

Diel variations in the photosynthetic parameters of coastal marine phytoplankton

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Abstract

The diel variations in the assimilation number, P_m^B , of natural assemblages of coastal marine phytoplankton were examined and a working model proposed to characterize the apparent diel rhythm. No rhythm could be distinguished for the initial slope of the light saturation curve, α , although α and P_m^B were highly correlated and the daily and hourly variations in α were as great as those in P_m^B . Diel variations in the derived parameter $I_k (\equiv P_m^B/\alpha)$ were described by a model similar to that proposed for P_m^B . The rhythm in P_m^B was found to have a significant effect on the estimation of daily productivity. Correlations with environmental covariates support the hypothesis that the photosynthetic rhythms observed in the field result both from intrinsic oscillations within the phytoplankton cells and from varying environmental factors.

Although considerable research has been carried out on diel rhythmicity in phytoplankton photosynthesis (see Sournia 1974), the investigations have rarely been designed with a view to improving our capacity to predict gross daily productivity (gdp). To reduce variance on estimates of gdp by allowing for the effects of diel rhythms we must understand how the relationship between photosynthesis and light changes through the day. In other words, we have to be able to answer the question: how stable are the parameters of the light saturation curve on time scales ≈ 24 h or less? A parallel question is: what can we learn from diel variations in the photosynthetic parameters about the physiological ecology of phytoplankton? Here we describe a set of experiments addressed to these questions for natural assemblages of coastal marine phytoplankton.

Mathematical framework

From zero light up to the threshold of photoinhibition, only two parameters are required to give a sufficient mathematical description of the light saturation curves.

Platt et al. (1977) have demonstrated that the various representations of this curve may all be recast in terms of the same two parameters: α , the initial slope [$\text{mg C}(\text{mg Chl } a)^{-1} \text{ h}^{-1}(\text{W m}^{-2})^{-1}$] and P_m^B , the specific productivity at saturating light [$\text{mg C}(\text{mg Chl } a)^{-1} \text{ h}^{-1}$]. These parameters satisfy the requirements of well chosen parameters (Ross 1970); further, their ratio, $P_m^B:\alpha$, is identical to the parameter I_k , frequently used to define the state of physiological adaptation of algal populations (Talling 1957; Steemann Nielsen 1962). Jassby and Platt (1976) have shown that of the various formulations of the light saturation curves, the hyperbolic tangent equation

$$P^B = P_m^B \tanh(\alpha I/P_m^B) - R^B \quad (1)$$

gives the best fit to field data, at least for coastal assemblages. In Eq. 1, R^B is the normalized dark respiration in $\text{mg C}(\text{mg Chl } a)^{-1} \text{ h}^{-1}$: it accounts for the difference between gross production and the net particulate production measured by the ^{14}C -method.

Methods

During the period from May to August 1975, a series of eleven diel experiments was carried out from a barge stationed in the Bedford Basin, Nova Scotia. An ac-

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count of the phytoplankton, nutrients, and hydrography of the basin is given in Platt et al. (1970). In each experiment, samples were taken about every 3 h, beginning at 0900, for a total of 9 or 10 time periods. (The single exception was the experiment from 5–8 August, in which samples were taken every 4 h for a total of 18 time periods.) At the beginning of each time period, water was pumped from 5 m with a submersible pump and filtered through 153- μ nylon netting into a large carboy. After a thorough mixing, ≈ 5 liters were poured from the carboy into each of three small carboys. Three replicate light saturation experiments were then begun, each using water from a different carboy. Two 1-liter samples were also removed from each carboy and filtered through Millipore filters (0.45 μ). These filters were frozen immediately and later used for chlorophyll *a* determination. Twenty plastic bottles (125-ml capacity) were filled with filtered seawater and quickly frozen in Dry Ice and methanol to be used later for analysis (in quadruplicate) of nitrate, nitrite, phosphate, silicate, and ammonia. A salinity sample was taken and water temperature recorded.

