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Analysis of diel variability in chlorophyll fluorescence

by John Marra[1]

ABSTRACT

Examples of the diel variability in chlorophyll and beam attenuation are presented using data from moored *in situ* fluorometers and transmissometers, and from profiles of the beam attenuation coefficient and fluorescence. The data are discussed in terms of the three primary processes thought to influence the diel variability in chlorophyll: (1) fluorescence yield per unit chlorophyll *a,* (2) chlorophyll *a* changes per cell (or, carbon), and (3) changes in phytoplankton carbon (growth). A simple, provisional, model is presented which incorporates these three biological processes, under the assumption that the corresponding diel variability in particle attenuation represents the change in phytoplankton carbon. The analysis produces qualitative agreement with the *in situ* data. The model suggests that while under high-light conditions fluorescence declines, chlorophyll can still increase during the day. Under low-light conditions, the diel variability of chlorophyll and fluorescence are in phase. The model is limited by (1) physiological understanding of the processes involved in producing fluorescence and chlorophyll changes over diel time scales; (2) biomass-independent variations in particle attenuation; and (3) not including, for the present, physical forcing.

1. Introduction

The variation in solar irradiance, from day to night, has profound influence not only on planktonic organisms (Enright, 1970) but on their environment (e.g., Price *et al.,* 1986). Diel variability in chlorophyll *a* in the ocean has been recognized since at least 40 years ago. Sournia (1974) and Harris (1978) have reviewed the earlier evidence, and ascribed the variations to effects from irradiance (Yentsch and Ryther, 1957; Glooschenko *et al.,* 1972), or from changes in biomass (Harris, 1978).

In earlier studies the data were usually not well resolved because the water column could not be easily sampled. Although repeated hydrocasts are usually impractical, Le Bouteillier and Herbland (1982) achieved a 13-day time series of chlorophyll as a function of depth in the equatorial Atlantic, sampling eight depths four times per day. There has been some success in doing repeated casts for continuous profiles of bio-optical properties (Siegel *et al.,* 1989), or casts at specified times over a period of days (Weller *et al.,* 1985; Marra *et al.,* 1987; Cullen *et al.,* 1992). However, the magnitude and significance of diel variability was not revealed until the use of moored or drifting bio-optical sensors (Hamilton *et al.,* 1990; Abbott *et al.,* 1990; Dickey *et al.,* 1991; Stramska and Dickey, 1992). For the study of diel

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variability, automated sampling and measurement are indispensable, and sampling programs have only recently been so configured.

In the last decade, there has been a reliance on *in vivo* fluorescence to provide estimates of chlorophyll, continuously and *in situ,* coupled with the use of beam transmissometers which offer a means to estimate particle biomass in a size range typical for phytoplankton. The benefit of these methods is the essentially continuous measurement over depth or time, which fulfills the condition mentioned above about automating the measurement of the variable of interest in diel studies. For fluorometry, a disadvantage is that it adds another component to the variability of the chlorophyll changes, making the signals often notoriously difficult to interpret (Cullen, 1982; Cullen *et al.,* 1988). In addition to the changes in chlorophyll induced by irradiance or from changes in biomass, a third effect must be added, changes in fluorescence per unit chlorophyll, or the fluorescence yield. Variation in fluorescence yield forces interpretive constraints, but also grants possible opportunities in estimating photosynthesis and physiological properties (Cullen *et al.,* 1988) and, indirectly, in the study of mechanisms by which phytoplankton are mixed through the euphotic zone (Therriault *et al.,* 1990).

Here, a preliminary biological model of the diel variability of chlorophyll is developed in order to interpret sequential observations in the ocean. Developing the model at this stage requires simplification in three areas. First, for the time being, physical forcing of diel properties is disregarded (Doney *et al.,* 1995); however, the potential importance of mixing processes on the signal observed is clear. The data primarily considered are not well-enough resolved in the vertical to allow straightforward analysis. Second, developing a model on the diel variations in chlorophyll requires a measure of autotrophic biomass. Therefore, it is assumed that particle attenuation measured on the mooring is a proxy for phytoplankton carbon, much as Siegel *et al.* (1989) assumed. The effects of this assumption are discussed in Section 4. Third, by convention, the moored fluorescence values are presented in units of chlorophyll *a.* Therefore, for the purposes of this analysis, fluorescence and chlorophyll are interchangeable.

Although only diagnostic at this point, the model does suggest directions for future work. And if the parameters of the model were better known, the net growth of phytoplankton *in situ* might be estimated from the diel variation in phytoplankton properties.

Stramska and Dickey (1992) have done statistical analyses of the diel variability of fluorescence and beam attenuation for the mooring experiment that we conducted south of Iceland (59°29′N/20°50′W) as part of the Marine Light-Mixed Layers (ML-ML) Program in 1989 (Marra, 1989). They also reviewed possible contributing factors. Here, a more mechanistic approach is attempted, using mooring data from a previous mooring experiment, Biowatt-II, and also profile data from ML-ML.

