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Utility of the light-saturation curve as an operational model for quantifying the effects of environmental conditions on phytoplankton photosynthesis

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ABSTRACT: The utility of the light-saturation curve as a tool to quantify effects of environmental conditions on the specific production rate of phytoplankton is assessed by comparing it with the more traditional approach which consists of directly relating the instantaneous rate of photosynthesis to the major factors believed to be affecting it. The internal consistency of data was tested by calculating the functional regression between measured and calculated values of the *in situ* production rate. Slope and y-intercept of the regression were not significantly different from slope 1 and y-intercept 0 ($r = 0.89$, $P < 0.1$ %). The light-curve method is shown to lead to a better understanding of the factors controlling the photosynthetic activity of phytoplankton in their natural environment. In particular it is shown that whereas changes in the pattern of photosynthesis (α^B, P_m^B) emphasized the profound effect that transient physical phenomena (passage of storms, periods of upwelling, etc.) had on the short-term dynamics of the phytoplankton production system, changes in the instantaneous rate of photosynthesis, $P^B(I)$ did not.

INTRODUCTION

In spite of the attention given by phytoplankton ecologists to the analysis of factors governing photosynthesis in natural phytoplankton assemblages, it still remains very difficult when analysing field data, to separate and quantify the effects of the various factors (chemical, physical, biological) which together control phytoplankton production (Morris, 1974; Jones, 1977; Harris et al., 1980). One approach often used consists of establishing statistical relations between the instantaneous rate of photosynthesis, $P^B(I)$ and the simultaneously observed values of the major environmental and biological factors believed to be affecting it (Margalef, 1965; Goldman et al., 1968; Platt and Subba Rao, 1970; Brylinski and Mann, 1973; Platt et al., 1973; Hameedi, 1976; Côté and Lacroix, 1979). The approach has generally emphasized the predominant influence of ambient light intensities on the photosynthetic rate, but has proven to be of limited utility in separating out the effects of other environmental covariates (Fogg, 1975; Platt et al., 1975).

Jassby and Platt (1976) and Platt and Jassby (1976) have suggested, as an alternative approach, that the importance of environmental factors in regulating the photosynthetic rate of natural phytoplankton assemblages could be assessed through their effect on the parameters describing the light-saturation curve. Photosynthesis-light curves are used extensively in primary productivity studies to predict the temporal and spatial variation in the instantaneous rate of photosynthesis resulting from fluctuations in environmental light intensities. Jassby and Platt (1976) found that the most consistently useful empirical relation between photosynthesis and light, for light fluxes lower than the threshold of photo-inhibition, was the hyperbolic tangent equation

$$P^B = P_m^B \tanh (\alpha^B I / P_m^B) / R^B$$

where α^B = initial slope of the curve (mg C mg Chla^{-1} h^{-1} w^{-1} m^2); P_m^B = specific productivity at saturating

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light (mg C mg Chla^{-1} h^{-1}); R^B = intercept at zero irradiance. These parameters correspond to physiological characteristics of the organism (see review by Harris, 1978) and can respond to changing environmental conditions including light intensity: they will not therefore be constant in space or time.

Côté and Platt (1983) presented data on the daily variations, over a 70 d period, of the photosynthetic parameters α^B and P_m^B and related the variations to changing environmental conditions through use of multivariate analysis. In the present paper a similar analysis is performed on the simultaneously measured values of the instantaneous rate of photosynthesis. By comparing the results of these 2 approaches we shall show that the traditional approach not only provides less information about the factors controlling photosynthesis in natural phytoplankton assemblages but much more importantly can result in grossly misleading information regarding the relative importance of a given factor. In particular it is shown that whereas changes in the pattern of photosynthesis (α^B, P_m^B) emphasized the profound effect transient physical phenomena (passage of storms, periods of upwelling, etc.) had on the short-term (daily-weekly) dynamics of the phytoplankton production system changes in the instantaneous rate $P^B(I)$, did not.

We first present the results of a regression analysis describing the relation between the instantaneous rate of photosynthesis as measured *in situ* and that calculated from knowledge of ambient light levels and the photosynthesis-light relation. This analysis indicated whether or not the photosynthesis-light curves adequately describes the photosynthetic behavior of the phytoplankton populations. Good agreement between the 2 values is a prerequisite to the use of the light-saturation curve as an aid in the assessment of the factors which influence photosynthesis.

METHODS

Bedford Basin is a small enriched marine inlet 70 m deep with a surface area of 17 km^2. It is separated from the sea by a channel Halifax Harbour, 10 km long and 400 m wide at the narrowest part. The channel, which is shallower than the Basin, constitutes a sill of 20 m depth. The waters in the basin above the sill depth exchange continuously with the open sea by a variety of mechanisms driven by tides, winds and freshwater runoff (Platt and Conover, 1971; Platt et al., 1972). A detailed account of the ecology of this inlet and others on the Atlantic coast of Nova Scotia is given in Platt and Conover (1975).