Light saturation experiments were carried out as outlined by Jassby and Platt (1976) using 10-chamber incubators. 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 infrared portion of the spectrum. Circulating seawater pumped from 5 m served to control temperature. Incubation lasted 2 h. The total radiation at each bottle position was determined as described by Jassby and Platt (1976). Irradiances ranged from 0–225 W m^{-2} . As many sets of light readings were taken as time permitted (usually 3 or 4 per incubator per diel experiment); readings were averaged over the experiment.

The uptake of ^{14}C and the concentration of chlorophyll *a* were measured by the methods of Jassby and Platt (1976). Nitrate, nitrite, and phosphate were determined according to Strickland and Parsons (1972); ammonia according to Solórzano (1969); and silicates according to Mullin

and Riley (1955). Salinity was measured by the conductivity method, with an auto-lab/601 inductively coupled salinometer. Hourly sunlight readings were taken from the official records at Citadel Hill, Halifax.

The two-step fitting procedure of Jassby and Platt (1976) was followed to estimate the photosynthetic parameters α , R^B , and P_m^B . The light-saturation experiments were made in triplicate so three separate estimates of α , R^B , and P_m^B were obtained for each sampling period.

A midmorning or noontime maximum and an early evening or nighttime minimum characterize the rhythms in P_m^B in most previously published data (see Sournia 1974). Within these limits, it has generally (if not always explicitly) been assumed that the variation follows a simple sine curve. Inspection of our plots of P_m^B against time indicated that there was, indeed, a noontime maximum, but that P_m^B was more or less constant at night (Fig. 1). It seemed, then, that a simple sine curve would not be the best way to represent the observed variation. We chose instead, to examine the following family of curves (Fig. 2):

$$P_m^B(t) = b_m + b_a 2^{-n} \cdot [1 + \cos(2\pi/24)(t - b_p)]^n, \quad (2)$$

where b_m = minimum value, b_p = phase, b_a = amplitude, and n , an integer ≥ 1 .

Data from each experiment were fitted to seven curves of the family represented in Eq. 2 (integer values from $n = 1$ to $n = 7$). To find the parameter values, the same nonlinear least-square techniques used in estimating P_m^B were used in a two-step fitting procedure. First, b_p was fitted, holding (estimates of) b_m and b_a constant; then, the fitted value of b_p was held constant while b_m and b_a were fitted simultaneously. The justification for this procedure is that b_m and b_a vary along the y -axis (and should be fitted together) whereas b_p varies along the x -axis (and can be fitted independently). Fitting all three parameters simultaneously gave results within 1% of the chosen method, but with wider confidence limits.

