
The kinetics of algal photoadaptation in the context of vertical mixing

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Abstract. The responses of phytoplankton to turbulent motions in the surface mixed layer can be measured to estimate the rate of vertical mixing. If the time scale for the response (photoadaptation) is shorter than that for vertical mixing, phytoplankton will exhibit a vertical gradient associated with adaptation to ambient light, whereas if mixing occurs with a time scale shorter than that of photoadaptation, the surface mixed layer will be uniform with respect to the photoadaptive parameter. To examine the physiological bases for a model of vertical mixing and photoadaptation, we grew the marine diatom *Thalassiosira pseudonana* (clone 3H) at three photon flux densities and subjected the cultures to reciprocal light shifts, measuring physiological and chemical changes over the following 10 h. Several parameters, easily measured in nature and attributable primarily to phytoplankton, responded to fluctuating light on different time scales. After cultures were exposed to relatively bright light, both the initial slope of the photosynthesis–irradiance curve and *in vivo* fluorescence were depressed on a time scale of less than an hour. Photosynthetic capacity was also reduced transiently, but recovered over many hours to a high level characteristic of an adapted state. First-order kinetics (the current model of choice for describing photoadaptation) reasonably described the rapid responses of phytoplankton to bright light, but other parameters (i.e. cellular chemical composition and photosynthetic capacity) changed as a result of unbalanced growth and required much longer to adapt from low to high light as compared to from high to low light. A logistic model of this adaptation is presented. The model suggests that hysteresis of adaptation during vertical mixing may have important consequences. The vertical distributions of photoadaptive properties in mixed layers not only reveal the rate of vertical mixing, but show how phytoplankton integrate environmental fluctuations.

Introduction

The relationship between photosynthesis and local irradiance for natural phytoplankton populations is fundamental to the study of aquatic productivity (Ryther and Yentsch, 1957; Talling, 1957; Platt, 1975) and has particular relevance to recent attempts to predict fluxes of carbon in the world's ocean. Many of the physiological processes that determine the photosynthesis–irradiance relationship are plastic; in particular they are responsive to fluctuations in irradiance incident on the algal cell. The resulting variability in the photosynthesis–irradiance relationship introduces uncertainty into estimates of primary production; this uncertainty can be reduced substantially through understanding the nature of the responses of phytoplankton to the fluctuations of irradiance which characterize planktonic existence in the upper water column.

It has long been recognized that phytoplankton respond physiologically to changes in ambient light [light–shade adaptation or photoadaptation; reviewed by Falkowski (1980), Richardson *et al.* (1983) and Harding *et al.* (1987)] and grow in environments where several dynamic processes expose them to fluctuations in light intensity over a wide range of temporal scales (Falkowski, 1980; Harris, 1980a, 1986; Marra and Heinemann, 1982; Lewis *et al.*, 1984a).

The effects of these changes in irradiance on the growth and chemical composition of phytoplankton have received considerable attention in both experimental and theoretical studies (e.g. Steemann Nielsen *et al.* 1962; Brooks, 1964; Tilzer and Goldman, 1978; Marra, 1978a,b; Prézelin and Matlick, 1980; Falkowski, 1984; Platt and Gallegos, 1980; Falkowski and Wirick, 1981; Lewis *et al.*, 1984a,b; Geider and Platt, 1986; Neale and Richerson, 1987). Many studies have focused on the responses of phytoplankton to vertical mixing in near-surface layers, where assessment of primary production is particularly problematic (Platt and Gallegos, 1980; Goldman and Dennett, 1984; Vincent *et al.*, 1984; Yoder and Bishop, 1985; Elser and Kimmel, 1985).

Photoinhibition is one of the processes encountered near the sea surface (Neale, 1987). Because photoinhibition is an observable response of phytoplankton to light, it is considered here as a photoadaptive process. This classification has some theoretical justification (Sakshaug *et al.*, 1987), but it is used here only to simplify discussions of algal responses to light in the context of vertical mixing.

The conceptual basis for a model of the biological responses of phytoplankton to vertical mixing was well established by the late 1950s (Steemann Nielsen and Hansen, 1959; Ryther and Menzel, 1959) and has been applied in limnological studies (e.g. Tilzer and Goldman, 1978; Gibson, 1978; Harris, 1980b); recent developments and historical perspectives are presented by Falkowski (1980, 1983), Lewis *et al.* (1984a) and Harris (1986). Simply, if the time scale for the response (photoadaptation) is shorter than for vertical mixing, phytoplankton in a mixed layer will exhibit a vertical gradient associated with adaptation to ambient light intensities, whereas if mixing occurs with a time scale shorter than that of photoadaptation, the near-surface mixed layer will be uniform. Adaptation to fluctuating light involves several physiological processes (photoadaptive properties) which respond over a wide range of temporal scales (Harris, 1980a, 1984, 1986). Vertical distributions of several photoadaptive parameters with known and different time scales can thus be used to establish the rate of vertical mixing of the upper mixed layer (Lewis *et al.*, 1984a). Clearly, prediction of the consequences of a turbulent irradiance field requires precise knowledge of the characteristic rates of change for photoadaptive properties and a good understanding of how photoadaptive state reflects the integration of a variable environment by phytoplankton.

Here we examine the kinetics of photoadaptation and the temporal scales of light-dependent change for a marine diatom grown in the laboratory. This information can be employed to use the characteristics of phytoplankton as monitors of the physical environment (cf. Harris, 1984). Estimates of growth and productivity of phytoplankton in nature can also be improved.

Materials and methods

Unialgal, but not axenic, cultures of the marine diatom, *Thalassiosira pseudonana* (clone 3H), were maintained under continuous irradiance from below in low-form culture flasks (culture volume, ≤ 1.71 ; culture depth, ≤ 4 cm). The cells were grown in a modified Aquil medium (Morel *et al.*, 1979) with

increased nutrient levels (nitrate = 0.3 mM; phosphate = 0.25 mM; silicate = 0.113 mM). Light was provided by tungsten-halogen lamps (Atlas OHS 2000) shone through heat filters of running seawater and, except at the highest intensities, through perforated nickel neutral density screen. Temperature was controlled at $21 \pm 0.5^\circ\text{C}$ by a circulating solution of CuSO_4 in water. The culture flasks were fitted with transparent feet so that they rested in copper sulfate solution about 1.5 cm above the glass bottom of the water bath. Thus the light field provided the cultures with approximated submarine irradiance (Jitts *et al.*, 1964; Lewis, 1983). The flasks were sealed with silicone rubber stoppers fitted with a port for bubbling with filtered air and also a silicone rubber siphon tube for adding and withdrawing media or culture aseptically. Appropriate amounts of culture were replaced with fresh media at regular intervals to maintain the cultures in exponential phase at low densities so that the light absorbed by the cultures was generally well below 10% of incident irradiance [estimated by assuming a specific absorption coefficient for chlorophyll *a* of $0.016 \text{ m}^2 \text{ mg}^{-1}$ (Smith and Baker, 1978)].

Cultures were maintained through several transfers at each of three light intensities (photosynthetically active photon fluence density, PPF) measured with a quantum scalar irradiance meter (Biospherical Instruments QSL-100): $20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ('low'), $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ('medium') and $2200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ('high'). Experiments were performed to determine the rate of change of several easily measured parameters after a step-change of PPF. Six transitions were imposed, corresponding to reciprocal shifts between pairs of light intensities. After the switch, a large aliquot from a pre-adapted culture was maintained at the original light intensity, serving as a control. Sampling of the well-mixed control and experimental cultures proceeded for about 10 h. Each experiment was repeated once, with different but overlapping sets of measurements made the second time.

Subsamples for particulate analysis were collected on Whatman GF/C glass fiber filters, precombusted when appropriate. Chlorophyll *a* was measured fluorometrically on samples extracted in 90% acetone in the dark at 0°C . This method compared favorably with other, more tedious methods in a thorough controlled experiment (data not shown). Carbohydrate was measured by the phenol-sulfuric acid method (Dubois *et al.*, 1956), modified to increase sensitivity by incubating samples at 85°C during color development (Sun *et al.*, 1982) and reducing total reactant volume to 2.6 ml. Protein was determined by the fluorescamine method (Udenfriend *et al.*, 1972) as described by Packard and Dortch (1975) except that the filters were ground in 1.6 ml of a 1% solution of Triton X-100 in distilled water rather than in 3 ml of water. Particulate organic carbon was measured according to Sharp (1974). Chlorophyll and carbohydrate were determined in triplicate; measurements of protein and particulate carbon were duplicated.