Water samples were collected on 70 consecutive days from 18 May to 26 July 1975 between 0830 and 0900 h from a station located in the southwesterly corner of Bedford Basin. All samples were collected from 5 m depth using a 30 l Niskin sampler. The water was filtered through 153 µm mesh netting to remove large herbivores and transferred to a large plastic carboy covered with an opaque plastic bag to prevent damage to the cells from strong surface radiation. The sample was then transported to a barge located in the vicinity of the sampling station where a field station had been set up for rapid processing of the sample. The water sample served for the determination among others, of chlorophyll *a*, pheopigments, particulate carbon, salinity, Coulter counter counts and primary production. A vertical profile of temperature was recorded with a bathythermograph. A detailed account of the physical, chemical and biological characteristics of the Basin during the sampling period is given in Côté and Platt (1983).

Primary production was measured by both the *in situ* and incubation (light-saturation curve) methods. For the *in situ* measurement (^{14}C technique), 5 light bottles and 1 dark bottle were attached with a special frame to a weighted nylon line and suspended over the side of the barge at 5 m depth. The samples were incubated for 3 h from approximately 1000 h to 1300 h local time. The amout of light available under water during the ^{14}C *in situ* experiments was measured either directly by use of a submersible integrating radiometer (Platt et al., 1970) or calculated from total incident light measurements made at Citadel Hill, Halifax (situated 3.5 km from the sampling station), with a Kipp CM6

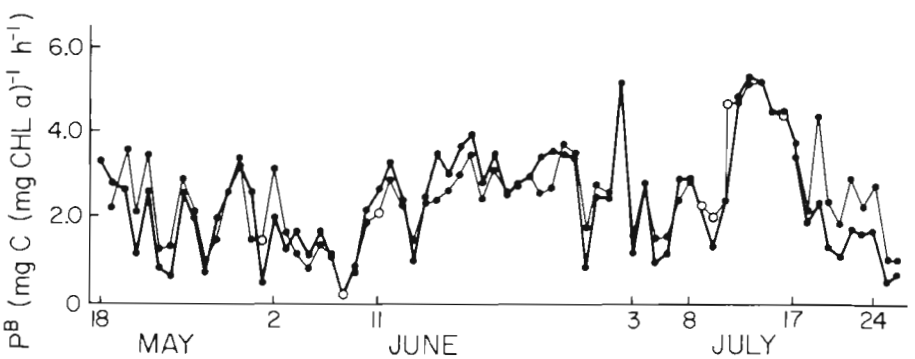


Fig. 1. Temporal variations in *in situ* specific production rate $P^B(I)$ (●——●) and computed values of P^B from corresponding light-saturation curves (●——●). Open circles: values obtained from Citadel Hill light measurements

pyranometer. In the latter case light intensity at 5 m depth was calculated using Beer's law; total incident light measurements were corrected according to Strickland (1958), and depth attenuation was estimated by averaging the extinction coefficients for the days prior to the sampling period and those following it.

Light-saturation experiments were carried out in triplicate for each sample using the methods outlined in Platt and Jassby (1976). A Plexiglas cuvette containing a 1 % solution of $CuSO_4$ was placed at the front of each incubator to filter out the far-red and infra-red portion of the spectrum. Incubation of samples were carried out simultaneously with the *in situ* experiments. The light-saturation curve was obtained by normalizing the production rates to chlorophyll *a* and plotting the rates as a function of light intensity, I ($W\ m^{-2}$). The hyperbolic tangent equation was fitted to the data by the two step fitting procedure of Jassby and Platt (1976).

From the fitted light-saturation curve for each sampling day, an estimate of the *in situ* production rate at 5 m was calculated by substitution of internal light field measurements.

Chlorophyll *a* and pheopigments were measured by the fluorometric technique of Yentsch and Menzel (1963), as modified by Holm-Hansen et al. (1965). Particulate carbon was determined using a Hewlett-Packard model 185 B CHN analyser. Salinity was measured by the conductivity method with an autolab 601 inductively coupled salinometer. Particle-size distribution (2 to 203 μm in diameter) was measured by a Coulter counter model T using 100, 180 and 400 μm tubes. Mean cell volume was calculated in the 4 to 128 μm size range. The diversity index of the nanoplankton size fraction (4 to 16 μm) was determined for each of the spectra using the Shannon-Weaver expression, Diversity = $\Sigma p_i \ln p_i$, where p_i = amount of particulate material in a given size category expressed as a function of the total volume of either nanoplankton or microplankton (Parsons, 1969). Daily internal light levels were estimated by summing the hourly sunlight readings over the 24 h period preceding the time of collection of the sample, and multiplying by the extinction coefficient. Hourly sunlight readings were first multiplied by 0.5 to give the fraction in the photosynthetically active band (380 to 725 nm) and further reduced by 10 % to allow for losses at the sea surface (Strickland, 1958).

