

Modeling phytoplankton dynamics in the northeast Atlantic during the initiation of the spring bloom

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Abstract. Primary productivity in the North Atlantic (59°29'N, 20°50'W) was estimated by applying a "light-pigment" productivity model (Kiefer and Mitchell, 1983) to mooring data collected during the spring of 1989. We show that the choice of the parametrization of the light captured by phytoplankton cells in a turbulent mixed layer has a significant effect on the calculated productivity estimates. It appears that the quality of such estimations benefits largely from using high-resolution time series data (minutes). We also examined phytoplankton dynamics by incorporating the Kiefer-Mitchell model into a one-dimensional model of the turbulent mixed layer (Mellor and Yamada, 1982). The calculated time-depth distribution of phytoplankton biomass compares relatively well with that measured in situ. The model results indicate that small changes in the water column stability can be sufficient to initiate phytoplankton bloom even before the apparent formation of the seasonal thermocline. The model also describes the diel cycle of biomass concentration, suggesting that near the sea surface the daytime losses of biomass by vertical diffusion can be much larger than nighttime losses. Thus, if not accounted for, such losses may bias estimates of primary production from diel variations in biomass concentration, for example, when using a method based on beam attenuation measurements. These losses should also be considered for the proper interpretation of in situ primary production measurements by incubation methods.

Introduction

The determination of the magnitude and distribution of primary production over a wide range of space and time scales is essential for improving our understanding of marine ecosystems and biogeochemical cycles. Unfortunately, the possibility of extensive in situ measurements of growth rates by carbon, oxygen, or nitrogen incubation methods is rather problematic, because these methods are time consuming and require considerable ship time. Such determinations will likely continue to be used routinely during oceanographic cruises, even though the results may be severely biased because of inaccuracies in the procedures [e.g., *Epply*, 1980; *Richardson*, 1991, and references therein] or contamination of the methods [e.g., *Fitzwater et al.*, 1982].

In recent years, much effort has been directed toward development of alternative ways of estimating primary production. Increased temporal resolution of measurements at a given point under water can now be achieved using moored instrumentation systems [*Dickey*, 1991; *Dickey et al.* 1991, 1993, also Bio-optical and physical variability in the northeast Atlantic Ocean (59°N, 21°W) during the spring of 1989, submitted to *Journal of Geophysical Research*, 1993 (hereinafter referred to as *Dickey et al.*, submitted manuscript, 1993)]. These systems allow the collection of bio-optical and physical data concurrently and provide information on the characteristics of the water column over timescales of minutes

to months. Importantly, the data obtained from moorings can be applied to estimate primary production. For this purpose, a number of procedures have been proposed, including methods based on the "light pigment" bio-optical models (see reviews by *Cullen* [1990] and *Bidigare et al.* [1992]), diel variability of the beam attenuation coefficient [*Siegel et al.*, 1989; *Cullen et al.*, 1992], oxygen budget [e.g., *Emerson*, 1987; *Jenkins and Goldman*, 1985], and solar-induced fluorescence [*Kiefer et al.*, 1989].

This study attempts to reevaluate the relationship between photosynthetically available radiation, phytoplankton production, and vertical mixing. First, primary productivity in the northeast Atlantic in the spring is estimated using time series of bio-optical data obtained with a mooring located south of Iceland. This estimation is based upon a simple version of a "light-pigment" bio-optical model [*Kiefer and Mitchell*, 1983]. The importance of the parameterization of light energy received by phytoplankton in the turbulent medium is considered. Finally, the Kiefer-Mitchell productivity model is incorporated into a one-dimensional model of the turbulent mixed layer [e.g., *Mellor and Yamada*, 1982]. Calculated and measured in situ time-depth biomass distributions are compared.

Such modeling of the phytoplankton dynamics aids in the interpretation of mooring data. For example, in contrast to classical models, our data suggest that the major outburst of spring phytoplankton bloom began prior to the apparent formation of the seasonal thermocline. This raises the question of whether the bloom was related to water mass advection or was a local phenomenon. It is hypothesized here that small changes in water column stability are sufficient to stimulate the initiation of the bloom. Such small changes in

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Table 1. Parameters for Phytoplankton Model

Symbol	Definition	Value
C/Chl	carbon:chlorophyll ratio	50
ϕ_m	maximum quantum efficiency	0.059 g atm C Einst ⁻¹
K_ϕ	irradiance at which $\phi = 1/2\phi_m$	10 Einst m ⁻² day ⁻¹
a_{chl}	chl specific absorption coefficient	9.5 m ² (g Chl a) ⁻¹
L	loss rate	0.12 day ⁻¹

the stability regulate the rate of loss of biomass by turbulent diffusion from surface to deep water. In addition, these changes likely influence the average light energy captured by the cells and, as a result, affect the phytoplankton production in the upper part of the water column. Thus a major goal of our modeling effort is to examine biological responses to physical forcing at the beginning of the spring bloom.

Methods

Primary Production Model

A number of "light-pigment" primary productivity models have been developed over the past years [e.g., Ryther and Yentsch, 1957; Bannister, 1979; Kiefer and Mitchell, 1983; Bidigare et al. 1987; Platt et al. 1988; Sathyendranath et al. 1989; Smith et al. 1989; Morel, 1991]. A basic assumption in these models is that phytoplankton production can be estimated from measurements of the incoming irradiance and phytoplankton pigment concentration. The number of equations and parameters used in such models can be fairly high, and some consider spectral distribution of underwater irradiance and phytoplankton absorption [e.g., Bidigare et al., 1987; Sathyendranath et al., 1989; Morel, 1991].

An original version of the Kiefer-Mitchell (KM) model [Kiefer and Mitchell, 1983] is selected for this study. This model is satisfactory for present purposes, and key points may be considered relatively easily since the model is not very complicated. It has been shown that the basic equation of the KM model is essentially consistent with other productivity models [Cullen, 1990]. Various versions of the model were recently validated with extensive data sets from laboratory and in situ experiments on primary productivity rates [Marra and Heinemann, 1987; Sakshaug et al., 1989; Marra et al., 1992]. In the KM model, the gross phytoplankton growth rate μ is represented as a product of the quantum yield for carbon fixation ϕ and the rate of energy absorption:

$$\mu = \phi a_{chl} E_0 \text{ Chl/C} \quad (1)$$

where E_0 is the scalar irradiance of photosynthetically available radiation (PAR), a_{chl} is the chlorophyll specific absorption coefficient, and Chl/C is the ratio of cellular chlorophyll to carbon concentration. The dependence of ϕ on irradiance is described by the Michaelis-Menton function:

$$\phi = \phi_m K_\phi / (K_\phi + E_0) \quad (2)$$

where ϕ_m is the maximum quantum efficiency of photosynthesis and K_ϕ is the irradiance at which ϕ is 0.5 ϕ_m . The numerical values of the model parameters used for our calculations are assumed to have no temporal, depth, or temperature dependence (Table 1).

The original formulation of the KM model was based on data

obtained with photoadapted phytoplankton cultures grown under a light/dark cycle. In order to apply the model to field data, two questions need to be examined. First, how should one quantify the light received by phytoplankton cells in a turbulent mixed layer? Second, what timescales should be resolved in the calculations? As a first step, four different parameterizations of irradiance E_0 , which can serve as input into equation (1), are compared. As will be shown later, the choice of parameterization has a significant effect on the primary productivity estimates.