The fluorescence of chlorophyll *a in vivo* was measured with a Turner Designs 10-005R fluorometer. Samples were held at 21°C in the dark until being dispensed into clean cuvettes and placed in the fluorometer for 1 min, while fluorescence was recorded on a chart recorder. Fluorescence *in vivo* (*F*) was

measured on independent subsamples after dark adaptation for 1 min. Fluorescence (F_d) of subsamples poisoned with the photosynthetic inhibitor DCMU [3-(3,4-dichlorophenyl)-1,1-dimethylurea; final concentration 3×10^{-6} M] was determined after 1 min exposure to the poison. Dark adaptation time was thus 2 min for F_d . Several experiments demonstrated that an incubation of 1 min with DCMU was enough to assure enhancement of fluorescence very close to maximal. Fluorescence yield (F/Chl) is expressed as the dimensionless ratio of *in vivo* fluorescence to the fluorescence of an equal concentration of chlorophyll in 90% acetone (Kiefer, 1973).

Photosynthesis was measured as a function of PPFD (Lewis and Smith, 1983). Illumination was from a tungsten-halogen lamp attenuated by water and neutral density screens. A filter of $CuSO_4$ in water would have matched the spectral quality of the light source for growth, but maximal irradiance would have been diminished. Temperature was controlled at 21°C. Sample preparation required about 10 min after an aliquot was withdrawn from a culture; an incubation of 20 min followed. Radioactive counts were corrected for quench and time-zero controls. Photosynthesis versus irradiance ($P-I$) curves were statistically analyzed by nonlinear curve fitting (Platt and Gallegos, 1980; Gallegos and Platt, 1981).

In the presentation of data, points correspond to the time the aliquot was removed from the culture. Measurements made during the time-course experiments were fit to kinetic models using the multivariate secant method (Ralston and Jennrich, 1978) of the NLIN procedure of SAS (SAS Institute, 1985).

Results and discussion

An analytical model was developed to determine the relationship between vertical mixing and photoadaptation in near-surface mixed layers (Lewis *et al.*, 1984a,b). The model was based on an equation in which the rate of change of a photoadaptive parameter Γ at depth z is determined by photoadaptation, modelled as a first-order reaction (cf. Falkowski, 1980, 1983, 1984; Rivkin *et al.*, 1982), and turbulent mixing, modelled as a diffusive process:

$$\frac{\partial \Gamma(z)}{\partial t} = \gamma(\Delta \Gamma) + \frac{\partial}{\partial z} \left(K_v \frac{\partial \Gamma(z)}{\partial z} \right) \quad (1)$$

where γ (units: time^{-1}) is the rate constant of photoadaptation, $\Delta \Gamma$ is the difference between the value of Γ at depth z [$\Gamma(z)$] and the steady-state value of Γ for ambient irradiance, and K_v (units: $\text{length}^2 \text{time}^{-1}$) is the coefficient of vertical eddy diffusion. Given a mixed layer of depth l and light extinction defined by a diffuse attenuation coefficient k_s (units: length^{-1}), we defined conditions under which vertical mixing and photoadaptation would have approximately equal influence on the vertical distribution of Γ (Lewis *et al.*, 1984a; Figure 1):

$$\frac{K_v}{l^2 \gamma} = 1 - e^{-k_s l} \quad (2)$$

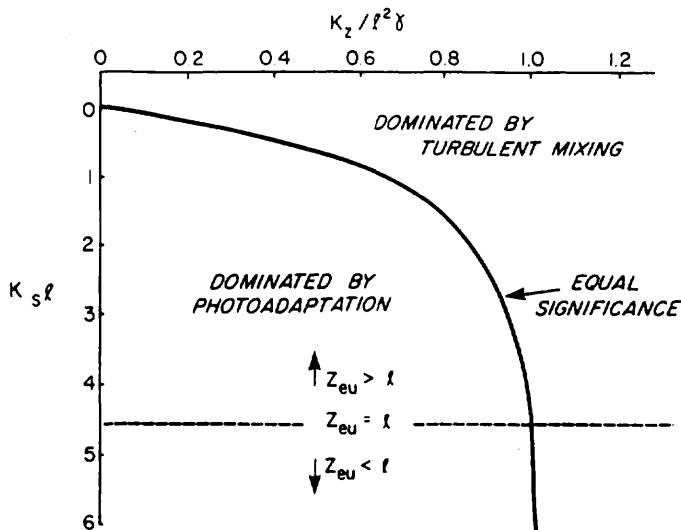


Fig. 1. Modeled relationship between vertical mixing and photoadaptation (equation 2). The line divides the parameter space into a region where photoadaptation dominates and a region where turbulent diffusion dominates. The depth of 1% surface irradiance is called Z_{eu} . From Lewis *et al.* (1984a).

In principle, the equation allows one to specify K_z , the difficult-to-measure coefficient of vertical eddy diffusion, given the diffuse attenuation coefficient, the mixed layer depth, and γ , the rate of photoadaptation at which mixing and photoadaptation share equal dominance. The diffuse attenuation coefficient and mixed layer depth are readily measured; the appropriate value for γ is determined by measuring in vertical profile a suite of photoadaptive parameters with known rates of change and determining the rate which corresponds to the boundary between mixing-dominated and photoadaptation-dominated, as outlined above.

We hoped to identify several characteristics of phytoplankton (photoadaptive parameters) that responded to light over different but definable scales. To be useful as a parameter in a model of photoadaptation and vertical mixing, a light-dependent property of phytoplankton must fulfill two requirements: the property must show monotonic dependence on PPFD with sufficient dynamic range to be easily detectable; and the rate of change of the photoadaptive parameter must be definable and comparable in scale to mixing processes. In testing our model we examine the empirical behavior of easily measured parameters rather than physiological processes *per se*.

Many properties of the cultures showed some correlation with irradiance, as exemplified by a limited set of measurements (Figure 2). The effect of PPFD on each parameter is quite pronounced, but the mathematical nature of the dependence cannot be clearly described on the basis of information from only three light levels. The data indicate the dynamic range of several properties; other studies present detailed data on the dependence of chemical composition

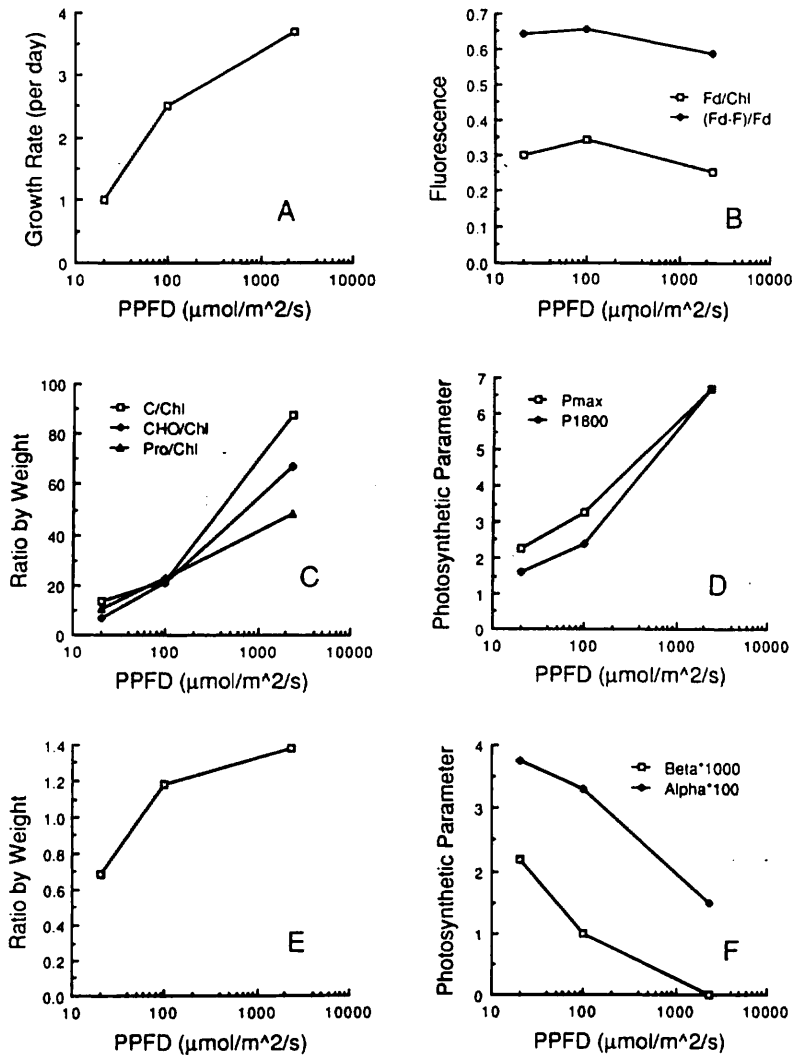


Fig. 2. Photoadaptive parameters as a function of PPFD for growth. Values are averages for control cultures. (A) Growth rate (day^{-1}); (B) fluorescence; (C) ratios by weight of particulate carbon, carbohydrate and protein to chlorophyll *a*; (D) photosynthetic parameters ($\mu\text{g C } \mu\text{g Chl}^{-1} \text{ h}^{-1}$), where P_{1800} is photosynthesis at $1800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ as determined from the fitted parameters; (E) the ratio of carbohydrate to protein; (F) photosynthetic parameters [$\mu\text{g C } \mu\text{g Chl}^{-1} \text{ h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$].

