g Chl)$^{-1}$ h^{-1}, $\alpha = 0.020$ g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$, and $I_k = 308\,\mu$mol m^{-2} s^{-1}. The model values for P^B_s and α are higher than average for natural populations, but certainly not atypical (HARRISON and PLATT, 1986). In fact, the value for α is close to the mean of 0.024 ± 0.005 g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$ reported by LANGDON (1988) for cultures. The photosynthetic parameters are also
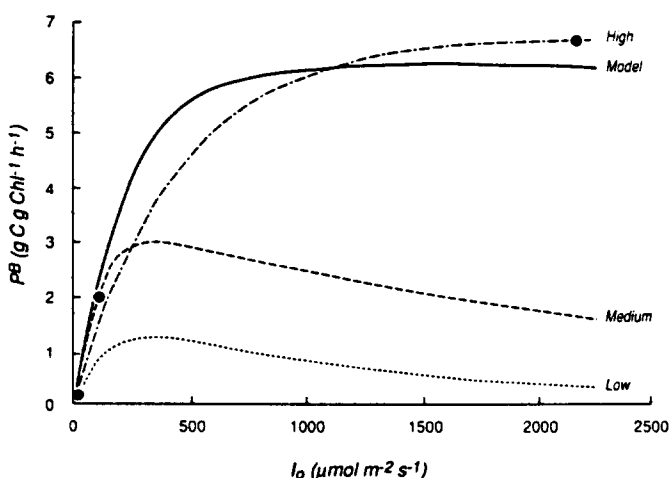
Fig. 2. Relationships between P^B and irradiance. The curves labeled Low, Medium and High are for cultures of the marine diatom *Thalassiosira pseudonana* (clone 3H) grown at 20, 100 and 2200 μmol m^{-2} s^{-1}, respectively (CULLEN and LEWIS, 1988). Photosynthesis was determined by measuring the uptake of ^{14}C-bicarbonate during 20 min incubations (LEWIS and SMITH, 1983). Lines are the best fits to the model of PLATT *et al.* (1980). The three points correspond to P^B at the growth irradiance. The model curve comes from the model of SAKSHAUG *et al.* (1989), as expressed in equation (6). This presentation demonstrates that adapted rates of photosynthesis have a relationship with irradiance that is not characteristic of the P^B vs I curve at any one growth irradiance. This point has been made repeatedly by Myers (cf. MYERS, 1970; MYERS and GRAHAM, 1971) and has recently been illustrated by KANA and GLIBERT (1987b). The excellent correspondence between the measured rates and the growth model should not be accepted uncritically because short-term measurements of carbon uptake do not correspond well to net carbon assimilation under all conditions.

strikingly consistent with data and a model presented and discussed by LAWS and BANNISTER (1980). An exception is that P^B at high growth irradiance is undiminished despite severe nutrient limitation. The results of SAKSHAUG *et al.* (1989) therefore indicate that the photosynthetic debilitation characteristic of nutrient starvation (WELSCHMEYER and LORENZEN, 1981) is not a feature of steady-state, nutrient-limited growth (OSBORNE and GEIDER, 1986; but see KOLBER *et al.*, 1988). This seems to be one of the fundamental differences between balanced and unbalanced growth.

APPLICATION OF THE MODEL: REMOTE SENSING

The advent of sensing phytoplankton pigments from space has generated considerable interest in relating pigment concentration to integral primary productivity (EPPLEY *et al.*, 1985; PLATT and SATHYENDRANATH, 1988; BALCH *et al.*, 1989). Phytoplankton production per unit area of sea surface (IP: g C m^{-2} d^{-1}) has been normalized to total pigment biomass in the water column (IB: g Chl m^{-2}) and IP/IB has been described as a function of incident irradiance (I_o: mol m^{-2} d^{-1}) (MALONE, 1976; FALKOWSKI, 1981; PLATT, 1986; CAMPBELL and O'REILLY, 1988). The slope of the relationship is Ψ [g C (g Chl)$^{-1}$ m^{-2} (mol photons)$^{-1}$], a parameter which has been shown to vary remarkably little in samples from a variety of environments (PLATT, 1986; but see CAMPBELL and O'REILLY, 1988). If Ψ is

known, integral primary production can be estimated given data on chlorophyll concentrations and solar insolation (MALONE, 1976; FALKOWSKI, 1981; PLATT, 1986). PLATT (1986) has reported that Ψ is usually about 0.4 g C (g Chl)$^{-1}$ m^2 (mol photons)$^{-1}$.

