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A mechanistic model of photoadaptation in microalgae

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ABSTRACT: A mechanistic model is presented that describes changes in the chlorophyll *a*:carbon ratio of microalgae growing in fluctuating light. A consideration of the mass budgets for cell carbon and chlorophyll during nutrient-sufficient microalgal growth illustrates that imbalances between rates of synthesis and degradation of the macromolecular components of a microalgal cell will result in changes in its biochemical composition. The dynamic equations describing the rate of response of the chl:C and C:chl ratios to a change in light level are shown to depend on the magnitude of the change. In particular, the cases of light-limited and light-saturated growth rate are considered. A previously described empirical model of photoadaptation kinetics is shown to be a special case of the new analytical model. In general, we conclude that for a photoadaptive variable defined as the ratio of 2 biochemical constituents of a cell where the denominator is the concentration of the catalyst that is rate-limiting for photosynthesis, then the new, mechanistic model simplifies to a first order differential equation describing the photoadaptation kinetics of the ratio.

INTRODUCTION

The dependence of the biochemical composition of microalgae on photon flux density (PFD) (Cook 1963, Parrot & Slater 1980, Foy & Gibson 1982) is one manifestation of physiological plasticity in microalgae (Myers 1970). Any observable property of a microalgal cell that depends on the PFD under which the microalga was grown can be considered as a photoadaptive variable. Examples include cell pigment content, enzyme activities, respiration rate and the parameters of the photosynthesis-light (PI) curve (Falkowski 1980, Richardson et al. 1983).

Several models have been developed to describe the physiological adaptation of phytoplankton to PFD for cells in balanced growth (Shuter 1979, Bannister 1979, Kiefer & Mitchell 1983). Their predictions are in good agreement with experimental observations of the C:chl*a* ratio and the parameters of the PI curve (Laws et al. 1983, 1985). Although derived independently, all 3 models (Shuter 1979, Bannister 1979, Kiefer & Mitchell 1983) have closely related formulations (Laws et al. 1983, 1985) and can be shown to be based on the application of the principles of energy and mass conservation (Geider 1984). They are all, however, static descriptions of microalgal physiology and are limited in that they cannot be used to investigate the time course of changes in chemical composition that occur in response to changes in PFD.

The importance of photoadaptation as part of the physiological response of microalgae to a fluctuating light regime in nature has been the subject of recent investigations (Jones 1978, Rivkin et al. 1982a, Falkowski 1983, Smith et al. 1983, Lewis et al. 1984a). Adaptation kinetics have been modelled empirically using a first order differential equation (Falkowski & Wirick 1981, Rivkin et al. 1982a, Liou & Eybergen 1982, Lewis et al. 1984a, b).

$$dR(t)/dt = k[R_w(t) - R(t)] \quad (1)$$

where R(t) = the photoadaptive variable of interest; $R_w(t)$ = the value which R(t) would have if the phytoplankton were in balanced growth at the instantaneous PFD, I(t); k = the rate constant for adaptation. Many photoadaptive variables can be characterized by first order rate constants 0.02 to 0.06 per hour (Falkowski 1980), which are of the same magnitude as the growth rate for many microalgae. It is well known that the rate

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constant for adaptation depends on the particular physiological process under consideration (Harris 1978). For example, the *in vivo* fluorescence properties of phytoplankton are characterized by faster response than chemical composition and the various parameters of the PI curve appear to adapt at different rates (Lewis et al. 1984a).

The empirical model (Eq. 1) has been applied in both theoretical (Falkowski & Wirick 1981, Lewis et al. 1984a) and experimental (Falkowski 1980, Falkowski 1983, Lewis et al. 1984b) studies of phytoplankton photoadaptation in a wind-mixed euphotic zone. Justification for its use has been obtained in experimental studies on the responses of photoadaptive variables in unialgal cultures subjected to step changes in PFD (Rivkin et al. 1982a, Falkowski 1984, Lewis et al. 1984a).