First, the irradiance E_0 at any depth z (where z is positive downward) was simply calculated from

$$E_0 = \text{PAR}(0) e^{-K_{\text{PAR}} z} \quad (3)$$

where K_{PAR} is the vertical diffuse attenuation coefficient for PAR and PAR(0) is the value of PAR just below the water surface. For this calculation, PAR(0) was taken as 47% of the total solar irradiance measured above the water surface [e.g., Siegel and Dickey, 1987]. The vertical diffuse attenuation coefficient, K_{PAR} , was estimated from PAR measured by moored instruments located at 10, 30, and 50 m. Such a parameterization of E_0 has some relevance for comparison of predicted photosynthetic rates with incubation experiments [e.g., Cullen et al. 1992; Mitchell and Holm-Hansen, 1991].

Second, the irradiance E_0 can be parameterized by taking into account the fact that phytoplankton cells actually undergo vertical displacement because of turbulence rather than remaining at a fixed depth. Let the vertical distance through which the cell i at depth z is moved by turbulent motion during the time interval Δt be denoted as H_i . The characteristic length scale H for vertical displacement of particle assemblage can be estimated by assuming that Lagrangian and Eulerian statistics are equivalent (Taylor's hypothesis) (see also Denman and Gargett [1983]) and taken as the standard deviation of H_i :

$$H = \sqrt{\frac{1}{N} \sum_{i=1}^N H_i^2} = \sqrt{2K_H \Delta t} \quad (4)$$

where K_H is the eddy diffusivity coefficient obtained here from the Mellor-Yamada model of the mixed layer (described later). In this case, the phytoplankton cells displaced from the depth z experienced over time Δt an average irradiance equal to

$$E_0 = \text{PAR}(0) e^{-K_{\text{PAR}} z} \left[e^{K_{\text{PAR}} H} - e^{-K_{\text{PAR}} H} \right] / (K_{\text{PAR}} 2H) \quad (5)$$

A similar parameterization has been used by Tett [1981]. Equation (5) accounts for turbulence, but not for any other mechanism of phytoplankton movement (e.g., internal waves) (see Denman and Gargett [1983] for discussion). A more detailed treatment of the problem will only be possible with an increase in our knowledge about the trajectories of phytoplankton cells.

Third, the parametrization of E_0 can be based upon information about the mixed layer depth (MLD). Here MLD was estimated from the mooring data as the depth at which the temperature differs from the surface value by 0.1°C. Then E_0 was calculated as the average value over the mixed layer:

$$E_0 = \text{PAR}(0) e^{-K_{\text{PAR}} \frac{\text{MLD}}{2}} \left[e^{K_{\text{PAR}} \frac{\text{MLD}}{2}} - e^{-K_{\text{PAR}} \frac{\text{MLD}}{2}} \right] / (K_{\text{PAR}} \text{MLD}) \quad (6)$$

This representation has essentially been used in the classical models of the seasonal cycle of phytoplankton [e.g., *Sverdrup, 1953; Wroblewski, 1989*].

Using the parameterizations described by equations (3), (5), and (6), primary production was calculated from equation (1) with a time step of 15 min. In contrast, in the fourth parameterization it was assumed that the irradiance E_0 is the daily integral of the scalar irradiance (equation (3)) from dawn (t_m) to dusk (t_e) [e.g., *Marra et al., 1992*]:

$$E_0 = \int_{t_e}^{t_m} \text{PAR}(t, z_i) \quad (7)$$

In all four cases, the production was calculated as a product of the specific growth production rate and chlorophyll a concentration estimated from stimulated fluorescence measured by moored instruments and interpolated to 0.5-m depth intervals. Note that we did not consider any photoadaptive and photoinhibitory processes in these calculations [e.g., *Lewis et al. 1984; Gallegos and Platt 1985; Cullen and Lewis, 1988*].

Model of Plankton Dynamics

The model of primary production rate described above provides the basis for the coupled biophysical model, which simulates the commencement of the spring bloom at the mooring site. The physical part is the level 2 1/2 version of the Mellor-Yamada model [*Mellor and Yamada, 1974, 1982; Mellor and Durbin, 1975; Blumberg and Mellor, 1983*]. This model belongs to the class of differential models. In contrast to integrated or "slab" models, it enables computation of vertical profiles of turbulent variables. Importantly, such a model includes realistic, stability dependent eddy diffusivity coefficients. These features of the model allow us to examine the relationship between the variable physical forcing and the dynamics of the biological processes.

Only a few basic equations of the Mellor-Yamada model are described here (see references given above for details). The model solves the turbulent forms of momentum and thermodynamic equations with some simplifying assumptions for closing the system. For a horizontally homogeneous ocean with no mean vertical water motion, the equations of conservation of momentum and heat are

$$\begin{aligned} \frac{\partial U}{\partial t} - f(V - V_d) &= \frac{\partial}{\partial z} \left[(K_M + v_M) \frac{\partial U}{\partial z} \right] \\ \frac{\partial V}{\partial t} + f(U - U_d) &= \frac{\partial}{\partial z} \left[(K_M + v_M) \frac{\partial V}{\partial z} \right] \\ \frac{\partial T}{\partial t} &= \frac{\partial}{\partial z} \left[(K_H + v_H) \frac{\partial T}{\partial z} \right] + \frac{1}{\rho_0 c_p} \frac{\partial I}{\partial z} \end{aligned} \quad (8)$$

where t is the time, z is the vertical coordinate, U and V are the mean horizontal velocity components, T is the mean temperature, I is the irradiance, f is the Coriolis parameter, K_M and K_H are the eddy coefficients for vertical turbulent diffusion within the mixed layer (ML), v_M and v_H are the coefficients for molecular viscosity and ambient diffusion below the ML, ρ_0 is the water density, and c_p is the specific heat of water. For simplicity, the geostrophical current components U_g and V_g were taken to be zero. The equation set (8) is closed using the following formulas for eddy coefficients:

$$K_M = lqS_M \quad (9)$$

$$K_H = lqS_H$$

where l is the turbulent length scale, $q^2/2$ is the turbulent kinetic energy, and S_M and S_H are the stability functions dependent on the local Richardson number.

In order to calculate $\partial I / \partial z$, which describes the penetration of the solar energy into the water column, it was assumed that half of the solar energy which is transmitted through the water surface is absorbed within the top 1 m of the water [*Smith and Baker, 1981, 1986; Siegel and Dickey, 1987*]. The other half corresponds to the irradiance from the visible spectral range, and its vertical distribution was estimated from PAR measured at the mooring instrument depths.

The biological part of the model is simple. The temporal evolution of the vertical distribution of phytoplankton is described by adding the following equation to set (8):

$$\frac{\partial \text{Chl}}{\partial t} = \frac{\partial}{\partial z} \left[(K_H + v_H) \frac{\partial \text{Chl}}{\partial z} \right] + \mu \text{Chl} - L \text{Chl} \quad (10)$$

where Chl is the biomass concentration expressed in mg Chl m^{-3} , μ is the gross production rate calculated from the Kiefer-Mitchell formula (equation (1)), and L is the phytoplankton specific loss rate.