RESULTS AND DISCUSSION

Temporal variations in $P^B(I)$

Temporal variations in the *in situ* specific production rate are shown in Fig. 1. Also shown are the specific production rates obtained from the corresponding light-saturation curve. The average magnitude, the standard deviation, the coefficient of variation and the range of $P^B(I_{5m})$ [hereafter referred to as $P^B(I)$], $P^B(I)/P^B_m$, I_{5m}, $I_{5m}/I_{surface}$ and $I_{5m}/I_{½k}$, are given in Table 1. The coefficient of variation of $P^B(I)$ compares with values respectively of 30.86 % and 28.85 % for α^B and P^B_m (Côté and Platt, 1983). The mean magnitude of the ratio $P^B(I)/P^B_m$, was not significantly different from 0.50.

Calculated *versus* measured *in situ* specific production rate

The internal consistency of the data was tested by calculating the functional regression between the measured and calculated values of the *in situ* production rate. Functional regression takes into account error measurement in both the x and y variables (Ricker 1973). It gave the following equation (Fig. 2):

$$P^B_{calculated} = 0.36 + 0.93\ P^B_{measured} \quad (1)$$

The slope and y-intercept of the line are not significantly different from slope 1 and y-intercept 0. The correlation coefficient (r = 0.89) is significant at the 99.9 % level.

Table 1. Mean magnitude, standard deviation (S.D), coefficient of variation (C.V.), and range (minimum-maximum) of *in situ* specific production rate (P^B [I]); ratio of P^B (I) to specific productivity at saturating light intensities (P^B_m); *in situ* light intensity (I_{5m}); ratio of I_{5m} to surface light intensity ($I_{surface}$); ratio of I_{5m} to I_k, i.e. the light intensity at which the linear part of the light saturation curve intersects the plateau; and ratio of I_{5m} to $I_{½k}$, i.e. the light intensity corresponding to ½ P^B_m

Parameter	Units	Mean	S.D.	C.V.	Range
$P^B(I)$	mgC (mgChl *a*)$^{-1}$ h^{-1}	2.38	1.22	51.3	0.18– 5.30
$P^B(I)/P^B_m$	——	0.48	0.21	43.6	0.05– 1.04
I_{5m}	$W\ m^{-2}$	23.76	10.05	42.3	3.44–47.45
$I_{5m}/I_{surface}$	%	27.08	9.61	35.5	4.62–52.82
I_{5m}/I_k	——	0.63	0.40	64.2	0.10– 1.95
$I_{5m}/I_{½k}$	——	1.17	0.69	58.9	0.17– 4.66

Further improvement in the accuracy of the measurement of $P^B(I)$ could be achieved by reducing the error variances of α^B and R^B. The mean relative error of these parameters, calculated as the width of the 90 % confidence interval divided by twice the parameter estimated, were respectively, 15 and 48 %. In comparison the mean relative error of P^B_m is 5 %.

Relation between *in situ* production rate P(I) and chlorophyll *a*

The plot of the *in situ* rate of photosynthesis, P(I), against chlorophyll *a* shows considerable scatter (Spearman's rank correlation coefficient = 0.37, $P < 1$ %) (Fig. 3A). Also noticeable is the lack of systematic change in the photosynthetic rate of the various algal assemblages sampled over the 70 d period. These observations contrast markedly with (1) the overall strong correlation between the non-normalized photosynthetic parameters, α and P_m, and chlorophyll *a* (Spearman's rank correlation coefficient = 0.82 and 0.79 respectively; $P < 1$ %), and (2) the systematic changes observed in the relationship between the photosynthetic parameters, α and P_m, and chlorophyll *a*, over the 70 d sampling period (Fig. 3B and C) (see discussion in Côté and Platt, 1983).

Environmental control of *in situ* specific production rate, $P^B(I)$

Table 2 shows the correlations of the instantaneous specific production rate with environmental and biological variables chosen on the basis of their known effects on phytoplankton photosynthetic rates.

Correlation coefficients to the right of the main diagonal are based on all 70 data points and those to the left on 41 data points. The correlations of the various variables with mean cell volume are shown only in the latter section of the correlation matrix. A reduced data set was used because mean cell volume was calculated from Coulter counter counts of seawater. Since these estimates can be unreliable when chain-forming species or colonies such as *Dinobryon balticum* are present, only those data points not including such forms were used. This left 41 data points in 2 blocks, 11 June to 2 July and 8 to 26 July. These periods were dominated by dinoflagellates and green flagellates.

