

Table 1. Parameters for Phytoplankton Model

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

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  $\mu$  is represented as a product of the quantum yield for carbon fixation  $\phi$  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  $\phi$  on irradiance is described by the Michaelis-Menton function:

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

where  $\phi_m$  is the maximum quantum efficiency of photosynthesis and  $K_\phi$  is the irradiance at which  $\phi$  is 0.5  $\phi_m$ . 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  $K_{\text{PAR}}$  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,  $K_{\text{PAR}}$ , 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  $\Delta t$  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  $\Delta t$  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.