Integral productivity is best estimated using experimental determinations of P^B vs I (PLATT and SATHYENDRANATH, 1988), but when appropriate data are lacking, it is instructive and useful to generalize the relationship (RYTHER and YENTSCH, 1957; PLATT, 1986). As a heuristic exercise, the model of SAKSHAUG et al. (1989) as reformulated here can be used to generate a general model of IP/IB vs I_o as a function of daylength (Fig. 3): integral primary productivity, normalized to chlorophyll, is estimated by using mean irradiance during daylight hours and averaging P^B to the 1% light level (i.e. through 4.61 optical depths) using equation (6). For any particular daily flux of sunlight, average quantum yield is lower for shorter days because more of the water column is at supersaturating irradiance in daylight. Daylength influences modeled relationships between IP/IB and I_o on an annual scale (cf. RYTHER, 1956). For example, a value for Ψ of about 0.64 g C (g Chl)$^{-1}$ m^2 (mol photons)$^{-1}$ can be generated by connecting points for combinations of I_o and daylength at mid-latitudes (Fig. 3). The slope of points from the summer months is about 0.4 g C (g Chl)$^{-1}$ m^2 (mol photons)$^{-1}$. A non-zero intercept on the ordinate, consistent with regressions on data from the field (PLATT et al., 1988), results from the nonlinearity of the P^B vs I model. This intercept can be fairly large so that IP/IB is not well described by $\Psi \cdot I_o$. Thus either the full regression equation with the intercept or a nonlinear P^B vs I model is preferable to the slope, Ψ, for describing primary production as a function of integrated biomass and solar insolation.

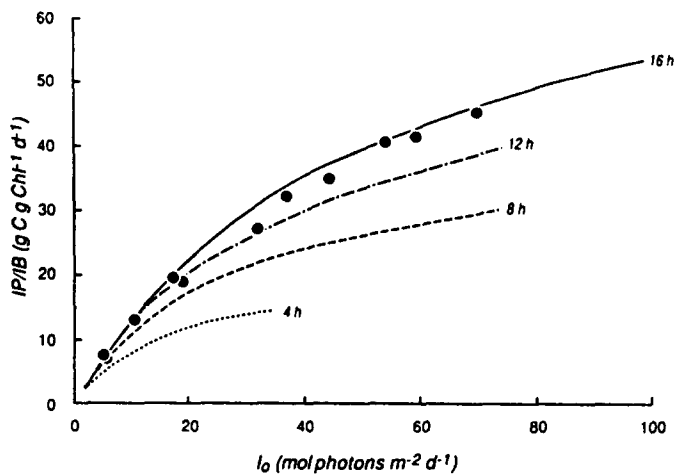General models of P^B vs I, with specified maximal rates, have played a small role in

Fig. 3. Phytoplankton production per unit sea surface area (gross production), normalized to chlorophyll as a function of solar insolation (i.e. IP/IB vs I_o). Results of the model of SAKSHAUG et al. (1989) as expressed in equation (6). Uniform chlorophyll concentration with depth is assumed. The ordinate is the average value of P^B from the surface to the depth of 1% I_o. The lines represent the relationship between IP/IB and I_o for different daylengths. The filled circles are representative combinations of daylength and I_o over a year for a temperate latitude (45°N): I_o for each month from HARRISON and PLATT (1980), daylength from PLATT (1971). The regression of IP/IB vs I_o on the 12 points has a slope of 0.64 g C (g Chl)$^{-1}$ m^2 (mol photons)$^{-1}$. This figure can be compared with Fig. 6 in RYTHER (1956).