The theoretical link between observations of the chemical composition of microalgae in balanced growth and the changes in chemical composition during unbalanced growth has not, however, been previously established. Nor has a mechanistic derivation for the empirical photoadaptation model (Eq. 1) previously been given.

In this paper we present a time-dependent theory of photoadaptation of the microalgal cell using as an example the evolution of chl*a*:C during unbalanced growth.

THEORY

Consider the following equations which are proposed to describe the carbon and chlorophyll *a* dynamics of a microalgal cell population:

$$dC(t)/dt = p\,C(t) - r_1\,C(t) \tag{2a}$$

$$dA(t)/dt = p\,f\,C(t) - r_2\,A(t) \tag{2b}$$

where C(t) = cell carbon concentration (mass of carbon per unit volume [M/L^3]); A(t) = cell chlorophyll *a* concentration (mass of carbon in chlorophyll *a* per unit volume [M/L^3]); p = the rate constant for photosynthesis (T^{-1}); r_1 and r_2 = the rate constants for the degradation of, respectively, cell carbon and chlorophyll *a* (T^{-1}); f = the fraction of photosynthate which is directed into chlorophyll *a* synthesis (dimensionless). The differential equations (Eq. 2a, b) describe changes in the carbon and chlorophyll *a* concentrations resulting from imbalances between rates of synthesis and degradation. Synthesis and degradation are assumed to follow first order kinetics. Note that the concentrations of cell carbon and chlorophyll *a* are expressed in terms of carbon equivalents such that the fraction of photosynthate directed into chlorophyll *a* synthesis (f) is dimensionless. The equations for the microalgal population (Eq. 1 & 2) are equally valid when recast in terms of individual microalgal cells. An advantage of Eq. 1 & 2 is that they are directly applicable to observations made on cells in batch cultures.

For light-limited growth the photosynthesis rate (p) is assumed to be proportional to the PFD incident on the cell and the chl*a*:C ratio:

$$P = \alpha\,\gamma\,I \tag{3}$$

where p = the rate constant for photosynthesis (s^{-1}); α = initial slope of the PI curve (units of [mg total C/mg C in chl*a*][m^2/μmol photons]); γ = the chl*a*:C ratio (units of [mg C in chl*a*] [mg C]$^{-1}$); I = the photon flux density (μmol photons $m^{-2}\,s^{-1}$). Under the assumption that the degradation rate constants (r_1 and r_2) and the initial slope of the PI curve (α) are invariant, and that the proportion of photosynthate which is directed into chlorophyll *a* synthesis (f) changes instantaneously with changes in PFD, Eq. 2a, 2b and 3 can be used to solve for the time dependence of the C:chl*a* ratio. Eq. 4 follows from Eq. 2a, 2b and 3 upon noting the identity $d(X/Y)/dt = [Y(dX/dt) - X(dY/dt)]/Y^2$ and making the substitutions X = A and Y = C:

$$d\theta(t)/dt = \alpha\,I\,f\,[(1/f) - \theta(t)] - \theta(t)\,(r_1 - r_2) \tag{4}$$

where $\theta = C(t)/A(t) = 1/\gamma$ is the ratio of total carbon to carbon in chlorophyll α. $r_1 = r_2$, Eq. 4 reduces to:

$$d\theta(t)/dt = \alpha\,I\,f\,[(1/f) - \theta(t)] \tag{5}$$

Eq. 5 is the same as the empirical photoadaptation model (Eq. 1) given the following identifications: $k = (\alpha If)$, $R_w(t) = (1/f)$, $R(t) = \theta(t)$. The adaptation rate constant, k, is equal to the specific rate of synthesis of chlorophyll *a* of fully adapted cells ($k = \alpha If = [A(t)^{-1}][dA(t)/dt]$).