or physiological capacities on irradiance levels for growth [reviewed by Falkowski (1980) and Harding *et al.* (1987); see also Sakshaug and Andresen (1986) and references in Rivkin *et al.* (1982)]. In our model a linear relationship between PPFD and photoadaptive state was originally assumed (Lewis *et al.*, 1984a).

Kinetics of photoadaptation

The time-dependence of the adaptation of unicellular algae to PPFD has been studied on several occasions (Stemann Nielsen *et al.*, 1962; Steemann Nielsen and Park, 1964; Brooks, 1964; Beardall and Morris, 1976; Falkowski, 1980, 1983, 1984; Marra, 1980; Prézelin and Matlick, 1980; Rivkin *et al.*, 1982; Post *et al.*, 1984; Geider and Platt, 1986, Harding *et al.*, 1987), but until recently very little information has been available to describe precisely the kinetics of photoadaptation.

Based on some experimental results and in the absence of contradictory evidence, it has been proposed that photoadaptive changes of cellular chlorophyll content follow first-order kinetics (Falkowski, 1980, 1983, 1984; Rivkin *et al.*, 1982; Post *et al.*, 1984; Lewis *et al.*, 1984a). This generalization has been extended to include the light-dependent changes of photosynthetic capacity (Falkowski and Wirick, 1981) and has also been used to describe photoinhibition and recovery of *in vivo* fluorescence (Vincent *et al.*, 1984; Neale and Richerson, 1987). The first-order model is particularly well suited for application in mathematical descriptions of photoadaptation. However, some aspects of the formulation that are important in general models have not been tested experimentally. Here we examine the consistency of the kinetics of photoadaptation with the first-order reaction model and propose an alternate description of the kinetics of photoadaptation for some light-dependent properties of phytoplankton.

First-order kinetics. By definition, a first-order reaction proceeds at a rate proportional to the concentration of the reactant (A):

$$\frac{\partial A}{\partial t} = k \cdot A \quad (3)$$

where k is the rate constant. In the context of light-dependent changes of a parameter, Γ , first-order kinetics are followed when the rate of change of Γ is proportional to the difference between Γ and the steady-state value for the parameter at ambient irradiance, Γ_{∞} ,

$$\frac{\partial \Gamma_t}{\partial t} = \gamma(\Gamma_{\infty} - \Gamma_t) \quad (4)$$

where γ is the rate constant or characteristic rate of change and $(\Gamma_{\infty} - \Gamma_t)$ is the same as $\Delta\Gamma$ in equation (1). Equation (4) is integrated to obtain a mathematical relationship that is well suited for statistical determination of the rate constant:

$$\Gamma_t = [(\Gamma_{\infty} - \Gamma_0)(1 - e^{-(\gamma t)})] + \Gamma_0 \quad (5)$$

or

$$\ln \frac{(\Gamma_t - \Gamma_{\infty})}{(\Gamma_0 - \Gamma_{\infty})} = -\gamma t \quad (6)$$

That is, the rate constant is defined by the slope of an appropriately scaled logarithmic regression of the photoadaptive parameter versus time (Rivkin *et al.*, 1982; Falkowski, 1983). We have found through experience that the task of fitting experimental results to the first-order model is greatly complicated unless the asymptotic value, Γ_{∞} , is clearly described by the data. Nonetheless, results of some time-course experiments are in good agreement with equation (6), suggesting that photoadaptation may follow first-order kinetics (Rivkin *et al.*, 1982; Falkowski, 1984).

Logistic adaptation. The process responsible for light-dependent changes in chemical composition of phytoplankton is unbalanced growth, the synthesis (or more precisely, the net accumulation) of some cellular components at different rates than others (cf. Shuter, 1979; Eppley, 1981; Cullen, 1985). The nature of unbalanced growth suggests an alternate description of the kinetics of photoadaptation.

Consider the time-course of particulate carbon and chlorophyll *a* concentrations in cultures subjected to shifts between high ($2200 \mu\text{mol m}^{-2} \text{s}^{-1}$) and medium ($100 \mu\text{mol m}^{-2} \text{s}^{-1}$) PPFD (Figures 3 and 4). The control culture

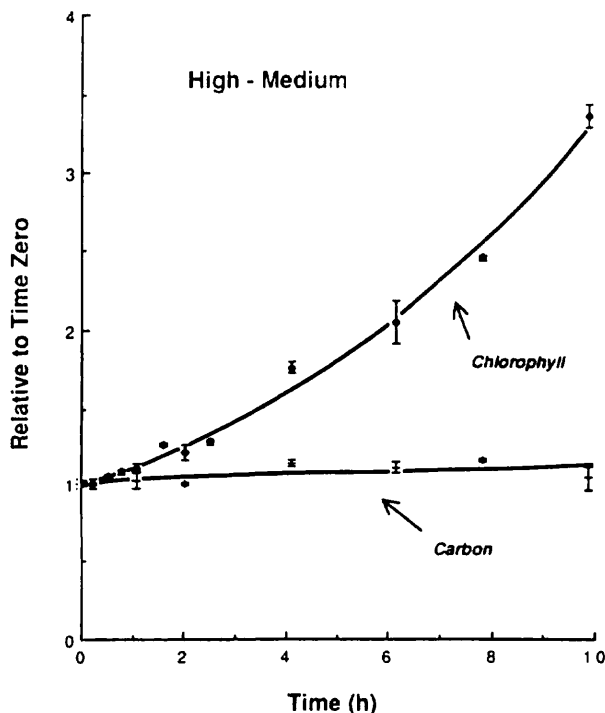


Fig. 3. Time course of particulate carbon and chlorophyll concentration after a switch from 2200 to $100 \mu\text{mol m}^{-2} \text{s}^{-1}$. Values are relative to time zero. Error bars are \pm SE for chlorophyll and the range for duplicate determinations of carbon. Curves are fit by logarithmic regression (see text).

maintained in high light grew at the exponential rate of $0.155 \pm 0.021 \text{ h}^{-1}$ (slope of logarithmic regression $\pm 95\%$ confidence limits), as determined from measurements of chlorophyll during exponential growth (cf. Brand and Guillard, 1981). As expected under conditions of balanced growth, the rate of increase as determined from measurements of particulate carbon was about the same ($0.137 \pm 0.025 \text{ h}^{-1}$). After the experimental culture was shifted to $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Figure 3), chlorophyll synthesis continued unabated for at least 5 h whereas the rate of increase of particulate carbon was sharply reduced due to the limitation of photosynthesis by light and the apparently substantial demands of respiration. During this period of unbalanced growth, the changes in chlorophyll and particulate carbon were indistinguishable from exponential: linear regression on logarithmically transformed data indicated that the accumulation of chlorophyll could be described by

$$(\text{Chl})_t = (\text{Chl})_0 \cdot e^{\rho_{\text{chl}} t} \quad (7)$$

where Chl_0 is chlorophyll at time zero and ρ_{chl} is the rate constant, $0.122 \pm 0.007 \text{ h}^{-1}$. For the purposes of this discussion, the increase of