This description of the biology is based on the following assumptions. First, no equation for nutrients is included, because our interests lie only in the bloom initiation. Nutrients are abundant in winter and become limiting only after the development of the bloom. This simplification is further justified by the relatively high surface nitrate (>7.0 mmol m^{-3}) and silicate (3-4 mmol m^{-3}) concentrations measured at the mooring site on Julian day 165, just after the period of our model simulation [*Weeks et al., 1993*]. Second, it is assumed that cells behave as passive tracers of the water movements and are transported only through the vertical diffusion. In addition, it is assumed that the diffusivity coefficient for heat transfer applies to phytoplankton. Third, in order to convert carbon based growth rate to Chl a, a constant C/Chl (weight/weight) ratio of 50 is used (see, for example, *Langdon [1987] and Li et al., [1993]* for discussion of this parameter). Fourth, the phytoplankton specific loss rate L represents the sum of losses of the biomass, such as algal respiration and grazing. This simple parameterization of biomass losses seems to be reasonable for the first phase of the bloom in the North Atlantic, when grazing pressure is very low [*Weeks et al., 1993*]. Finally, cell sinking is neglected. Previous studies suggest that diatoms do not sink effectively during the first stage of the bloom as long as light and nutrients are not limiting the growth [*Anderson and Sweeney, 1977*].

For the purpose of numerical calculations, equations (8) and (10) are transformed into finite difference equations using the implicit Crank-Nicholson scheme [Richtmyer and Morton, 1967]. The vertical grid spacing is optimized to obtain high vertical resolution of the parameters near the water surface. The distance between computational grid points increases with depth according to a geometrical progression. The interval is 0.04 m at the surface and there were 300 levels down to a depth of 740 m. The time step is 15 min.

Experimental Data

The model described above was run using time series data obtained with multivariable moored systems (Dickey *et al.*, 1991, 1993). The measurements were carried out from April 13 through June 12, 1989, in the North Atlantic (59°29'N, 20°50'W) as a part of the Marine Light in the Mixed Layer program. The full details of the methodologies and the description of the data are given by Dickey *et al.* (submitted manuscript, 1993).

Boundary conditions for the model, including wind stress, heat flux, and incoming solar insolation were obtained from the meteorological sensors on the surface mooring (see Stramska and Dickey, 1993 for details). Wind stress was obtained using bulk aerodynamic formula [Large and Pond, 1982; Geernaert, 1990]. The heat flux was taken as a sum of the heat loss leaving directly from the water surface and the solar radiation absorbed within the water column. The heat loss is the sum of the latent, sensible and longwave radiative heat fluxes, which were estimated using standard bulk formulas [Large and Pond, 1982; Geernaert, 1990] and a net longwave radiation formula [Bunker, 1976]. The model was initiated using temperature and chlorophyll profiles constructed from the mooring data taken at the beginning of the experiment (day 103).

Results

Estimates of Primary Production

Estimates of carbon production obtained with the Kiefer-Mitchell model using four different parameterizations of light received by the cells (equations (3), (5), (6), and (7)) are given in Figure 1. Note that all these estimates fell within the range of values observed in the region at that time of the year [Williams, 1975; Martin *et al.* 1993; Weeks *et al.* 1993]. However, the estimate based on the parametrization of E_0 taken as an average PAR for the mixed layer (equation (6)) displays a clearly different pattern in vertical distribution than the other three estimates.

The column-integrated estimates of the production for the top 200 m of the ocean are shown in Figure 2. The estimates involving parametrizations by equations (3) and (5) gave very similar results, which suggests that the influence of turbulence on the light energy captured by cells had only a minor effect on the integrated production. While a significantly higher productivity estimate resulted from applying the daily integral of light (equation (7)), the lower estimate was obtained when the light was averaged over the MLD (equation (6)).

It is important to emphasize that our calculations cannot be used as a general quantification of the differences between various estimates of primary productivity. This is because the final results depend also on the vertical distribution of Chl *a* in the water column. Figures 1 and 2 only serve as examples.

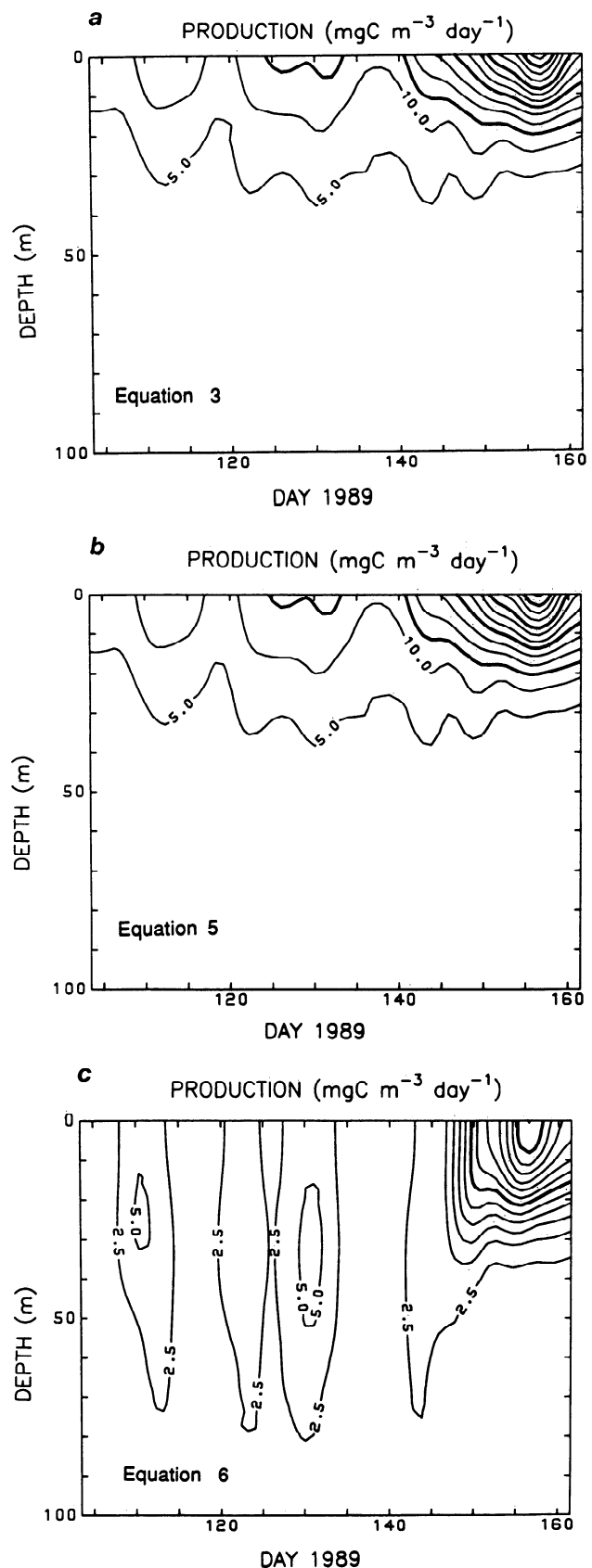


Figure 1. Contours of gross primary production estimated using Kiefer-Mitchell model [Kiefer and Mitchell, 1983], Marine Light in the Mixed Layer mooring data, and equations (3), (5), (6), and (7) to parametrize E_0 . See explanations in the text.