The dynamics of chl*a*:C (i.e. $1/\theta(t) = \gamma(t)$) derived from Eq. 2a, 2b and 3 will not yield such a simple equation. This can be shown as follows. Note the identity $d[1/Z(t)]/dt = -Z(t)^{-2}\,[dZ(t)/dt]$ and substitute $\theta(t) = Z(t)$ to obtain Eq. 6 describing the time dependence of the chl*a*:C ratio:

$$d\gamma(t)/dt = I\,[f\,\gamma(t) - \gamma(t)^2] \tag{6}$$

Because of the $\gamma(t)^2$ term, this equation is non-linear.

The difference between the dynamics of chl*a*:C (Eq. 5) and C:chl*a* (Eq. 6) following a hypothetical step change in PFD is illustrated in Fig. 1 and 2. The ordinate is expressed in units of dimensionles time (i.e. the product of the photosynthesis rate and time). The trajectories followed by C:chl*a* for reciprocal shifts in

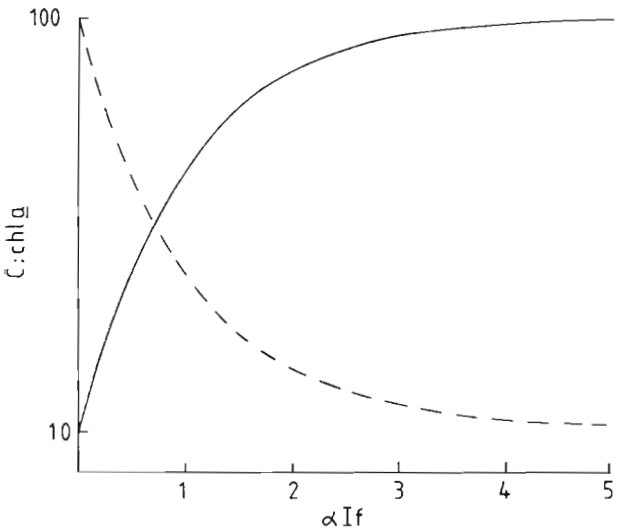

Fig. 1. Trajectory of the C:chl*a* ratio predicted by Eq. 5 for hypothetical reciprocal shifts in PFD. The scale for the ordinate is dimensionless being set equal to the product of the adaptation rate constant (α I f) and time. Note the symmetry of the 2 trajectories

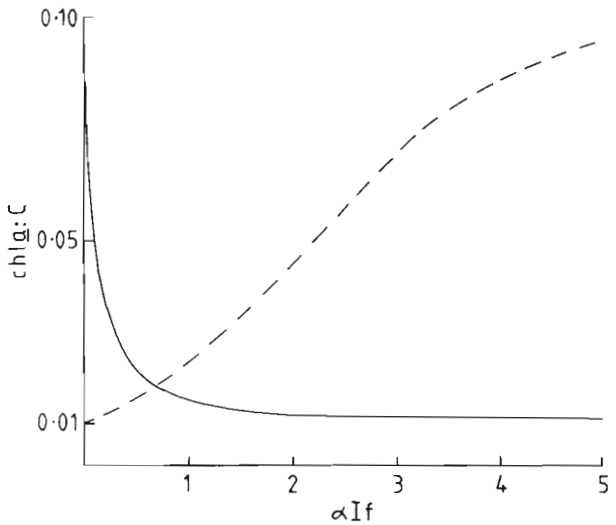

Fig. 2. Trajectory of the chl*a*:C ratio predicted by Eq. 6 for the same hypothetical reciprocal shifts in PFD as are illustrated in Fig. 1. The scale for the ordinate is the same as in Fig. 1. Note that the magnitude of the asymmetry between the trajectories for the shift-up and shift-down experiments will depend on the range of values of the chl*a*:C ratio which are produced by the PFD shift. The asymmetry is very pronounced for an order of magnitude change in the ratio but would be less marked for a 2-fold change

PFD are symmetric, but the trajectories followed by chl*a*:C are markedly asymmetric.