Fig. 4. Phytoplankton production per unit sea surface area normalized to chlorophyll as a function of solar insolation (i.e. IP/IB vs I_o). Models of integrated primary production compared with data in the literature (cf. PLATT, 1986). Filled circles are from the model of SAKSHAUG et al. (1989) as presented in Fig. 3. Open circles are results from the method of RYTHER and YENTSCH (1957), modified as described in the text (equation 11) and applied to the same combinations of insolation and daylength. Dotted line is the regression presented by FALKOWSKI (1981) and the solid line is MALONE's (1976) regression, in terms of surface insolation (MALONE, 1987).
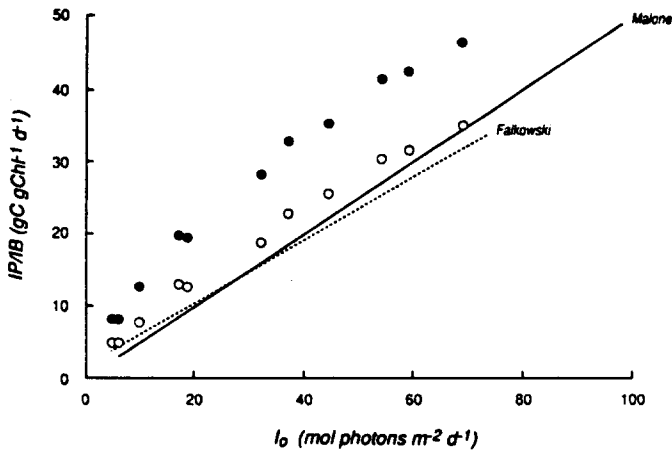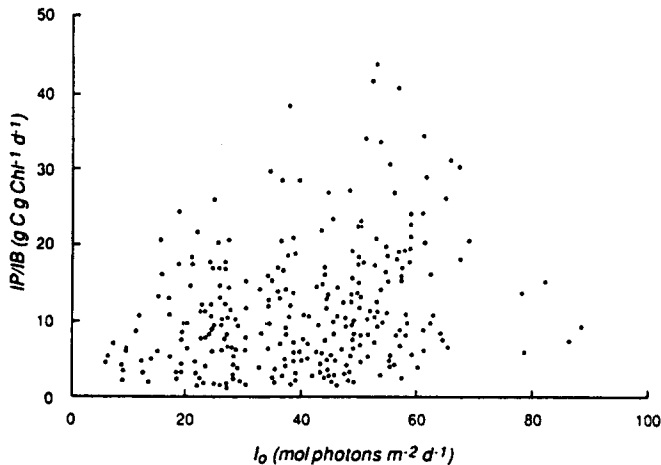

Fig. 5. Phytoplankton production per unit sea surface area, normalized to chlorophyll as a function of solar insolation (i.e. IP/IB vs I_o). Data from the Southern California Bight survey, 1974–1987, compiled by W. M. Balch and R. W. Eppley. There are 310 points and the correlation coefficient is 0.25 (6.1% of the variance explained). Data provided by W. M. Balch.

recent efforts to model primary production, presumably because years of research have shown how variable the P^B vs I relationship can be. The data of SAKSHAUG et al. (1989) suggest that under steady-state conditions, the adapted rate of photosynthesis normalized to biomass is a function solely of irradiance and thus the concept of general P^B vs I relationships has some newfound credibility. In this context, it is instructive to compare the relationship in the model of Sakshaug et al. to the P^B vs I relationship presented by RYTHER (1956) and RYTHER and YENTSCH (1957). A major difference is that photoinhibition is a prominent feature of the general P^B vs I curve presented by Ryther, whereas P^B is not depressed at high irradiance for the well-adapted cultures studied by SAKSHAUG et al. (1989). Complete adaptation of cultures to high irradiance was not demonstrated in the early experiments carried out by Ryther, and there is reason to believe that with special precautions (KANA and GILBERT, 1987a) much higher rates would have been achieved under bright light. Parameters can be compared between models if the photoinhibitory part of Ryther's general model is ignored and the mathematical form of equation (7) is chosen to describe the saturation function. Maximum photosynthesis of 3.7 g C (g Chl)$^{-1}$ h^{-1} is given by Ryther and Yentsch. A saturation irradiance (I_k) of 1400 foot candles solar irradiance ($=270\,\mu$mol m^{-2} s^{-1}; conversion in McCREE, 1972) is determined by inspection of Ryther's Fig. 2. The parameter α is the ratio of P_s^B to I_k [$\alpha = 0.013$ g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$]. It should be noted that Ryther and Yentsch calculated chlorophyll concentration on the basis of spectrophotometric equations (RICHARDS and THOMPSON, 1952) which have since been shown to overestimate the concentration of Chl a (BANSE and ANDERSON, 1967; WARTENBURG, 1978). The error is likely to be about 30% (LORENZEN and JEFFREY, 1980), so one should represent the parameters of the Ryther and Yentsch model as $P_s^B = 4.8$ g C (g Chl)$^{-1}$ h^{-1} and $\alpha = 0.018$ g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$. The saturation parameter is unchanged. In simple form, the modified Ryther and Yentsch model is then:

$$P^B = 4.8(1 - e^{-0.00456 \cdot I_o}), \tag{11}$$

where I_o is in μmol m^{-2} s^{-1}. The seasonal variation of IP/IB from the modified Ryther and Yentsch model can be compared with other models (Fig. 4). The slope of the regression (Ψ) is 0.44 g C (g Chl)$^{-1}$ m^2 (mol photons)$^{-1}$.

