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Lack of agreement among models for estimating the photosynthetic parameters

Abstract—Comparisons were conducted between estimates of photosynthetic capacity (P_{\max}) and photosynthetic efficiency (α) calculated with different models of the photosynthesis vs. irradiance curve. Values computed on the same data sets are different according to the models used. Estimates for P_{\max} with the exponential and hyperbolic tangent models (without a term for photoinhibition) are in good agreement (4% difference). The same comparison for α shows poor agreement (24% difference between the two models). When a parameter for the intercept is added to the two models, the lack of agreement increases to 8% for P_{\max} and 46% for α . When the mean photosynthetic parameters calculated with the two models are introduced into various published models for calculating primary production, differences in the resulting estimates range between 20 and 133%. Comparing the exponential model with a term for photoinhibition to the hyperbolic tangent model (without a term for photoinhibition) shows a 24% difference in the estimate of α . Equations are given for transforming values calculated with the various models.

In aquatic environments, the photosynthetic uptake of C by phytoplankton may determine to a large degree the abundance of renewable resources (e.g. Iverson 1990) and the biogeochemical flux of C (e.g. Volk and Hoffert 1985). Several mathematical models, ranging in complexity from simple equations to multiparameter formulations, have been developed to describe photosynthesis as a function of irradiance

(see Cullen 1990). Parameters that characterize the photosynthesis vs. irradiance ($P-I$) curve correspond to physiological characteristics (see Harris 1978) and are under the influence of environmental conditions. Such factors as time of day, quantum scalar irradiance, photoperiod, temperature, availability of nutrients, and phytoplankton community structure can affect photosynthesis and thus primary production (Harding et al. 1982; Coté and Platt 1983; Vincent 1992). The importance of these environmental factors can be assessed through their effects on the photosynthetic parameters.

Many researchers are thus interested in the initial slope of the light-limited portion of the $P-I$ curve (α), but few seem to realize that values of α are not interchangeable between mathematical $P-I$ models. When one deals with a family of $P-I$ curves with and without photoinhibition, consistency should be maintained by avoiding the simultaneous use of incompatible models for curves showing photoinhibition and for those without photoinhibition. We show that large differences in values of α , computed on the same data sets with different models, may lead to serious misinterpretations. These could affect conclusions in such important fields as diel variations of photosynthetic parameters or the estimation of areal daily production with the remote sensing approach.

Potential sources of experimental errors include incubation and filtration procedures, measurements of low irradiances (Richardson 1991), sampling and temporal alias of the sampling (Platt et al. 1984), differences in the spectral quality of experimental and natural irradiance, and algal response to the spectral distribution of light (Rochet et al. 1986; Sathyendranath et al. 1989). Larger analytical variability associated with α as compared to P_{\max} has also been noted in earlier studies (Jassby and Platt 1976; Peterson et al. 1987; Richardson 1991). In most papers, a single model is used to compute the $P-I$ parameters. However, in some studies (e.g. Harrison and Platt 1986; Prézelin et al. 1986), different models

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have been used simultaneously to minimize the residual sums of squares and thus obtain a best fit to the data.

The choice of a particular model to estimate the P - I parameters may lead to different values of P_{\max} and α and thereby to different integrated primary production. Among the most extensively used models are those dealing with the representation of the P - I curve below the onset of photoinhibition (e.g. Jassby and Platt 1976) and those that allow the possibility of photoinhibition (e.g. Platt et al. 1980).

The two most widely used P - I models without photoinhibition (i.e. Webb et al. 1974; Jassby and Platt 1976) result in different values for P_{\max} and α because of differences in the approximation underlying each model. As discussed by Gallegos and Platt (1981), Chalker (1980) showed that the rate of change of P vs. I is a function of P , i.e. $\partial P/\partial I = f(P)$, which can be expanded as a power series:

$$\frac{\partial P}{\partial I} = a_0 + a_1P + a_2P^2 + a_3P^3 + \dots \quad (1)$$