Now consider the application of Eq. 2a, b to photoadaptation under conditions of light-saturated photosynthesis. In this case the photosynthesis rate (p) can be considered to be independent of both the PFD and the chl*a*:C ratio, consistent with the observations of Myers (1970) for *Chlorella vulgaris* and Geider (1984) for *Thalassiosira pseudonana*. Under the assumption that the rate constant for light-saturated photosynthesis is constant, the coupled pair of differential equations describing changes in cell carbon and chlorophyll *a* content are:

$$dC(t)/dt = (P_m - r_1)\, C(t) \quad (7a)$$

$$dA(t)/dt = P_m\, f\, C(t) - r_2\, A(t) \quad (7b)$$

where P_m = the light-saturated photosynthesis rate constant (T^{-1}). Solving Eq. 7a, b for chl*a*:C yields Eq. 8:

$$d\gamma(t)/dt = P_m[f - \gamma(t)] - \gamma(t)\,(r_2 - r_1) \quad (8)$$

If $r_1 = r_2$, Eq. 8 reduces to:

$$d\gamma(t)/dt = P_m\,[f - \gamma(t)] \quad (9)$$

At saturating light levels chl*a*:C follows adaptation kinetics (Eq. 9) consistent with the empirical model (Eq. 1) when the following indentities are noted; $k = P_m$, $R_w(t) = f$, and $R(t) = \gamma(t)$. By analogy with the derivation of Eq. 6 from Eq. 5, the dynamics of C:chl*a* for growth within the light-saturated region of the PI curve can be derived from Eq. 9 to yield:

$$d\theta(t)/dt = P_m\,[\theta(t) - f\,\theta(t)^2] \quad (10)$$

The preceding analysis shows that even a simple model of carbon and chlorophyll *a* synthesis and degradation can lead to complex patterns of response of microalgal biochemical composition in fluctuating light. The non-linearity of the photosynthesis-light curve has significant effects on the rates of response of the chl*a*:C and C:chl*a* ratios following step shifts in PFD. The C:chl*a* ratio is an example of a photoadaptive variable that is consistent with the empirical photoadaptation model (Eq. 1) for light-limited growth, whereas the chl*a*:C ratio is consistent with the empirical model for light-saturated growth. The analysis shows that considerable care must be exercised in defining photoadaptive variables for use in empirical models if mechanistic interpretations are desired.

Explicit models of carbon flow through the microalgal cell, of which Eq. 2a, b are simple examples, will further our understanding of the physiological aspects of photoadaptation kinetics in microalgae. The details made explicit in this approach may be unnecessary, and perhaps also computationally or analytically prohibitive, for some ecological applications. The physiological approach (Eq. 2a, b), however, does provide insight into choice of appropriate photoadaptive variables for use with the analytically tractable first order model (Eq. 1).

The results presented here for the C:chl*a* and chl*a*:C ratios suggest that the photoadaptive variable appropriate for use in the empirical model is a ratio of biochemical properties of the algal cell in which the term in the denominator is proportional to the photosynthesis rate. In other words the denominator can be considered as the catalyst that limits the rate of photosynthesis. In the light-limited region of the PI curve, the photosynthesis rate is proportional to the chlorophyll *a* concentration because light harvesting limits photosynthesis. Chlorophyll *a* is thus the catalyst limiting the rate of photosynthesis, and the photoadaptive variable which follows the first order adaptation model (Eq. 1) is the C:chl*a* ratio. For light-saturated photosynthesis we have assumed that the photosynthesis rate is proportional to cell carbon, consistent with observations of Myers (1970) and Geider (1984). Although cell carbon is clearly not the catalyst which limits photosynthesis, the assumption that the carbon-specific, light-saturated photosynthesis rate is constant implies that the concentration of the rate-limiting catalyst is correlated with cell carbon. For light-saturated photosynthesis the photoadaptive variable which follows the kinetics described by Eq. 1 is the chl*a*:C ratio.

