JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 97, NO. C11, PAGES 17,873–17,887, NOVEMBER 15, 1992

Variability of Bio-optical Properties of the Upper Ocean Associated with Diel Cycles in Phytoplankton Population

MALGORZATA STRAMSKA AND TOMMY D. DICKEY

Ocean Physics Group, Department of Geological Sciences, University of Southern California, Los Angeles

The variability of bio-optical properties of seawater associated with planktonic responses to the daily light cycle was examined. We performed a spectral analysis of a 60-day time series of open ocean mooring measurements of the scalar irradiance (photosynthetically available radiation, PAR), beam attenuation coefficient at 660 nm (c_{660}), stimulated fluorescence, and dissolved oxygen concentration. The measurements were done from April through May 1989 in the North Atlantic south of Iceland, as a part of the Marine Light in the Mixed Layer program. We have shown that the statistical significance of the daily cycles of bio-optical properties of the open ocean varies in time throughout the spring season. The diurnal periodicity of c_{660} and O_2 was especially well pronounced during the development of the phytoplankton bloom in May. The fluorescence signal was dramatically affected by the ambient light intensity. The measurements at depths of 10 and 30 m showed fluorescence rhythms completely out of phase with each other. The comparison between the 10- and 30-m beam attenuation signals suggests that the 30-m signal was more sensitive to within day PAR variability. Further investigations are needed to determine how widespread the daily variations of bio-optical properties in the ocean are, what conditions favor this cycling, and how this variability may impact procedures for estimating the phytoplankton biomass and production.

INTRODUCTION

Large variability of bio-optical properties in the open ocean is thought to be caused primarily by phytoplankton populations [e.g., *Kirk*, 1983]. In recent years there has been an increased use of in vivo fluorescence, beam attenuation, and oxygen evolution measurements to investigate natural phytoplankton. When applied in mooring systems, these techniques have a great advantage of providing automatic sampling over time periods of months [*Dickey*, 1991; *Dickey et al.*, 1991]. However, the interpretation of mooring data, and even more so of shipboard data, is not simple because of many sources of signal variability, which reflect not only phytoplankton concentration, composition, and physiological processes but also concentrations of detritus and heterotrophs. The knowledge of this variability is therefore critical for understanding the measurement results and developing bio-optical models of photosynthetic production.

Phytoplankton depend on light energy for growth, so they have evolved a variety of adaptations to light variability, especially to its most regular component, the daily cycle of light. It is important to focus attention on a diel periodicity, since this time scale coincides with the generation time of individual phytoplankters. An extensive literature describes daily cycles exhibited by phytoplankton. Diel periodicity has been reported for cell division patterns [e.g. *Nelson and Brand*, 1979; *Harding and Heinbokel*, 1984; *Campbell and Carpenter*, 1986], photosynthetic parameters [e.g. *Doty and Oguri*, 1957; *Lorenzen*, 1963; *Prézelin and Sweeney*, 1977; *Harding et al.*, 1981*a*, *b*, 1982*a*, *b*; *Côté and Platt*, 1983; *Putt and Prézelin*, 1985; *Putt et al.*, 1988; *Prézelin et al.*, 1986; *Erga and Skjoldal*, 1990], carbon incorporation rates [*Malone*, 1971; *Glover and Smith*, 1988], cellular pigment concentration [e.g., *Yentsch and Scagel*, 1958; *Owens et al.*, 1980], nutrient assimilation [*Eppley et al.*, 1971; *Chisholm et al.*, 1978], chlorophyll fluorescence [e.g., *Kiefer*, 1973*a*; *Prézelin and Ley*, 1980; *Brand*, 1982; *Setser et al.*, 1982], and phytoplankton biomass in the water volume [*Fuhrman et al.*, 1985; *Litaker et al.*, 1988; *Prézelin and Glover*, 1991]. Daily patterns have been also observed in bio-optical properties of the ocean [*Siegel et al.*, 1989; *Hamilton et al.*, 1990; *Olson et al.*, 1990; *Cullen et al.*, 1992]. In spite of all the effort, any generalizations and comparisons based on previous studies are very difficult to make. Sometimes the investigators arrived at contradictory conclusions. For example, while in some studies the maximal division rate of the diatom *Skeletonema costatum* was found during the dark period [*Eppley et al.*, 1971; *Hitchcock*, 1980], others have reported the opposite behavior [*Jørgensen*, 1966; *Cosper*, 1982].

There are several reasons why our knowledge of the daily cycles in phytoplankton is limited. First, biological responses to variability of ambient light are strongly modified by many environmental and physiological factors including temperature [*Hitchcock*, 1980], nutrient availability [*Kiefer*, 1973*b*], average light intensity, length of photoperiod, and cell light history [e.g., *Yentsch and Scagel*, 1958; *Cosper*, 1982; *Putt and Prézelin*, 1985], and cell size distribution, storage capacity, and growth rates [*Malone*, 1971; *Chisholm and Costello*; 1980]. Second, although laboratory studies have been developed to separate various effects, comparisons between such experiments are difficult because of the differences in experimental procedures and choices of parameters measured during culture growth. Third, major problems arise when trying to relate laboratory models to natural oceanic conditions. For example, most laboratory studies have been conducted using a light:dark scheme in which the intensity of light was constant during the light part of the cycle. Ignoring natural variations of light is expected to change cell physiological responses and may invalidate extrapolation of laboratory results to the ocean.

Paper number 92JC01570.
0148-0227/92/92JC-01570$05.00

TABLE 1. Symbols and Units

Symbol	Definition	Unit
PAR	photosynthetically available radiation	μEin m^{-2} s^{-1}
c_{660}	beam attenuation coefficient at 660nm	m^{-1}
c_w	beam attenuation coefficient for water	m^{-1}
FLUO	stimulated fluorescence	V
T	water temperature	°C
O_2	dissolved oxygen content	μM

Finally, difficulties in interpreting the data are also related to insufficient sampling rate, which in most experiments have been a few hours. Such low sampling resolution most likely distorts the interpretation of the time evolution of diel cycles.

The main goal of this work is to examine the variability of bio-optical properties of seawater associated with planktonic responses to the daily light cycle. Our approach is unique because it is based upon an in situ experiment, which provided data at a high-frequency sampling rate for an extended period of time. Specifically, we analyze a 60-day time series of open ocean mooring measurements of scalar irradiance (photosynthetically available radiation, PAR), beam attenuation coefficient at 660 nm (c_{660}), stimulated chlorophyll fluorescence, and dissolved oxygen concentration.

MEASUREMENTS AND DATA ANALYSIS

The measurements were carried out from April through May 1989, in the North Atlantic (59° 29' N, 20° 50' W), as a part of the Office of Naval Research sponsored Marine Light in the Mixed Layer (MLML) program. Time series data were obtained with a multi-variable moored systems (MVMS) located in the upper 250 m. The technical details of the MVMS are given elsewhere [*Dickey et al.*, 1991] and a separate paper will describe the general mooring results, so we limit ourselves to a brief description. The configuration of the MVMS included a vector measuring current meter (VMCM) [*Weller and Davis*, 1980], a thermistor for water temperature measurements, a PAR sensor with a spherical collector for measuring scalar irradiance within a visible spectral range [*Booth*, 1976], a beam transmissometer (light wavelength of 660 nm [*Bartz et al.*, 1978]), an in situ stimulated fluorescence meter (blue excitation filter and red emission filter [*Bartz et al.*, 1988]), and a pulsed electrode dissolved oxygen sensor [*Langdon*, 1984]. In addition, surface meteorological measurements including wind speed and direction, barometric pressure, air and sea surface temperatures, and incoming solar radiation (250-2500 nm) were made from a surface buoy.