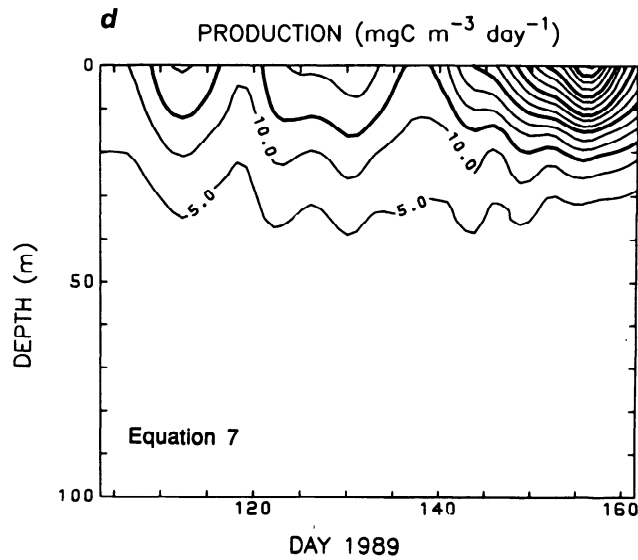


Figure 1. (continued).

which are helpful in comparing trends in the differences between various estimates. In addition, as noted before, we do not attempt to model the kinetics of photoadaptive and photoinhibitory responses [e.g., *Lewis et al.* 1984; *Gallegos and Platt*, 1985; *Cullen and Lewis*, 1988] but rather the average photosynthetic rates. In our model, the vertical mixing affects the photosynthetic rates, because phytoplankton cells are exposed to different average light intensities than if they were to remain at a fixed depth and, additionally, because of the implications of the curvilinearity of the P versus I relationship for the integration of primary productivity (see discussion in the last section).

Comparison of Model-Simulated Plankton Dynamics with Experimental Data

The results of the biophysical model of the phytoplankton bloom are considered below. Unfortunately, we could not make any direct comparison of the estimated productivity and specific loss rate L with in situ data, because such measurements were not done concurrently with the mooring measurements in 1989. Note that combining the biological and physical mixed layer models allows us to examine the relative balance between biomass production and losses. In our model, an increase in growth rate μ can be compensated by an increase in specific loss rate L . The results presented below were obtained with the numerical values for the model parameters summarized in Table 1.

The modeled vertical distribution of the water temperature is shown in Figure 3a. A comparison of this result with the temperature contours from the mooring data (Figure 3b) indicates that our model does not reproduce all of the temperature variability, especially events that appear deep in the water column. These features are likely to be attributable to mesoscale water mass variability, which cannot be

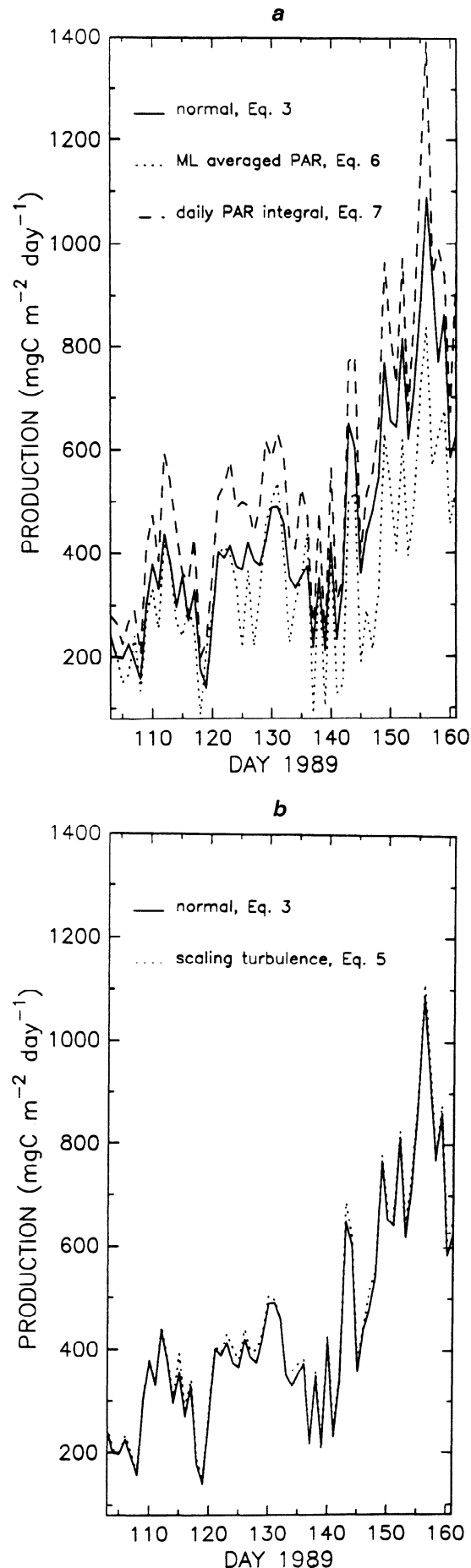


Figure 2. Time series of water column integrated gross primary production estimated using Kiefer-Mitchel model [*Kiefer and Mitchell*, 1983], mooring data, and equations (3), (5), (6), and (7) to parametrize E_0 . See explanations in the text.

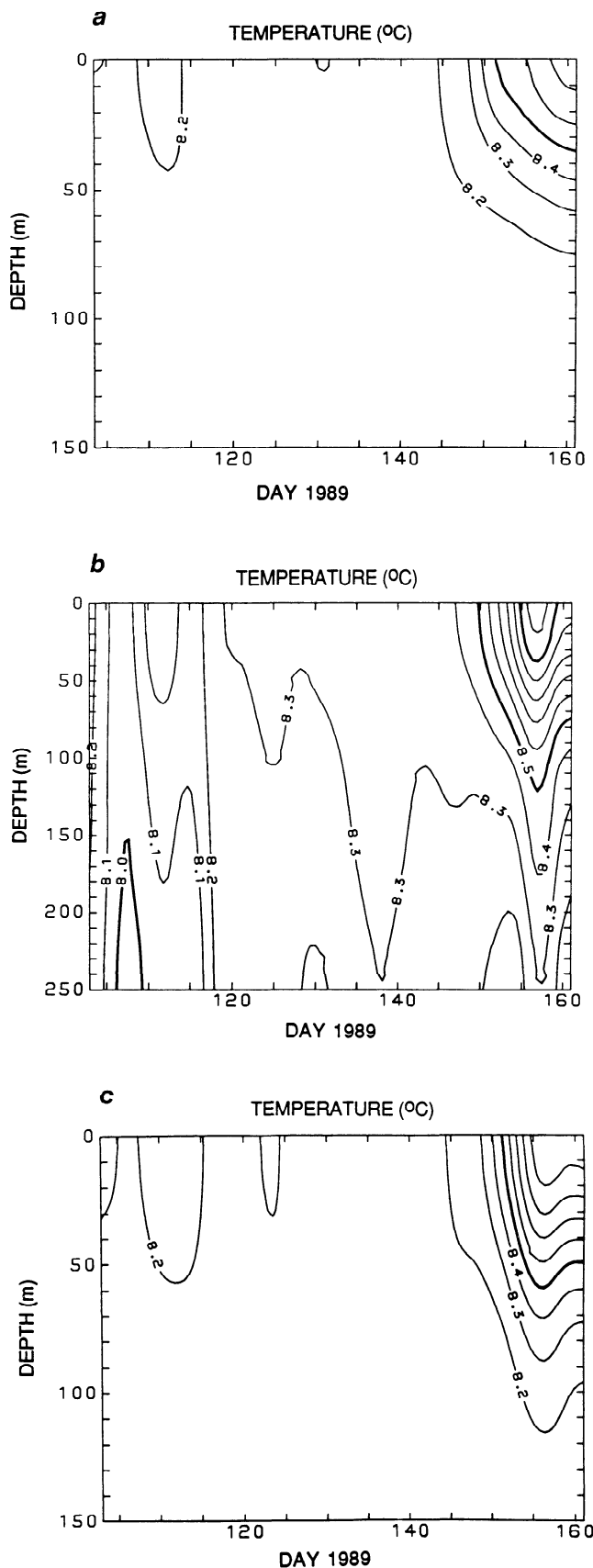


Figure 3. Time versus depth contours of water temperature: (a) one-dimensional Mellor-Yamada model simulation [Emellor and Yamada, 1982], (b) mooring data, and (c) mooring data after subtracting temperature variability at 150 m.

reproduced by a one-dimensional model. Therefore we feel that a meaningful comparison of the calculated temperature with the data can only be made in terms of the relative rather than the absolute distributions. In order to separate "local" from "nonlocal" changes in water temperature (and following Price *et al.* [1986], we subtracted the temperature changes at 150 m from the temperature data. The temperature contours based on this calculation are shown in Figure 3c. Now the agreement between in situ temperature structure in the upper 150 m and the model simulation is fairly good. Because changes in salinity during the experiment were small, this temperature distribution is expected to be a good descriptor of the water density in the upper layer of the ocean.