In addition to identifying 'appropriate' photoadaptive variables, the mechanistic model (Eq. 2a, b) provides an interpretation of the first order rate constant for photoadaptation (k in Eq. 1). If a photoadaptive variable is defined as a biochemical ratio in which the denominator is the catalyst limiting the rate of photosynthesis (or is directly correlated with the concentration of the rate-limiting catalyst), it follows that the adaptation rate constant (k) will equal the balanced growth rate at the new light level. For the response of cell carbon and chlorophyll *a*, $k = P_m$ under light-saturating conditions and $k = \alpha I f$ under light-limiting conditions.

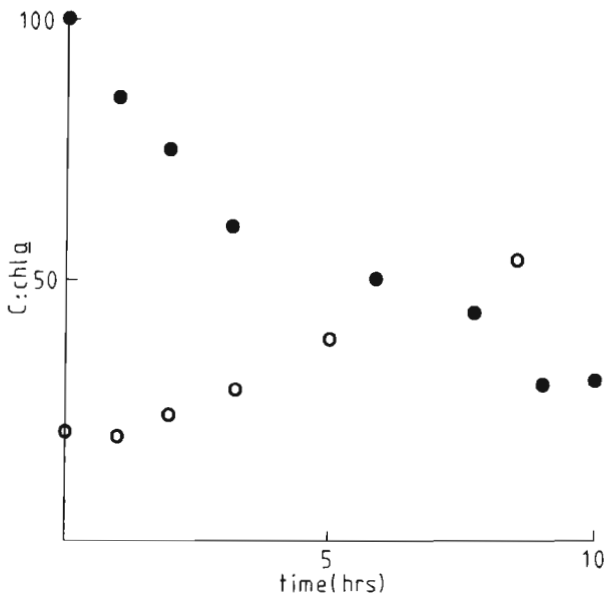

Fig. 3. Observations of changes in the C:chl*a* ratio for *Thalassiosira pseudonana* cultures following reciprocal shifts in PFD between 100 and 2400 µmol photons m^{-2} s^{-1}. Open circles are observations for the shift-up in PFD. Closed circles are observations for the shift-down in PFD. Observations are taken from Lewis et al. (1984a)

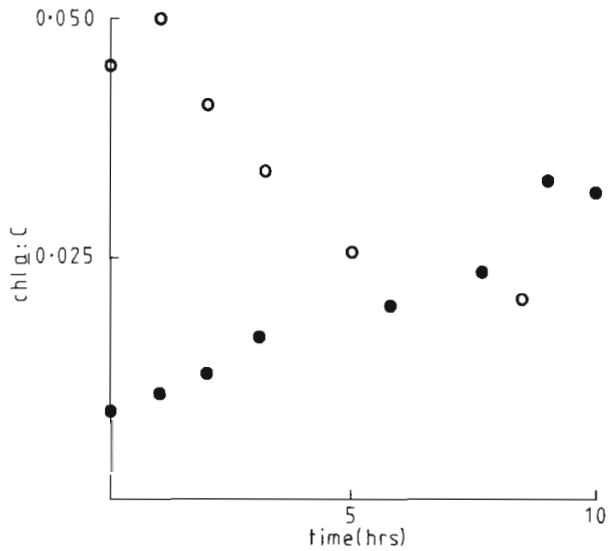

Fig. 4. Observations of changes in the chl *a*:C ratio for *Thalassiosira pseudonana* following reciprocal shifts in PFD between 100 and 2400 µmol photons $m^{-2}s^{-1}$. Open circles are observations for the shift-down in PFD for the same observations as are illustrated in Fig. 3

MODEL VERIFICATION

The experimental study of the response of biochemical composition and photosynthesis rates of microalgae to step changes in PFD has been pursued for almost 25 yr (Steemann Nielsen et al. 1962, Sheridan 1972a, b, Beardall & Morris 1976, Marra 1978, 1980, Prézelin & Matlick 1980, Rivkin et al. 1984a). Most of these studies do not provide observations that can be used to test unambiguously the assumptions and predictions of the preceding theoretical analysis. One study (Lewis et al. 1984a), however, does provide observations which can be compared with the first order model (Eq. 5 and 9). We consider these observations next.