The linear approximation of Eq. 1 is

$$\frac{\partial P}{\partial I} = a_0 + a_1P \quad (2)$$

which leads to the solution of Webb et al. (1974):

$$P = P_{\max}[1 - \exp(-\alpha I/P_{\max})]. \text{ Model 1. } (3)$$

Whereas the quadratic approximation of Eq. 1:

$$\frac{\partial P}{\partial I} = a_0 + a_1P + a_2P^2 \quad (4)$$

leads to the solution of Jassby and Platt (1976):

$$P = P_{\max} \tanh(\alpha I/P_{\max}). \text{ Model 2. } (5)$$

Concerning P - I models with photoinhibition, the frequently used model of Platt et al. (1980) allows for photoinhibitory response after reaching P_{\max} but is the same as model 1 when no photoinhibition occurs. It is expressed as a continuous exponential function equation:

$$P = P_S[1 - \exp(-\alpha I/P_S)][\exp(-\beta I/P_S)]. \text{ Model 3. } (6)$$

P_S is a scaling parameter defined as the maximum, potential, light-saturated photosynthetic rate, and β characterizes the negative

slope of the curve at high irradiance (i.e. the photoinhibition parameter). P_{\max} is calculated from the equation

$$P_{\max} = P_S[\alpha/(\alpha + \beta)][\beta/(\alpha + \beta)]^{\beta/\alpha}$$

and is equivalent to P_S when $\beta = 0$.

Different approximations thus lead to different numerical solutions of the same initial relationship. P_{\max} and α from model 2 are not directly comparable to those from models 1 and 3, contrary to the suggestion of Gallegos and Platt (1981). Using the quadratic approximation (i.e. Jassby and Platt 1976) introduces an additional (second degree) term in the power series, which should increase the precision of the mathematical solution. This term does not exist in the linear approximation of Webb et al. (1974). Since this last model also describes the curve up to the threshold of photoinhibition in the Platt et al. (1980) model, the same remark also applies to this last case, which means that P_{\max} and α calculated with the models of Jassby and Platt (1976) and Platt et al. (1980) are not the same.

It has also been proposed to include an additional parameter, R_b , that allows the Y -intercept to take a non-0 value, and reduces the mean residual sum of squares when fitting models to data. The purpose of the present study is to assess the degree of agreement between estimates of the photosynthetic capacity (P_{\max}) and of the initial slope of the P - I relationship (α), calculated with different models.

Field measurements were made in Lake Tantaré (47°04'N, 71°32'W; 457 m asl), an oligotrophic, head-water lake with one shallow and two deep basins. Sampling was carried out between 19 May and 13 July 1990. Samples comprised depth profiles and diel cycles (24 h). The depth profiles included four depths in one of the deep basins (15 m deep) and one depth in the shallow basin (5 m deep) and were sampled at noon and midnight on two occasions, i.e. during the day before and the day after the diel cycles. For the diel cycles, integrated water samples were collected at 4-h intervals. During the thermally unstratified period (May), integrated samples were over the whole water column, whereas during the thermally stratified period (July), each thermal stratum (epi, meta, and hypolimnion) and the chlorophyll maximum were sampled individually. The shallow-basin station remained un-

stratified during the entire study period. Water was collected with a submersible low-volume diaphragm pump and a 1.25-cm (i.d.) silicone hose. Integrated samples correspond to three round trips of the pump in each thermal zone. The effluent of the pump was collected in 2-liter Nalgene polypropylene brown bottles when sampling at discrete depths and in a 20-liter polypropylene container for the integrated samples. All containers were rinsed with the sampled water.

At each sampling time, Chl *a* concentration was determined by filtering duplicate 100-ml subsamples onto Nuclepore filters of the same size and porosity as described below for ^{14}C uptake. Pigments were extracted in 10 ml of 90% acetone at 4°C in the dark for 24 h. Chl *a* concentrations were determined fluorometrically and corrected for pheopigments (Parsons et al. 1984).

Dissolved inorganic C (DIC) was measured with the syringe gas-stripping procedure for gas chromatographic determination described by Stainton (1973). Water was collected on each sampling occasion by slowly filling a 125-ml serum bottle by means of a silicone tube (5-mm i.d.) and was allowed to overflow three times to avoid air-bubble formation. Bottles were capped, sealed with a metal ring, and kept in the dark at 4°C until analysis (within 24 h).

Twelve 70-ml subsamples were taken from the sample bottles and dispensed with a calibrated pipette into Corning 70-ml polystyrene culture bottles (10 clear and 2 dark). These rectangular flat plastic containers were used instead of the usual round glass bottles to minimize bottle effects due to light refraction. $\text{NaH}^{14}\text{CO}_3$ was inoculated with a Nichyrio re-pipette to a final activity of $0.02 \mu\text{Ci ml}^{-1}$. Phytoplankton samples were then incubated 2 h under artificial light, with water thermostatically controlled to simulate the in situ temperature. A 250-W Optimarc high-pressure sodium lamp provided irradiances ranging from 12 to $996 \mu\text{Einst m}^{-2} \text{s}^{-1}$. Irradiance (PAR, 400–700 nm) was measured in each incubation bottle with a Biospherical quanta meter (4π collector).