2. Methods

a. Moored observations. Descriptions of the methods used for acquiring the data from the moored fluorometers and transmissometers on the Multi-Variable Moored Sensors have

been presented previously (Dickey *et al.*, 1991; Marra *et al.*, 1992). The moored fluorescence data are presented in units of chlorophyll *a* (see also Marra and Langdon, 1993). Transmissometer voltages were converted to transmittance (T) according to instructions from the manufacturer, and the beam attenuation coefficient, c_{tot} (at 660 nm), was calculated by

$$c_{tot} = \frac{-\ln(T)}{l} \tag{1}$$

where l is the pathlength, 25 cm. The beam attenuation coefficient was corrected for the attenuation by pure water to obtain the coefficient for particles by,

$$c_p = c_{tot} - 0.364.$$

The contribution to attenuation by dissolved material is neglected.

b. Profiling observations. Vertical profiles of properties were collected with a Seabird CTD (SBE, Bellevue, WA) to which were incorporated (1) a transmissometer (25 cm pathlength, with a light source at 660 nm; SeaTech, Corvallis, OR), (2) a fluorometer (SeaTech), and (3) a PAR sensor (QSP-200L, Biospherical Inst., San Diego, CA). Profiles were taken 4–5 times per day at selected stations. The raw profile data were processed and binned to 1 m intervals. Fluorescence (F1) is reported as a voltage. Transmissometer data were treated in the same manner as for the moored sensors. Chlorophyll *a* analysis followed standard methodology.

3. Observations

As mentioned above, the significance of the diurnal signals in chlorophyll and bio-optical properties was first recognized in the data from the Biowatt Mooring Experiment in 1987 (Dickey *et al.*, 1991), and occurred throughout the 9-month record (Dickey *et al.*, 1993; Marra, 1994). Two examples of those data are shown to illustrate the role of irradiance in shaping the diel variability.

The response in F1 in the moored-sensor data seems to be driven by the magnitude of the irradiance (Fig. 1). The diel change in c_p is the same as found in earlier studies (e.g., Siegel *et al.*, 1989), that is, a minimum at sunrise and a maximum at sunset. In March, early in the year (Fig. 1a), F1 and particle attenuation co-vary closely, suggesting that the change occurring in particles during the day is almost entirely associated with phytoplankton. Again, the diel variability is characterized by increases during the day and declining values at night. Later in the season, in October (Fig. 1b), irradiances are much higher, with noontime values of about 400–500 μmols photons m^{-2} s^{-1}. In this case, F1 declines sharply during the day, and is more or less constant at night. Particle attenuation continues to exhibit the same behavior as in March. For both time periods, fluorescence and particle

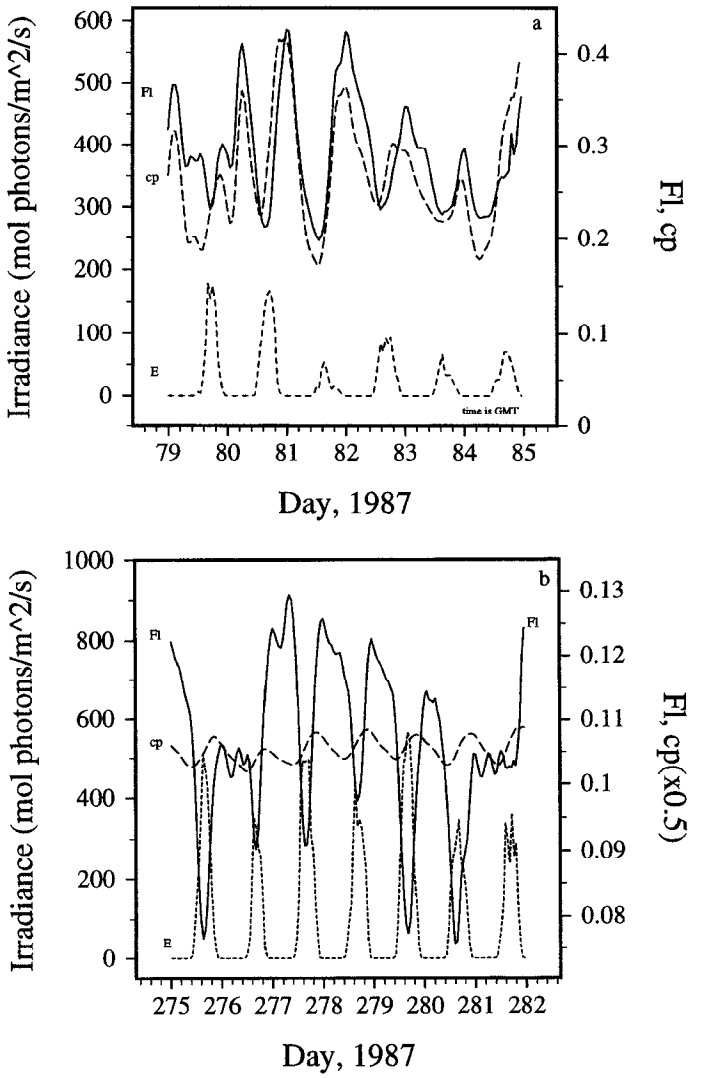


Figure 1. Diel variability of *in vivo* chlorophyll *a* fluorescence (F1) and particle attenuation (c_p) from moored sensors at 20 m depth. For the mooring data, the convention has been to report moored fluorescence in units of chlorophyll *a* (mg m^{-3}). Irradiance (PAR) is in μmols photons m^{-2} s^{-1}. (a) March, 1987; (b) October, 1987.

attenuation show little overall trend. These data are but two examples of similar behavior observed throughout the mooring experiment.

a. Correlations between beam attenuation and fluorescence. Under certain circumstances, it is possible to study diel variations from profiles of chlorophyll *a* fluorescence. Because

the water column may change between casts, or between the up and down portions of the cast, it can be useful to plot c_p and F1 together. This way, F1 can be studied in relation to a measure of particle, typically phytoplankton, abundance. If we plot c_p on the y-axis and F1 on the x-axis, any changes in the x-direction should be proportional to increases in chlorophyll per particle (or cell). Changes in the y-direction may reflect changes in the number of particles (and their scattering properties) relative to F1. Changes in the positive direction of the slope of the relationship may indicate increases in phytoplankton, that is, particles and chlorophyll together.