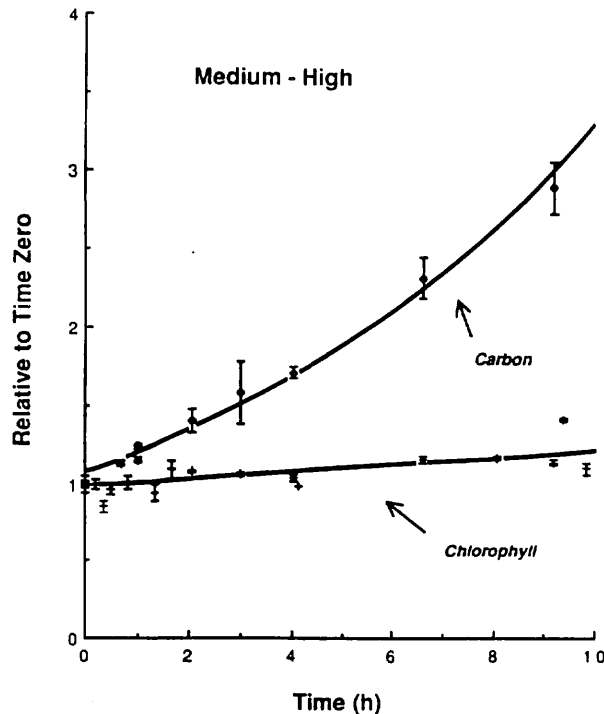


Fig. 4. Time course of particulate carbon and chlorophyll concentration after a switch from 100 to $2200 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Values are relative to time zero. Error bars are $\pm \text{SE}$ for chlorophyll and the range for duplicate determinations of carbon. Curves are fit by logarithmic regression (see text).

particulate carbon can be similarly represented, with the rate constant for carbon, $\rho_c = 0.009 \pm 0.011 \text{ h}^{-1}$. Results for the first hours after the reverse shift, from medium to high PPF, were likewise consistent with this simple exponential model: the growth rate at $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ was $0.097 \pm 0.012 \text{ h}^{-1}$; after the switch to high light, the rate of accumulation of particulate carbon did not change significantly, maintaining throughout the experiment an apparently exponential rate of $0.104 \pm 0.017 \text{ h}^{-1}$ (Figure 4). The net synthesis of chlorophyll, however, was sharply curtailed to $0.017 \pm 0.007 \text{ h}^{-1}$ [see Falkowski (1980) for a suggested mechanism for repression of chlorophyll synthesis by high irradiance].

A useful photoadaptive parameter is the ratio of carbon to chlorophyll (C/Chl: Laws and Bannister, 1980; Falkowski and Wirick, 1981; Geider and Platt, 1986). The change of C/Chl during the first hours of each experiment (Figure 5) can be described as

$$(C/Chl)_t = (C/Chl)_0 \cdot e^{(\rho_c - \rho_{chl})t} \quad (8)$$

Exponential increases or decreases of C/Chl can therefore be attributed to disparate rates of accumulation for C and Chl (cf. Falkowski, 1984). The general form of equation (8) is

$$\Gamma_t = \Gamma_0 \cdot e^{\rho t} \quad (9)$$

Exponential kinetics persist only during the initial phase of photoadaptation when the differing rates of synthesis are relatively constant: as cellular composition approaches the photoadaptive optimum (cf. Shuter, 1979), unbalanced exponential rates converge on a new steady state corresponding to equal rates of synthesis at the new growth rate. For a first approximation, we will assume a linear feedback on ρ as Γ_t approaches Γ_∞ :

$$\frac{\partial \Gamma_t}{\partial t} = \rho \Gamma_t \left(\frac{\Gamma_\infty - \Gamma_t}{\Gamma_\infty} \right) \quad (10)$$

This kinetic model is mathematically the same as the logistic model of population growth and will be referred to in this discussion as the logistic model of adaptation. The solution is

$$\Gamma_t = \frac{\Gamma_\infty}{1 + [(\Gamma_\infty - \Gamma_0)/\Gamma_0] e^{-\rho t}} \quad (11)$$

The observed changes of C/Chl during reciprocal shifts between high and medium PPF are consistent with logistic adaptation (Figure 5). This formulation is similar to that proposed by Geider and Platt (1986). As pointed out by Geider and Platt, it is important which measurement is in the denominator when a photoadaptive parameter is expressed as a ratio. In the logistic model the photoadaptive parameter must be positively related to growth irradiance, i.e. C/Chl must be used rather than Chl/C.

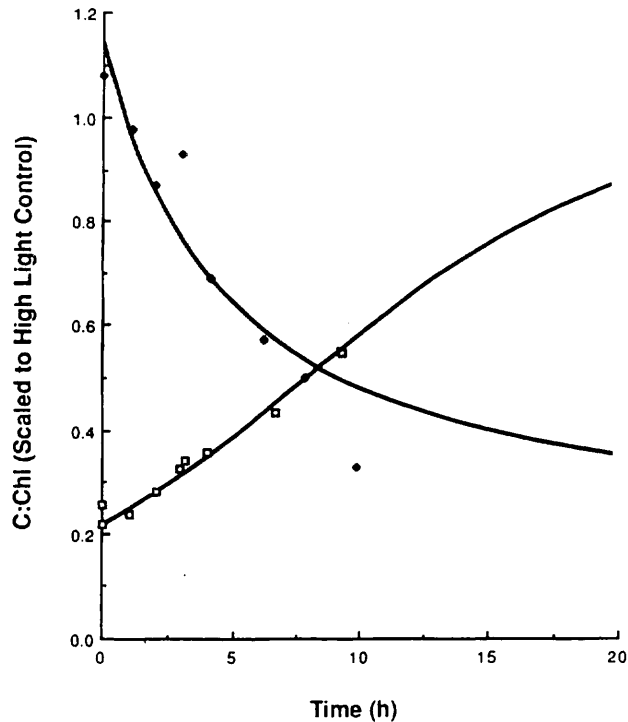


Fig. 5. Time course of C/Chl after shifts between 2200 and 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Values are scaled to the high light control. Boxes represent the shift from 100 to 2200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Filled diamonds represent the shift from 2200 to 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Curves are best fits to the model of logistic adaptation (see text).

Differences between the kinetic models. A comparison of the predictions of the first-order and logistic models (Figure 6) shows that in many situations both kinetic models predict similar behavior. Some fundamental differences exist, however, and these have significant consequences in models describing growth and photosynthesis in fluctuating light. Assume that Γ is positively related to growth irradiance. It can be seen that the two models predict different forms of exponential change. After a shift from a high to low PPFD, the first-order decline of Γ would be very difficult to distinguish from the mathematically distinct pattern predicted by the logistic model. For the reciprocal shift from low to high PPFD, however, the shapes of the two curves are distinctly different (cf. Geider and Platt, 1986). With precise measurements it might be possible to determine which model is the better fit.

A more dramatic and important difference between models is in time scales for adaptation. The first-order model specifies that the time for adaptation depends only on the rate parameter γ and is therefore independent of the magnitude or direction of change whereas the temporal scale for logistic adaptation depends on starting and ending conditions: for comparison between