After incubation, the samples were sequentially filtered under low vacuum (<120 mm of Hg) onto 2- and $0.2\text{-}\mu\text{m}$ pore-size Nuclepore filters (47-mm diam) mounted in a Nalgene swinlock cartridge system on an ABS filtration

manifold unit. Filters were individually placed into Petri dishes for fuming over concentrated HCl for 20 min and then transferred into scintillation vials containing 10 ml of Cytosint ES scintillation cocktail (ICN) and $50 \mu\text{l}$ of 1 N NaOH to avoid pH changes of the cocktail. All samples were counted on a LKB-Wallac (1211 Minibeta) liquid scintillation counter, counts being corrected for quenching by the channels-ratio method. The rate of ^{14}C fixation (Parsons et al. 1984) was calculated for the picoplankton fraction ($0.2\text{--}2.0 \mu\text{m}$), the nanoplankton fraction ($>2.0 \mu\text{m}$), and total phytoplankton. Dark-bottle values were subtracted from the counts. Photosynthesis was normalized to unit Chl *a*.

Comparison of P_{max} and α was conducted for models 1 and 2 with 137 data sets showing no photoinhibition (either total phytoplankton, $>2.0\text{-}\mu\text{m}$ fraction, or picoplankton). The same comparisons were conducted between these two models and model 3 for 63 data sets showing photoinhibition. In this case, computations with model 3 were on the original data sets, while those with models 1 and 2 were data sets from which the photoinhibited points had been excluded. Data sets where maximum photosynthesis corresponded to the highest irradiances were considered nonphotoinhibited. In cases where the maximum observed photosynthesis was followed by lower values (at higher irradiances), these were identified as the photoinhibited points. A nonlinear curve-fitting procedure (NLIN; SAS computer package) was used to calculate the parameters of the P - I curves with the Gauss-Newton method (Bard 1974). A subsample of 27 data sets showing no photoinhibition was used to compare results obtained with this method to those from the derivative-free secant method (DUD) provided by NLIN.

Partial derivatives used for fitting Eq. 3 are

$$\frac{\partial P}{\partial \alpha} = I[\exp(-\alpha I/P_{\text{max}})] \quad (7)$$

and

$$\frac{\partial P}{\partial P_{\text{max}}} = 1 - [\exp(-\alpha I/P_{\text{max}})][1 + \alpha I/P_{\text{max}}]. \quad (8)$$

Partial derivatives used for fitting Eq. 5 are

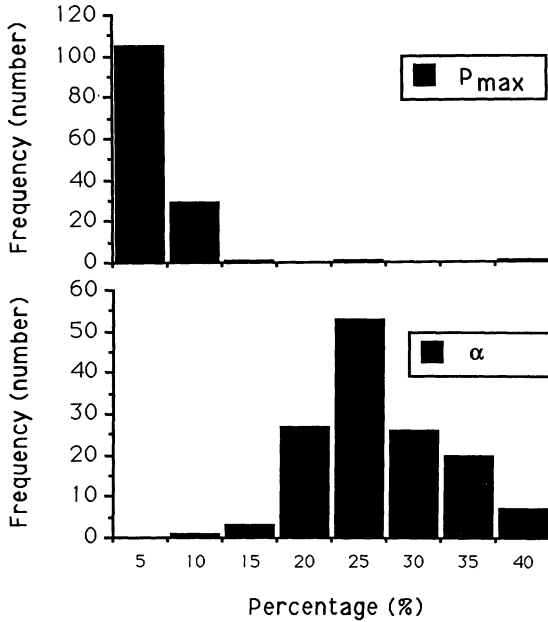


Fig. 1. Frequency distribution of percent differences $[100 \times (\text{model 1} - \text{model 2})/\text{model 2}]$ between the values of P_{max} and α calculated with the models of Jassby and Platt (1976) and of Webb et al. (1974) without an intercept parameter (R_b). Values on abscissa refer to the upper limits of the classes.