In this paper we will focus on data from depths of 10 and 30 m. The sampling was done at 1- and 7.5-min intervals for the 10- and 30-m depths, respectively. The meteorological data were acquired at 7.5-min intervals. In order to obtain the same time resolution for all data sets, we calculated 15-min averages before further analysis. Time series analyses using algorithms described by *Bendat and Piersol* [1966] were performed. Symbols and units of the parameters used for the analyses are listed in Table 1. The power spectra of the data sets were obtained using a Fourier transform of the autocovariance function. To describe the joint properties of the processes, we estimated squared coherence and phase functions between the pairs of data sets. The Parzen weighting function was applied to the covariance functions in order to maintain the coherence within the theoretical range $coh^2 \leq 1$. The confidence limits for coherence were calculated following the method of *Bloomfield* [1976]. Because the original time series in this study were

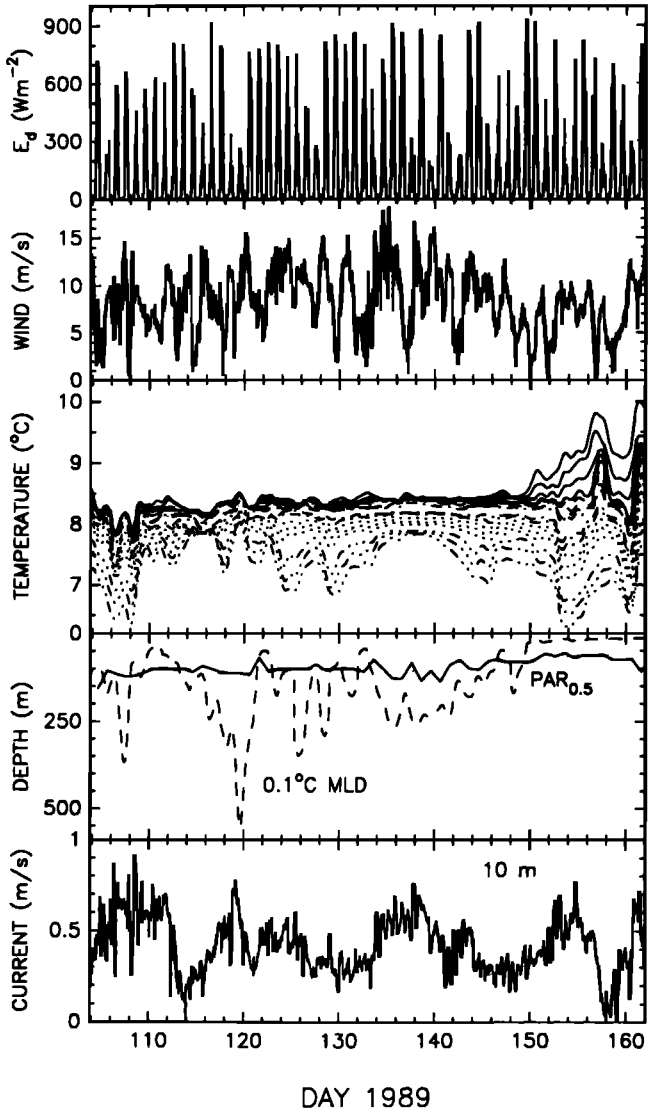

Fig. 1. Time series of the surface irradiance (E_d), wind speed, water temperature for 16 depths (10, 30, 50, 90, 110, 150, 200, 250, 350, 400, 450, 500, 550, 650, 700, 750 m), mixed layer depth (MLD) and 0.5 μEin m^{-2} s^{-1} PAR level depth ($PAR_{0.5}$), and 10-m current speed. These data were collected during the MLML 1989 experiment and are 15-min averages.

nonstationary, we removed the slow trends by high-pass moving average filtering, using a 3-day window width.

RESULTS

The physical and dynamical conditions at the mooring site during the MLML 1989 experiment will be discussed in greater detail in a separate paper. These conditions are summarized in Figure 1. Briefly, the experiment was conducted at the transition period from winter conditions with a very deep mixed layer to the summer characterized by thermal stratification of the surface water. Throughout the experiment the current speed varied between 0.2 and 0.9 m s^{-1}, and winds were highly variable, at times exceeding 15 m s^{-1}. The seasonal temperature stratification became evident after day 149 of the year and was coincident with some decrease of the wind speed. Note that during the course of the experiment, a few episodic events of shallowing and deepening of the mixed layer occurred before the seasonal thermal stratification was established. The mixed layer depth estimated using the 0.1°C criterion is compared in Figure 1 with the depth of the PAR level of 0.5 μEin $m^{-2}s^{-1}$.

Time series of PAR, beam attenuation coefficient (c_{660}), stimulated fluorescence (FLUO), and dissolved oxygen concentration (O_2), measured at 10 and 30 m are shown in Figures 2*a* and 2*b*. One of the most striking features is a general trend of increasing c_{660} and fluorescence starting at about day 140. This trend was likely due to the onset of a phytoplankton bloom. It was accompanied by an increase in vertical PAR attenuation which resulted in a significant decline in irradiance at 10 and 30 m. Oxygen concentration at 10 m showed also a tendency to increase and likely reflects the increase of net primary production. The average decrease of the 30-m oxygen signal after day 135 can be related to the decrease of the net production due to much lower light intensity at that depth, and to the large input of particles from the water above.

In Figures 3-5 we present the coherence and phase functions for PAR-FLUO, PAR-c_{660}, and PAR-O_2 relationships at 10 m, as estimated for a period of 15 consecutive days (days140-154). The distinct maxima for the coherence between PAR and bio-optical parameters corresponding to diel periodicity occur at the frequency band of 0.0417 cph. However, the statistical significance of correlations between changes in PAR, c_{660}, FLUO, and O_2, was not constant in time during the 2 months of deployment.

Figures 6-8 summarize the time evolution of the diel cycle at

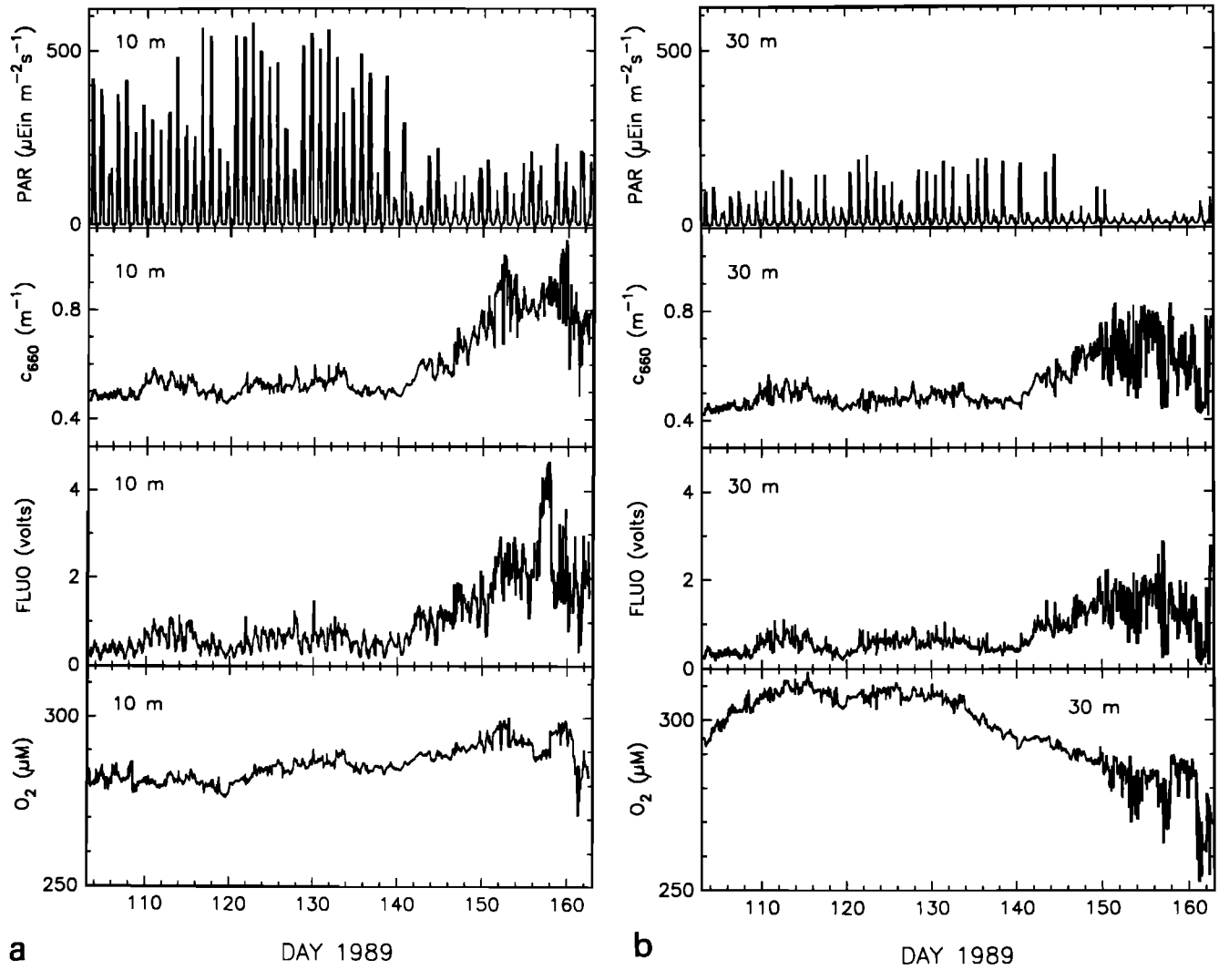

Fig. 2. Time series of PAR, c_{660}, stimulated fluorescence, and dissolved oxygen measured at (*a*) 10-m depth and (*b*) 30-m depth.