The pheopigment : Chl *a* ratio is included in the study as a potential measure of nutrient regeneration resulting from grazing activity. It is assumed that the major portion of the pheopigments produced in the Basin result from the passage of chlorophyll *a*

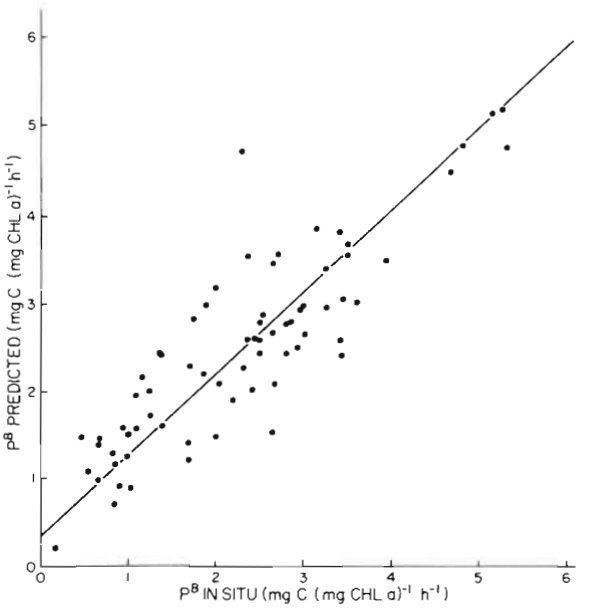
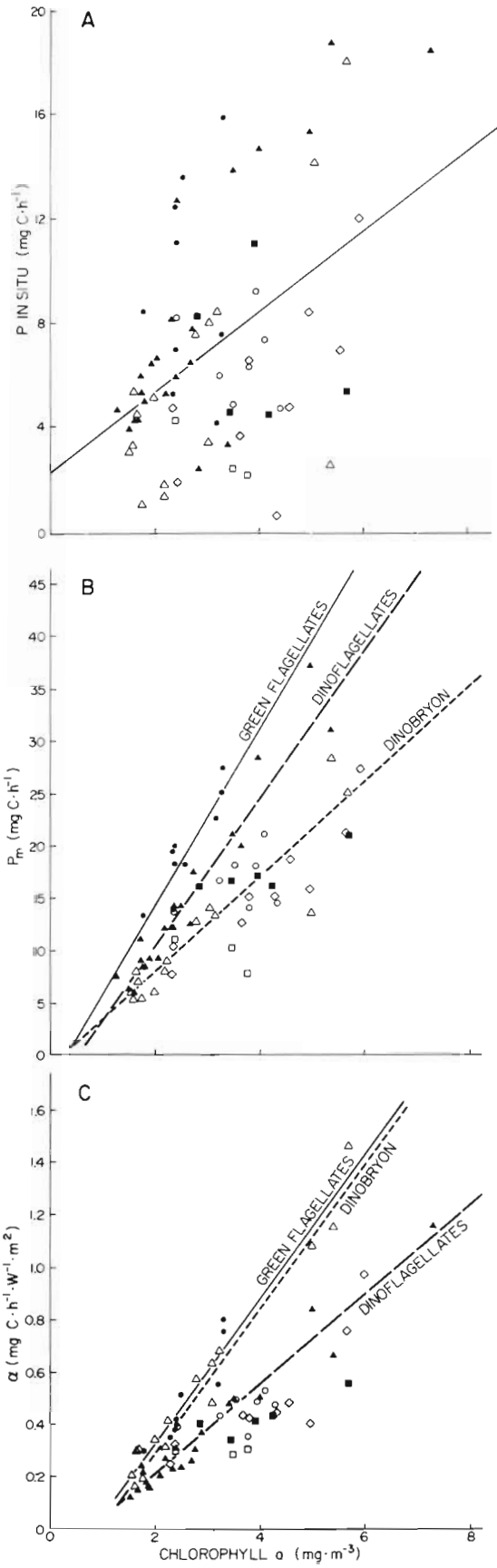


Fig. 2. Relation between values of specific production rate measured *in situ* ($P^B_{in\ situ}$) and values computed from the corresponding light-saturated curves ($P^B_{predicted}$)

molecules through the digestive tract of planktonic herbivores (copepods and microplankton) (Daley, 1973; Shuman and Lorenzen, 1975) and is not the result of dying cells (Daley and Brown, 1973). Lorenzen (1967) found a positive correlation between zooplankton abundance and the pheopigment : Chl *a* ratio, and suggested using this ratio as an indicator of grazing activity. Similar relations have been found by Malone (1971), Glooschenko et al. (1972), and Eppley et al. (1978). In the present study, the pheopigment : Chl *a* ratio varied inversely with tidal height throughout much of the sampling period (see Côté and Platt, 1983: Fig. IU & O). This is as would be expected if the pheopigment : Chl *a* ratio reflected a measure of grazing activity since, maximum concentrations of both phytoplankton and zooplankton are frequently found at low tide in Bedford Basin, as a result of a dilution effect (Platt and Conover, 1971). It should also be noted that the pheopigment : Chl *a* ratio was only slightly correlated with internal light levels (Table 2A). Gieskes et al. (1978) have demonstrated the importance of irradiance in determining the distribution of chlorophyll degradation products. In the present study, irradiance could account for only 10 % of the variability of the pheopigment: Chl *a* ratio. This factor should not interfere therefore with the pheopigment : Chl *a* ratio being used as a measure of grazing pressure.