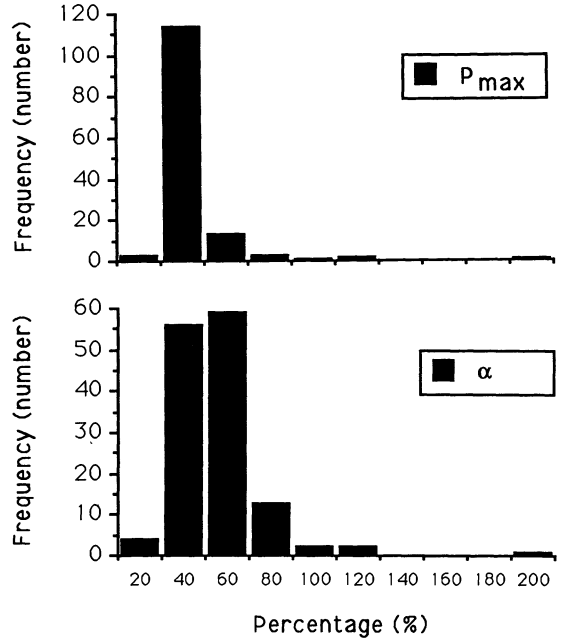


Fig. 2. As Fig. 1, but with an intercept parameter (R_b).

$$\frac{\partial P}{\partial \alpha} = I[1 - \tanh^2(\alpha I/P_{max})] \quad (9)$$

and

$$\frac{\partial P}{\partial P_{max}} = -\frac{\alpha I}{P_{max}} [1 - \tanh^2(\alpha I/P_{max}) + \tanh(\alpha I/P_{max})]. \quad (10)$$

Partial derivatives used for fitting Eq. 6 are given by Platt et al. (1980).

Mean values of P_{max} , α , and the residual sums of squares were compared with the 95% confidence intervals calculated for the two models. The confidence intervals for P_{max} and α were estimated as

$$[P_{max} \text{ or } \alpha] \pm 1.96[\Sigma(SE^2)/n^2]^{1/2}$$

where n is the number of data sets. For the mean residual sum of squares (SS), the confi-

Table 1. Mean values and 95% confidence intervals for P_{max} [$\mu\text{g C } (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$], α [$\mu\text{g C } (\mu\text{g Chl } a)^{-1} \text{ h}^{-1} (\mu\text{Einst m}^{-2} \text{ s}^{-1})^{-1}$], and the residual sums of squares (SS) and mean relative errors (%) for P_{max} and α calculated with the P - I models of Jassby and Platt (1976) and Webb et al. (1974). The 137 curves were fitted with and without an intercept parameter (R_b).

P - I models	P_{max}	α	Residual SS	Relative errors	
				P_{max}	α
Without R_b					
Jassby and Platt	3.82 (3.76, 3.87)	0.02 (0.02, 0.02)	0.15 (0.13, 0.16)	5.7	10.3
Webb et al.	4.03 (3.95, 4.11)	0.03 (0.03, 0.03)	0.16 (0.14, 0.17)	6.8	12.7
With R_b					
Jassby and Platt	3.97 (3.89, 4.05)	0.03 (0.02, 0.03)	0.13 (0.12, 0.14)	9.3	21.4
Webb et al.	4.30 (4.20, 4.40)	0.04 (0.03, 0.05)	0.13 (0.12, 0.15)	10.3	26.3

Table 2. Model 2 linear regressions on 137 pairs of P_{\max} and α (data sets without photoinhibition) calculated for different combinations of the Webb et al. (1974) and the Jassby and Platt (1976) models. The equations ($P < 0.001$) can be used to transform published values of P_{\max} and α as calculated with various models.

Model 2 linear regressions	P_{\max}		α	
	Equations	r^2	Equations	r^2
Webb et al. without R_b vs. Jassby and Platt without R_b	$Y = 1.134x - 0.300$	0.983	$Y = 1.335x - 0.002$	0.996
Webb et al. with R_b vs. Jassby and Platt with R_b	$Y = 1.092x - 0.036$	0.998	$Y = 2.069x - 0.013$	0.935
Webb et al. without R_b vs. Webb et al. with R_b	$Y = 1.018x - 0.222$	0.970	$Y = 0.387x + 0.012$	0.685
Jassby and Platt without R_b vs. Jassby and Platt with R_b	$Y = 1.057x - 0.514$	0.947	$Y = 0.600x + 0.006$	0.817

dence limits (C.L.) were estimated as

$$C.L._1 = \Sigma(df \text{ rms})/\chi^2_{\alpha/2, \Sigma df}$$

and

$$C.L._2 = \Sigma(df \text{ rms})/\chi^2_{(1-\alpha/2), \Sigma df}$$

where df is the residual degrees of freedom for each data set and rms the residual mean square.