Validation of analytical productivity models requires comparison with real data (cf. PLATT, 1986). Observations reported by FALKOWSKI (1981) seem to be about half what would be expected if the model of Sakshaug et al. applied, but are fairly consistent with the modified Ryther and Yentsch model (Fig. 4). Some data sets seem to bear no relationship to any simple model. CAMPBELL and O'REILLY (1988) found a poor correlation between IP/IB and I_o for a large set of determinations from the continental shelf off the northeast United States. Measurements from the Southern California Bight (Fig. 5; see also BALCH et al., 1989) likewise indicate that a stable relationship between IP/IB and I_o does not exist, even though, for the average of many points from individual depths, there is a clear relationship between P^B and I (EPPLEY and HOLM-HANSEN, 1986; their Fig. 5.8; see also BALCH et al., 1989). It is important to understand why a relationship works well in some regions and not in others.

DISCUSSION

Models of phytoplankton growth

Many models of phytoplankton growth are based on similar principals, but it is difficult

to decipher the models and discern the important similarities and differences between them. For example, KIEFER and MITCHELL (1983) showed that their model was in many ways similar to those of LAWS and BANNISTER (1980) and SHUTER (1979). To discuss the models they had to introduce about 34 symbols. LAWS et al. (1985) compared the predictive model of KIEFER and MITCHELL (1983) to a modified version of a theoretical model by SHUTER (1979). Laws et al. effectively and informatively demonstrated that the two models made very similar predictions, but their discussion required the use of about 26 different symbols. These rather complicated presentations dealt with important physiological processes which are inextricably linked to photosynthesis and growth; yet models of phytoplankton growth can be simplified to an extreme: the major features of growth can be described by a simple energy budget (cf. GEIDER et al., 1986) using one of several 2-parameter functions that describe light dependence of gross photosynthesis (cf. JASSBY and PLATT, 1976). Such a model can be constructed by using equations (8) and (10) to simplify equation (1):

$$(\mu + r) = \frac{Chl}{C} \cdot D \cdot P_s^B \cdot (1 - e^{(-I_c/I_k)}). \tag{12}$$

Here the parameters P_s^B and I_k refer to the adapted rate of photosynthesis as a function of irradiance, which has been shown in the data of SAKSHAUG et al. (1989) to be substantially independent of daylength or nitrogen limitation (Fig. 1). The ratio of chlorophyll to carbon can be treated as one variable and described as a function of irradiance and temperature (GEIDER, 1987) as well as nutrition (LAWS and BANNISTER, 1980), and possibly daylength (GEIDER, 1987).

Equation (12) describes growth simply and effectively, but it explains little. The explanations come from considering the processes that are represented in detailed models of light utilization and chemical composition of phytoplankton.

Physiological implications

General models of photosynthesis have been around for a long time (RYTHER, 1956). However, the P^B vs I relationship described by the data of SAKSHAUG et al. (1989; equations 5–7; Fig. 1) is novel and significant because it is based on real data obtained under a wide variety of steady-state growth conditions, including nutrient limitation and variable daylength. That nutrient-limited cultures do not deviate from a general P^B vs I relationship is especially noteworthy. Previous studies on photosynthesis during nutrient starvation (unbalanced growth) have indicated that photosynthetic efficiency declines substantially after nitrogen is depleted (WELSCHMEYER and LORENZEN, 1981). If this were true for steady-state cultures (balanced growth), P^B at growth irradiance would be a function of nutrient-limited growth rate. For the cultures studied by SAKSHAUG et al. (1989), P^B at growth irradiance is essentially the same, regardless of nitrogen-limitation of growth. In contrast, LAWS and BANNISTER (1980) showed that P^B at growth irradiance was nearly constant only if nutrient-limited growth rate was above about 0.25 of maximal. It is not clear why the results of Laws and Bannister differ from those of Sakshaug et al. at low growth rates. Regardless, it seems possible that nitrogen-limited balanced growth is fundamentally different from nutrient starvation (unbalanced growth) in that photosynthetic efficiency does not differ much as a function of nutrient supply.