Water density at 5 m depth is used in the study as a measure of the stability of the water column. High values of density correspond with periods when the water column is strongly stratified and low values with



periods of weak stratification (Côté and Platt, 1983: Fig. 1A & E).

In Table 2A, the *in situ* specific production rate, $P^B(I)$, is seen to be strongly correlated with internal light levels received during the 3 h incubation period, I_{5m}. This variable alone accounts for up to 51 % (n = 70) of the variance in $P^B(I)$. $P^B(I)$ is also correlated, although to a lesser extent, with most other variables. The strength of the correlations of $P^B(I)$ with the various variables differs, however, depending on whether they are based on all 70 data points or on the reduced data set. Similarly, the rank order in importance of the various variables, based solely on the strength of the correlations, differs in the two segments of the matrix.

The percentage of the variance in $P^B(I)$, attributable to variables other than internal light intensities, was determined by carrying out a stepwise regression between the residuals, $P^B_{residual}$, of the functional regression between $P^B(I)$ and internal light levels, and possible covariates. The correlations between $P^B_{residual}$ and the various covariates are given in Table 2B. $P^B_{residual}$ was most strongly correlated with the pheopigment : Chl *a* ratio, whether the correlation was based on all 70 data points, or on the reduced data set. In the case, however, of the reduced data set, $P^B_{residuals}$ was as equally strongly correlated with mean cell volume.

The results of the stepwise regression using the reduced data set are shown in Table 3 (Regression 1). The only variable that significantly reduced the unexplained variance in $P^B_{residual}$ was the pheopigment : Chl *a* ratio. It accounted for 62 % of the variability in $P^B(I)$ not explained by internal light intensities. Given, however, that mean cell volume and the pheopigment : Chl *a* ratio are strongly correlated, a second stepwise regression was carried out (Table 3, Regression 2). This time $P^B_{residual}$ was first regressed against mean cell volume, and additional variables were then entered in the regression equation following the standard procedure (Nie et al., 1975, pp. 320–367). In the latter case, mean cell volume accounted for 50 % of the unexplained variance in $P^B_{residual}$ and the

Fig. 3. (A) Relation between the *in situ* production rate P(I) and chlorophyll *a* [P(I) = 2.30 + 1.52 Chl *a*]. (B) and (C) Relation between the non-normalized photosynthetic parameters α and P_m and chlorophyll *a*. Regression lines for Periods 1, 3 and 5 are: Period 1 (– – – –) P_m = 0.65 + 3.63 Chl *a*, α = −0.25 + 0.28 Chl *a*; Period 3 (— — — —) P_m = −4.06 + 7.03 Chl *a*, α = −0.13 + 0.17 Chl *a*; Period 5 (——) P_m = −2.94 + 8.43 Chl *a*, α = −0.36 + 0.32 Chl *a*. Symbols refer to the 7 periods discussed in Côté and Platt (1983): Period 1: (△), 18 May to 1 June, Dinobryon; Period 2: (◇) 2 to 10 June, Diatoms; Period 3: (▲) 11 June to 2 July, Dinoflagellates; Period 4: (■) 3 to 7 July, Diatoms; Period 5: (●) 8 to 16 July, Green flagellates; Period 6: (○) 17 to 23 July, Green flagellates and dinoflagellates; Period 7: (□) 24 to 26 July, Dinoflagellates

Table 2. (A) Correlation matrix for *in situ* specific production rate, P^B (I). Correlations to the right of the main diagonal are based on all 70 data points; those to the left, on 41 data points (11 June to 2 July and 8 to 26 July). I_{5m} = light intensity received at 5 m during the 3 h incubation period; Pheo : Chl *a* = pheopigment : chlorophyll *a* ratio; Temp. = water temperature at 5 m; I_0 = total amount of light received at 5 m during the 24 h period preceding collection of the sample; C : Chl *a* = carbon : Chlorophyll *a* ratio; σ_t = water density at 5 m; diversity = logarithm to the base 10 of the nanoplankton diversity measure. (B) Correlations between residuals, $P^B_{residual}$, of the functional regression between P^B (I) and I_{5m}, and the variables given in (A). Correlations are based on both 70 and 41 data points