Observations of changes in C:chl*a* in cultures of the marine diatom *Thalassiosira pseudonana* were interpreted by Lewis et al. (1984a) to indicate that chemical composition responded more slowly to a shift-up in PFD than to the reciprocal shift-down (Fig. 3). Reciprocal shifts in PFD were performed on cultures of *T. pseudonana* previously acclimated to light levels of 100 and 2400 µmol photons m^{-2} s^{-1}. Changes in C:chl*a*

for the reciprocal shifts are illustrated in Fig. 3 and changes in chl*a*:C are illustrated in Fig. 4. Note the distinct asymmetry between the trajectories of both ratios for the reciprocal shifts in PFD.

The adaptation rate constants (k of Eq. 1) for the kinetics of C:chl*a* during the first 10 h following a shift in PFD were determined from non-linear, least squares fits of the data of the integrated form of Eq. 1. The rate constants for shift-up and shift-down are respectively 0.05 h^{-1} and 0.2 h^{-1}. The adaptation rate constants for shift-up and shift-down of chl*a*:C are are respectively 0.14 and 0.083 h^{-1}. The range of calculated adaptation rates (k) for response of carbon and chlorophyll *a* varies by about a factor of 3 for the shift-up and 2 for the shift-down depending on the choice of photoadaptive variable. Using C:chl*a* as a photoadaptive variable with Eq. 1 leads to the conclusion that photoadaptation following a shift-up in PFD occurs more slowly than adaptation to a shift-down in PFD; however, using chl*a*:C as the photoadaptive variable leads to the opposite conclusion that adaptation following a shift-up occurs more rapidly than adaptation following a shift-down in PFD. Rather than choosing between these 2 paradoxical interpretations based on fitting the observations to an empirical model, we can refer to the mechanistic model for insight into the underlying processes.

The high PFD (2400 μmol m^{-2} s^{-1}) is saturating for both growth and photosynthesis. The rate constant for the changes in the chl*a*:C following the shift-up in light level should be $k = P_m$ (Eq. 9), which, for *Thalassiosira pseudonana* growing at 100 μmol m^{-2} s^{-1}, is 0.15 h^{-1}. This value is similar to the light-saturated growth rate of 0.14 h^{-1} (M. Lewis unpubl. data). The adaptation rate constant (k of Eq. 1) calculated for this shift is 0.14 h^{-1}, consistent with the maximum growth rate and light-saturated photosynthesis rate as predicted by the mechanistic model (Eq. 9). The low light level (100 μmol m^{-2} s^{-1}) is within the linear, initial slope region of the PI curve for both the high-light and low-light acclimated cultures. As shown previously (Eq. 5), the adaptation rate constant for C:chl*a* following a shift within the light-limited region of the PI curve should be $k = (\alpha I f)$, which for $\alpha = 0.02$ (g C/g chl*a*) (m^2/μmol photons), I = 100 μmol m^{-2} s^{-1}, and f = 0.05 g chl*a* (g C)$^{-1}$, leads to $k = 0.1$ h^{-1}. This is only $^1/_2$ of the value of $k = 0.2$ h^{-1} obtained from fitting Eq. 1 to the observed changes in C:chl*a*. This inconsistency between observation and the mechanistic model (Eq. 5) may be due to a rapid utilization of energy reserves immediately following the shift-down in PFD. Consistent with this explanation is a reduction in total carbohydrate from 35 to 12 % of the cell carbon within the first 2 h of the shift-down in PFD (calculated from Fig. 3 of Lewis et al. 1984a). We return to the potential role of energy reserves for adaptation kinetics in the discussion.