In Figure 4 we have plotted mooring data, that is, fluorometrically determined concentration of Chl *a* (Figure 4a), and beam attenuation coefficient at 660 nm (c_{660} , Figure 4b). As a first approximation, c_{660} can be considered as a measure of the concentration of phytoplankton cells. The Chl *a* distribution predicted by the biophysical model with the E_0 parameterization based on equation (5) is shown in Figure 5a. Relatively good agreement exists between model output and observations. Specifically, the slow increase of the Chl *a* concentration around day 110 is reproduced well by the model. This trend was perturbed near day 115 and again on day 140 apparently by high wind speeds and enhanced cooling of the surface water, which produced greater mixing (see time series of heat fluxes, Stramska and Dickey, 1993). Note also that our model results reproduce the bloom initiation before the seasonal thermocline is apparent in the temperature contours.

The model was also run using E_0 parameterizations with equations (3) and (6) (equation (7) was not applied). The parameterization using Equation (3) gave similar results (not graphed here) to those associated with equation (5). In contrast, the model run with E_0 described by equation (6) (Figure 5b, PAR averaged over the ML) did not reproduce the same phytoplankton pattern as parameterization by equations (3) and (5). The bloom occurred later, and a difference in the Chl *a* between the beginning and the end of the simulation period was greater than the observed one. This suggests that the vertical structure of the primary productivity in the water column (nearly exponential decrease with depth) is an important feature which should be included in phytoplankton models.

It is of interest to further consider the results of our calculations, focusing on the daily timescale. Biological variability on this timescale is thought to be in phase with the diel thermal cycle in the upper ocean [Woods and Onken, 1982; Taylor and Stephens, 1993]. This cycle is associated with the daytime absorption of solar radiation, which tends to warm and stabilize the near surface layer, and nighttime cooling, which together with wind mixing, acts to destabilize the water column [e.g., Dickey and Simpson, 1983; Price *et al.*, 1986; Woods and Barkmann, 1986].

Figure 6 shows vertical profiles of gains and losses of Chl *a* by vertical mixing (Figure 6a), losses representing respiration and grazing (Figure 6b), and gross primary production (Figure 6c), over a diel cycle. The changes of Chl *a* concentration in our model (Figure 6d) result from a local balance of these three components (see equation (10)). Figure 6a shows that vertical mixing always acts to reduce biomass in the surface waters but can cause a gain at greater depths. Biomass losses by respiration and grazing (Figure 6b) are assumed to be proportional to the phytoplankton concentration. The

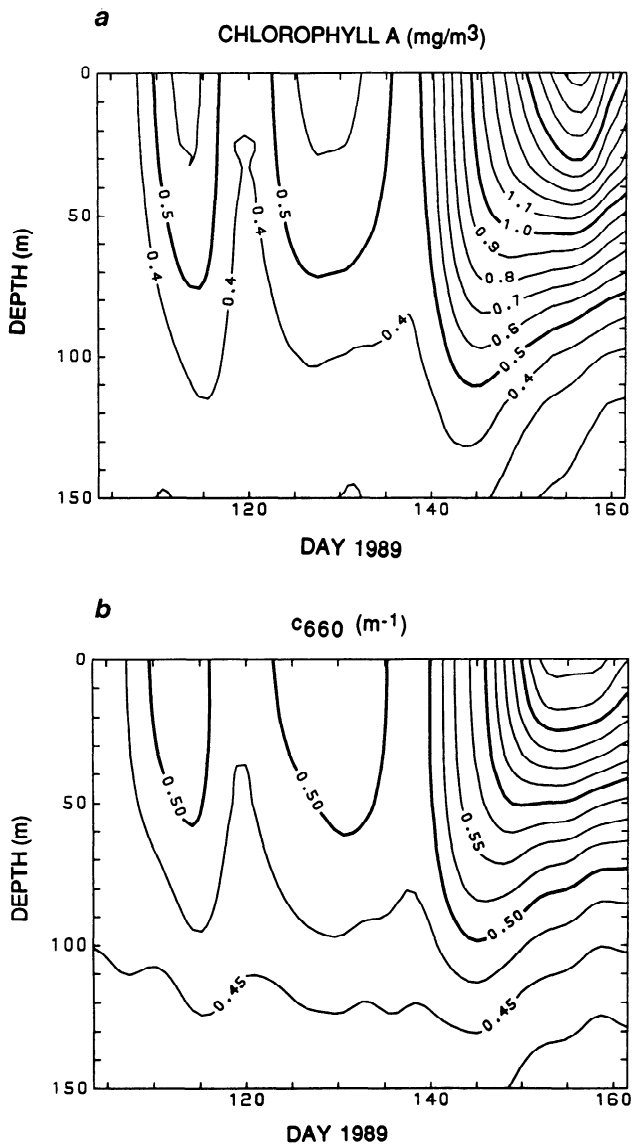


Figure 4. Time versus depth contours of (a) fluorometrically determined concentration of chlorophyll a and (b) beam attenuation coefficient at 660 nm from mooring measurements.

maximum losses occur in the evening when phytoplankton concentration is highest. Primary production (Figure 6c) is equal to zero at night and positive during the day, when it displays a strong decrease with depth.

All three components of the biomass balance are shown in Figure 7 as time series at a depth of 2 m. Regarding the loss term caused by mixing in the surface waters, it is apparent that this effect is much greater during the day than at night. This pattern is induced by the strong decrease of productivity with depth, which in turn leads to larger vertical gradients in phytoplankton distribution during the day than at night. Thus the model results presented here suggest that the diel cycle in phytoplankton concentration in the surface water results from the changing balance of phytoplankton gains and losses, with the losses being much larger during the day than at night.

This observation is important for estimating primary productivity from any method based on the diel variability of the biomass concentration, for example, using beam

attenuation coefficient data [Siegel *et al.*, 1989; Cullen *et al.*, 1992]. In order to avoid errors, such methods should account for the losses described above. It is worth stressing here that the diel pattern in the components of the biomass balance can generally change in time in response to mixed layer dynamics and light availability for primary production. In particular, dramatic changes may occur during time periods of increased heat loss from the sea surface and during high winds. Under such conditions, phytoplankton are efficiently mixed downward, in consonance with the mixed layer deepening. The result is that while phytoplankton concentration decreases significantly in surface waters, it can reach relatively high values at greater depths, even though local production is very low there because of low light levels (Figures 8 and 9).