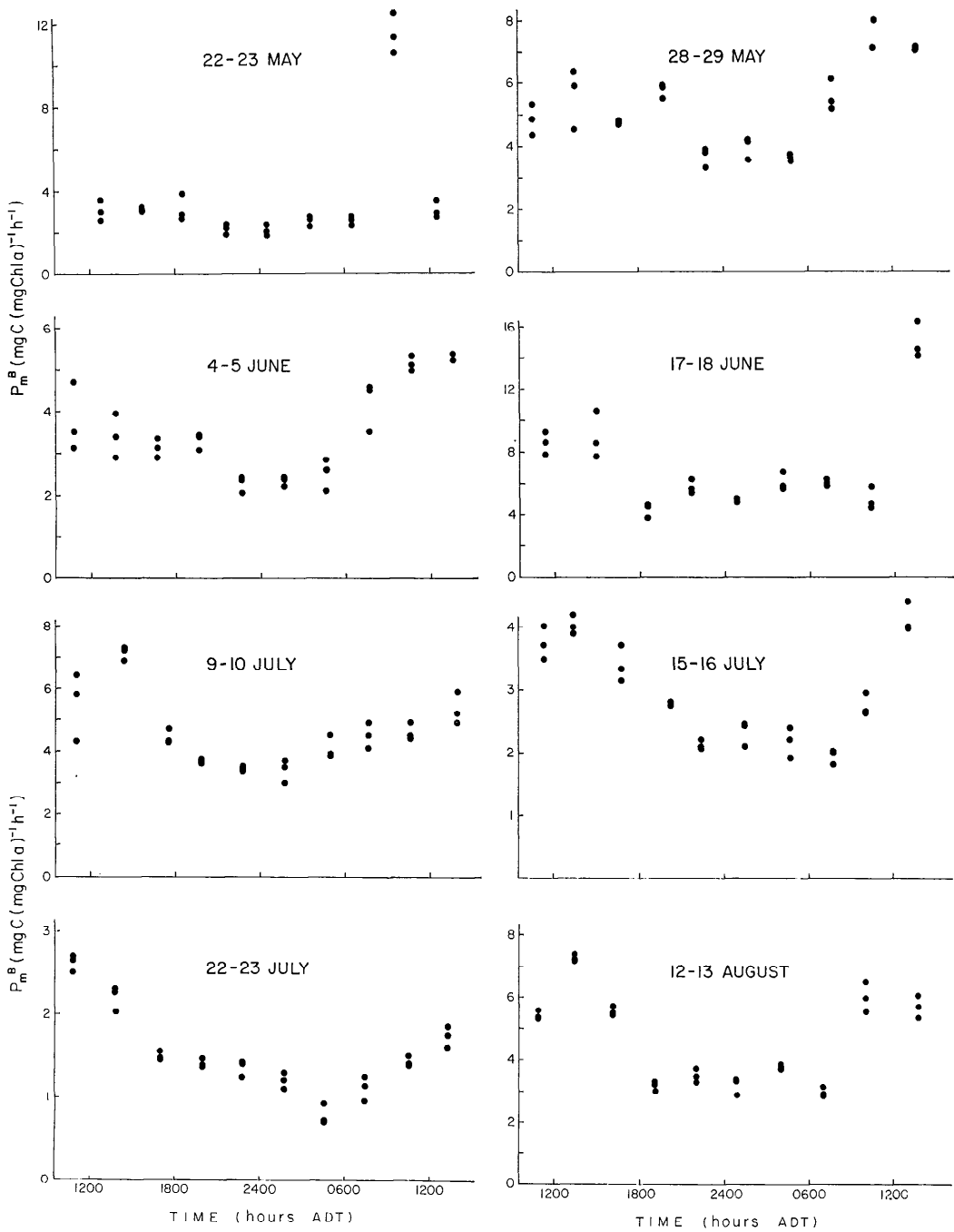


Fig. 1. Plots of P_m^B over time for eight diel experiments in Bedford Basin. Except for ninth time period on 28-29 May and fifth time period on 17-18 June, three values of P_m^B were available for each sampling period.

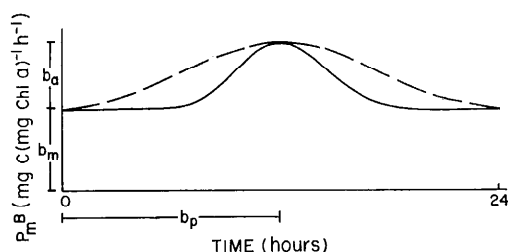


Fig. 2. Curve $P_m^B(t) = b_m + b_a 2^{-n} [1 + \cos(2\pi/24)(t - b_p)]^n$ for $n=5$. Indicated on graph are minimum value, b_m ; amplitude, b_a ; and phase, b_p . With $n > 5$ (< 5) amplitude would be more sharply (less sharply) peaked. For comparison, broken line shows simple sine curve ($n=1$ in above equation).

The average precision (relative error) on each of the three parameters [defined as half the (90%) confidence interval divided by the fitted value] in Eq. 2 improved monotonically with n . For values of n larger than 4, the values of the parameters remained relatively constant and changes in precision were slight. The value $n=5$ was therefore selected for subsequent analysis of the diel rhythm. That is, the following equation was used to represent the diel rhythm in P_m^B :

$$P_m^B(t) = b_m + b_a 2^{-5} \cdot [1 + \cos(2\pi/24)(t - b_p)]^5. \quad (3)$$

Use of Eq. 3 implies that the variation in P_m^B deviates strongly from a pure sinusoid (Fig. 2).