Again, the three processes mentioned above operate during a series of casts taken over a single day, and within a single water mass. With data from profiles, there is never enough temporal resolution. However, unlike the mooring data, the depth distributions can be examined in greater detail. Two examples are shown. The first is from the ML-ML site (circa 59N/21W) in August, 1991 (Fig. 2). The temperature structure suggests a deepening of the surface mixed layer over the day (Fig. 2a) and perhaps consequently, for this day, c_p declines in the afternoon. Chlorophyll a is constant throughout the mixed layer, however, near-surface fluorescence declines appreciably for the two daytime casts and the decline intensifies from morning to afternoon (Fig. 2c). When c_p is plotted against F1, the diel behavior of fluorescence can be visualized better (Fig. 2d). There is evidence for an increase in fluorescence with respect to c_p by 1500 h; however, this cannot be verified as an increase in chlorophyll a (Fig. 2c). The near-surface decline in fluorescence can be seen, as in the depth profiles, producing the '7' shape to the distribution (e.g., Kitchen and Zaneveld, 1990).

In contrast, for the Gulf of Maine in July (Fig. 3), there exists a subsurface F1 maximum that is also a maximum for chlorophyll a (Fig. 3c) and the distributions are more stable (Fig. 3b). There is evidence of phytoplankton production and chlorophyll increases during this particular day, characterized by overcast conditions and low surface irradiances (see Marra *et al.,* 1993). The shapes of the curves indicate concurrent particle and F1 maxima. There is little photoinhibition of F1; instead, the distributions suggest a higher chlorophyll biomass at the F1 maximum. By dusk, phytoplankton production is apparent, as well as chlorophyll production.

4. Analysis

From the above discussion, diel variability in chlorophyll can be subdivided into three components: changes in fluorescence yield (F1 per chlorophyll a), changes in chlorophyll a per unit phytoplankton carbon (photoadaptation), and changes in phytoplankton carbon (growth).

Fluorescence changes per unit chlorophyll a are primarily caused by irradiance, are noted especially near the surface where irradiances are high (Kiefer, 1973; Vincent, 1979), and they are rapid (time scale of minutes) and reversible (Sakshaug *et al.,* 1987). Demers *et al.* (1991) show evidence of fluorescence quenching at irradiances above about 100 μmols photons m^{-2} s^{-1}, and occurring in less than ten minutes. Those authors also remark on a

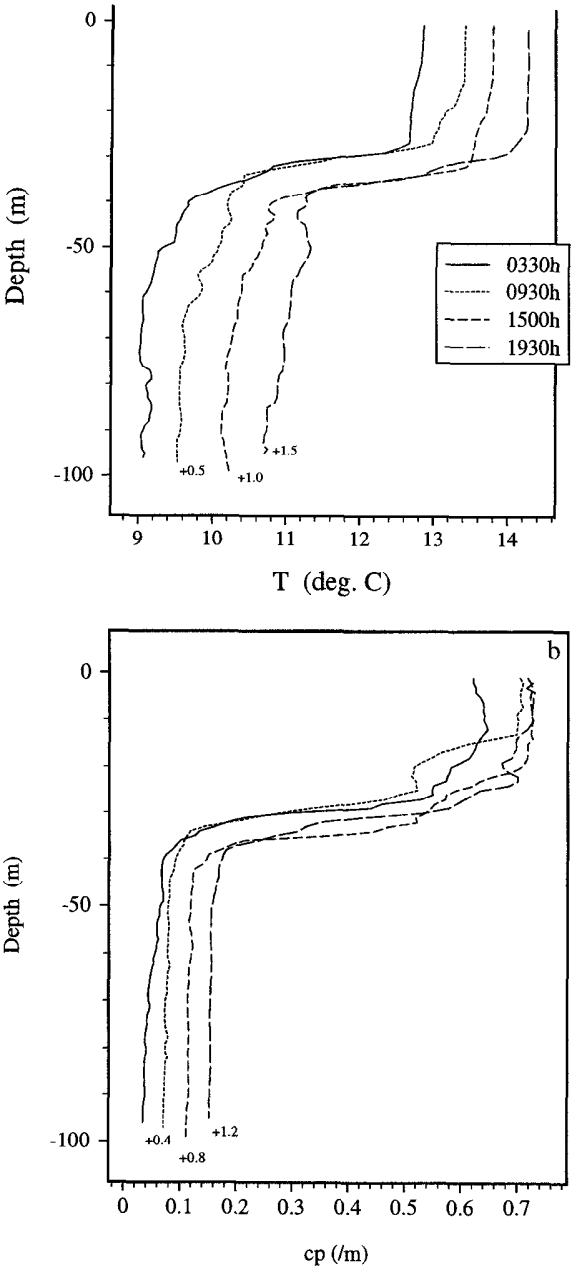
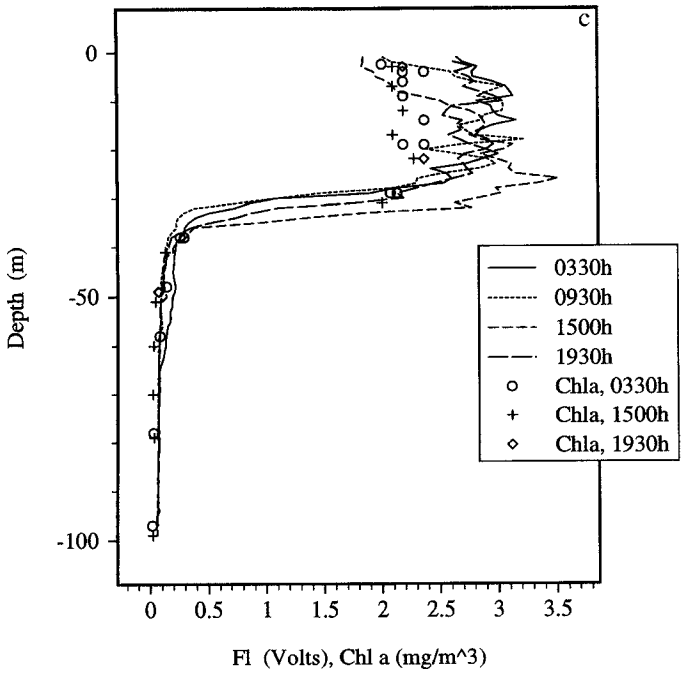