Estimates of P_{\max} and α , computed with the two SAS methods (Gauss-Newton and derivative-free) for models 1 and 2 with and without parameter R_b differed by $<0.1\%$. The precision provided by the two methods being comparable, all results in the remainder of this paper refer solely to the Gauss-Newton method.

Estimates of P_{\max} from models 1 and 2 (Fig. 1) are in good agreement, with 77% of the curves having $<5\%$ difference. The same comparison for estimates of α shows rather poor agreement between the two models, with 78% of the curves having $>20\%$ difference. When an intercept value (R_b) is added to the models, the lack of agreement increases (Fig. 2), with 83% of the curves showing 5–10% difference for P_{\max} and 56% showing $>40\%$ difference for α . In all cases, values for the parameters calculated with the model of Webb et al. (1974) were higher than with that of Jassby and Platt (1976).

The 95% confidence intervals for P_{\max} and α (Table 1) show no overlap between the mean values of the parameters estimated by the two models when fitted with or without an intercept parameter. The 95% confidence intervals for the mean residual sums of squares show complete overlap, indicating no significant differences in precision with either model. How-

ever, the relative error of each parameter (SE divided by the value of the derived parameter and multiplied by 100) is smaller for the Jassby and Platt (1976) model, showing a precision higher by 11 and 20% for P_{\max} and 23 and 24% for α calculated with and without R_b respectively. This result agrees with the findings of Chalker (1980) and reflects the inclusion of an additional term in the power series (*see above*).

Constraining the P - I curve to the origin ($R_b = 0$) has a major impact on the estimation P_{\max} and α . Upon addition of R_b , the lack of agreement between the two models (calculated as the mean percent difference between models) increases from 4 to 8% for P_{\max} and from 24 to 46% for α .

Model 2 linear regression for P_{\max} , computed with various combinations of the Webb et al. (1974) and Jassby and Platt (1976) models (Table 2), shows good agreement between the two models with values of the slope varying between 1.018 and 1.134. The same analyses for α corroborate the disagreement already found between the models, with values of the slope varying between 0.387 and 2.069. Again, adding the intercept parameter (R_b) to the models produces a drastic increase in lack of agreement for α . Regressions confirm the greater sensitivity of the Webb et al. model to the inclusion or not of R_b . Equations in Table 2 can be used to transform published values of P_{\max} and α as calculated with various models.

Comparisons for the two models without a term for photoinhibition (Table 3) indicate that model 1 is the most sensitive to the addition or not of R_b , with 10 and 28% differences for

Table 3. Values of α and P_{max} calculated with $P-I$ models in the columns compared with those calculated with models in the rows. Mean values (%) and ranges of percent differences [$100 \times (\text{model in row} - \text{model in column}) / \text{model in column}$] are given for 137 data sets without photoinhibition and for 63 data sets with photoinhibition. Curves were fitted with and without an intercept parameter (R_b), except for the Platt et al. (1980) model.

	Without photoinhibition and without R_b	Without photoinhibition and with R_b		With photoinhibition and without R_b
		Webb et al. 1974	Jassby and Platt 1976	Platt et al. 1980
α	Webb et al.	28.4 (1.7, 110.5)	21.2 (0.0, 213.5)	5.7 (0.1, 32.5)
	Jassby and Platt	39.8 (1.9, 85.1)	21.4 (0.1, 161.3)	23.7 (4.8, 37.7)
P_{max}	Webb et al.	9.8 (0.1, 59.1)	7.0 (0.2, 75.4)	8.5 (0.1, 54.3)
	Jassby and Platt	12.2 (0.8, 59.4)	7.4 (0.0, 45.5)	4.9 (0.0, 30.1)

P_{max} and α respectively, vs. 7 and 21% for model 2. Differences can reach 12 and 40% for P_{max} and α respectively, when comparing model 2 without R_b to model 1 with R_b . Analysis of data sets showing photoinhibition indicates that a major error may be generated when combining models 2 and 3 for analyzing data sets with and without photoinhibition, which can lead to a difference in α as high as 24%. The same analysis shows that models 1 and 3 are closely related with percentage differences of 8 and 6% for P_{max} and α respectively. Models 1 and 3 should therefore be used when dealing with such data sets, even if a better fit (lower residual SS) would result from the use of model 2 on those data sets without photoinhibition.