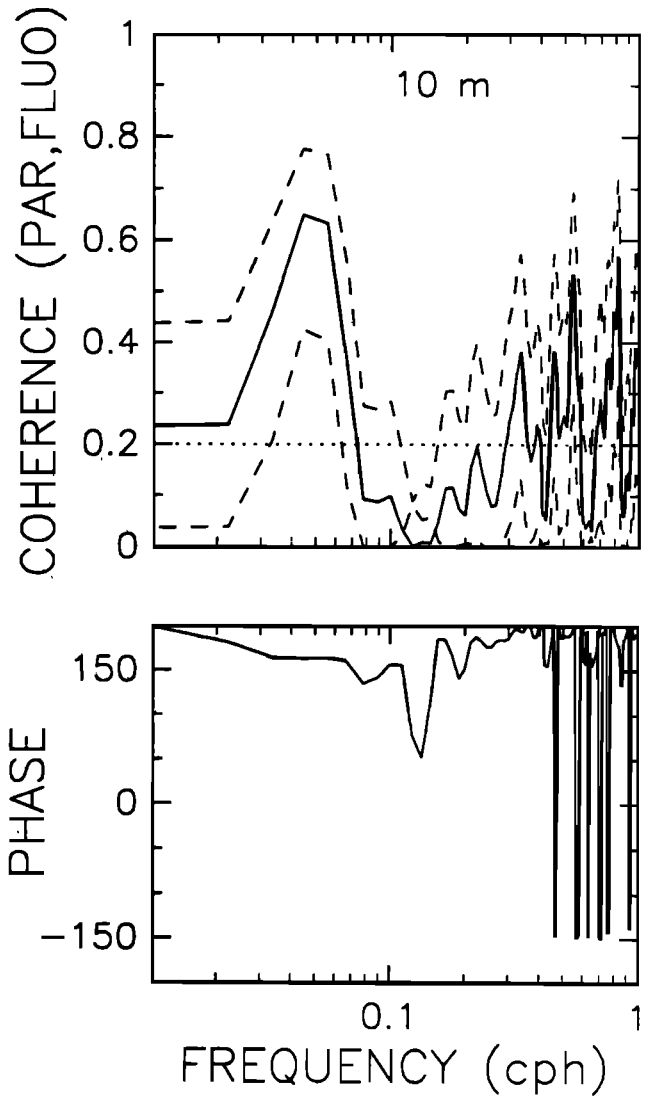

Fig. 3. Squared coherence and phase function between PAR and fluorescence estimated for 15 days of the time series at 10-m depth (days 140-154). Dashed lines are 95% confidence intervals; the dotted line is the cutoff value.

10 m depth. These plots were created as follows. First, we calculated 50 squared coherence and phase functions for the 10 day subsamples of the filtered time series. Then we plotted (Figures 6-8, solid line) the values of those estimates for the diurnal frequency. The scale on the horizontal axis indicates the time of the beginning of each data subsample, so for example, if we refer to the day 140 on these plots, we actually consider the results of cross-spectral analysis for data that include days 140-149. The dotted and the dashed lines in Figures 6-8 indicate a cutoff value of the coherence and 95% confidence intervals, respectively. The coherence function is significantly different from zero when it is greater than the cutoff value (~0.2 in this case), and then the confidence intervals apply [e.g., *Bloomfield*, 1976].

The diurnal variability of stimulated fluorescence at 10 m was significantly correlated with the diel periodicity in PAR throughout the deployment ($0.5<coh^2<0.8$ most of the time; Figure 6). The phase function was close to 180°, indicating that an increase in light was accompanied by a decrease in the fluorescence signal and vice versa. In contrast to fluorescence, the coherence at the diel frequency between PAR and c_{660} (Figure 7), as well as between PAR and O_2 (Figure 8), was rather low and often not significantly different from zero during the first part of the experiment. Then it increased significantly after day 140 (coh^2 >0.5). This indicates that the diel cycle in the beam attenuation and oxygen becomes more pronounced when the biological production intensifies in spring. We observe that when the PAR-c_{660} and PAR-O_2 coherence is high, the phase function assumes the value of about 70°-90° in both cases. It is also worth noting that the small maxima in the coherence function for the PAR-c_{660} relationship coincide with the timing of the short events of the shallowing of the mixed layer shown in Figure 1. The results of the cross-spectral analysis between all the pairs of parameters are summarized in Table 2.

In order to illustrate diel patterns in greater detail, we have plotted a few examples of expanded time series of PAR, c_{660}, fluorescence, and O_2 (Figure 9). We have chosen three subsamples from the beginning (days 112-113, Figure 9*a*), middle (days 130-131, Figure 9*b*) and the end of the experiment (days 148-150, Figure 9*c*). One can easily observe a persistent diel rhythm in fluorescence, with the daytime values being about twofold lower than nighttime values. The c_{660} daily cycle

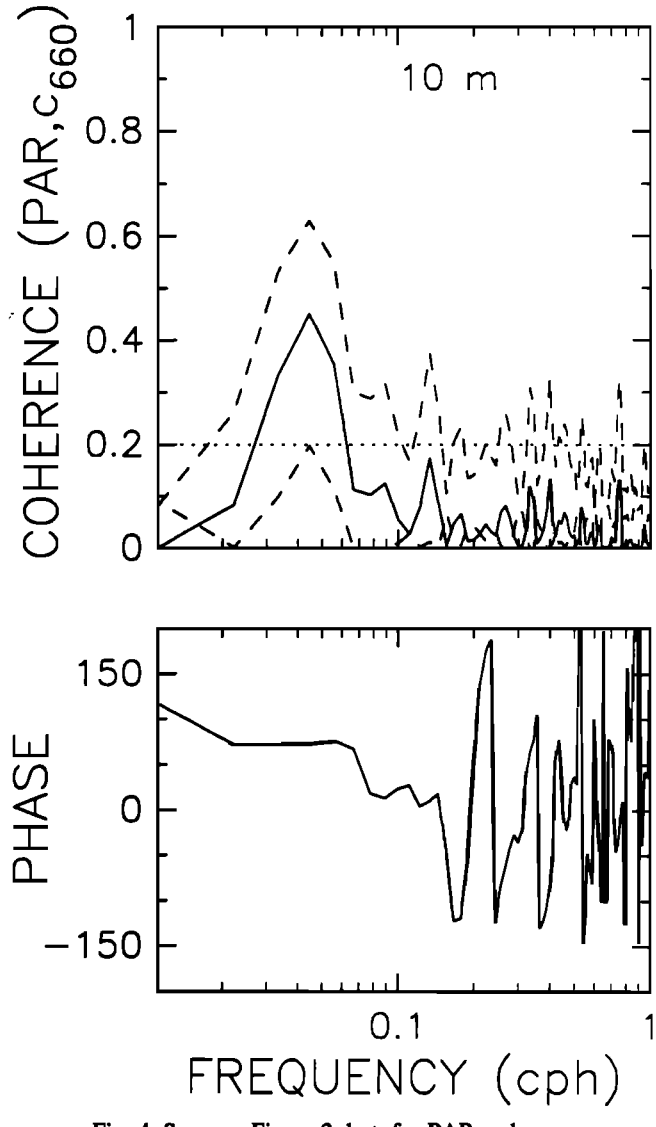

Fig. 4. Same as Figure 3, but for PAR and c_{660}.