Figure 2. Data on water column properties at various times of the day from the ML-ML site (circa 59W/21N), 27 August, 1991. These data are from drift stations during single 24 hour periods. The times of the casts are local and are shown in the legend. T-S plots of these casts do not indicate a change in water mass over the period of sampling. For temperature and particle attenuation, the profiles are offset (for visibility) by the amounts given at the bottom of the traces. (a) Temperature, (b) particle attenuation (c_p), (c) fluorescence (F1) and chlorophyll *a* (mg m^{-3}) and (d) c_p vs. F1.



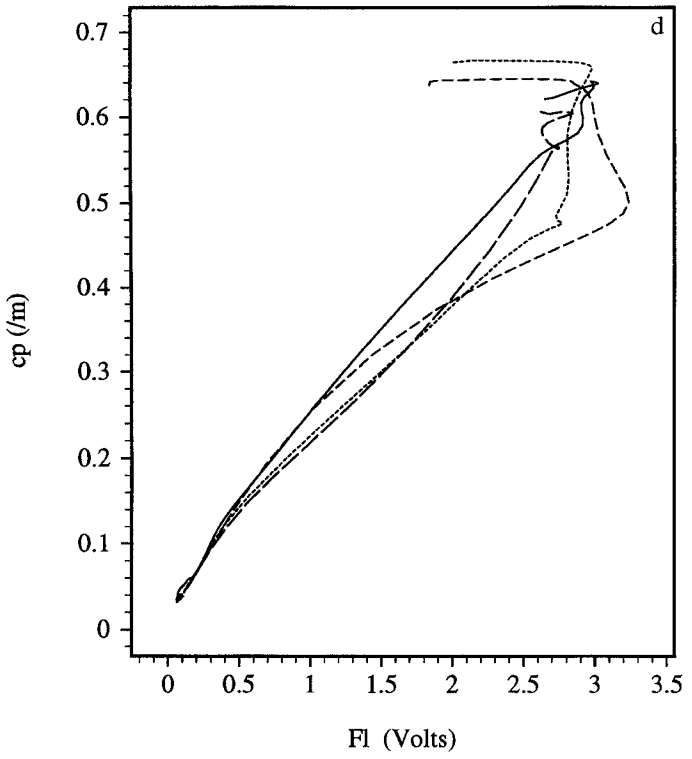


Figure 2. (Continued)