We are not aware of a suitable, quantitative measure of the significance of the fit to a nonlinear function such as the one we have chosen. However, various estimates of the confidence intervals on the fitted parameters are available (Conway et al. 1970). Taking the widest of these, we find the average precisions associated with the parameters in Eq. 3 are $b_m = 15\%$, $b_a = 43\%$, and $b_p = 5\%$. In two of the eleven experiments (11–12 June; 29–30 July) the confidence interval on the amplitude, b_a , slightly overlapped the confidence interval on the minimum, b_m , so that the existence of a rhythm could not be demonstrated. For the eight experiments shown in Fig. 1,

Table 1. Fitted parameters characterizing each diel curve for $P_m^B(t)$. b_m —minimum value; b_a —amplitude; b_p —phase.

Date	b_m	b_a	b_p
22–23 May	1.9	7.0	9.4
28–29 May	4.4	2.2	12.1
4–5 Jun	2.8	2.0	11.8
11–12 Jun	5.9	1.1	16.3
17–18 Jun	4.9	7.0	13.6
9–10 Jul	3.8	2.5	13.7
15–16 Jul	2.3	1.9	13.6
22–23 Jul	1.2	1.0	12.5
29–30 Jul	1.8	0.4	11.8
12–13 Aug	3.4	3.5	12.8
5–8 Aug *	2.4	0.5	21.2

*The phase for the experiment of 5–8 August was not considered reliable because of the wider sampling interval compared to the other experiments. For this reason, fitted parameters for this experiment were not used in any calculations.

the fitting procedure explained two-thirds of the variance in P_m^B .

The plots of I_k against time were similar to those of P_m^B , but less sharply peaked. The data were fitted in the same manner using the analogous equation

$$I_k(t) = c_m + c_a 2^{-n} \cdot [1 + \cos(2\pi/24)(t - c_p)]^n. \quad (4)$$

After applying the same criteria for stability of parameter estimates and precision with increasing n , we chose a value of $n=3$ to give the working model for the diel rhythm in I_k . The precisions associated with the fitted parameters were $c_m = 10\%$, $c_a = 48\%$, and $c_p = 8\%$. In four of the eleven experiments (22–23 May; 17–18 June; 29–30 July; 5–8 August) the confidence interval on the amplitude, c_a , overlapped the confidence interval on the minimum, c_m .

Results

The values of the parameters for the diel curves of $P_m^B(t)$ are presented in Table 1. The parameters b_m and b_a were highly variable among experiments, with coefficients of variation (\equiv standard deviation/mean) of 0.46 and 0.82. b_p was fairly constant, compared to these parameters,

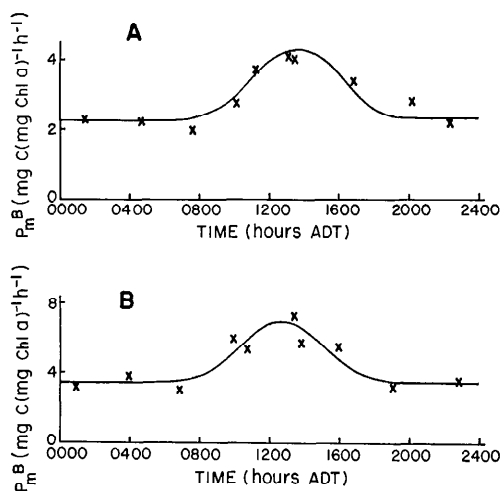


Fig. 3. Fitted curve and empirical observations, \times , (averaged over three incubators) for diel cycle in P_m . A—15–16 July; B—12–13 August.

with a coefficient of variation of 0.14. Figure 3 shows two examples of the fitted diel curves together with the corresponding observed values (averaged over the three incubators).

Presented in Table 2 are the values of the parameters for the $I_k(t)$ curves. The parameters c_m and c_a were less variable among experiments than b_m and b_a (coefficients of variation of 0.19 and 0.28) while the coefficient of variation of c_p was the same as that for b_p . Figure 4 shows two