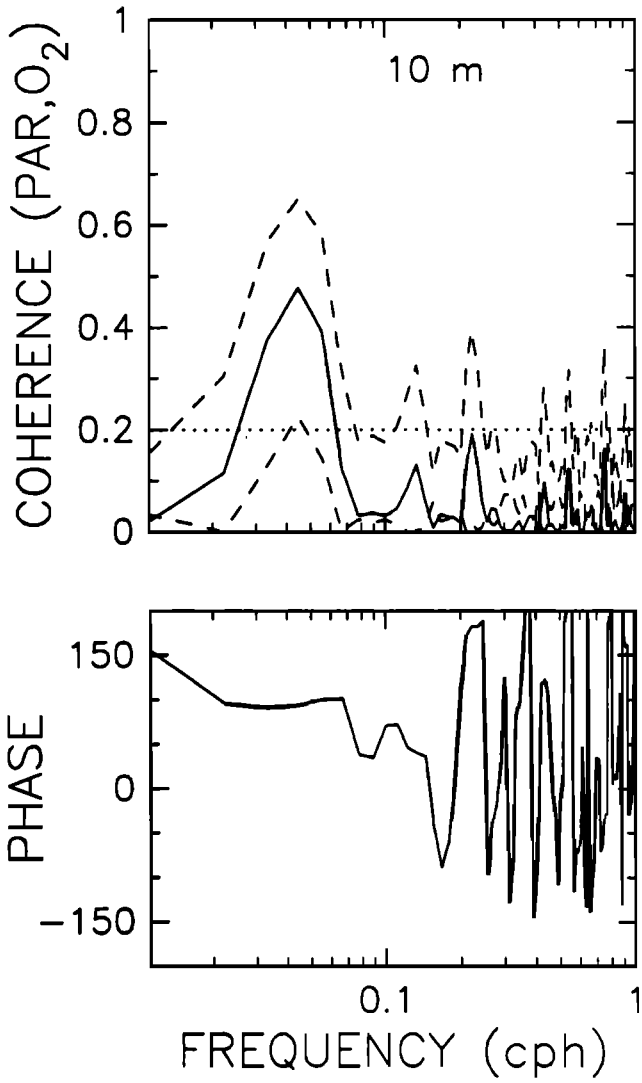

Fig. 5. Same as Figure 3, but for PAR and oxygen.

shows the peak-to-peak amplitude at the end of the deployment reaching as much as 0.1 m^{-1} (Figure 9*c*). The daily variability of c_{660} can be seen during days 112-113 as well (Figure 9*a*), but it is not apparent during days 130-131 (Figure 9*b*). The diel changes in oxygen signal at the end of experiment reached 5 μM (Figure 9*c*).

Similar analysis was performed for the time series from the 30-m depth. The evolution of the diel cycle throughout the deployment is shown in Figures 10-12. In general, the coherence between PAR and other parameters is lower at 30 m than at 10 m. We observe that the coherence for the diel cycle of PAR and FLUO becomes significant only during the final portion of the deployment after day 136 (Figure 10). Note that the phase function is not greater than 50°, compared to about 180° at the 10 m depth. The coherence for PAR and c_{660} is low, although it remains above the cutoff value most of the time from the beginning of the experiment until day 140 (Figure 11). The coherence between PAR and oxygen is significantly different from zero for only a short time interval around days 135-140 (Figure 12).

An interesting observation is that the estimates of the PAR-FLUO and PAR-c_{660} coherence functions at 30 m are characterized by the maxima at higher frequencies with distinctive semidiurnal peaks (0.083 cph, Figures 13 and 14). There was also a change of the phase from about 100° (diurnal periodicity) to about 180° (semidiurnal) in the case of c_{660}, and from about 50° (diurnal) to about 0° (semidiurnal) in the case of fluorescence. At the same time, there was no significant correlation between PAR and oxygen at that frequency (plots not shown; see Table 3).

The evidence indicating that the patterns of daily rhythms of bio-optical properties at 30 m differed from those at 10 m is also supported by the expanded plots of time series (Figure 15). At 30 m the fluorescence has a pronounced maximum during the light period and appears to track the PAR signal. This is in contrast to the FLUO pattern at 10 m. The daytime beam attenuation at 30 m has a pattern which is generally inverse to that of PAR signal. This includes even the relatively short-term variations due to cloudiness. The comparison between 10- and 30-m beam attenuation suggests that at 30 m, c_{660} was much more sensitive to this short-term PAR variability. The time series of oxygen at 30 m were generally very variable and it is difficult to assess any periodicity visually.

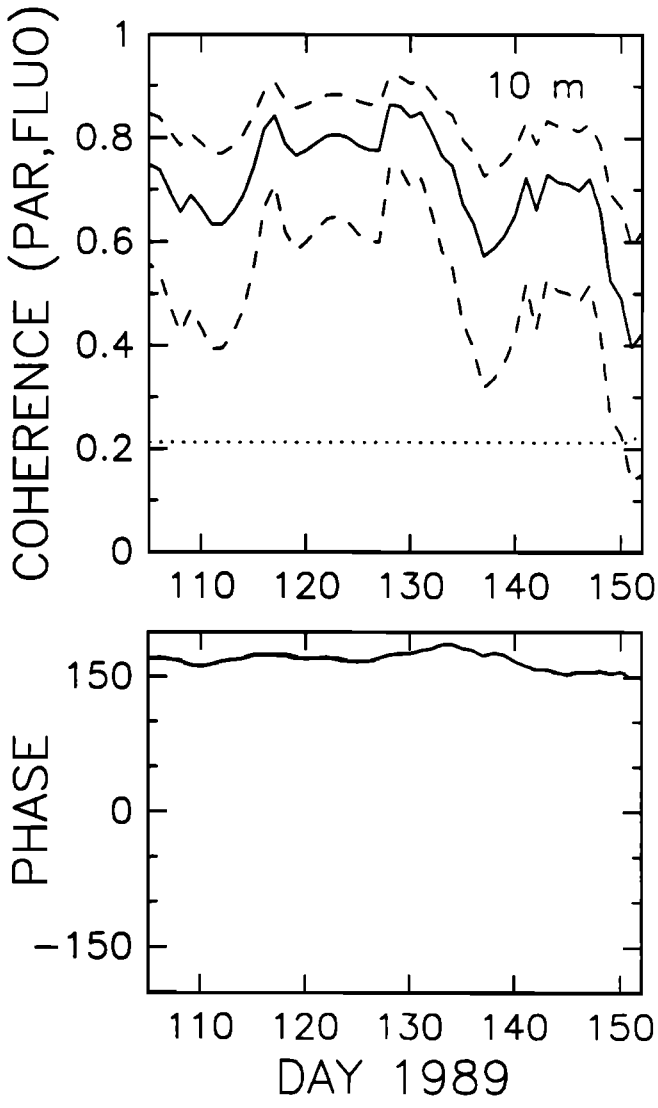

Fig. 6. Time evolution of the squared coherence and phase functions between PAR and fluorescence at 10 m, at the diurnal frequency (0.0417 cph). Dashed lines are 95% confidence intervals; the dotted line is the coherence cutoff value.