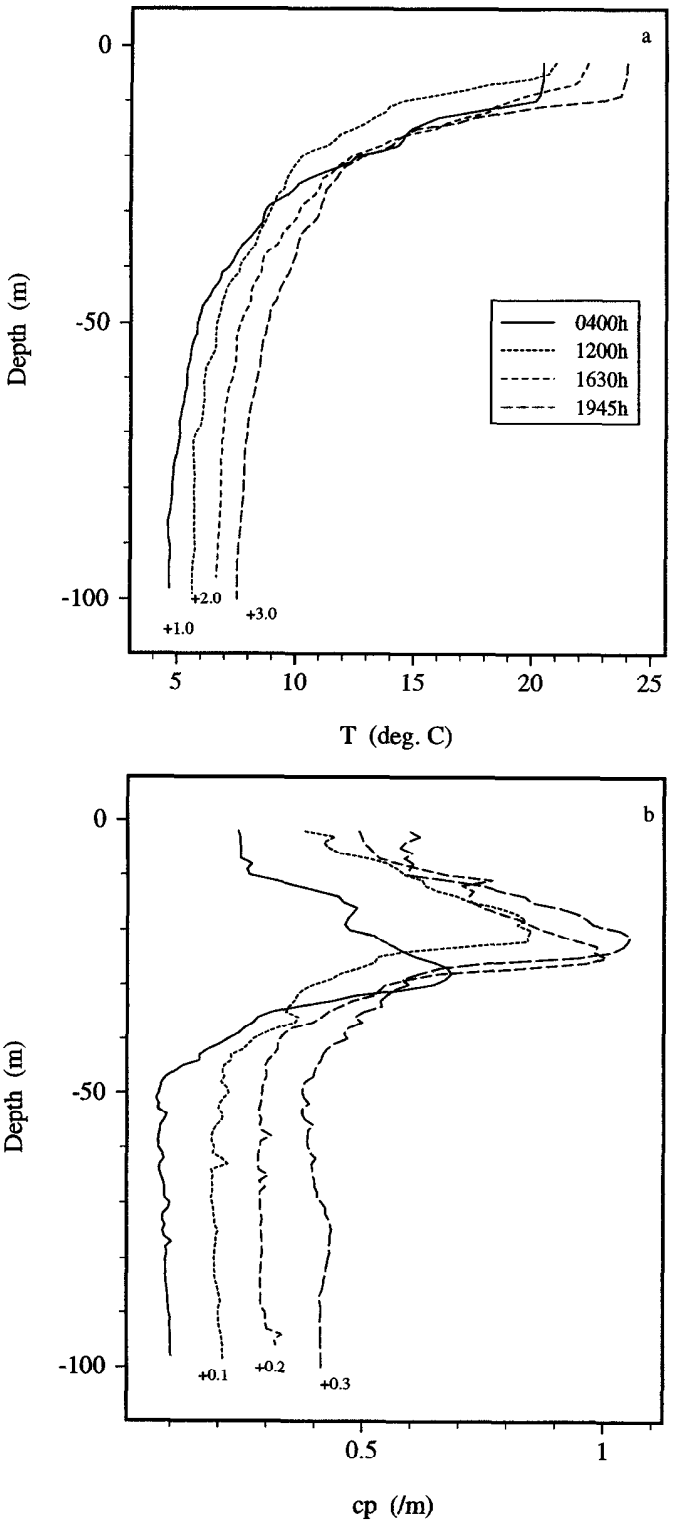


Figure 3. Same as Figure 2 but for the Gulf of Maine (42N/69W), 29 July, 1990.

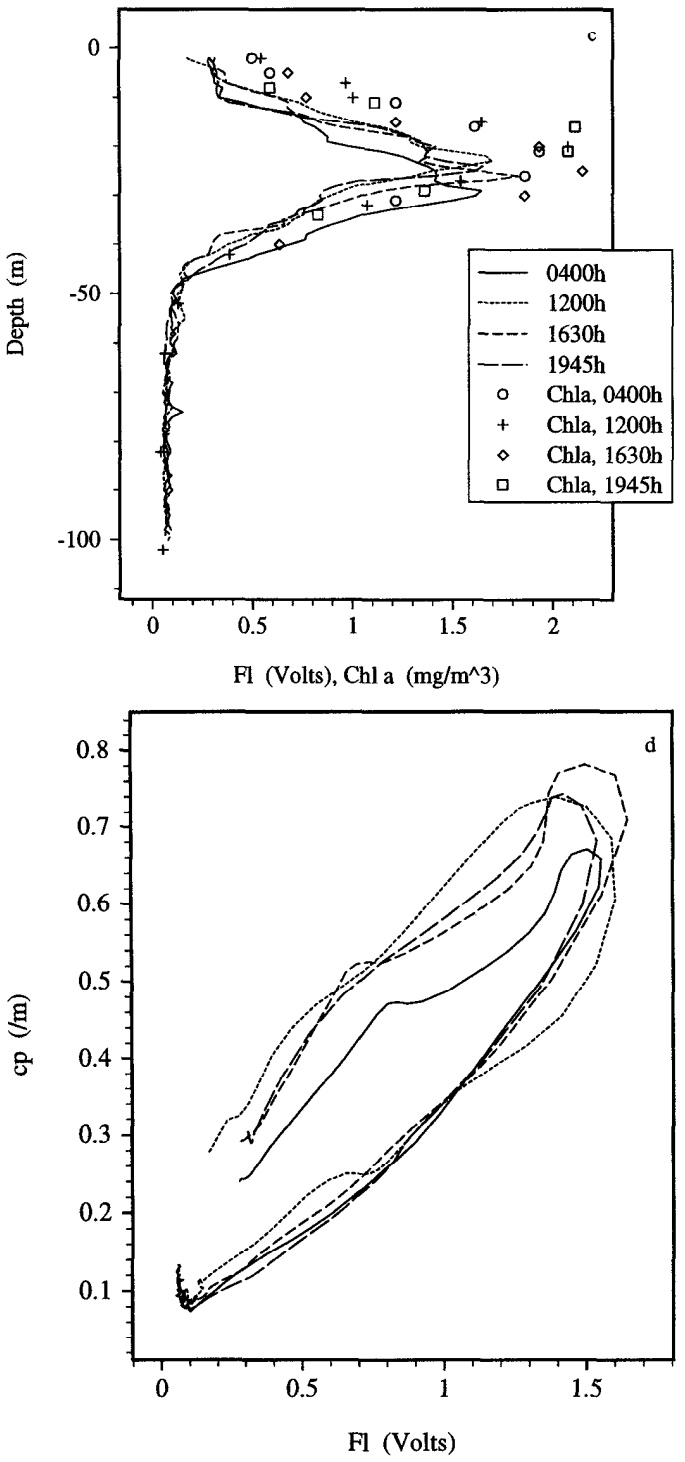


Figure 3. (Continued)

variation between the two species tested in the susceptibility to photoinhibition. Demers *et al.* (1991) argue that the changes in fluorescence yield which they observed are a form of nonphotochemical quenching, controlled by the xanthophyll cycle (Demmig-Adams, 1990), a short-term mechanism involving photo-protectant carotenoids to protect the photosynthetic units from damage caused by high photon fluxes. At high irradiances, nonphotochemical quenching should dominate other quenching of fluorescence, such as that caused by photochemistry (Holmes *et al.,* 1989).