Discussion and Conclusions

The crucial variable in phytoplankton models is the light energy captured by phytoplankton cells, since it controls the

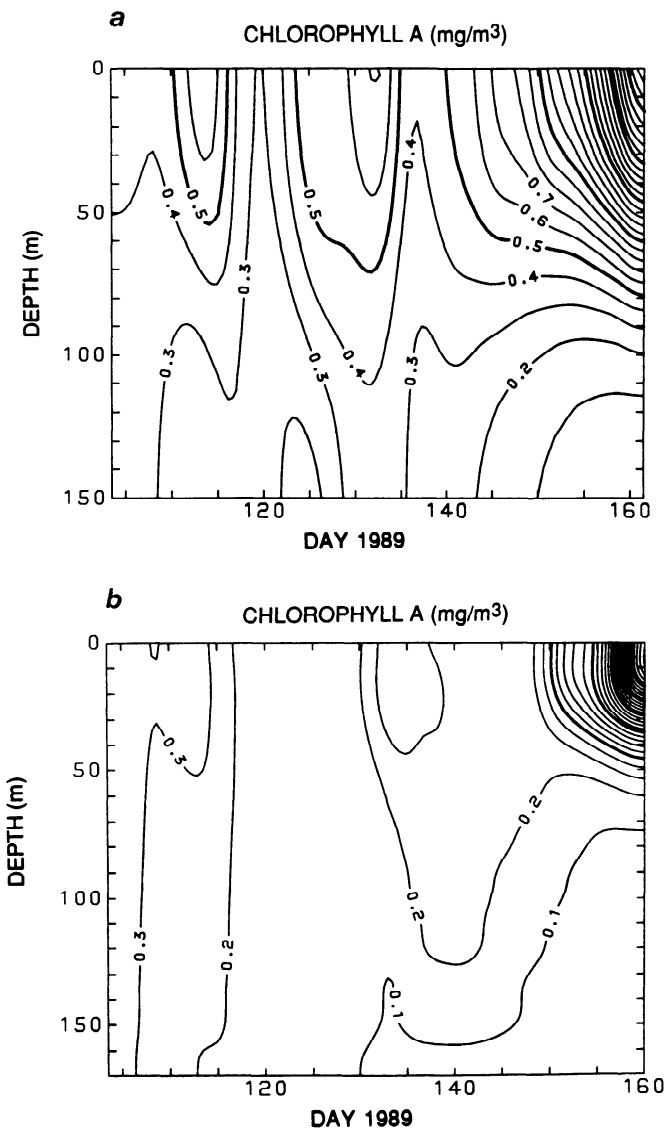


Figure 5. Results of coupled biophysical model simulation (see text for details). (a) Concentration of chlorophyll a obtained using equation (5). (b) Concentration of chlorophyll a obtained using equation (6).

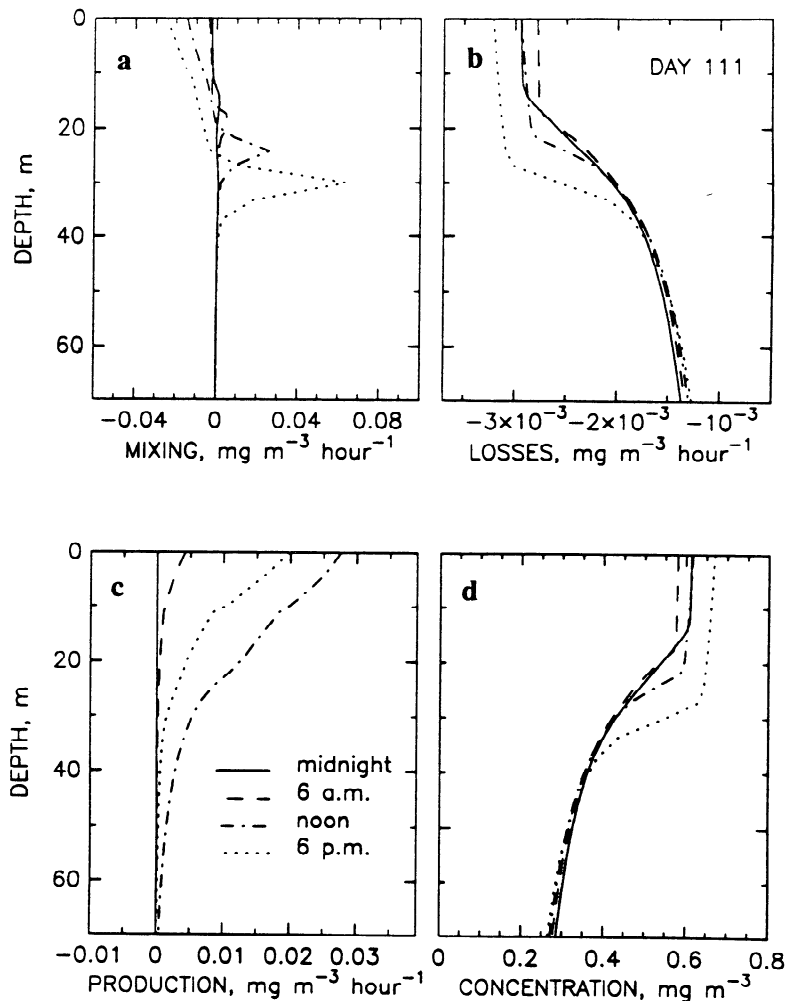


Figure 6. Results of coupled biophysical model simulation (equation (5)). Vertical profiles for day 111 at midnight, 0600, 1200, and 1800 UT for (a) net phytoplankton transport by vertical mixing in $\text{mg Chl a m}^{-3} \text{ hr}^{-1}$, (b) biomass losses by respiration and grazing in $\text{mg Chl a m}^{-3} \text{ hr}^{-1}$, (c) phytoplankton production, in $\text{mg Chl a m}^{-3} \text{ hr}^{-1}$, (d) phytoplankton concentration in mg Chl a m^{-3} .

growth and cellular physiology of the plankton. The amount of light reaching phytoplankton varies on timescales from fractions of seconds to climatic scales because of the variability of the radiant flux penetrating into the water and because of the vertical movements of the individual cells within the water column. In recent years, there have been several attempts to examine phytoplankton responses to light variability associated with clouds [e.g., *Gallegos et al.*, 1977, 1980; *Abbott et al.*, 1982; *Marra and Heinemann*, 1982; *Stramska and Dickey*, 1992a,b], vertical water movements [e.g., *Marra*, 1978, 1980; *Gallegos and Platt*, 1982], and wave action at the sea surface [e.g., *Dera et al.*, 1975; *Walsh and Legendre*, 1983; *Stramski et al.*, 1993]. These studies have provided evidence that phytoplankton can respond to rapid changes in irradiance, but they did not answer how these changes affect the depth-integrated primary production.

The effects of fluctuating light on the mean photosynthetic rate in higher plants were examined by *Thornley* [1974] using a two-step reaction kinetics model. He distinguished two extreme types of responses representing fast and slow light fluctuations. If light fluctuations are fast compared with the time response of the photosynthetic apparatus (seconds or less), the mean photosynthetic rate is the same as the rate the

plant would achieve at a constant irradiance equal to the mean level of fluctuating light. However, if light fluctuations are relatively slow (minutes and more), plants integrate photosynthetic rate so that the measured photosynthetic rate is the average of the photosynthetic rates at light levels during fluctuations. Thus, in this case, the mean photosynthetic rate may be lower compared to the rate measured at the mean irradiance (see also *McCree and Loomis* [1969], *Gross and Chabot* [1979] and *Gross* [1982]).