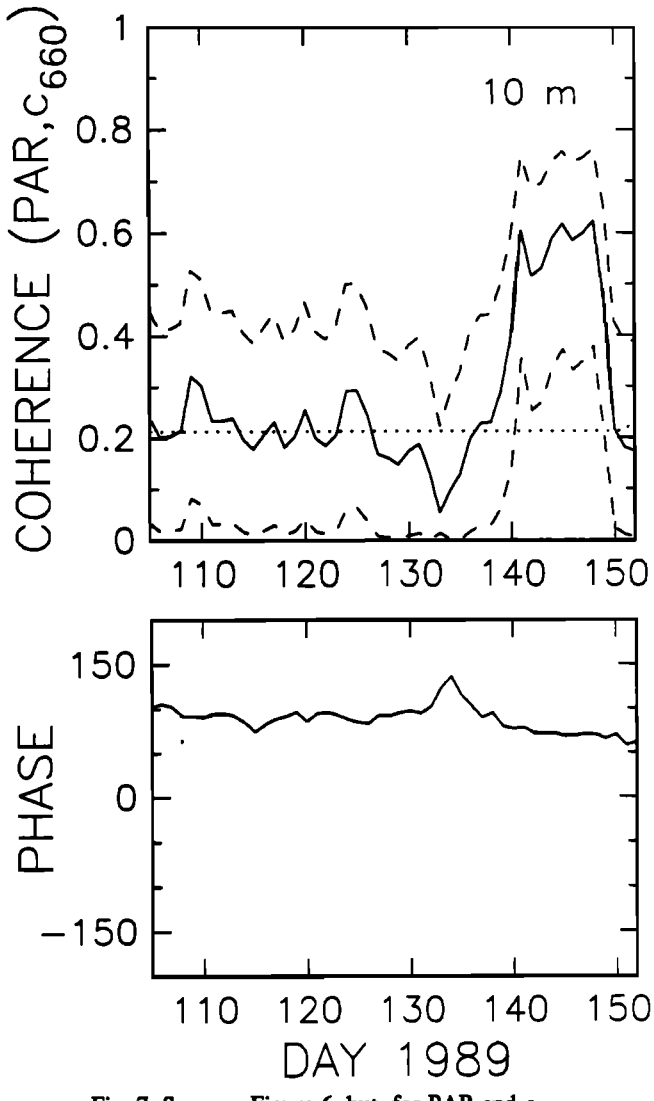

Fig. 7. Same as Figure 6, but for PAR and c_{660}.

DISCUSSION

The North Atlantic has been an area of long term oceanographic observations for many years, and a considerable background of information has accumulated [e.g., *Williams*, 1975; *Colebrook*, 1979; *Mann and Lazier*, 1991; and references therein]. Early spring blooms in this region are associated with the onset of surface warming and the formation of a shallow mixed layer, and are dominated by diatoms. They develop under conditions of high nutrient concentration and relatively weak stratification [*Cushing*, 1989]. A potential source of cell loss, grazing pressure, is rather low in North Atlantic, contrary to some Pacific areas [*Daro*, 1988; *Mann and Lazier*, 1991; *Morales et al.*, 1991; *Nielsen and Richardson*, 1989]. In addition, another source of cell loss, sinking, may be significantly reduced if phytoplankton decrease falling velocity in the thermocline [*Lande and Wood*, 1987]. A periodically deepening mixed layer might then cause the resuspention of particles back from the thermocline to the interior of the mixed layer. The historical data from the vicinity of the location of MLML mooring (Ocean Weather Station India, 59°N, 19°W) indicate that usually *Thalassiosira* spp. are the most abundant diatom in early spring (April-May), and *Calanus finmarchicus* the dominant copepod [*Williams*, 1975; *Longhurst and Williams*, 1979].

In this paper we have focused on diurnal variability of bio-optical properties of the water column in the North Atlantic throughout the spring season. As shown, the measured parameters can vary significantly during a day. The interpretation of this is limited by our understanding of the sources of such variability. In general, the variability of bio-optical properties at a fixed point in the ocean represents the superposition of local biological processes and the advection and mixing of different patches of the water.

As reported in the past, the degree of control of physical over biological processes may be reflected in significant coherence between Chl *a* and physical parameters like temperature [*Denman and Platt*, 1975; *Denman*, 1976], although the argument is limited to the situations when the variables are related by a monotonic function [*Star and Cullen*, 1981]. It might be argued that diel variability in optical properties was caused by the cycle of diurnal heating and nocturnal mixing, and dilution of surface water as cooler fluid is entrained from greater depth. Diurnal oscillations in the mixed layer depth associated with strong diurnal changes in the net heat exchange are often important features of the mixed layer dynamics in temperate

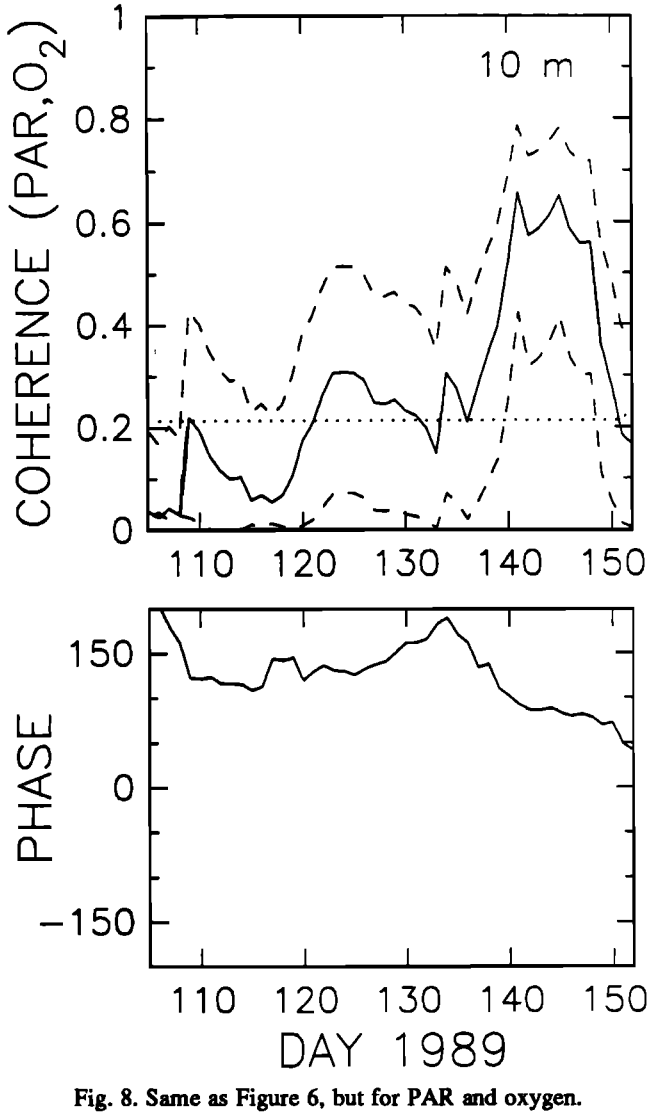

Fig. 8. Same as Figure 6, but for PAR and oxygen.

TABLE 2. Results of the Cross-Spectral Analysis for 24- and 12-Hour Periods at 10-m Depth

		Squared Coherence / Phase		
	Day	FLUO	c_{660}	O_2
PAR	110	0.75/170	0.35/80	NS
	(110)	(0.60)/(180)	(0.25)/(180)	NS
	140	0.65/160	0.50/70	0.45/90
	(140)	NS	NS	NS
T		NS	NS	NS
Current		NS	NS	NS
FLUO	110		0.60/30	0.25/0
	(110)		(0.80)/(0)	(0.30)(0)
	140		0.65/50	0.70/60
	(140)		(0.40)/(0)	(0.50)/(0)
c_{660}	110			0.80/0
	(110)			(0.80)/(0)
	140			0.35/0
	(140)			(0.40)/(0)

The coherence and phase functions were calculated for 15 day time series starting at days 110 and 140. The numbers in parentheses are for 12-hour period. NS, not significantly cross-correlated.

oceans [*Kondo et al.*, 1979; *Price et al.*, 1986; *Woods and Barkmann*, 1986; *Woods and Onken*, 1982]. However, we did not find significant coherence between bio-optical properties and the water temperature, mixed layer depth or the speed (kinetic energy) of the water motion in the diurnal and semidiurnal frequencies. Such observations favor the importance of biological diel rhythms in phytoplankton population.

It has been suggested in the literature that in order to study photoadaptive processes it is useful to relate fluorescence to beam attenuation [eg., *Denman and Gargett*, 1988; *Cullen et al.*, 1988, 1992]. When measured in the open ocean, both parameters often covary lineary with chlorophyll concentration, but when photoadaptive processes become important c_{660} and FLUO are expected to change on different time scales, with beam attenuation being more conservative. With this in mind we have plotted $(c_{660}\text{-}c_w)$/FLUO ratio as a function of time (Figure 16) and PAR (Figure 17). As might have been expected from the patterns of daily variability of c_{660} and FLUO presented before (Figures 9 and 15), $(c_{660}\text{-}c_w)$/FLUO displays the daily cycle, with the maximum at noon at 10 m and the minimum at 30 m. This again suggests that photoadaptive processes were involved and supports the interpretation of our data primarily in terms of biological processes rather than hydrodynamical ones. However, it needs to be recognized that we likely observe a rather delicate balance between mixing and biological responses. This is especially true for c_{660}, which is expected to be function of PAR integrated through some time interval and not a direct function of instantaneous irradiance. The responses of FLUO and O_2 to light changes include time scales of tens of seconds to hours [e. g., *Abbott et al.*, 1982; *Marra and Heinemann*, 1982; *Cullen et al.*, 1988; *Stramska and Dickey*, 1992]. As was shown in the previous section, the statistical significance of the coherence between PAR, c_{660}, FLUO, and O_2, was not constant in time during the 2 months of deployment. Only when favorable physical conditions prevailed (i.e., low turbulent mixing) were phytoplankton cells caught within the upper water layer and exposed to certain light intensities long enough to display biological responses to PAR.