Second, fluorescence changes will arise from changes in chlorophyll per cell (carbon), or photoadaptation. Photoadaptation can operate at the diel scale but also over periods of a few days. On the diel time scale, it has often been observed that in cultures placed in the light, phytoplankton cells make chlorophyll *a* (e.g., Eppley *et al.,* 1967; Owens *et al.,* 1980; Marra, 1980; Hitchcock, 1980). When phytoplankton cultures are transferred to a reduced irradiance, they often produce more chlorophyll *a* over the period of one to a few days (e.g., Richardson *et al.,* 1983). The two time scales to photoadaptation are perhaps best seen in the study by Post *et al.* (1984), where a diel oscillation in chlorophyll per cell of the same magnitude occurs when exposed to either high or low irradiance. Thus there are two components to consider in photoadaptational change. On a light:dark cycle, cells will produce chlorophyll in the light, but also, the level of irradiance will determine the quantity of chlorophyll in the cell, a level that may prevail over longer than the photoperiod. We might expect that the diel variation in chlorophyll *a* per cell may be driven by a separate cellular process than longer-term (two or more days) changes in chlorophyll in the cell.

Another problem is that the most-reported change is on a per-cell basis and not carbon. Given photosynthesis and balanced growth (all cellular components increasing together), the chlorophyll:C ratio (Chl:C) in the cultures may be invariant at the diel time scale. There are very few data on the changes in Chl:C over a day; Owens *et al.* (1980) show data from one 24 h period in a natural population which indicate day-to-night changes in Chl:C, but relatively constant values during the day. Stramski and Reynolds (1993) show two-fold variations, but which may in part be driven by the atypical diurnal irradiance variation in their culture.

Finally, chlorophyll will change as biomass changes with balanced growth in phytoplankton. This was the conclusion of Le Bouteillier and Herbland (1982) in their 13-day study of diel variations in the equatorial Atlantic. Importantly, in the water column, growth must be considered to include zooplankton grazing, making this part of the diel variability in chlorophyll *a* net growth rate.

A model for the diel variations in chlorophyll begins with the net growth rate of phytoplankton. As stated above, it is assumed that the diel change in c_p is representative of phytoplankton growth and loss, although the model is not dependent on the specific kinds of variability included in the diel change in c_p. For example, for some populations, there can be carbon-independent changes in c_p over the day (Stramski *et al.,* 1995), and the autotrophs will constitute only a portion of the c_p. Assuming therefore, the general shape of

the diel change in c_p (Fig. 1), phytoplankton growth is written as,

$$C_{t+1} = C_t \cdot e^{(p-r)t} \tag{2}$$

where C is phytoplankton carbon, t is time, p is the rate of photosynthesis and r is the rate of respiration (both with units of T^{-1}). The photosynthesis rate is made a function of irradiance, using the hyperbolic tangent function (Jassby and Platt, 1976),

$$p = p_{max}\tanh(E/E_k) \tag{3}$$

for $E > 0$, and E being the irradiance and p_{max} the maximum growth rate. E_k marks the irradiance above which $p = p_{max}$. Respiration is parameterized as a two-component process to incorporate a diel change. Thus, respiration consists of a light-dependent rate (r_E), a fraction of p, and a maintenance respiration rate, r_m (Shuter, 1979). Combined, we have

$$r = r_E + r_m \,. \tag{4}$$

Included in the maintenance respiration are any losses from grazing on phytoplankton carbon. The increase in phytoplankton carbon is the difference between p and r.

Irradiance is assumed to vary with time of day as,

$$E(t) = E_{max} \cdot \sin\left(\pi \frac{t-6}{D}\right)^3 \tag{5}$$

where E_{max} is the irradiance at $(t - 6)$ h, or noon, and D is the day length, 24 h.

As the next step, we need to be able to parameterize how chlorophyll changes relative to phytoplankton carbon as the phytoplankton are growing in the light, that is, an equation for the photoadaptation process. From evidence cited above an equation of the form,

$$\theta_t = \theta_0 + mE(t)e^{-nE(t)} \tag{6}$$

is appropriate, where θ_0 is an initial or reference Chl:C ratio, n is a constant and m a scaling factor. Eq. (3) accounts for decreases in chlorophyll relative to carbon at high irradiances, but allows an increase in chlorophyll relative to carbon at low irradiances, depending on the choice of n. The above relationship is also implied by the data of Hitchcock (1980).