This reanalysis of the observations of Lewis et al. (1984a) for carbon and chlorophyll *a* dynamics is consistent with the predictions of the theoretical analysis. The interpretation of the observations in terms of the mechanistic model leads to the conclusion that the adaptation rates for the reciprocal shifts between 2400 and 100 mol photon m^{-1} s^{-1} will occur at approximately the same rate, but that the 'appropriate' variable for use with Eq. 1 is C:chl*a* for the shift-down and chl*a*:C for the shift-up. This conclusion would not have been obtained by simply fitting an arbitrarily chosen photoadaptive variable (i.e. either chl*a*:carbon or carbon:chl*a*) to the empirical model (Eq. 1).

DISCUSSION

The mechanistic theory of photoadaptation kinetics proposed in the preceding section consists of a pair of differential equations describing the mass balances of chlorophyll *a* and carbon during microalgal growth. The mechanistic model (Eq. 2a, b) reduces to a previously described empirical model (Eq. 1) under certain conditions. It provides a theoretical basis for choosing 'appropriate' photoadaptive variables for use in the empirical model and insight into the physiological significance of the coefficients of Eq. 1 as follows.

(1) The photoadaptive variable for use in the empirical model is defined as the ratio of the concentrations of 2 biochemical components of a microalgal cell in which the denominator of the ratio is the rate-limiting catalyst for photosynthesis (or is proportional to the concentration of the rate-limiting catalyst).

(2) For a step change in PFD the rate constant 'k' will equal the balanced growth rate (*sensu* Eppley 1980) that would eventually be obtained under the new experimental conditions.

(3) The coefficient R_w of Eq. 1 is equal to the ratio of the amounts of photosynthate directed into synthesis of the biochemical components making up the numerator and denominator of the ratio defining the photoadaptive variable.

Our theoretical treatment of adaptation does not consider the biochemical mechanisms that are responsible for adaptation. These physiological processes are taken into account by the specification of a coefficient which describes the fraction of photosynthate (f) directed into the synthesis of the biochemical compound of interest. In the differential equations used to model carbon and chlorophyll *a* dynamics (Eq. 2a, b) it was assumed that this coefficient (f) responds instantaneously following changes in PFD. Thus, although the photoresponse of biochemical composi-

tion is observed on a time scale associated with the rate of photosynthesis, implicit in the model is a much shorter time scale (assumed to be infinitesimally small for our analysis) associated with changes in f. Research into the mechanism that underlies photoadaptation should then be directed into an evaluation of the factors controlling the synthesis of key biochemical components of the photosynthetic apparatus. One such mechanism has been discussed by Falkowski (1980) for control of chlorophyll synthesis in microalgae.

It is possible, without going into a detailed consideration of algal biochemistry, to derive values for the coefficients of the photoadaptation models (Eq. 1, 5 & 9) from an intracellular compartment model of microalgal growth (Shuter 1979). This model is based on the flow of energy and carbon through 4 intracellular compartments: the photosynthetic apparatus, the synthetic apparatus, the structural material, and the energy reserves. Under conditions of constant temperature and saturating nutrient availability, the model describes the distribution of carbon among the intracellular compartments and the growth rate as a function of PFD given the specification of 2 rate constants (i.e. a rate constant for photosynthesis, and a rate constant for the elaboration of the initial products of photosynthesis into new cells) and the energy costs of synthesis and maintenance. This model can be used to describe the dependencies of C:chl*a* and growth rate on PFD for microalgae in balanced growth and thus provides a means for specifying the coefficient f and the adaptation rate constant k.