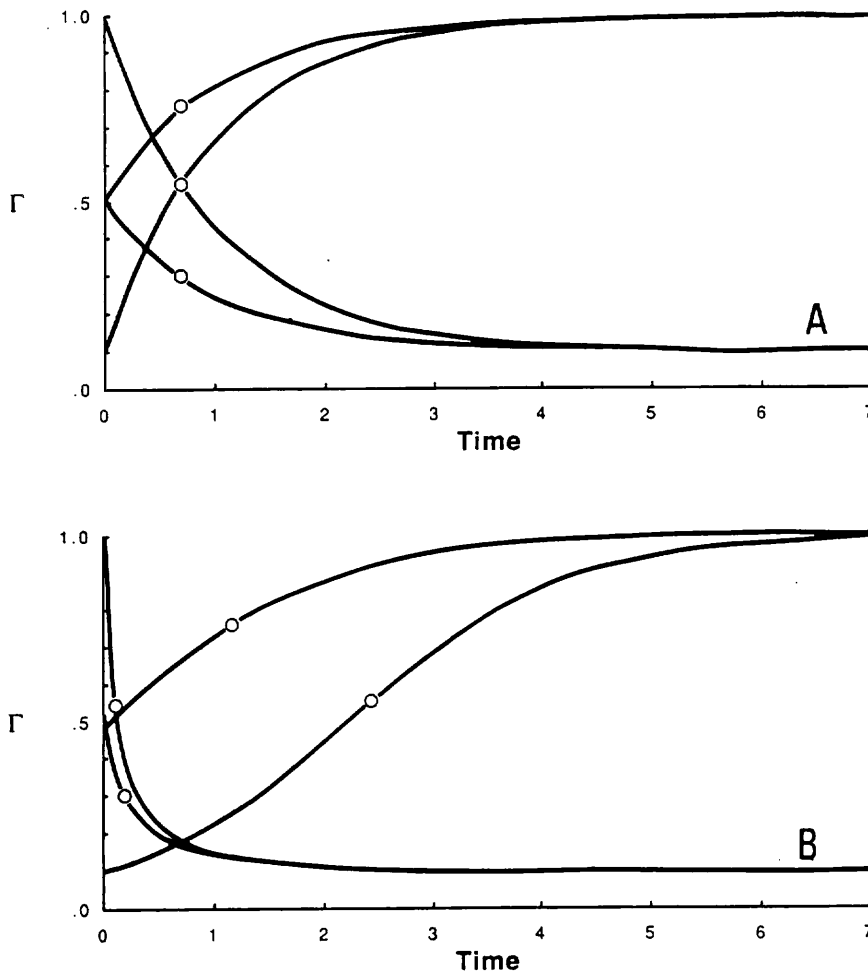


Fig. 6. Models of the kinetics of photoadaptation. The parameter Γ represents a photoadaptive parameter that is positively related to PPFD. Circles mark 50% completion of the change from Γ_0 to Γ_∞ . (A) First-order kinetics: the time scale for change is independent of the magnitude or direction of the change in PPFD. (B) Logistic adaptation (see text): the time scale for change is a function of both the magnitude and direction of change; the shapes of the curves therefore also depend on the nature of the change.

models we can define the time scale of adaptation as $\tau_{0.50}$, the time required for 50% of full response from Γ_0 to Γ_∞ . This temporal scale is calculated by solving the model equation for t when $\Gamma_t = (\Gamma_0 + \Gamma_\infty)/2$. In the first-order model,

$$\tau_{0.50} = \frac{0.693}{\gamma} \quad (12)$$

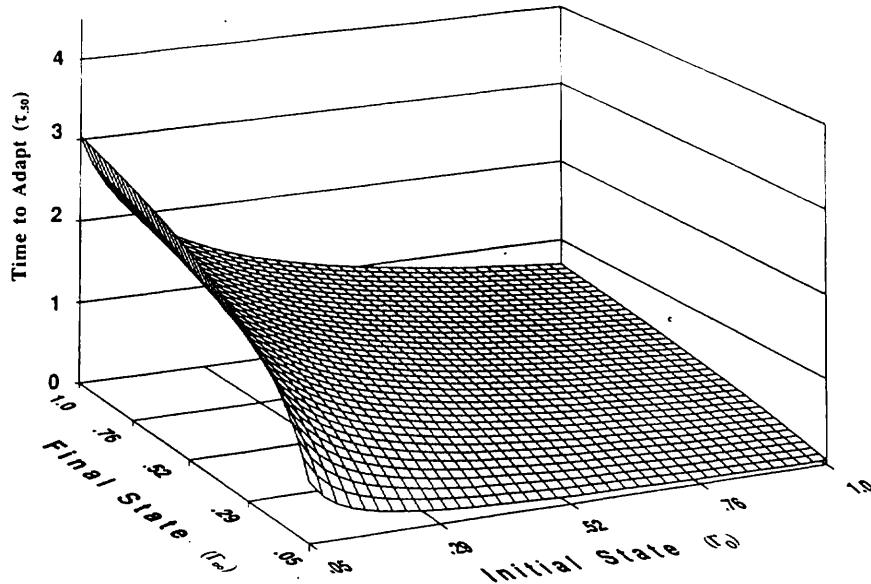


Fig. 7. Logistic adaptation: time to adapt as a function of initial state (Γ_0) and final state (Γ_∞). The parameter $\tau_{0.50}$ is the time required for 50% completion of the change from Γ_0 to Γ_∞ . According to the model, it takes longer to adjust to an increase of PPFD than to a decrease and it takes longer to adjust to a large change of PPFD as compared to a small change. The first-order model, strictly interpreted, predicts that $\tau_{0.50}$ is the same regardless of the magnitude or direction of the change in PPFD. Note that when $\Gamma_0 = \Gamma_\infty$, $\tau_{0.50}$ is meaningless.

The temporal scale is independent of the magnitude of Γ_0 and Γ_∞ . The logistic model (equation 10; Figure 6B) is fundamentally different:

$$\tau_{0.50} = -\ln \left(\frac{\Gamma_0}{\Gamma_0 + \Gamma_\infty} \right) / \rho \quad (13)$$

The time scale for change is dependent on the relative magnitude of the change in irradiance, the starting condition, and the direction of change (Figure 7). Given the same rate constant and the same absolute change, $|\Delta\Gamma|$, the logistic process will approach completion more rapidly for changes between high-light states as opposed to changes between low-light states, and for down-shifts as opposed to up-shifts in PPFD. This is all a consequence of the assumed nature of unbalanced growth, including the implicit assumption that the rate of synthesis in balanced growth (i.e. growth rate) is proportional to Γ .

Time scales of adaptation. Results from the light-shift experiments were fit to both the first-order and logistic models and time scales ($\tau_{0.50}$) were calculated (Table I). For several sets of measurements, adaptation was incomplete by the end of sampling and an asymptote could not be reliably determined by the curve-

Table 1. Kinetics of adaptation for *Thalassiosira pseudonana* (3H)—results of curve-fitting procedures

Switch	Γ_0	s.e.	Γ_x	s.e.	γ	s.e.	$T_{0.50}$
<i>First-order model</i>							
α [$\mu\text{g C } \mu\text{g Chl}^{-1} \text{h}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1}$]							
HL	0.016	(0.0020)	0.057	(0.0253)	0.09	(0.086)	7.53
HM	0.014	(0.0035)	0.031	(0.0054)	0.32	(0.272)	2.17
LH	0.033	(0.0017)	0.008	(0.0009)	1.84	(0.428)	0.38
LM							
MH	0.034	(0.0019)	0.020	(0.0009)	1.62	(0.653)	0.43
ML	0.031	(0.0009)	0.055	(0.0398)	0.05	(0.104)	13.86
P_{max} ($\mu\text{g C } \mu\text{g Chl}^{-1} \text{h}^{-1}$)							
HL	6.78	(0.300)	3.69	(0.15)	1.32	(0.379)	0.53
HM	6.03	(0.422)	3.28	<i>fixed</i>	0.07	(0.043)	9.63
LH	1.11	(0.025)	6.70	<i>fixed</i>	0.03	(0.001)	21.00
LM	2.25	(0.201)	4.37	(1.85)	0.11	(0.158)	6.30
MH	3.47	(0.296)	8.77	(10.53)	0.06	(0.151)	11.55
ML							
P_{1800} ($\mu\text{g C } \mu\text{g Chl}^{-1} \text{h}^{-1}$)							
HL	5.76	(0.236)	3.14	(0.19)	0.69	(0.196)	1.01
HM	6.03	(0.357)	2.38	<i>fixed</i>	0.13	(0.034)	5.52
LH	1.03	(0.039)	6.00	<i>fixed</i>	0.04	(0.001)	17.86
LM	1.46	(0.171)	2.26	(0.58)	0.19	(0.296)	3.65
MH	2.96	(0.267)	6.39	(1.30)	0.16	(0.118)	4.25
ML							
C/Chl (g g^{-1})							
HL	72.2	(3.8)	13.6	<i>fixed</i>	0.12	(0.019)	5.82
HM	98.6	(5.0)	22.0	<i>fixed</i>	0.16	(0.023)	4.33
LH	13.4	(3.1)	87.8	<i>fixed</i>	0.04	(0.009)	16.90
LM	9.5	(3.9)	22.0	<i>fixed</i>	0.42	(0.243)	1.65
MH	17.4	(1.0)	87.8	<i>fixed</i>	0.06	(0.004)	11.95
ML	23.4	(1.1)	13.6	<i>fixed</i>	0.05	(0.026)	13.59
CHO/Chl (g g^{-1})							
HL	95.1	(5.6)	10.0	(7.8)	0.28	(0.074)	2.46
HM	54.9	(3.9)	18.5	(3.7)	0.52	(0.170)	1.34