Combining the growth and photoadaptation equations, we arrive at an equation for the variation in chlorophyll a at any time during the 24 h period,

$$Chl_t = C_t \cdot \theta_t \,. \tag{7}$$

Finally, there is the light-dependent change in fluorescence per unit chlorophyll, which, as argued above, is nonphotochemical quenching. Fluorescence is the property normally measured on profiling and moored sensors. If we suppose that the decline in fluorescence per unit chlorophyll is reversible (Demers *et al.*, 1991), then it should not involve the destruction of pigment. Therefore, we might expect the relationship between nonphoto-

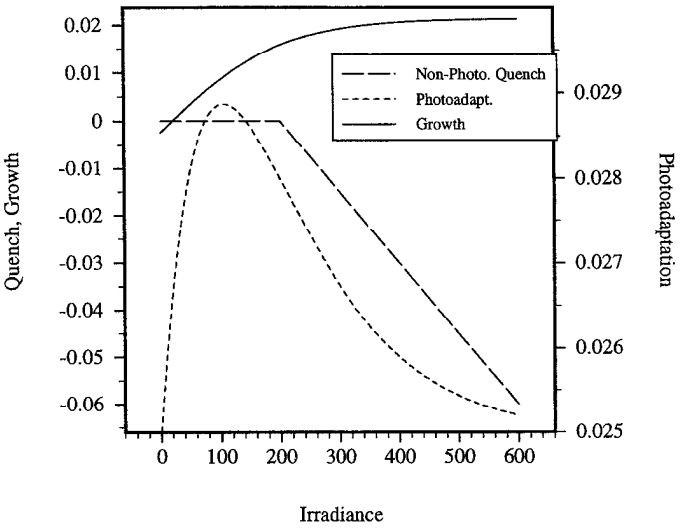


Figure 4. Output of Eqs. (2), (6) and (8) (see text) illustrating the irradiance dependencies used to generate the model output in Figure 5. The constants for growth are those for the "high" light condition, analogous to Figure 1b. The values of the constants used are as follows: p_{max} = 0.03 h^{-1}, r_m = 0.007 h^{-1}, $r_E = 0.2 \cdot p$, m = 0.00015, n = −0.0095, k = 0.001, and b = 0.03 and the C:Chl ratio for E = 0 is 0.025.

chemical quenching and irradiance to be linear, or

$$Q_{NP}(t) = kE(t) + b \qquad E > E_c$$
$$Q_{NP}(t) = 0 \qquad E \leq E_c \tag{8}$$

where k and b are constants. These equations imply that below a critical irradiance E_c, Q_{NP} will be zero, whereas above that, chlorophyll (as measured by fluorescence) will decline proportional to E. Weeks *et al.* (1993) use an equation for quenching that uses an exponential decline in chlorophyll as a function of E. Since their relationship is empirically derived, it may also include variability in Chl:C. Nonphotochemical quenching will be superimposed on the observed chlorophyll *a* signal, thus, combining its effect with the previous, we have,

$$Chl_t = C_t \cdot \theta_t + Q_{NP}(t)\,. \tag{9}$$

There is little guidance in the literature to assign values for the various constants identified in Eqs. (6) and (8). However, a critical irradiance level for many physiological properties of phytoplankton is in the range 100–300 μmols photons m^{-2} s^{-1}, the onset of saturation for photosynthesis. In that sense, the constants describing the decreases are less important. Nevertheless, the functions for growth, photoadaptation, and nonphotochemical quenching are shown in Figure 4.

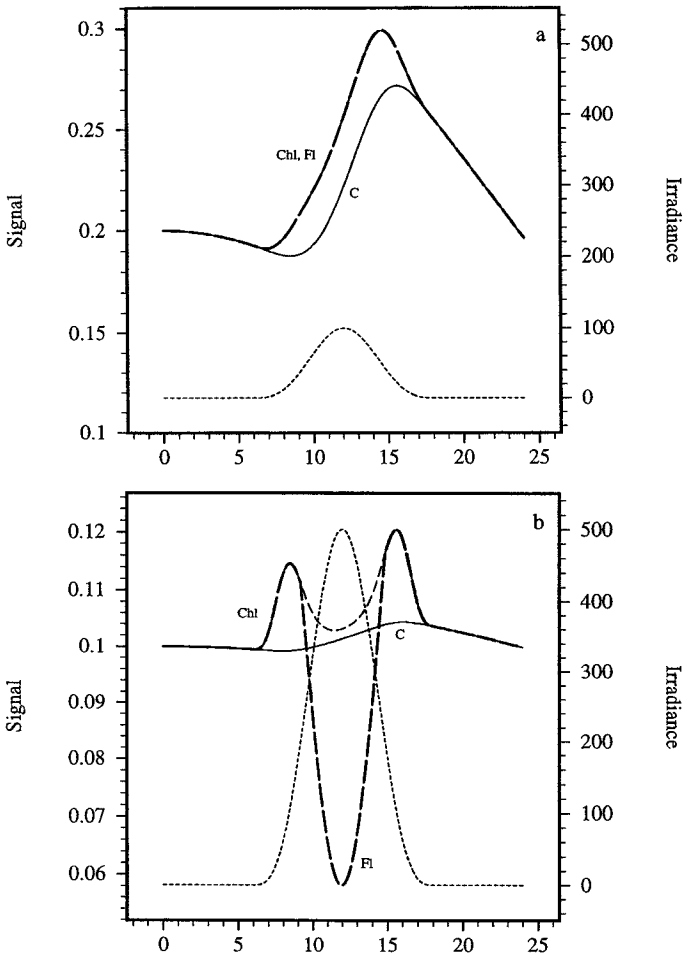


Figure 5. Model output for (a) low and (b) high noontime maximum irradiance (PAR). Irradiance variation was produced using Eq. (5) in the text. The maximum photosynthesis rate and maintenance respiration were adjusted to give the approximate average amplitudes of the signals observed in Figure 1. For the low-light condition (Fig 1a), $p_{max} = 0.6\ h^{-1}$, $r_m = 0.05\ h^{-1}$, $m = 0.00015$, $n = -0.0095$, $a = 0.001$, and $b = 0.03$. For the high-light condition, only photosynthesis and maintenance respiration parameters were changed, to $p_{max} = 0.03\ h^{-1}$ and $r_m = 0.007\ h^{-1}$. The initial Chl:C ratio is 0.025. E is in units of mols photons $m^{-2}\ s^{-1}$. The high irradiance corresponds to 500 and the low irradiance, 100 μmols photons $m^{-2}\ s^{-1}$.