Several lines of evidence suggest that α is the most critical parameter when estimating phytoplankton production. First, photosynthesis normally takes place at nonsaturating irradiances (Kirk 1983) and, since irradiances over most of the euphotic zone are nonsaturat-

ing, good estimates of α are usually required for modeling primary production. In the same vein, based on a study of 722 $P-I$ curves from the world oceans, Lewis et al. (1985) showed that errors in α have a greater effect on estimates of integrated production than equivalent relative errors in P_{max} on a daily average basis. In addition, samples from several depths in the euphotic zone off the leeward coast of Oahu, Hawaii, indicated that changes in the light-limited layer accounted for most of the variation in total primary production observed throughout the year (Bienfang et al. 1984). It follows that saturating irradiances, which are responsible for photoinhibition, represent only a small percentage of the euphotic zone, suggesting a rather small impact of photoinhibition on daily productivity. Finally, daily variations of α and not of P_{max} have been shown to be responsible for circadian variations in the daily specific productivity of phytoplankton (Harding et al. 1982; Vandevelde

Table 4. Production estimates for various published production models. For each model, primary production was calculated with each of the four pairs of P_{max} and α values listed in Table 1. For the equations without and with R_b , percent differences [$100 \times (\text{model 1} - \text{model 2}) / \text{model 2}$] were calculated between the estimates derived from the models of Webb et al. and Jassby and Platt.

Models used to calculate P I or $I_0 = 100 \mu\text{Einst m}^{-2} \text{ s}^{-1}$ $I_k = P_{max}/\alpha$ $K = 0.33$ (extinction coefficient)	Source	Parameters estimated with $P-I$ models	
		Without R_b	With R_b
$P = P_{max}[1 - \exp(-\alpha I/P_{max})]$	Webb et al. 1974	20.1	38.1
$P = P_{max} \tanh(\alpha I/P_{max})$	Jassby and Platt 1976	21.2	38.5
$P = P_{max} \alpha I / [(P_{max})^2 + (\alpha I)^2]^{1/2}$	Smith 1936	19.9	35.3
$P = P_{max} \ln(I_0/0.5I_k) / K$	Talling 1957	111.1	133.2
$P = \alpha I$	Vandevelde et al. 1989	26.6	58.8
$\Delta = (P_{max}/4.6) \ln\{I_0/I_k + [1 + (I_0/I_k)^2]^{1/2}\}$	Sathyendranath et al. 1989	24.1	49.4

Table 5. Production estimates calculated with the models of Webb et al. (1974), Jassby and Platt (1976), and Platt et al. (1980) for different irradiances. Five $P-I$ models were used to estimate P_{\max} and α which were reintroduced in the original equations to calculate production at different irradiances. Values calculated with the models in the columns are compared with those calculated with models in the rows for the same irradiance. Mean values of the percent differences [$100 \times (\text{model in row} - \text{model in column})/\text{model in column}$] are given in each case (0.0 for self-comparisons). In the last column, no calculations were made for irradiance higher than I_{\max} (see text).

	137 data sets without photoinhibition				63 data sets with photoinhibition
	Models without R_b		Models with R_b		Model without R_b
	Webb et al.	Jassby and Platt	Webb et al.	Jassby and Platt	Platt et al.
Without R_b					
Webb et al.					
$I = 100 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	0.0	2.6	2.4	4.2	3.0
$I = 300 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	0.0	4.0	3.5	6.1	—
$I = 500 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	0.0	2.2	1.6	3.1	—
Jassby and Platt					
$I = 100 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	2.6	0.0	3.3	2.7	3.4
$I = 300 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	4.0	0.0	2.0	2.9	—
$I = 500 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	2.2	0.0	1.4	1.4	—
With R_b					
Webb et al.					
$I = 100 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	2.4	3.3	0.0	3.2	—
$I = 300 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	3.5	2.0	0.0	3.0	—
$I = 500 \mu\text{Einst m}^{-2} \text{ s}^{-1}$	1.6	1.4	0.0	1.8	—

et al. 1989). However, P_{\max} can also be quantitatively important. For example a study of 138 stations in the eastern tropical Pacific (including no data on α) showed P_{\max} to be the best predictor for integral water-column production (Banse and Yong 1990).