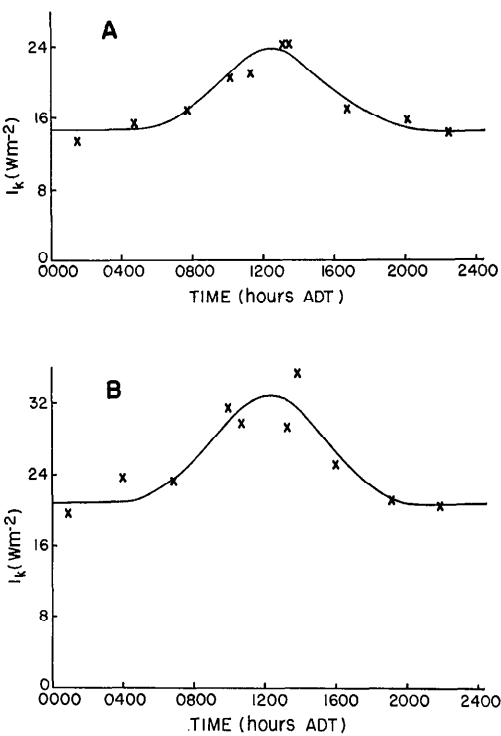


Fig. 4. Fitted curve and empirical observations, \times , (averaged over three incubators) for diel cycle in I_k . A—15–16 July; B—12–13 August.

examples of the fitted diel curves together with the corresponding observed values.

The variation of $\alpha(t)$ was not consistent. In some experiments, α appeared to undergo random variations within the day; in other experiments, it followed a unimodal curve. A one-way analysis of variance was made on the results of each experiment with the null hypothesis $H_0: \langle \alpha_1 \rangle = \langle \alpha_2 \rangle = \dots = \langle \alpha_s \rangle$ (where s = number of sampling periods for the particular experiment and the angle brackets indicate an average over the three replicates). As shown in Table 3, the results were not conclusive.

In most experiments, R^B appeared to undergo random variations with time. A one-way analysis of variance was made with the null hypothesis $H_0: \langle R_1^B \rangle = \langle R_2^B \rangle = \dots = \langle R_s^B \rangle$, and again results were inconclusive (Table 4).

Table 2. Fitted parameters characterizing each diel curve for $I_k(t)$. c_m —minimum value; c_a —amplitude; c_p —phase.

Date	c_m	c_a	c_p
22–23 May	14.1	3.4	8.9
29–28 May	15.6	6.5	11.6
4–5 Jun	17.4	10.1	10.8
11–12 Jun	21.3	6.6	10.4
17–18 Jun	18.9	5.1	13.2
9–10 Jul	21.6	11.0	12.0
15–16 Jul	14.5	9.2	12.5
22–23 Jul	13.9	7.0	14.3
29–30 Jul	13.7	4.6	13.4
12–13 Aug	21.0	11.8	12.3
5–8 Aug	19.2	0.9	9.9

Table 3. F-values for one-way analysis of variance with null hypothesis $H_0: \langle \alpha_1 \rangle = \langle \alpha_2 \rangle = \dots = \langle \alpha_s \rangle$. (s = number of sampling periods within experiment and angle brackets indicate average over three replicates.)

Date	df	F
22-23 May	7, 19	82.7567
28-29 May	7, 21	2.6585
4-5 Jun	7, 22	1.1567
11-12 Jun	7, 22	1.0661
17-18 Jun	7, 18	12.5655
9-10 Jul	7, 22	6.4422
15-16 Jul	7, 22	4.6241
22-23 Jul	7, 22	1.5532
29-30 Jul	7, 22	1.4764
12-13 Aug	7, 22	3.0880
5-8 Aug	5, 48	2.7939

A significant diel rhythm was not, therefore, established in either α or R^B . In view of the ambiguity of the results, each of the curves $\alpha(t)$ and $R^B(t)$ was characterized by a constant value (the daily mean) in all subsequent analyses.

Discussion

Estimation of gdp—Table 5 gives examples of the magnitude of the error which could be incurred in estimating *gdp* if the diel rhythm in P_m^B were ignored. In each example, Eq. 3 and the fitted parameter estimates (b_m , b_a , and b_p) were used to calculate hourly values of P_m^B . Using incident illumination recorded during the experiment (corrected according to Strickland 1958), and the daily means of α and R^B , we estimated hourly specific productivities with Eq. 1 (photosynthetically active radiation at 5 m was consistently below photoinhibiting levels). The sum of the hourly values gave one estimate of daily specific productivity. Let us call this result the “true” value.