Figure 5 shows model output, and an attempt to mirror the variations shown in Figure 1 by adjusting the variables. At this point, we are not able to constrain the variables to the extent that meaningful quantitative agreement can be demonstrated. The transitory peaks in fluorescence near dawn and dusk are a function of the way that Eq. (6) is written, but there is a hint of this behavior in the mooring data under high irradiances (Fig. 1b).

The model is provisional and can be faulted on several grounds. First, the three processes are all referenced to the same irradiance and are independent. It is probably true that Q_{NP} and θ affect growth, but little is known of the nature of the interaction between these properties. Equally possible is that Q_{NP} and θ are under metabolic (such as internal rhythmic control) rather than irradiance forcing. It would be better to write the equations as a hierarchy of responses over time, with the biophysical response, Q_{NP} acting faster than physiological changes, and both of these faster than cell division. A further assumption that could be made is that nonphotochemical quenching and photoadaptation affect the irradiance absorbed and used for growth. But there is little experimental justification for incorporating these variants, and how coupled the processes are in phytoplankton cells is not known. The equations ignore nutrient (Kiefer, 1973), temperature (Hitchcock, 1980), and physical (e.g., Doney *et al.,* 1995) effects. The maintenance respiration term is important in maintaining a roughly steady-state biomass, which is seen in the moored data over time periods of several days (Fig. 1). Still, the equations are a beginning, and, appropriately, serve as a basis for new experiments and observational work. The equations also suggest that if Q_{NP} and θ are better understood, there may, under some conditions, be a means to estimate phytoplankton growth rates.

The model depends on a diel variation in phytoplankton carbon, much as observed in the diel variation in particle attenuation from the moored transmissometer (Fig. 1). However, to what degree the amplitude of c_p represents phytoplankton carbon production is uncertain. In one laboratory study (Stramski and Reynolds, 1993), using a diatom, the carbon-specific attenuation coefficient was relatively constant over the day, suggesting that the diurnal increase is representative of increases in cell carbon. Other studies have also suggested minor changes in this parameter over time scales of hours (Ackleson *et al.,* 1993; S. Ackleson, personal communication). A more recent study, with *Synechococcus,* on the other hand, found significant irradiance-induced, carbon-independent changes in carbon-specific attenuation (Stramski *et al.,* 1995). The data from Figure 1 are from times where *Synechococcus* is unlikely to be dominant (Iturriaga and Marra, unpublished data), however, we have no way of verifying population structure for the moored-sensor data. It is clear, however, that care must be exercised in attempting to use a diurnal change in c_p as a phytoplankton production proxy.

Cullen *et al.* (1992) and Cullen and Lewis (1992) have also pointed out the difficulties in interpreting c_p with respect to the relative biomasses of autotrophs, heterotrophs, and bacteria. However, there is the more basic problem of relating c_p to the amount of POC *in situ.* For example, while c_p will increase with phytoplankton carbon, it will not increase proportionately if the increase in phytoplankton includes types with inorganic tests such as diatoms and coccolithophorids. Bishop (1986) and Bishop *et al.* (1992) have formulated relationships between suspended particulate matter and c_p, but the relationship between suspended matter and POC is more variable (J. K. B. Bishop, personal communication).

5. Hypothesis for the variations

The simplest hypothesis for the diel variation in chlorophyll is that phytoplankton grow during the day and are grazed at night (Le Bouteillier and Herbland, 1982; Marra, 1994). This hypothesis also agrees with the diel c_p signals analyzed by Siegel *et al.* (1989). Both these signals are complicated by competing processes, which may be expressed as corollary hypotheses. Diel photoadaptation increases chlorophyll (per unit biomass) during the day, and chlorophyll is broken down (or diluted by cell-division) at night (Post *et al.,* 1984). Scattering by particles can have a diel signal, as cells change size through growth and photosynthesis during the day (Olson *et al.,* 1990; Ackleson *et al.,* 1993). The loss terms at night are difficult to specify quantitatively, the nearly growth-compensating losses at night (e.g. Fig. 5a) requiring large respiration and grazing (Marra, 1994) and changes in cell-size through cell division. Grazing losses from diel migrators in the zooplankton have impacts that are typically 10–20% of phytoplankton growth rates (Marra *et al.,* 1987), and mesozooplankton would not be expected to graze efficiently the smaller organisms thought to constitute the bulk of the autotrophic particle abundances in the open ocean (Stramski and Kiefer, 1991). However, Waterbury *et al.* (1986) have hypothesized a discontinuous grazing by microflagellates as being a possible cause of diel variability in the cyanobacterium *Synechococcus.* Finally, different populations of phytoplankton may have differing diel characteristics with respect to F1 and (perhaps) scattering properties. None of these hypotheses explain all the variability associated with the observed diel changes.

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