A consideration of the intracellular compartmental model of Shuter (1979) also highlights some of the limitations of the description of carbon and chlorophyll *a* dynamics by Eq. 2a, b. By considering only chlorophyll *a* and carbon dynamics, our analysis has been limited to a treatment of photosynthesis, implicitly neglecting the rate of elaboration of the products of photosynthesis into the complex macromolecules which make up the cell. One may suspect that this latter process will control the adaptation rate under some circumstances. Also neglected in our analysis is the role of an energy storage pool that could act as a buffer in temporary exposures to extremes of PFD, providing an energy reserve to maintain synthesis rates at low PFD and a means of collecting energy in excess of the demands for cell synthesis at high PFDs. The importance of this energy reserve is illustrated by the observation of Rivkin et al. (1982b) that a steady division rate can be maintained at the expense of stored carbon for 2 generations following a step-down in PFD in the dinoflagellate *Gonyaulax polyhedra*. In another paper, Rivkin et al. (1982a) note that changes in the cell chlorophyll *a* content of *Pyrocystis noctiluca* do not occur until 2 d following a shift-down in PFD after which time Eq. 1 adequately describes the photoresponse of cell chlorophyll. One area in which further theoretical work should proceed is in the extension of Shuter's (1979) model of balanced growth into a dynamic model applicable to the description of microalgal metabolism in a changing environment.

One of the assumptions allowing the derivation of Eq. 5 and 9 from Eq. 2a, b is that the degradation rate constants for carbon and chlorophyll *a* (r_1 and r_2) have the same value. This assumption is required to make the derivation of the mass balances for carbon and chlorophyll *a* collapse to the empirical model. Carbon-14 labelling experiments with microalgae in balanced growth indicate that total carbon and chlorophyll *a* label at the same rates (Redalje & Laws 1981, Welschmeyer & Lorenzen 1984) consistent with the assumption that $r_1 = r_2$. Observations of rapid chlorophyll turnover (Grumbach et al. 1978, Riper et al. 1979), however, may indicate that this assumption is not universally valid.

Differences in degradation rate constants for chlorophyll *a* and carbon will not significantly alter the kinetics of response of biochemical composition provided the synthesis rate constant (p) is large relative to the degradation rate constants (see Eq. 4 & 8). The linear first order models (Eq. 5 & 9) and by implication the empirical model (Eq. 1) may adequately describe changes in chemical composition in rapidly growing cultures subjected to shifts in PFD (Falkowski 1984, Lewis et al. 1984a) because the synthesis rates are much larger than the degradation rate in these cultures. Under conditions in which the degradation rate constants are of the same magnitude as the synthesis rate constant, such as might be expected for extreme light- or nutrient-limitation, the empirical adaptation model (Eq. 1) may prove inappropriate. To the best of our knowledge this model has not been applied to such extreme situations.

One of the interesting conclusions of the theoretical analysis is that the adaptation rate parameter of the empirical model (k in Eq. 1) is expected to be variable. It is not our intent to consider in detail the implications of variability in k; however, we note that the adaptation rate will covary with the photosynthesis rate. Thus, photoadaptation rates of nutrient-sufficient microalgae will be faster at high light levels than at low light. The ecological implications are that phytoplankton in a mixed layer will become acclimated to light levels in excess of the mean PFD and that 'adaptation' will be faster during the day than at night.

The significance of the results presented here relates to the success of a simple mass balance in explaining major features of the adaptation kinetics of biochemical composition in microalgae. A coupled pair of first

order differential equations is used to describe the rate of change of C:chl*a* in microalgae. Other photoadaptive variables that can be expressed as the ratio of 2 chemical components should be able to be treated by a similar formulation. The model is not intended to apply to rapid changes in the fluorescence properties or photosynthesis rates (Kiefer 1973, Harris 1978) caused by changes in the biophysical or biochemical activity of a particular molecule or assemblage of molecules such as the photosynthetic unit. Neglect of variability in the activity of rate-limiting catalysts may be an important limitation of our treatment since both Lewis et al. (1984a) and Falkowski (1984) report that the initial slope of the PI curve can change following a shift in PFD. Our treatment also does not apply to diel periodicities in the value of a photoadaptive variable which result from cell cycle entrainment into a light: dark cycle or to circadian periodicities (Chisholm 1981). Rather, the model formulated in this paper applies to the synthesis and degradation of the various components which make up the algal cell. There is, however, no reason why the treatment cannot be extended to include a consideration of variable activity of the catalysts which limit the rate of photosynthesis.

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