We calculated two extreme estimates of *gdp* using as constants in Eq. 1, first, the lowest fitted value of P_m^B for the day (which might be measured, for example, in a single experiment made at early morning or evening) and, second, the highest fitted value of P_m^B (which might be measured in a single experiment conducted

Table 4. As Table 3, but with null hypothesis $H_0: \langle R_1^B \rangle = \langle R_2^B \rangle = \dots = \langle R_s^B \rangle$.

Date	df	F
22-23 May	7, 19	5.9111
28-29 May	7, 21	2.2307
4-5 Jun	7, 22	0.9403
11-12 Jun	7, 22	1.8026
17-18 Jun	7, 18	4.4285
9-10 Jul	7, 22	1.6635
15-16 Jul	7, 22	3.0820
22-23 Jul	7, 22	0.3398
29-30 Jul	7, 22	2.6798
12-13 Aug	7, 22	5.4091
5-8 Aug	5, 48	1.9890

around noon). Clearly, the discrepancy between the true value and each of the extreme estimates is not negligible even when P_m^B showed less than a twofold variation through the day (e.g. 15–16 July).

It is true that an estimate of productivity made without considering the diel rhythm on days when b_a is small compared to b_m would be close to the true value, but, in fact, the experiments showed that generally the magnitude of b_a was comparable to that of b_m .

Saijo and Ichimura (1962) reported that the diel fluctuation in productivity was generally confined to the surface layer and concluded that the error due to the diel rhythms on the estimation of column productivity would be rather small (they gave one example of $\approx 4\%$), at least in eutrophic waters. Our results indicate that the rhythm is more significant than this. Because of the relatively high extinction coefficient in Bedford Basin, only $\approx 22\%$ of the photosynthetically active light reaches the experimental depth (5 m) where the rhythm in P_m^B is still pronounced. At least three-fourths of the column productivity occurs at light levels greater than 22% in this environment.

The examples of possible errors that might be incurred in estimating daily productivity using a constant P_m^B (Table 5) are of roughly the same order as the horizontal spatial variability in productivity observed by Platt (1975) for four sampling stations in the Bedford Basin (at 5 m, the

Table 5. Estimates of daily specific productivity [mg C (mg Chl a)⁻¹ d⁻¹] using (1) fitted diel curve, $P_m^B(t)$; (2) lowest fitted value of P_m^B ; and (3) highest fitted value of P_m^B . Column 1 gives the "true" results.

Date	(1)	(2)	(3)
22-23 May	50	22	86
17-18 Jun	91	54	114
15-16 Jul	39	28	49

coefficient of variation between stations was 52%). In the estimation of primary productivity on a given day it is therefore as important to correct for the diel rhythm as it is to account for the spatial variability. On an annual basis, rhythmicity is the more significant factor. The coefficient of variation between stations of the annual production rate (calculated by integrating over depth and time) was only 4% (Platt 1975), reflecting the fact that spatial patterns are not consistent from day to day. Assuming that the rhythm is of the same significance throughout the rest of the year as it is in the summer, we think it is of greater value, in the estimation of annual production rate, to determine the diel variations at one station than to sample once at many stations on each sampling day.

Variability of α —It has been suggested (Dunstan 1973; Bannister 1974) that α might be a rather stable parameter compared to P_m^B , since it is a function of the basic photochemical reactions of the chlorophyll and should therefore be species and temperature independent. Aside from theoretical considerations (Platt and Jassby 1976) several factors lead us to believe that it is, in fact, no more constant than P_m^B on any time scale for natural assemblages of phytoplankton. The coefficient of variation of the *daily mean* α was 0.37 while that for the *daily mean* P_m^B was 0.44; thus on a time scale of days, α and P_m^B were of comparable variability. The average coefficient of variation of (α) *within days* (0.21) was not significantly different ($t_{20} = 0.97$) from that of (P_m^B) (0.29) *within days*, indicating that on a time scale

of hours the two were equally variable. Platt and Jassby (1976) showed that the magnitudes of the seasonal variations of the two parameters were about the same.