	A									B	
	P^B(I)	I_{5m}	Pheo: Chl *a*	Temp.	I_o	C: Chl *a*	σ_t	Diversity	Salinity	$P^B_{residual}$ (n = 70)	$P^B_{residual}$ (n = 41)
P^B(I)	—	0.71•	0.49•	0.39•	0.47•	0.28#	−0.37••	0.07	0.01	—	—
I_{5m}	0.62•	—	0.08	0.26#	0.41•	0.47•	−0.06	0.13	0.20	—	—
Pheo: Chl *a*	0.43••	−0.25	—	0.64•	0.01	−0.06	−0.48•	0.03	0.12	0.54•	0.79•
Temp.	0.53•	0.07	0.66•	—	0.30#	0.01	−0.56•	0.11	0.36••	0.18	0.54•
I_o	0.36#	0.33#	−0.32#	0.14	—	0.50•	0.00	0.20	0.31••	−0.23	−0.28
C: Chl *a*	0.11	0.49••	−0.37#	−0.37#	0.52•	—	0.05	0.06	0.05	−0.25#	−0.43••
σ_t	−0.58•	−0.02	−0.55•	−0.39••	0.26	0.22	—	0.42•	0.56•	−0.42•	−0.64•
Diversity	−0.17	0.17	−0.34#	−0.01	0.39#	0.01	0.64•	—	0.56•	−0.30#	−0.40••
Salinity	−0.20	0.03	−0.08	−0.34#	0.31#	−0.05	0.74•	0.64•	—	−0.25#	−0.26
Cell Vol.	−0.44••	0.17	−0.78•	−0.73•	0.43••	0.49••	−0.02	0.17	0.03	—	−0.71•

• Significant at $P < 0.001$; •• Significant at $P < 0.01$; # Significant at $P < 0.05$

Table 3. Summary of results of stepwise regression analysis for $P^B_{residual}$. R = correlation coefficient; R^2 = coefficient of determination; RSQ change = percentage of variance of $P^B_{residual}$ attributed to each of the variables. In Regression 1 and 2 the reduced data set (n = 41) was used, whereas in Regression 3 all 70 data points were used. Regression 2 was obtained by first regressing $P^B_{residual}$ against mean cell volume. Other regressions were carried out following the standard procedure

Step	Variable	F-value	Significance	R	R^2	RSQ Change
			Regression 1			
1	Pheo:Chl *a*	60.87	0.000	0.79	0.62	62.2
2	σ_t	6.78	0.013	0.83	0.68	6.0
3	C:Chl *a*	2.55	0.119	0.84	0.70	2.2
4	Temp.	0.05	0.820	0.84	0.70	0.0
			Regression 2			
1	Cell vol.	37.81	0.000	0.71	0.51	50.5
2	Pheo:Chl *a*	14.12	0.001	0.80	0.64	13.9
3	σ_t	5.00	0.032	0.83	0.69	4.4
4	C:Chl *a*	1.65	0.207	0.84	0.70	1.4
			Regression 3			
1	Pheo:Chl *a*	27.63	0.000	0.54	0.29	29.2
2	Salinity	11.01	0.001	0.63	0.39	10.1
3	C:Chl *a*	4.98	0.029	0.66	0.44	4.3
4	Temp.	1.14	0.289	0.67	0.45	1.0

pheopigment : Chl *a* ratio for a further 14 %. When the stepwise regression is carried out using all 70 data points, the pheopigment : Chl *a* accounts for 29 % of the unexplained variance in $P^B_{residual}$ and salinity for 10 % (Table 3, Regression 3). In Regressions 1 and 2 roughly 65 % of the variance in $P^B_{residual}$ can be explained while in Regression 3, 39 % of the variance $P^B_{residual}$ is explained.

The positive correlation between P^B(I) and internal light levels was to be expected. As for the negative correlation between $P^B_{residual}$ and mean cell volume, 2 possible explanations may be given depending on whether the *in situ* specific production rate is situated in the light-limited or light-saturated range of the photosynthesis-light curve. If P^B(I) is in the light-limited range, the negative correlation is best explained by self-shading of the chlorophyll *a* molecules within the cells. Platt and Jassby (1976) have concluded from geometrical arguments that there should be an inverse relation between the initial slope

of the light-saturation curve, α^B, and the mean cell volume of the individual cells of the phytoplankton population provided that the chlorophyll *a* concentration per unit cell volume is kept constant. Taguchi (1976, 1981) has verified the inverse dependence of α^B on mean cell volume for cultures of the diatom *Coscinodiscus centralis* and for field populations of the dinoflagellate *Ceratium longipes.* If $P^B(I)$ is in the light-saturated range, however, control could be through nutrient uptake rates depending on the surface to volume ratio of cells (Eppley et al., 1969; Taguchi, 1976). In Côté and Platt (1983), α^B and P^B_m were both found to be strongly negatively correlated with mean cell volume. The relation between $P^B_{residual}$ and mean cell volume is shown in Fig. 4. Open circles indicate days on which the *in situ* light intensities were lower than the light intensity observed at ½ P^B_m. Throughout the 70 d period, approximately half of the values of $P^B(I)$ were found to be below the value taken at the half-saturation constant ($P^B_m/2$) and thus were located on the linear portion of their respective light-saturation curves. The remaining half were located for the most part between the values of $P^B(I)$ taken at the half-saturation constant and the value of $P^B(I)$ taken at I_k, that is the light intensity at which the extrapolation of the linear part of the light-saturation curve intersects the plateau, P^B_m. Only a few data points had values of $P^B(I)$ greater than I_k; however, these values were still lower than the corresponding value of P^B_m. The negative correlation between $P^B_{residual}$ and mean cell volume is therefore likely to be the result of both explanations.

