



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