We found pronounced diel cycles in in situ fluorescence, although the patterns were quite different at 10- and 30-m depths. It is unlikely that these differences were due to different composition of the planktonic community, because the patterns were present when the sampling was done well within the mixed layer during the first part of the experiment.

Fluorescence represents a loss of energy which might otherwise have been converted to chemical energy (photosynthesis) or dissipated as heat. The basic assumption of the in vivo Chl *a* fluorescence technique is that there exists a constant ratio between fluorescence intensity and the amount of extractable chlorophyll *a* and pheopigments. Accordingly, the source of the changes in fluorescence on a time scale of a day is the variability of the concentration of those pigments in the water volume. Assuming no advection of water, such effects as changes of the biomass due to phytoplankton growth, zooplankton grazing, cell sinking, cell senescence and mortality, fecal pellet sinking and photodegradation, as well as change of cellular pigment concentration due to photoadaptation, all might cause variation in total pigment concentration. A model developed by *Welschmeyer and Lorenzen* [1985] suggests that growth and grazing are probably most important in this respect. Thus part of the variability of the fluorescence signal in our experiment is likely attributable to the dynamical balance between those processes.

The strength of the fluorescence signal is not a simple

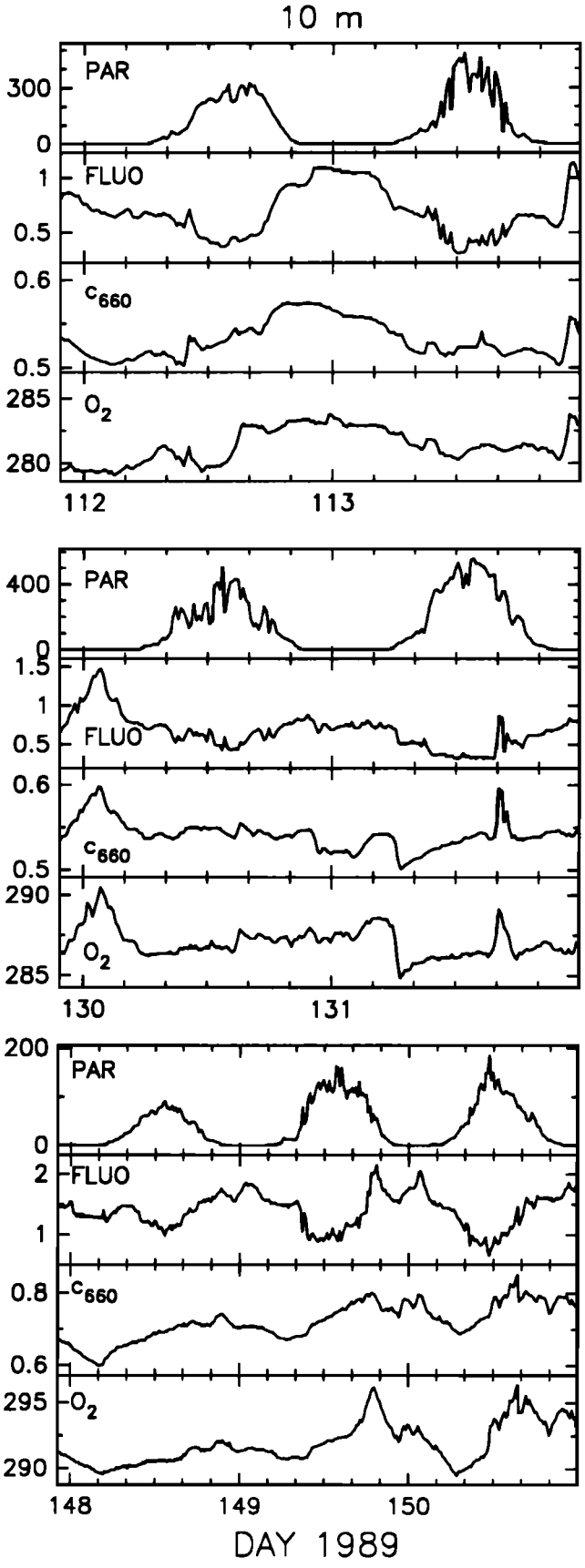

Fig. 9. Examples of daily time courses of bio-optical parameters: PAR, c_{660}, fluorescence, and oxygen as measured at 10-m depth.

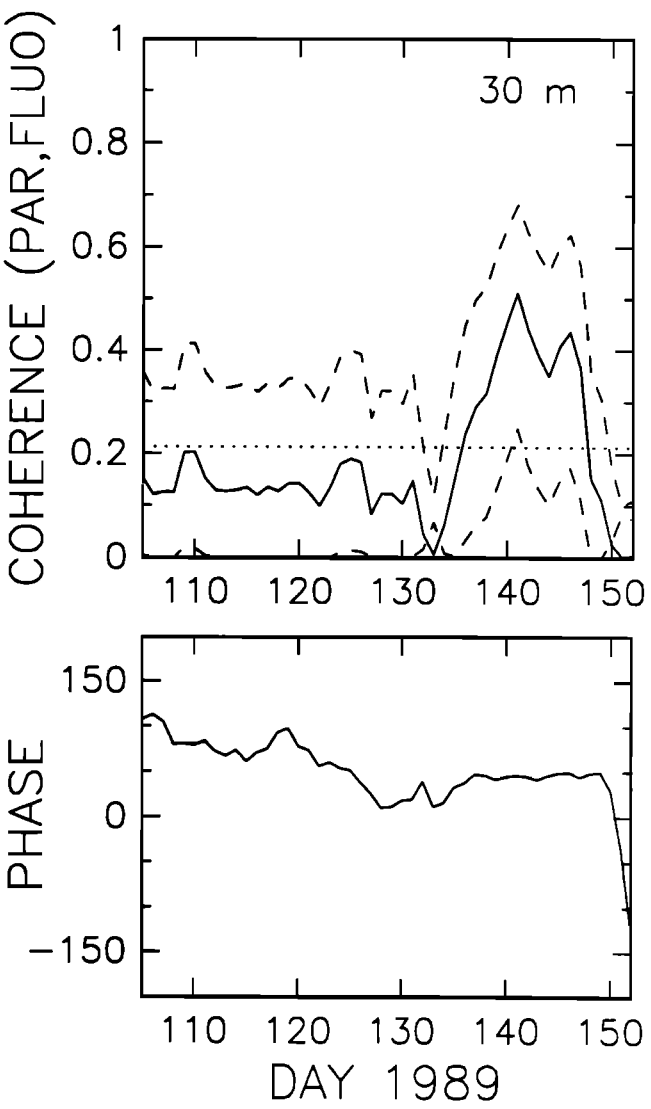

Fig. 10. Time evolution of the squared coherence and phase functions between PAR and fluorescence at 30 m, at the diurnal frequency (0.0417 cph). Dashed lines are 95% confidence intervals; the dotted line is the cutoff value.

function of chlorophyll concentration, however. On a time scale of a day, changes in pigment specific fluorescence are probably related to one or a combination of a few types of responses described previously in the literature. First, the decrease of the fluorescence with light can be caused by the changes in the concentration of quinone-type quenchers, redistribution of the energy between two photosystems, and changes in fluorescence yield [*Bannister and Rice*, 1968; *Bonaventura and Myers*, 1969; *Falkowski and Kiefer*, 1985; *Vincent*, 1979]. It can also be associated with changes in chloroplast shape and position affecting cellular absorption [*Kiefer*, 1973b]. Second, the increase of fluorescence with light can be attributed to the decrease of self-shading of the chloroplasts [*Loftus and Seliger*, 1975]. Finally, the fluorescence can vary due to the light-shade adaptation of phytoplankton cells, which occurs on a time scale of several hours, and is associated with the change of cellular pigment concentration and composition [e.g., *Falkowski*, 1980; 1984].

