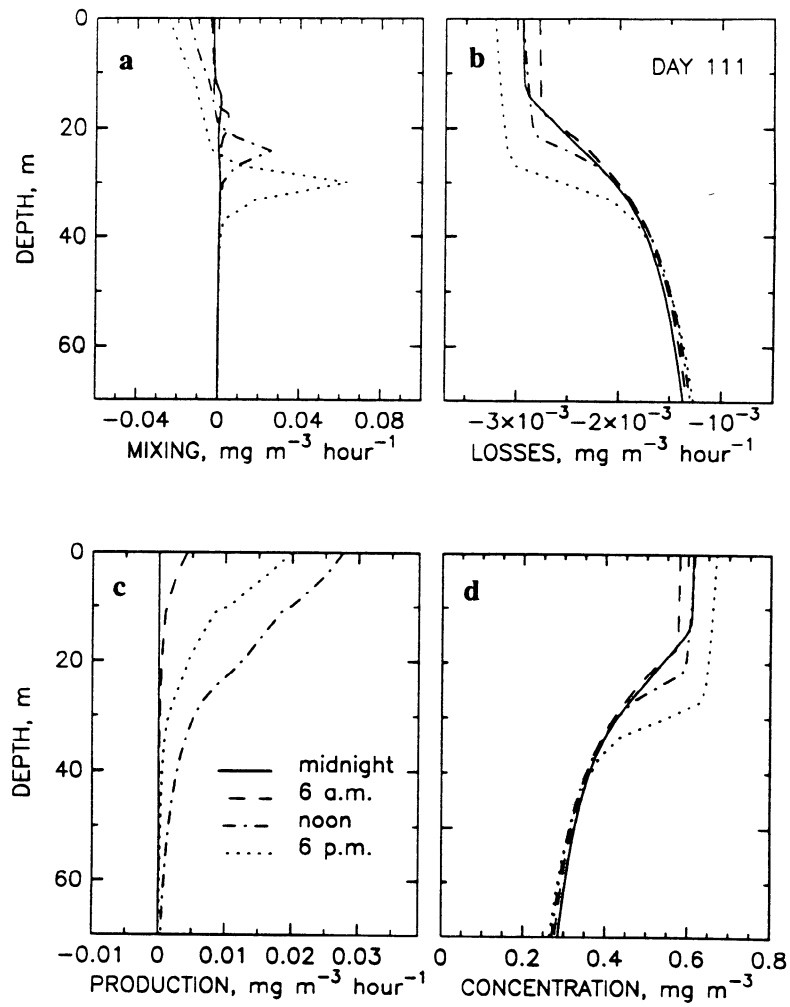

Figure 6. Results of coupled biophysical model simulation (equation (5)). Vertical profiles for day 111 at midnight, 0600, 1200, and 1800 UT for (a) net phytoplankton transport by vertical mixing in mg Chl a m^{-3} hr^{-1}, (b) biomass losses by respiration and grazing in mg Chl a m^{-3} hr^{-1}, (c)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