An interesting product of this analysis is the comparison of the rearranged SAKSHAUG et al. (1989) model (equation 5) with the well-established exponential equation for describ-

ing P^B vs I (WEBB *et al.*, 1974; PLATT *et al.*, 1980; DUINSKY *et al.*, 1986). A mechanistic basis for exponential photosynthesis models is evident. The correction for multiple hits of the rate-limiting photosystem (equation 2) is the essence. This target theory is the basis for several descriptions of photosynthesis (ARNOLD, 1932; KOHN, 1936; MYERS and GRAHAM, 1971; LEY and MAUZERALL, 1982; DUBINSKY *et al.*, 1986; PETERSON *et al.*, 1987; EILERS and PEETERS, 1988). A correction term governs quantum yield, so one might infer that ϕ_{max} can be considered a constant. DUBINSKY *et al.* (1986), however, have concluded that the maximum quantum yield is not constant as a function of growth irradiance, and KOLBER *et al.* (1988) state that the efficiency of photosynthesis declines under nitrogen limitation. In contrast, OSBORNE and GEIDER (1986) determined that maximum quantum yield was not significantly different from the theoretical upper limit despite severe nitrate deficiency in continuous cultures. It is clear that some questions concerning the effects of nutrient limitation on photosynthesis have yet to be resolved fully.

It must be recognized that the model P^B vs I curve (equation 7) does not necessarily represent the relationship between photosynthesis and irradiance for any of the cultures studied (Fig. 2). Rather, it can be viewed as a composite with one point, corresponding to the growth irradiance, contributed by each culture which has its own instantaneous P^B vs I curve (cf. MYERS, 1970). Even though a single P^B vs I curve, specified by parameters with biophysical meaning, describes photosynthesis of a marine diatom over a very broad range of conditions, it cannot be concluded that certain properties of the photochemical mechanism of the diatom (i.e. the composite "constants", $a_p \cdot \phi_{max}$ and $\sigma\tau$; equations 3 and 4) are invariant. Because P^B_s, α and I_k are known to vary with growth conditions (HARRISON and PLATT, 1980; RICHARDSON *et al.*, 1983; HARRISON and PLATT, 1986; OSBORNE and GEIDER, 1986), the products $a_p \cdot \phi_{max}$ and $\sigma\tau$ must also change (equations 8–10; FALKOWSKI, 1981; GALLEGOS and PLATT, 1981; DUBINSKY *et al.*, 1986). We are presently studying how these changes of the photochemical machinery work in concert to produce one general P^B vs I curve to describe adapted photosynthesis (CULLEN and KIEFER, in preparation).

The biophysical interpretation of the general model of growth in *Skeletonema* is not as simple as it may seem at first inspection [see also FALKOWSKI *et al.* (1985) and DUBINSKY *et al.* (1986), for other considerations]. The utility of the model as a descriptive tool does not depend on our complete understanding, though.

MYERS (1970) stated that the relationship between growth rate and light intensity is a genetic characteristic of an alga whereas the photosynthesis vs irradiance relationship is an adaptive characteristic (see also RICHARDSON *et al.*, 1983). The data of SAKSHAUG *et al.* (1989), as presented here, suggest that the relationship between the *adapted* rate of photosynthesis (normalized to chlorophyll) and light is also a genetic characteristic of a species. The implications of this suggestion are quite important to biological oceanography. Specifically, the results indicate that for an alga grown at a given temperature the adapted rate of photosynthesis, P^B is a function solely of growth irradiance—*it is independent of growth rate*. It will be interesting to determine if other species of phytoplankton conform to this strategy of photoadaptation (cf. RICHARDSON *et al.*, 1983).