The lack of agreement between P_{\max} and α estimated with the Webb et al. (1974) and the Jassby and Platt (1976) models is, in all cases, greater for α than for P_{\max} . This lack of agreement represents an additional source of error, which might have a cumulative effect when calculating areal photosynthesis. The estimation of daily production often involves the integration over time (24 h) of areal production calculated with photosynthetic parameters derived from nonlinear (as discussed above) or linear ($P = \alpha I$) photosynthetic models and the measured irradiance profile (see Platt et al. 1984). Similarly in the remote-sensing approach, water-column production normalized to total biomass (Λ) is a function of surface irradiance (I_0) with a slope Ψ (same dimensions as α). In this context, it has been found that Ψ is directly proportional to α , so that primary production can be calculated as $\Lambda = \Psi I = (\alpha/4.6)I_0$ (Platt et al. 1988). Linear models with the Ψ parameter can also be replaced by a $P-I$ curve (Cullen 1990), thereby elimi-

nating prediction of primary production in the dark. When the mean photosynthetic parameters calculated with models 1 and 2 are introduced into various published models (Table 4), differences in the resulting production estimates range between 20 and 133% for a non-saturating irradiance (I or I_0) of $100 \mu\text{Einst m}^{-2} \text{ s}^{-1}$. The largest differences occur for linear models, as could be expected. It must be noted that more sophisticated, nonlinear algorithms have been published recently (e.g. Platt et al. 1990).

When the photosynthetic parameters are reintroduced into the original nonlinear models, percent differences between production estimates are minimal, ranging between 3 and 6% for different irradiances (Table 5). Comparisons with the Platt et al. (1980) model were made at $100 \mu\text{Einst m}^{-2} \text{ s}^{-1}$ only, which is an irradiance below

$$I_{\max} = P_S/\alpha \ln[(\alpha + \beta)/\beta],$$

representing the threshold for photoinhibition.

The precision of primary production estimates is thus directly related to the measurement of α , and improved predictions would result from standardizing the calculation of parameters derived from the $P-I$ curve. Care should be taken when choosing a model to

describe $P-I$ relationships or comparing the results from different studies with different models. The equation of Platt et al. (1980) is a very useful and widely accepted model that takes into account photoinhibition. However, when one deals with a family of $P-I$ curves with and without photoinhibition, consistency should be maintained by avoiding the simultaneous use of their model for curves showing photoinhibition and of model 2 (Jassby and Platt 1976) for curves without photoinhibition.

Another approach in modeling $P-I$ curves does not require calculation of α . It considers 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 (*see* Cullen 1990) and can be described by an exponential function mathematically identical to that of Webb et al. (1974; Dubinsky et al. 1986; Cullen 1990). The approach is based on studies of the kinetics of photosynthesis.

Peterson et al. (1987) discussed the additional problem of subjectivity in parameter estimation when using the linear model ($P = \alpha I$), with possible bias in the choice of the linear or apparent linear range in irradiances. This problem can be avoided by nonsubjective simultaneous fitting with all the observations, as in our study. The simple linear determination of α may lead to underestimation and is therefore not recommended.

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Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment

Abstract—Water motion can be an important variable affecting the recruitment, metabolism, growth rates, feeding efficiency, and distribution of aquatic organisms. Recent studies suggest that flow speed may be an important factor regulating primary productivity of reef algal turf communities. We mea-

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sured profiles of flow speed over algal turfs with different canopy heights and over algal turfs growing on substrata that varied in microtopography. Profiles over sea urchin-grazed algal turfs with low canopy heights and algal turfs growing on topographical high points indicate that the boundary layer is dominated by turbulent eddies. In contrast, flow over algal turfs with higher canopy heights and those growing within depressions in the substratum is influenced more by viscous forces that may lead to diffusion-limited metabolism of these algal communities. These data demonstrate that flow speeds over coral reef algal turfs exhibit spatial variation over small spatial scales and temporal variation that is dependent on ambient flow speeds. Our results predict microscale variation in algal turf metabolism and suggest that photosynthetic rates of this component are likely to be below maximum capacity for a significant portion of the time.

Aquatic organisms experience costs and benefits of living in a moving, relatively vis-