Four possible estimates of primary productivity have been applied here. For the present data set, estimates using equations (3) and (5) gave relatively similar results, suggesting that turbulent mixing was not very important for the production rates. However, the effect of turbulence on productivity can be greater in other situations, for example, when the vertical distribution of Chl *a* is characterized by a deepwater maximum. In contrast to small differences between estimates using equations (3) and (5), averaging the PAR over the MLD or integrating PAR over a day leads to significantly different productivity estimates. Assuming that the model of *Thornley* [1974] for the average photosynthetic rate of plants in variable light holds for phytoplankton, the use of such estimates of primary productivity becomes problematic.

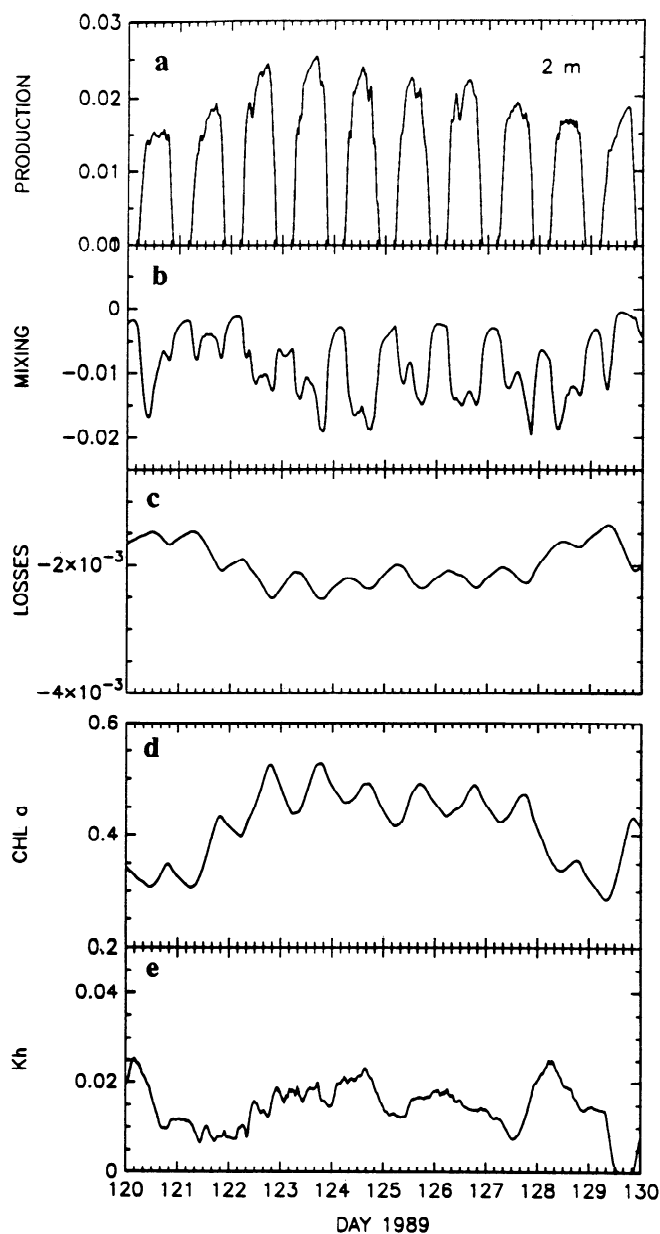


Figure 7. Results of coupled biophysical model simulation, at 2 m depth. Time series of (a) phytoplankton production in $\text{mg Chl a m}^{-3} \text{hr}^{-1}$, (b) net phytoplankton transport by vertical mixing in $\text{mg Chl a m}^{-3} \text{hr}^{-1}$, (c) biomass losses by respiration and grazing, in $\text{mg Chl a m}^{-3} \text{hour}^{-1}$, (d) phytoplankton concentration in mg Chl a m^{-3} , (e) eddy coefficient for vertical diffusion in $\text{m}^2 \text{s}^{-1}$.

However, more experimental evidence is needed in order to better understand the effect of light variability on the average photosynthetic rate of phytoplankton.

The variability of phytoplankton concentration in the open ocean is forced not only through conditions limiting growth rates but also through processes responsible for phytoplankton losses. Because of the numerous physical and biological factors controlling both growth and losses of phytoplankton, models describing annual phytoplankton cycles must be rather exhaustive and contain a considerable number of equations and parameters [e.g., *Fasham et al.*, 1990; *Hoffmann and Ambler*, 1988]. As a result, it is often difficult

to evaluate to what degree the modeling results are affected by a particular assumption [e.g., *Jamart et al.*, 1977; *Steele and Henderson*, 1992]. In contrast, the phytoplankton model presented here is simple and would not suffice for a description of the annual cycle. This model cannot simulate effects related to horizontal variability, processes such as photoadaptation and photoinhibition, or biological diversity of plankton populations. However, we have applied the model to specific conditions, namely a relatively short period of time when the bloom initiation in the North Atlantic took place. This provided an opportunity to minimize many complications, including nutrient limitation and cell losses due to grazing and sinking, and allowed us to focus on the relation between phytoplankton and mixed layer dynamics.

It has been pointed out in the past that in situ vertical distribution of the biomass concentration is very sensitive to changes of the water column stability (see also *Pingree et al.* [1976] *Bishop et al.* [1986, 1992] and *Gardner et al.* [1993]). The model presented here was inspired by these observations and includes only three terms responsible for the local changes of Chl a concentration: gross primary production, losses by biological processes (respiration and grazing), and vertical mixing. In our model, the latter is the dominant mechanism of phytoplankton cell removal from the surface waters. This is in agreement with in situ data which show that, despite the strong decrease of primary production rate with depth, the vertical profiles of phytoplankton concentration are usually relatively uniform. Thus continuous vertical redistribution of the phytoplankton stock within the mixed layer is intuitively expected to take place, and any changes in the stability structure of the surface waters should be reflected in the phytoplankton concentration profiles. In the case of extremely deep mixing events due to strong winds and surface heat loss, significant removal of phytoplankton stock from the euphotic zone occurs (Figures 8 and 9). Note that any changes in the vertical distribution of phytoplankton will in turn affect total phytoplankton production, which for the constant specific growth rate decreases with the decrease of chlorophyll concentration. The physical/biological feedbacks also involve the vertical redistribution of radiative flux in the water column in response to changes in phytoplankton concentration, which is expected to influence the mixed layer dynamics [e.g., *Zaneveld et al.*, 1981, *Lewis et al.*, 1983, 1990, *Stramska and Dickey*, 1993].

The relatively successful simulation of the chlorophyll distribution during the development of the bloom supports the notion that vertical turbulent diffusion is important for biology. The model results described here indicate that the phytoplankton bloom could have been a local phenomenon and that considerable primary production in the northeast Atlantic took place before the seasonal thermocline was fully established. The possibility that the spring bloom may precede the seasonal stratification of the surface water, so surprising in the light of classical bloom models, has already been suggested [*Colebrook*, 1979, 1982; *Townsend et al.*, 1992]. To our knowledge, this effect is supported here for the first time by high temporal resolution field data representing both prebloom and bloom initiation phases, together with the meteorological data, allowing us to reproduce such a situation by the model.