Oceanographic implications

Three decades ago, RYTHER and YENTSCH (1957) proposed a method for calculating integral primary production on the basis of chlorophyll and light data. Central to the model

was a general description of P^B vs I for marine phytoplankton (RYTHER, 1956). Over the years it became clear, however, that P^B vs I is very responsive to growth conditions (MYERS, 1946; STEEMANN NIELSEN and HANSEN, 1959; MYERS and GRAHAM, 1971; BEARDALL and MORRIS, 1976; FALKOWSKI, 1980; HARRISON and PLATT, 1980; HARDING et al., 1987; CULLEN and LEWIS, 1988). It would be reasonable to conclude that photosynthesis in the sea is much too complicated to describe with one formulation. Nonetheless, the availability of unprecedented quantities of data on pigment distributions in the ocean from remote sensing has stimulated a substantial effort to develop simple, general algorithms to relate pigment concentration to primary productivity (EPPLEY et al., 1985; PERRY, 1986; PLATT, 1986; BALCH et al., 1989).

General models of P^B vs I can be used to estimate integrated primary productivity normlized to chlorophyll in the water column as a function of solar insolation. The data presented by SAKSHAUG et al. (1989) lend legitimacy to such formulations, at least with respect to adapted rates of photosynthesis. The model describing those data is an improvement on other descriptions of phytoplankton growth because it has been validated by comparison with growth rates under a very broad range of conditions. When the model is reformulated to describe photosynthesis, the results are similar to early models (RYTHER, 1956) and are consistent with the analysis of several sets of data by PLATT (1986). A remarkable agreement between RYTHER and YENTSCH (1957) and PLATT's (1986) analysis is demonstrated (Fig. 4). It appears that the photosynthetic performance of natural phytoplankton is often similar to steady-state cultures.

The model does not describe photosynthesis in all parts of the ocean. The poor relationship in Fig. 5 and similar results presented by CAMPBELL and O'REILLY (1988) attest to that. Why would a model work sometimes and not others? Taxonomic differences are certainly a consideration (LANGDON, 1988), especially because the general patterns of photoadaptation may differ between species (RICHARDSON et al., 1983). Factors not considered here, such as variation in the relative rate of respiration, may also be important (FALKOWSKI et al., 1985). The potential effects of temperature are not fully resolved (PLATT and SATHYENDRANATH, 1988), but corrections can be made with some success (BALCH et al., 1989). Vertical structure of chlorophyll (CULLEN, 1982; HAYWARD and VENRICK, 1982; PLATT and HERMAN, 1983) is an added complication, but it can be dealt with (PLATT et al., 1988; PLATT and SATHYENDRANATH, 1988; BALCH et al., 1989). It is also possible that the nature of steady-state growth is central to an explanation. Phytoplankton adapted to the light and nutrient regime at the depth of sampling should conform to the general model whereas fluctuations in light and nutrient supply would lead to unbalanced growth and, possibly, large changes in the relationship between P^B and I (Fig. 2; see also KANA and GLIBERT, 1987b). The Southern California Bight (source for the data in Fig. 5) is a dynamic region with considerable admixture of water masses (EPPLEY, 1986). Steady-state growth may not be common. The fundamental differences between steady-state and unbalanced growth must be appreciated before the consequences of light and nutrient limitation of phytoplankton growth can be fully understood. The better we understand steady-state growth, the easier it will be to discern how unbalanced growth differs.

CONCLUSIONS

Many models of photosynthesis and growth of phytoplankton have been developed and most have performed well in describing aspects of their subject. The number of equations

and symbols generated in this pursuit is staggeringly high and probably not matched by a corresponding level of comprehension among biological oceanographers. The growth model presented by SAKSHAUG et al. (1989) is simple, yet powerful. It describes aspects of growth (nutrient-limited under different photoperiods) that were left out of many earlier models. The formulation of the model is theoretically justifiable and the parameters are not only real but measurable. The model could be deceptive, though, because the best-fit values for the parameters are composites, and probably not representative of any one growth state. Nonetheless, careful consideration of the model is fruitful, as possible mechanisms underlying the relationship between photosynthesis and irradiance are exposed in the process (DUBINSKY et al., 1986; PETERSON et al., 1987).

When modified to describe the adapted rate of photosynthesis as a function of irradiance, the model does remarkably well in complementing the analysis by PLATT (1986) and renewing interest in the general P^B vs I models such as RYTHER and YENTSCH (1957). Simply, the data of SAKSHAUG et al. (1989) validate the idea that under certain conditions, one model of photosynthesis vs irradiance can describe primary productivity in the water column. Although positive results are worthy of note, the failures of models to fit some sets of observations (Fig. 5; CAMPBELL and O'REILLY, 1988) demonstrate that much is yet unexplained.

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