The positive association of $P^B_{residual}$ and the pheopigment : Chl *a* ratio suggests that the specific production rate is being limited not by *in situ* nutrient concentrations, low as they may have been (e.g. the average concentration of NH_3 over the 70 d sampling period was 0.6 mg-atoms m^{-3}), but rather by the rate at which they were being made available through grazing activity. It is important to note that the relation between $P^B(I)$ and the pheopigment : Chl *a* ratio holds whether P(I) is first normalized to chlorophyll *a* or regressed upon this variable. The possibility therefore that the observed relation is simply the result of both parameters having been normalized to the same variable can be excluded. Further support for the argument that $P^B(I)$ was being limited by the rate of supply of nutrients comes from the fact that the calculated nitrogen requirement was positively correlated with the pheopigment : Chl *a* ratio ($r = 0.61$; $P < 1$ %) but not correlated with total nitrogen content (nitrate + nitrite + ammonia) (Côté and Platt, 1983: Fig. 7).

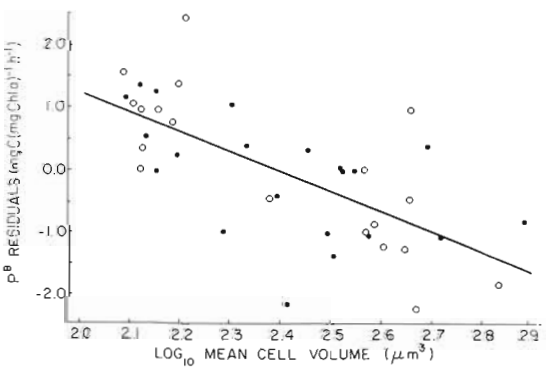


Fig. 4. Relation between residuals of the functional regression between $P^B(I)$ and incident solar radiation received during 3 h incubation period ($P^B_{residual}$) and logarithm to the base 10 of mean cell volume. Regression based on 41 data points ($P^B_{residual}$ = 7.63 – 3.16 mean cell volume, $r = -0.72$; $P < 1$ %). Open circles: days on which *in situ* light intensity was lower than light intensity observed at half-saturation constant ($I_{½k}$)

Utility of light-saturation curve as operational model for quantifying effects of environmental conditions on phytoplankton photosynthesis

Côté and Platt (1983) presented data on day-to-day variations of the photosynthetic parameters α^B and P^B_m and of the derived parameter I_k ($= P^B_m/\alpha^B$), and related the variations to changing environmental conditions. In the present paper a similar analysis has been performed on the simultaneously measured values of the *in situ* specific production rate. By comparing the results of both approaches, we shall show that systematic study of the variations in the photosynthetic parameters leads to a better understanding of the factors controlling the photosynthetic activity of the phytoplankton in their natural environment.

The temporal fluctuations in the photosynthetic parameters α^B and P^B_m were shown in Côté and Platt (1983) not to be stationary, i.e. the mean and the variance of the time-series depended not only on their length but also on absolute time. Most variations in these parameters were associated with episodic atmospheric phenomena. Three events during the 70 d period were shown to have a profound effect on the physico-chemical characteristics of the Basin and on the short-term dynamics of the phytoplankton production system. These events consisted of a storm on 6 to 7 June, a period of strong southwesterly winds between 17 and 23 July, and a hurricane on 28 July. The importance of these 3 events to the dynamics of the phytoplankton production system was apparent upon examination of the relation between the non-normalized photosynthetic parameters α and P_m and chlorophyll *a*. Systematic changes in the relation of the photosynthetic parameters to chlorophyll *a* were noted and shown to coincide with the 3 events. No such systematic change was noted however when the *in situ* production rate was plotted against chlorophyll *a*. The

latter data provided no indication that the productivity of the phytoplankton production system was affected by the physical transients.