Although no significant rhythm in α could be demonstrated from our experiments, several investigators have indicated that its variations are, in fact, rhythmic. Sorokin and Krauss (1961) and Sorokin (1963) observed that the photochemical as well as the enzymatic part of the photosynthetic apparatus changes with the course of cell development in synchronous cultures. Hellebust et al. (1967) observed that *Acetabularia crenulata* has a photosynthetic rhythm at light-limiting as well as light-saturating intensities, although the amplitude of the rhythm was less pronounced at the lower intensities. Senger and Bishop (1967, 1969a,b), using synchronized cultures of *Scenedesmus obliquus*, showed that the rhythm in P_m^B was related to development of the cell and that α was proportional to P_m^B at least at the maximum and minimum points of the diel cycle in P_m^B .

The experiments presented here lend some support to these suggestions: a significant correlation was found between $\langle \alpha \rangle$ and $\langle P_m^B \rangle$ ($r_{114} = 0.89$) and between the daily means of α and P_m^B ($r_9 = 0.90$). (The Spearman rank correlation coefficients, nonparametric statistics, were equally as significant.) However, if α and P_m^B were indeed proportional through the diel cycle, $I_k(t)$ would be a straight line parallel to the x -axis, and the observed fluctuations about this line would be random. In fact, the variations of I_k with time appeared to be other than random, indicating a changing proportionality between P_m^B and α during the diel cycle. Further, Walther and Edmunds (1973), in an investigation of synchronous cultures of *Euglena gracilis*, found no major changes in the light-limited region of light saturation curves during a cell cycle. Clearly, the question of rhythmicity in α has yet to be resolved.

Possible explanations for the rhythm—As outlined by Stross et al. (1973), there are two categories of explanations for photo-

synthetic rhythms: the *phasing* hypothesis, which is based on an intrinsic capacity in phytoplankton for cell processes to be entrained by a light-dark cycle; and the *forcing* hypothesis, which proposes that some rhythmic limiting factor (nutrients) or destructive agent (photodestruction) drives the oscillation. Neither explanation is wholly supported by our data. That the rhythm is not fully intrinsic in nature is suggested by the high variability between days in the parameters b_m and b_a . That the oscillations are not forced is indicated by the essentially random nutrient fluctuations within each diel period and by the fact that light levels at the experimental depth never exceed the threshold of photo-inhibition (MacCaull 1976).

Enright (1970) suggested that rhythms in the field should not be categorized simply as intrinsic or forced; rather, that the behavior of the organism in its natural environment is a (p. 236) "mixture of responses to exogenous stimuli superimposed on an endogenous readiness to respond in a given way." In their examination of factors responsible for photosynthetic rhythms in phytoplankton, Stross et al. (1973) adopted this approach: they suggested that the variation in photosynthetic capacity observed in the field was a (p. 207) "compromise between a forcing oscillation in the environment and an inherent rhythmicity in the potential of the organism." The inherent rhythmicity was in the *photosynthetic potential*—the photosynthetic rate achieved when both light and nutrients are saturating.

Several lines of evidence indicate that certain environmental parameters are significant covariates of the various photosynthetic parameters (for the dependence of P_m^B on temperature see Eppley 1972; for the dependence of P_m^B and α on sunlight and temperature see Platt and Jassby 1976). Multiple regression analysis with the environmental covariates (inorganic nutrients, temperature, salinity, and sunlight) from the experiments reported here showed that salinity and temperature made significant reductions in residual variance about regression equations for the daily means of

α , R^B , P_m^B , and I_k , and also that ammonia concentration was a significant covariate in regression equations for the parameters b_m and b_p (see MacCaull 1976). The dependence of the phase (b_p) on ammonia concentration agrees with Malone's (1971) suggestion that the phase of the diel curve in P_m^B is partly dependent on the degree to which nutrients are limiting.

Conclusions

The effect of the diel rhythms in the phytoplankton assimilation number, P_m^B , on estimates of gross daily productivity can no longer be ignored.

No diel rhythm could be established for the initial slope, α , of the light saturation curves, but this may be due to the relatively poor precision with which it is measured (Platt and Jassby 1976).

On a time scale of days or hours, α was found to be no less variable than P_m^B .

Evidence suggests that the photosynthetic rhythms observed in the field result both from an intrinsic oscillation in the phytoplankton cells and fluctuating environmental factors.

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