	LH	7.5	(1.7)	67.3	fixed	0.03	(0.006)	24.75	
	LM	20.1	(2.0)	42.0	fixed	0.13	(0.033)	5.21	
	MH	20.2	(4.1)	87.0	(58.5)	0.09	(0.108)	8.15	
	ML	20.9	(2.1)	7.0	fixed	0.07	(0.042)	10.34	
F_p/Chl	HL 1	0.240	(0.018)	0.431	(0.010)	1.02	(0.23)	0.68	
	HL 1	0.348	(0.027)	0.451	(0.018)	0.97	(0.67)	0.71	
	HM 1								
	HM 2	0.387	(0.035)	0.476	(0.023)	0.94	(1.09)	0.73	
	LH 1	0.264	(0.013)	0.101	(0.006)	1.73	(0.30)	0.40	
	LH 2	0.305	(0.022)	0.119	(0.011)	3.75	(1.35)	0.18	
	LM 1	0.304	(0.008)	0.375	(0.016)	0.35	(0.21)	1.99	
	LM 2								
	MH 1	0.416	(0.020)	0.168	(0.006)	2.94	(0.47)	0.24	
	MH 2	0.393	(0.022)	0.211	(0.008)	5.73	(1.75)	0.12	
	ML								
<i>Exponential model</i>									
	α [$\mu\text{g C } \mu\text{g Chl}^{-1} \text{h}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1}$]								
	HL	0.016	(0.0016)	0.044	(0.0049)	0.30	(0.089)	4.43	
	HM	0.014	(0.0029)	0.030	(0.0031)	0.59	(0.320)	1.98	
	LH	0.034	(0.0027)	0.009	(0.0015)	0.72	(0.348)	0.31	
	LM								
	MH	0.034	(0.0021)	0.020	(0.0011)	1.16	(0.617)	0.40	
	ML	0.031	(0.0009)	0.048	(0.0157)	0.11	(0.105)	8.79	
P_{max} ($\mu\text{g C } \mu\text{g Chl}^{-1} \text{h}^{-1}$)	HL	6.78	(0.348)	3.69	(0.19)	0.92	(0.346)	0.47	
	HM	6.09	(0.436)	3.28	fixed	0.05	(0.027)	9.17	
	LH	1.28	(0.038)	6.70	fixed	0.10	(0.005)	17.73	
	LM	2.26	(0.192)	3.99	(0.88)	0.21	(0.167)	4.80	
	MH	3.45	(0.277)	6.69	(0.23)	0.18	(0.154)	5.89	
	ML								
P_{min} ($\mu\text{g C } \mu\text{g Chl}^{-1} \text{h}^{-1}$)	HL	5.68	(0.267)	3.09	(0.28)	0.41	(0.184)	1.05	
	HM	6.06	(0.422)	2.38	fixed	0.06	(0.019)	5.53	
	LH	1.23	(0.060)	6.00	fixed	0.11	(0.008)	15.98	

Table I. Continued

Switch	Γ_0	s.e.	Γ_∞	s.e.	γ	s.e.	$T_{0.50}$
LM	1.46	(0.167)	2.19	(0.38)	0.28	(0.320)	3.25
MH	2.98	(0.240)	5.93	(0.64)	0.31	(0.127)	3.56
ML							
C/Chl (g g^{-1})							
HL	74.2	(4.9)	17.1	(30.1)	0.04	(0.115)	4.71
HM	99.9	(7.3)	22.0	<i>fixed</i>	0.05	(0.010)	4.04
LH	14.3	(1.9)	87.8	<i>fixed</i>	0.15	(0.025)	12.87
LM	11.0	(2.1)	37.7	(21.6)	0.21	(0.155)	6.98
MH	19.1	(0.8)	78.7	(20.1)	0.17	(0.036)	9.45
ML	23.4	(1.2)	13.6	<i>fixed</i>	0.03	(0.017)	14.13
CHO/Chl (g g^{-1})							
HL	95.8	(8.2)	7.0	<i>fixed</i>	0.03	(0.007)	2.14
HM	54.7	(4.7)	14.9	(13.4)	0.16	(0.162)	1.50
LH	8.1	(1.4)	67.3	<i>fixed</i>	0.13	(0.025)	17.15
LM	20.6	(1.9)	42.0	<i>fixed</i>	0.20	(0.049)	5.55
MH	20.0	(3.3)	60.7	(8.4)	0.34	(0.125)	4.07
ML	21.3	(2.2)	7.0	<i>fixed</i>	0.03	(0.017)	10.12
F_{β} /Chl							
HL 1	0.248	(0.016)	0.430	(0.009)	1.35	(0.30)	0.74
HL 1	0.348	(0.026)	0.451	(0.017)	1.13	(0.73)	0.74
HM 1	0.365	(0.046)	0.393	(0.025)	1.19	(4.69)	0.61
HM 2	0.388	(0.035)	0.476	(0.022)	1.02	(1.12)	0.78
LH 1	0.269	(0.015)	0.100	(0.077)	0.93	(0.24)	0.34
LH 2	0.320	(0.022)	0.120	(0.010)	2.78	(1.18)	0.11
LM 1	0.305	(0.008)	0.373	(0.014)	0.41	(0.22)	1.97
LM 2							
MH 1	0.421	(0.020)	0.166	(0.007)	1.62	(0.30)	0.21
MH 2	0.395	(0.022)	0.210	(0.008)	3.88	(1.33)	0.11
ML							

Light-shifts are abbreviated with the initial condition followed by the new condition: H (high), M (medium) and L (low). When data were insufficient to discern an asymptote, Γ_∞ was fixed. For some experiments, no strong pattern was discerned and data are not reported.

fitting procedure. In those cases, Γ_{∞} was set to the control value for the new PPFD and the curve-fitting routine determined only Γ_0 and the rate constant.

Photoadaptive parameters which could be modified by redistribution of energy in the photosynthetic apparatus [*in vivo* fluorescence and α , the initial slope of the $P-I$ curve; cf. Neale (1987)] changed more rapidly than parameters whose changes are associated with the synthesis of cellular material [e.g. cellular chemical composition and photosynthetic capacity; cf. Harris (1980a)]. Differences in the time to adapt for these two groups are most pronounced for the experiments shifting from lower to high irradiance (Figures 8 and 9): fluorescence and α changed rapidly (order 20 min) as a manifestation of photoinhibition of photosynthesis (Figure 10A). These results show clearly that photosynthesis is related to fluorescence during photoinhibition (Belay, 1981; Vincent *et al.*, 1984; Whitlam and Codd, 1984; Samuelsson *et al.*, 1985; Neale and Richerson, 1987). Photosynthetic capacity (P_{max}) was also depressed transiently soon after a switch to high irradiance (Figure 10B). Thus, the response to high light was characterized by rapid inhibition and, concurrently, slower repair (Samuelsson *et al.*, 1985) and adaptation. The logistic model of adaptation, developed to describe unbalanced growth in fluctuating light, is inappropriate for describing the rapid responses to bright light. For this reason, the logistic model of adaptation will be considered only as a description of the slower responses of photosynthetic capacity and chemical composition to light.

The time to adapt ($\tau_{0.50}$) can be used as a criterion to compare the first-order and logistic models as descriptors of experimental results for measures of cellular chemical composition and photosynthetic capacity. The predictions of the logistic model are (Figures 6 and 7):

- (i) It takes longer to adjust to an increase of PPFD as compared to the reciprocal decrease.

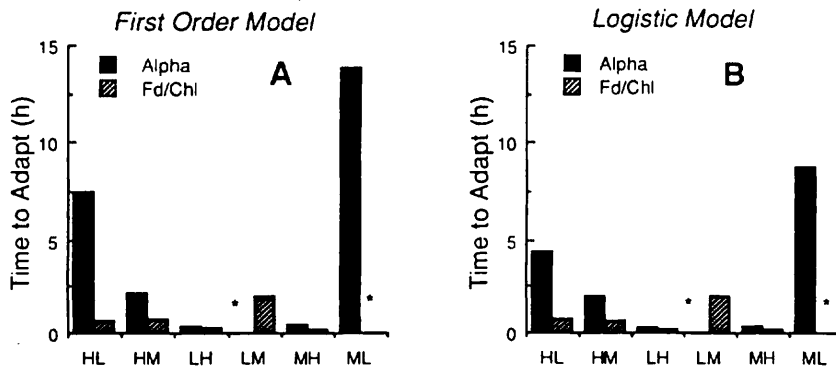


Fig. 8. Photosynthetic parameters of *Thalassiosira pseudonana* (3H). Time to adapt ($\tau_{0.50}$) for different shifts of PPFD. Light shifts are abbreviated with the initial condition followed by the new condition: H (high), M (medium) and L (low). Stars mark experiments for which no strong temporal pattern was observed during the experiment. Time to adapt was determined by best fits to (A) the first-order model and (B) the logistic model of adaptation. The parameters α and F_d/Chl are treated separately here because the dominant changes in response to bright light occur rapidly and do not involve substantial synthesis of cellular constituents.