As for the potential covariates of the photosynthetic parameters, these were found, for those periods when reliable measurements of mean cell volume were available, through correlation and regression analysis carried out on the normalized values of the photosynthetic parameters. The variance in P_m^B was attributed to variations in mean cell volume, the pheopigment : Chl *a* ratio, species diversity, water temperature and the stratification of the water column. The variances in α^B and I_k were attributed respectively to variations in mean cell volume and light intensity. In contrast (present study), aside from incident light intensity, only mean cell volume and the phaeopigment : Chl *a* ratio were found to reduce significantly the variability of $P^B(I)$. Furthermore, Table 4 shows that although all 3 parameters, $P^B(I)$, P_m^B and α^B, were significantly correlated with mean cell volume, it accounted for only 32 % of the variability of $P^B(I)$ compared with respectively 58 % and 52 % of the variability of P_m^B and α^B. We suppose that in the case of $P^B(I)$ the variance explained by mean cell volume is smaller because noice is introduced by not dissociating the effects of cell size on the 2 processes responsible for the observed correlation: self-shading of the chlorophyll *a* molecules within the cell and nutrient uptake.

Moreover the pheopigment : Chl *a* ratio accounts for roughly 10 % of the variability of $P^B(I)$ compared with 20 % of the variability of P_m^B (Table 4). This is understandable, given the equally strong dependence of $P^B(I)$ on the light reactions as on the dark reactions of photosynthesis but illustrates that the importance of a particular environmental factor in regulating the photosynthetic activity of phytoplankton populations may be underestimated if the instantaneous rate of photosynthesis is the only measure of photosynthetic activity available.

Finally, in the case of the photosynthetic parameters, additional variables were found, by examining the residuals of the relation between the photosynthetic parameters and the environmental and biological variables for discrepancies between periods, to affect the photosynthetic activity of the phytoplankton populations. For instance, examination of the relation between P_m^B and mean cell volume indicated lower values during the period of southwesterly winds (17 to 23 July). This, as suggested in Côté and Platt (1983), was possibly the result of deep off-shore water moving into the Basin and consequently the phytoplankton populations being shade-adapted. Similarly, examination of the relation between α^B and mean cell volume revealed a number of outliers for experiments made during the period when chlorophytes were most abundant, suggesting that superimposed on the cell size effect was a species effect. Examination of residuals also suggested that on the last few days of the sampling period (24 to 26 July), the phytoplankton community was responding in a stressful manner, as evidenced by reduced photosynthetic capacities, to turbulent conditions being generated by the approaching hurricane.

Table 4. Summary of the percentage of the variance of P^B (I), P_m^B and α^B attributed to various environmental and biological factors (based on results of stepwise regression with the reduced data set)

	$P^B(I)$	P^B	α^B
I_{5m}	35.0	–	–
Cell volume	32.0	57.5	52.0
Pheo: Chl *a*	9.1	18.2	–
σ_t	–	6.0	–
Temp.	–	4.0	–

As for those periods when reliable measurements of mean cell volume were not available, there is no reason – based on the relation between $P^B(I)$ and the various environmental factors examined – to suspect any change in inferred causal mechanisms at these times. In the case of photosynthetic parameters, it was possible to compare the photosynthetic behavior of the various phytoplankton assemblages, given the systematic changes in the relation between the non-normalized photosynthetic parameters and chlorophyll *a* and to show that the relative importance of the various covariates varied throughout the 70 d period. In particular, it was shown that species composition could be as important as mean cell volume in explaining the variability in the photosynthetic parameters. For instance, it was shown that during the 2 periods when diatoms were abundant the photosynthetic capacities of the phytoplankton assemblages were similar in spite of differences in cell size. A further possible species effect was noted during the period when the chrysophyte *Dinobryon balticum* dominated numerically the phytoplankton community (18 to 28 May). The relation between α and chlorophyll *a* and that between P_m and chlorophyll *a* were asymetrical, i.e. the slope of the regression line in Fig. 3B was the lowest observed over the 70 d period while the slope of the regression line in Fig. 3C was among the highest observed. Thus cell size could account for the magnitude of at most one or the other of the parameters but not both.

From these comparisons, it is apparent that a better understanding of the factors controlling the photosynthetic activity of the phytoplankton in their natural environment may be achieved by monitoring changes in the instantaneous rate of photosynthesis.

The main reason for the poor performance of the

traditional approach is that the instantaneous rate of photosynthesis is a function of the photosynthetic parameters. Therefore, unless the relation between α^B and P_m^B is invariant, attempts to relate the instantaneous rate of photosynthesis to variations in environmental conditions will be difficult. Côté and Platt (1983) show that while α^B and P_m^B are often strongly correlated the relation between these parameters is not constant.

CONCLUSION

The present study shows that systematic study of the photosynthesis-light relation offers a superior approach to resolving environmental effects on photoplankton photosynthesis. Consistent use in the field of this approach should aid in discovering the mechanisms by which the phytoplankton production system operates. This type of analysis has, so far, been successfully applied in both marine and freshwater environments on the seasonal time-scale and on the diel time-scale (Platt and Jassby, 1976; MacCaull and Platt, 1977; Lastein and Gargas, 1978; Williams, 1978; Harrison and Platt, 1980).

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