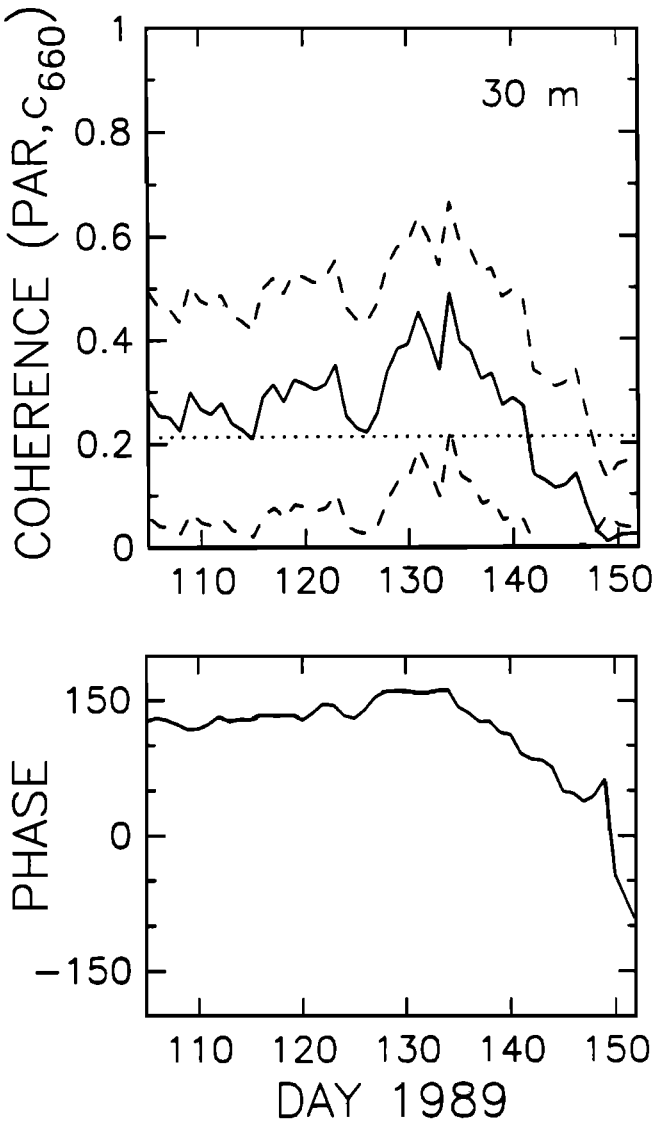

Fig. 11. Same as Figure 10, but for PAR and c_{660}.

Although little is known about the relative importance of these effects in the field, changes in quantum yield are thought to be a major source of fluorescence variation [*Falkowski and Kiefer*, 1985].

Our plots of $(c_{660}-c_w)$/FLUO ratio versus irradiance (Figure 17) (and fluorescence versus irradiance, not shown here), show no evidence of a critical PAR value when fluorescence quenching starts. This is in the contrary to the suggestions in the literature [e.g., *Vincent*, 1979]. It is possible that the differences in the fluorescence response to PAR at 10 and 30 m in our experiment resulted to some extent from adaptation to average light intensity reaching the phytoplankton cells. At 10 m, where PAR exceeded 400 μEin m^{-2} s^{-1} at noon, the fluorescence inhibiting processes prevailed during the day and the pattern was analogous to that described previously in the literature [*Kiefer*, 1973a; *Loftus and Seliger*, 1975; *Setser et al.*, 1982]. At 30 m, where PAR was not greater than 200 μEin m^{-2} s^{-1}, the fluorescence at day rather closely paralleled the light intensity.

If one excludes the possibility of hydrodynamical effects, the changes in oxygen concentration represent a superposition of production by photosynthesis and consumption by respiration. Our 10 m data show that a diel cycle for oxygen was especially pronounced after the onset of the phytoplankton bloom (day 140). The phase function for PAR and oxygen assumed a value of about 90°. It appears that during that period, there was a positive net production throughout the day and respiration prevailed at night.

The diel cycle of oxygen at 30 m was significant for a short period of time around day 138. The later disappearance of that cycle could be due to the decrease of the daily net production at that depth. The average decrease of the 30-m oxygen signal after day 135 supports the hypothesis that there was a negative net community production, even if a gross primary production occurred. In contrast to 30 m, oxygen concentration at 10 m showed a tendency to increase during that period of time. This is in agreement with historical data for the study region, which show that more than 95% of total carbon production occurs usually in the upper layer less than 30 m deep [*Williams*, 1973].

The beam attenuation coefficient is defined as the sum of the absorption and scattering coefficients and it is an inherent

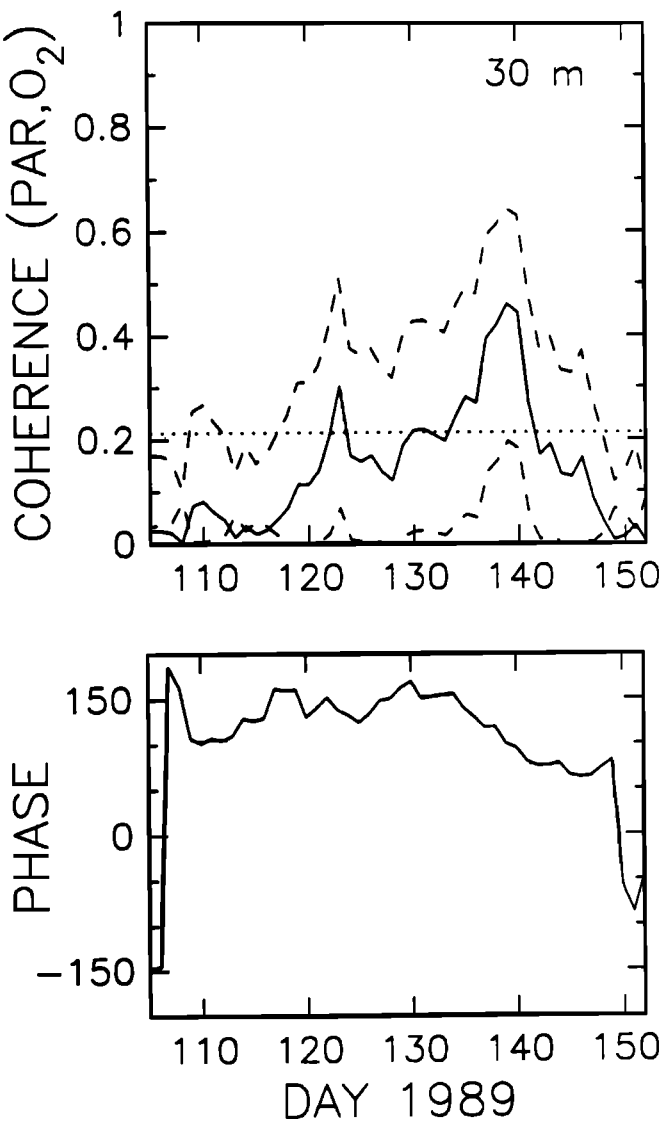

Fig. 12. Same as Figure 10, but for PAR and oxygen.