In summary, it should be recognized that classical phytoplankton bloom models involve considerable simplification and cannot be expected to give a good

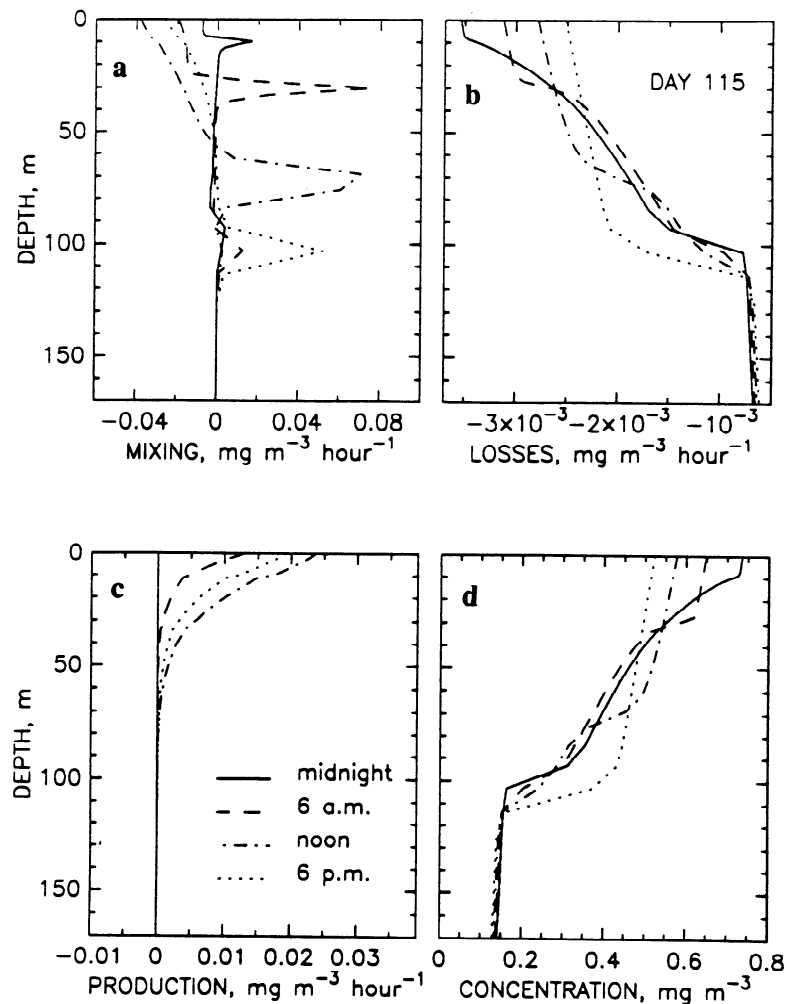


Figure 8. Same as Figure 6, but for day 115.

description of all the details of the temporal bloom evolution in its initial phase. This is because they are based on a mixed layer concept, assuming that such a layer is uniform and mixing actively at all times. Measurement techniques which could indicate modest thermal stratification in the upper layer were not available to early workers, including Sverdrup, and thus it is understandable that hypotheses and models were based on "truly uniform" mixed layers. However, that assumption is not strictly valid, and surface waters are often somewhat stratified and at times not actively mixing. Our results show that models resolving vertical stability structure of the upper ocean are more adequate for the description of biological/physical feedbacks.

Another aspect of our modeling effort is the simulation of the diel cycle of biomass concentration [e.g., Siegel *et al.*, 1989; Cullen *et al.*, 1992; Stramska and Dickey, 1992b]. In order to reproduce diel variations of Chl *a*, $p\text{CO}_2$, and oxygen concentration observed in the region of our experiment, Taylor and Stephens [1993] imposed diurnal variation of the phytoplankton mixing in a two layer model. Our approach was different, as no assumptions were made about the MLD or turbulent exchange, but rather a model was run with observed surface heat and momentum fluxes. The diel cycle of phytoplankton concentration in our model resulted from the

net gain of phytoplankton biomass during a daytime and the net loss at nighttime. However, unlike the Taylor and Stephens model, in our model the loss rate of phytoplankton owing to removal from the upper part of the water column by mixing could be much larger during the daytime than during the nighttime. We conclude that rigorous interpretation of the apparent accumulation of biomass in the water layer in terms of primary production estimates should account for these losses.

Finally, our simple model should help with the interpretation of in situ productivity measurements by incubation methods. Incubation methods do not allow for the mixing of phytoplankton. Thus artificial accumulation of the biomass may occur in incubation bottles located close to the sea surface (no loss by mixing is allowed). This will lead to an overestimation of production. In contrast, the increase of the biomass in deepwater bottles may be smaller than in the surrounding water at that depth (no gain by mixing is allowed), which will lead to underestimation of primary production. Such errors do not occur in the bio-optical models, which are based on the actual concentration of Chl *a* in the water. Thus such model calculations cannot generally be expected to show very good agreement with in situ productivity measurements.

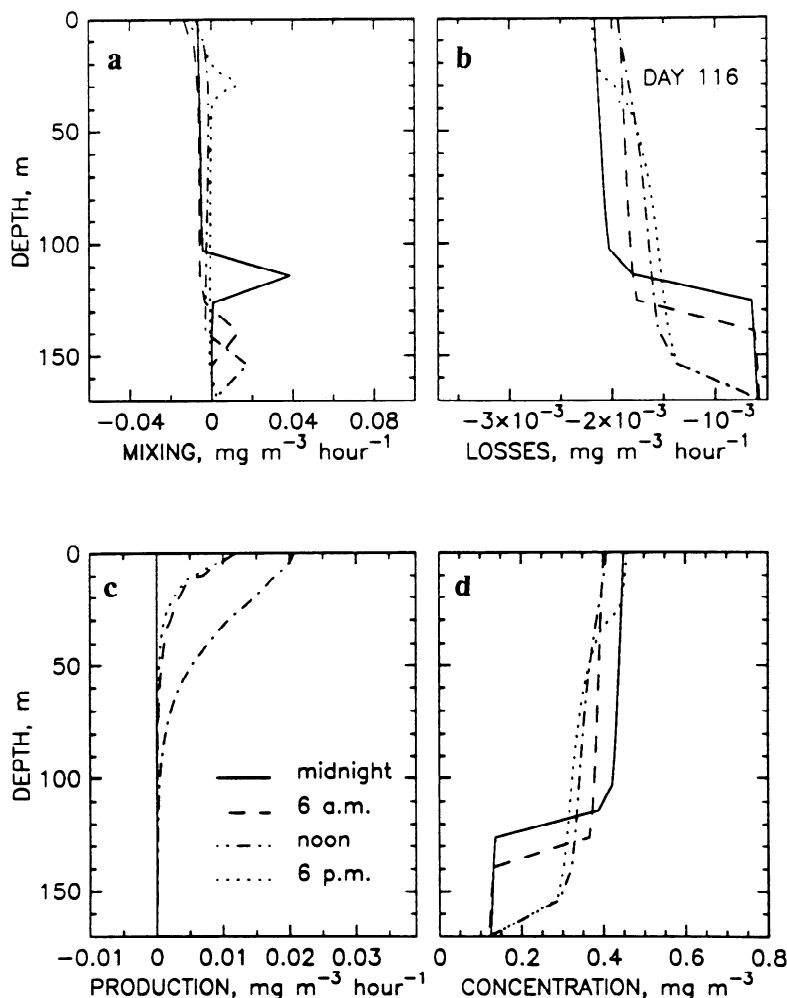


Figure 9. Same as Figure 6, but for day 116.

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