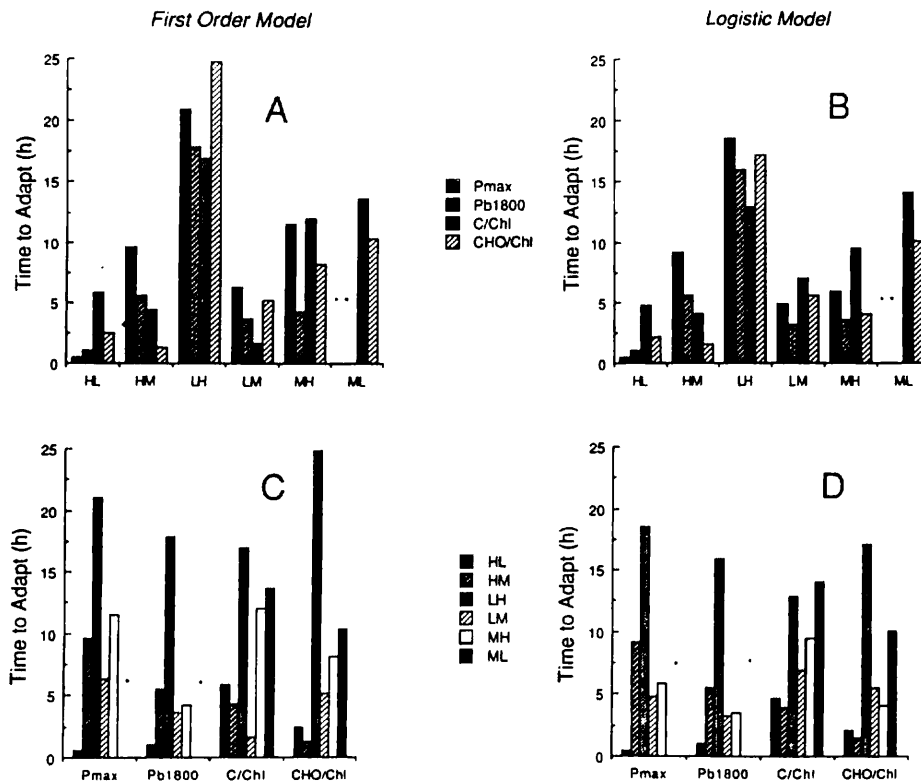


Fig. 9. Photosynthetic parameters of *Thalassiosira pseudonana* (3H). Time to adapt ($\tau_{0.50}$) for different shifts of PPFD. Abbreviations as in Figure 8. Data are presented two ways to facilitate comparisons: (A) and (B) are grouped to compare time scales for different light shifts, as determined by fits to the first order and logistic models, respectively. (C) and (D) are grouped to compare time scales of change for different photosynthetic parameters (P_{max} , P_{b1800} , C/Chl and carbohydrate/Chl). Changes of these parameters can be associated with unbalanced growth and might not be well described by the first-order model. If the first-order model explained perfectly the kinetics of photoadaptation, the rate constant for each parameter would be the same for any switch of PPFD, but might differ for each photoadaptive parameter.

- (ii) It takes longer to adjust to a large increase of PPFD as compared to a smaller increase.
- (iii) It takes longer to adjust to a smaller decrease of PPFD as compared to a larger decrease.

The logistic model predicts the biggest differences between time scales for shifts from high to low light (fast) as compared to shifts from low to high light (slow). For the logistic model of adaptation to be accurate, the rate constant, ρ , must be the same for any photoadaptive parameter, regardless of light shift.

The prediction of the first-order model is simple: $\tau_{0.50}$ and the rate constant, γ , are the same for any photoadaptive parameter, regardless of light shift.

The kinetics of photoadaptive responses to experimental light shifts are not entirely consistent with either model. Clearly, for any given parameter the time

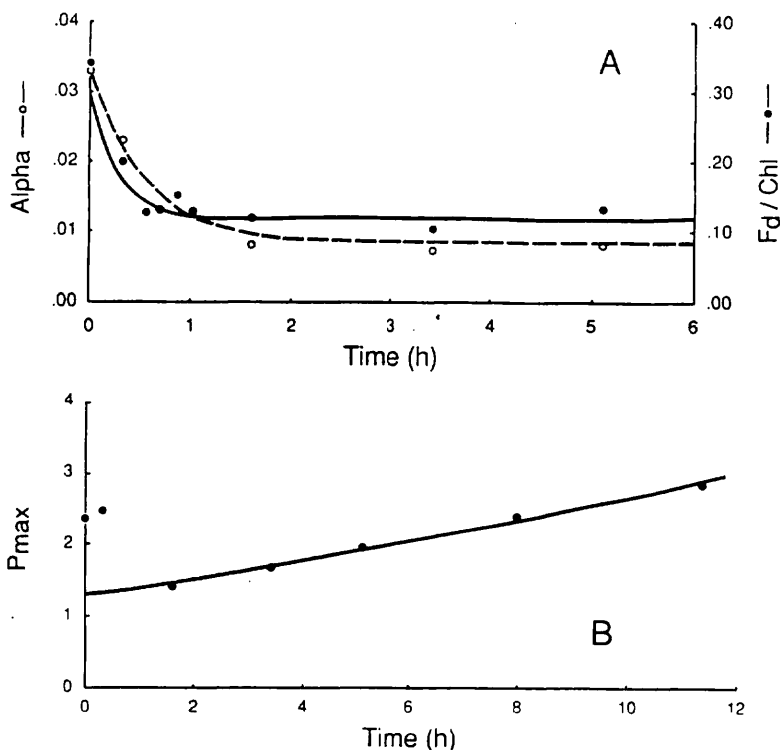


Fig. 10. Responses of *Thalassiosira pseudonana* (3H) to a shift from low ($20 \mu\text{mol m}^{-2} \text{s}^{-1}$) to high ($2200 \mu\text{mol m}^{-2} \text{s}^{-1}$) PPFD. (A) Fluorescence (F_d/Chl) and the initial slope of the $P-I$ relationship [α , $\mu\text{g C } \mu\text{g Chl}^{-1} \text{ h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$]. Curves are fits to the first order model. (B) Photosynthetic capacity (P_{max} , $\mu\text{g C } \mu\text{g Chl}^{-1} \text{ h}^{-1}$). A transient depression was followed by a slow increase toward the adapted state for high light. The curve fit is for the logistic model, Γ_{∞} set to $6.7 \mu\text{g C } \mu\text{g Chl}^{-1} \text{ h}^{-1}$.

scale for change is not the same for all light shifts (Figures 8 and 9). The first-order model is therefore incapable of describing fully our results. Consistent with prediction (i) for the logistic model, the time for adaptation for the switch from low to high PPFD was much longer than for the reciprocal shift. Other comparisons were reasonably consistent with the predictions (ii) and (iii) (Table II), especially considering that the expected differences in time scales are not large for some comparisons. For the results presented here, the logistic model explains some consistent deviations from first order kinetics. The model is by no means perfect, however: for any parameter, the rate constant is not the same for all light shifts (Figure 11), indicating that the logistic model does not fully describe the kinetics of photoadaptation for the experiments reported here. It should also be noted that other experiments have shown little or no differences between the times to adapt to reciprocal light shifts (Falkowski, 1984; Post *et al.*, 1984).

Table II. Comparisons of the time scales for photoadaptation: *Thalassiosira pseudonana* (3H)

$\tau_{0.50}$		HL/LH	HM/MH	HL/HM	LM/LH
First-order model	P_{\max}	0.03	0.83	0.05	0.30
	P_{1800}^b	0.06	(1.30)	0.18	0.20
	C/Chl	0.34	0.36	(1.35)	0.10
	CHO/Chl	0.10	0.16	(1.85)	0.21
Logistic model	P_{\max}	0.03	(1.56)	0.05	0.27
	P_{1800}^b	0.07	(1.55)	0.19	0.20
	C/Chl	0.37	0.43	(1.16)	0.54
	CHO/Chl	0.12	0.37	(1.43)	0.32

Abbreviations and units as in Table I. Data are the ratios of time scales ($\tau_{0.50}$) for the designated comparisons. The first-order model predicts that all ratios will be 1.0. The logistic model predicts that all ratios reported above should be <1. Deviations from the prediction of the exponential model are in parentheses.

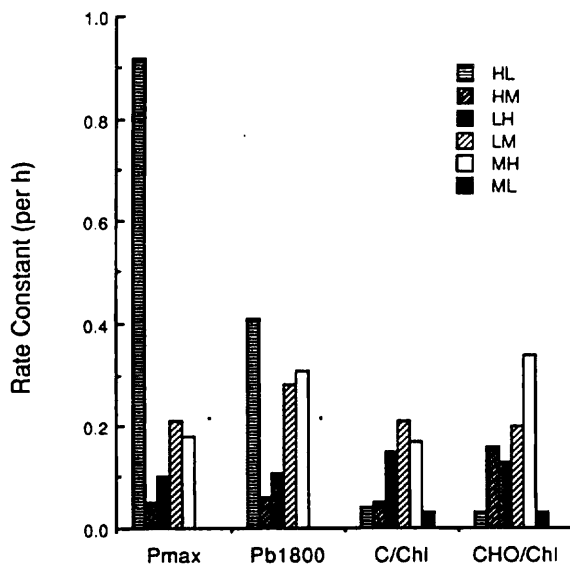


Fig. 11. Photosynthetic parameters of *Thalassiosira pseudonana* (3H). Adaptation rate constant, ρ , for the logistic model (equations 10 and 11). If the model explained perfectly the kinetics of photoadaptation, the rate constant for each parameter would be the same for any shift of PPFD, but might differ for each photoadaptive parameter.

Comparisons and implications

The choice of kinetic model for describing photoadaptation is not critical if one needs only to describe the temporal scale of the response: estimates of $\tau_{0.50}$ were similar for both models examined here (Figures 8 and 9) and other methods for describing kinetics (e.g. Prézélin and Matlick, 1980; Falkowski 1983, 1984; Post *et al.*, 1984) fit the data for any one experiment. When algal responses to vertical

mixing are considered, however, the distinctions between models might be crucial. Principally, pronounced differences in time scales for responses to reciprocal shifts of PPFD would lead to hysteresis effects which might change fundamentally the predictions of algal responses in mixed layers.

The photoadaptive parameters examined here fall into two categories: fairly rapid responses attributable to changes in the photochemical apparatus (photoinhibition) and slower changes due to unbalanced growth. It is useful to consider the two types of response separately.

Consistent with other studies, changes in the photochemical apparatus were reflected in *in vivo* fluorescence and parameters of the *P-I* curve (especially α), which declined in response to bright light with a temporal scale of less than an hour (Neale and Richerson, 1987, and references therein). The time scale of this rapid depression seems to be rather insensitive to growth temperature (Lewis *et al.*, 1984a). We did not study the recovery from photoinhibition. Recovery is not a mirror-image of inhibition, rather it is slower and a function of the prior exposure (Belay, 1981; Neale, 1987). The first-order model can describe some changes of fluorescence and photosynthesis in response to bright light, but for mixed-layer models some refinement is clearly warranted.

It should be recognized that there is substantial taxonomic variability in short-term responsiveness to bright light. *Thalassiosira pseudonana* was shown to be much more responsive to bright light than the oceanic clone *T. oceanica* (Sakshaug *et al.*, 1987). Because the flexibility of *T. pseudonana* is associated with better survival in strong light as compared to the oceanic clone, it is expected that the flora in mixed layers will be flexible like our test organism. This assumption can be tested in the field.

Post *et al.* (1984) pointed out that the first-order model had no inherent physiological meaning, yet they could detect no departures from first-order kinetics in their data. Our observations of large differences in time scales for adaptation from low to high light as compared to high to low light are not consistent with the first-order model. The logistic model, based on a simple description of unbalanced growth, therefore does a better, but incomplete job of accommodating the observed differences in rates of adaptation. Future models of algal responses to fluctuating light should at least consider that the rate of adaptation for any one parameter might not be independent of the magnitude or direction of the change of PPFD.

Diurnal variability can have a substantial influence on the kinetics of photoadaptation (Post *et al.*, 1984; Harding *et al.*, 1987), especially for processes with time scales on the order of days. In this study we have used cultures grown in continuous light and have measured parameters that in nature can change significantly in less than a day (Lewis *et al.*, 1984b). We feel that our experimental results are meaningful. Nonetheless, there is good justification for further work with more natural fluctuations of irradiance.

Implicit in the logistic model of adaptation is the dependence of the rate of adaptation on the rate of growth. The expectation, supported by some experimental results (Prézelin and Matlick 1980; Post *et al.*, 1984), is that under similar conditions, slowly growing algae would take longer to adapt than more

rapidly growing microalgae. By scaling appropriately the results from controlled experiments, it should be possible to examine the degree to which the rate of adaptation depends on the rate of growth.

The logistic model of photoadaptation (equation 10) is an alternative to the first-order model which can be incorporated into an equation to describe the relationship between vertical mixing and photoadaptation in near-surface mixed layers (see equation 1):

$$\frac{\partial \Gamma(z)}{\partial t} = \rho \Gamma(z) \frac{\Delta \Gamma}{\Gamma_{\infty}} + \frac{\partial}{\partial z} \left(K_v \frac{\partial \Gamma(z)}{\partial z} \right) \quad (14)$$

Our experimental results indicate that this may be better than equation (1) as a description of some forms of photoadaptation. There are several interesting implications of equation (14) which will be the topic of another study.

Patterns of fluorescence, cellular chemical composition and photosynthetic parameters in mixed layers show how phytoplankton integrate a variable environment (Harris, 1984, 1986). On the time scale of minutes to hours, *in vivo* fluorescence and *P-I* parameters are useful indicators. For example, if vertical mixing is sufficiently rapid (residence time less than the time scale for depression of photosynthesis), photosynthesis near the surface is maximal and neither fluorescence (measured appropriately) nor *P-I* parameters will be depressed near the surface (Marra, 1978a,b; Harris, 1984; Vincent *et al.*, 1984; Elser and Kimmel, 1985). Vertical uniformity therefore indicates efficient utilization of light in the near-surface layer. In contrast, on the time scale of hours to days, vertical differentiation of phytoplankton is due to photoadaptation rather than photoinhibition. If mixing is slow enough to allow the light-shade adaptation of phytoplankton in the water column, rates of growth and production will vary with depth, tending to maximize productivity (Tilzer and Goldman, 1978) and leading to vertical patterns of chlorophyll concentration (Cullen, 1982) and species composition (Cullen *et al.*, 1982; Venrick, 1982).

Conclusions

The changes of photoadaptive parameters observed during these experiments were only partially described by general models. Nonetheless, important generalizations can be drawn:

- (i) Several parameters, easily measured in nature and attributable primarily to phytoplankton, are responsive to fluctuating light on different time scales.
- (ii) In response to bright light, both the initial slope of the *P-I* curve and *in vivo* fluorescence are depressed on a time scale of less than an hour. Photosynthetic capacity is depressed transiently, but can recover over many hours to a high level characteristic of an adapted state. First-order kinetics reasonably describe the rapid responses of phytoplankton to bright light. The kinetics of recovery should be examined to refine models of photoinhibition and vertical mixing.

(iii) Some parameters of photoadaptation (i.e. cellular chemical composition and photosynthetic capacity) change as a result of unbalanced growth. A mathematical description of this process (the logistic model) suggests that, in contrast to predictions of the first-order model, the time scales for adaptation should depend on the initial and final irradiance. Some of our experimental results are in general agreement with predictions of the logistic model: particularly, adaptation from low to high light took longer than adaptation from high light to low light. The potential consequences of hysteresis during vertical mixing should be assessed.

Although the concept of photoadaptation is reasonably simple, the details are complicated. The same goes for vertical mixing in aquatic environments. By observing the vertical patterns of photoadaptive parameters near the surface, we can learn more about each process.

Acknowledgements

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