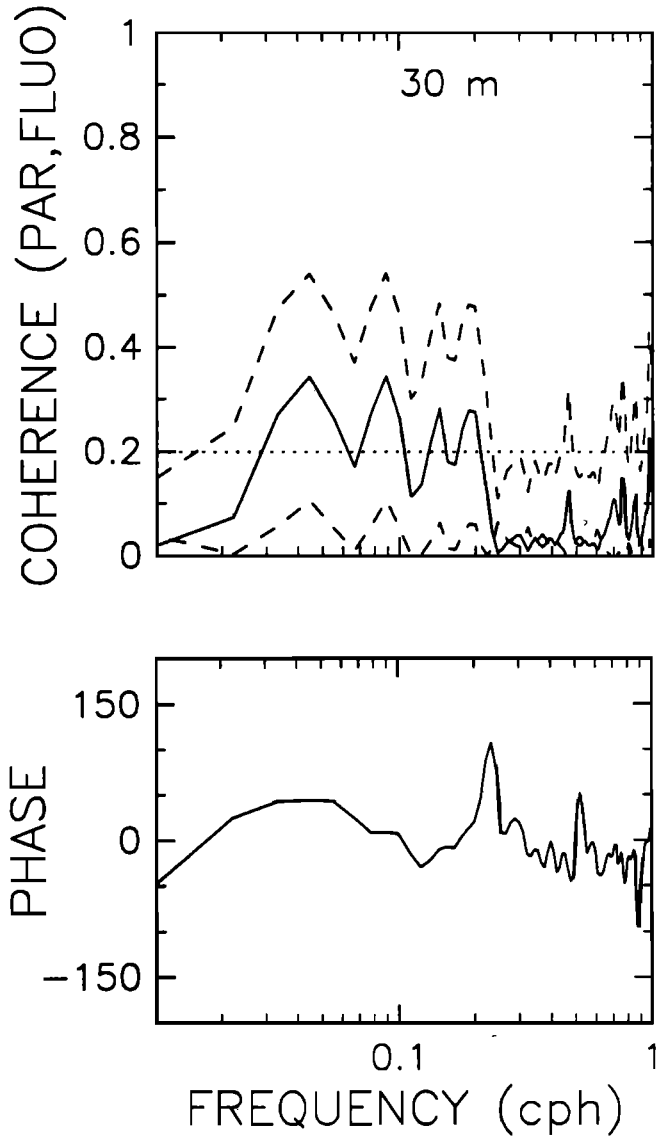

Fig. 13. Squared coherence and phase function between PAR and fluorescence estimated for 15-day time series at 30-m depth (days 140-154). Dashed lines are 95% confidence intervals; the dotted line is the coherence cutoff value.

optical property of the medium [*Jerlov*, 1976]. In the open ocean, light attenuation at 660 nm can change because of variations of particle (mainly phytoplankton cells) concentration, size distribution, shape, and refractive index [e.g., *Kitchen et al.*, 1982; *Baker and Lavelle*, 1984; *Morel and Bricaud*, 1986]. Previous studies have shown that the variability in c_{660} is well correlated with suspended particle concentration, primarily because of particle scattering [e.g., *Bishop*, 1986; *Spinrad et al.*, 1989]. During the spring bloom in the North Atlantic, c_{660} is expected to be dominated by nanoplankton and microplankton species. This is due to the high concentrations exceeding at times 10^{11} cells m^{-3} [*Erga and Heimdal*, 1984; *Skjoldal and Lannergren*, 1978] and large scattering cross-sections of these microorganisms [*Stramski and Kiefer*, 1991]. The diurnal cycle in c_{660} has been suggested to reflect the balance between particle production by photosynthesis and losses through grazing [*Siegel et al.*, 1989], but simple models might not explain phytoplankton growth accurately [*Cullen et al.*, 1992]. In general, the diel variability of phytoplankton abundance can be attributed to one or a combination of two processes: diel variability of production and diel variability of losses. Diel variability of production can be related to periodicity of photosynthesis and cell division rates [e.g., *Nelson and Brand*, 1979; *Harding et al.*, 1981b; *Harding and Heinbokel*, 1984; *Campbell and Carpenter*, 1986]. The important factors affecting phytoplankton losses are expected to be particle sinking and zooplankton grazing. The previous studies in North Atlantic show that phytoplankton grazing during the spring bloom is carried out mainly by copepods [*Williams*, 1973; *Longhurst and Williams*, 1979; *Nielsen and Richardson*, 1989; *Morales et al.*, 1991]. It has also been documented that copepods can be nocturnal feeders [e.g. *Daro*, 1988]. Therefore the diel periodicity in c_{660} may result from variability in both productivity and grazing.

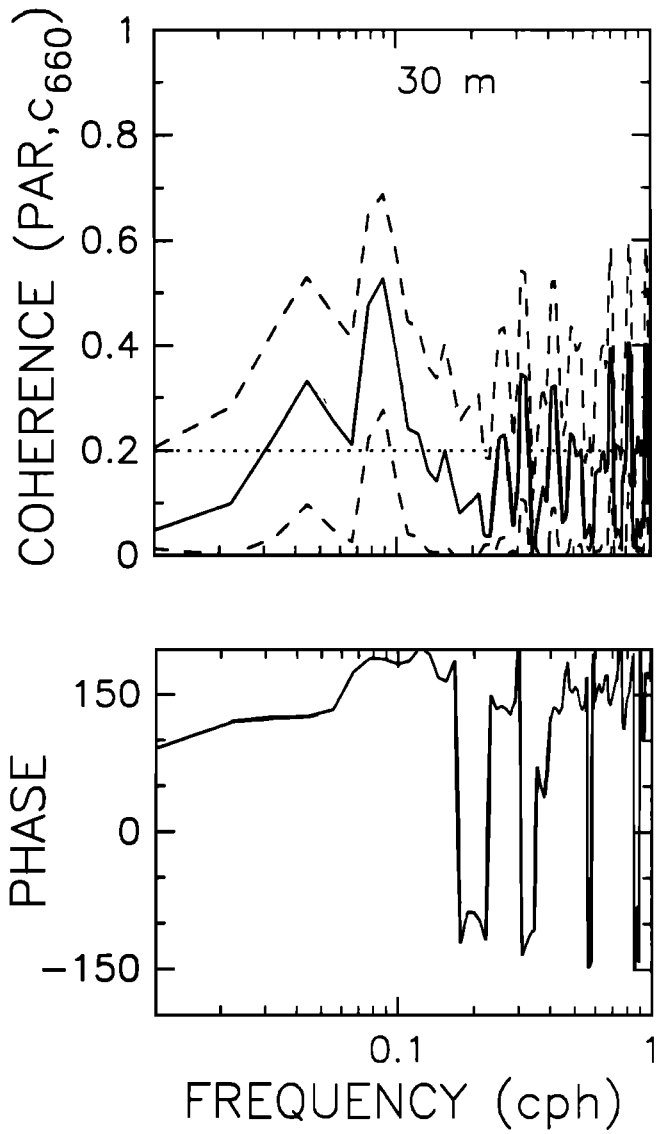

Fig. 14. Squared coherence and phase function between PAR and c_{660} estimated for 15-day time series at 30-m depth (days 110-114). Dashed lines are 95% confidence intervals; the dotted line is the coherence cutoff value.

TABLE 3. Results of the Cross-Spectral Analysis for 24- and 12-Hour Periods at 30-m Depth

		Squared Coherence / Phase		
	Day	FLUO	c_{660}	O_2
PAR	110	0.25/90	0.30/100	NS
	(110)	(0.50)/(0)	(0.50)/(180)	NS
	140	0.35/50	NS	0.30/90
	(140)	(0.35)/0	NS	NS
T		NS	NS	NS
Current		NS	NS	NS
FLUO	110		0.80/0	0.60/0
	(110)		NS	NS
	140		0.60/0	0.60/0
	(140)		(0.60)/(0)	(0.30)/(0)
c_{660}	110			0.70/0
	(110)			(0.35)/(0)
	140			0.80/0
	(140)			(0.35)/(0)

The coherence and phase functions were calculated for 15 day time series starting at days 110 and 140. The numbers in parentheses are for 12-hour period. NS, not significantly cross-correlated.

The point to be emphasized is that this simplistic concept of c_{660} variability reflecting phytoplankton abundance is modulated by other processes. First, a possible mechanism for varying c_{660} by the plankton population has been recently described by *Ackleson et al.* [1990]. They have provided laboratory evidence of phytoplankton cell swelling in response to increased light intensity. Phytoplankton swelling was accompanied by the change of cell size and refractive index, which eventually leads to changes of c_{660}. In situ diel changes in phytoplankton cell size were hypothesized to be the cause of the diel patterns in forward-angle light scatter observed in the Atlantic Ocean [*Olson et al.*, 1990]. Second, the change of cellular optical properties (refractive index and absorption) can be brought about by chloroplast configuration [*Kiefer*, 1973b] and by change in cellular pigments, due to photoadaptation [*Falkowski*, 1980, 1984]. The diel cycles in cellular Chl *a* concentration, observed in the laboratory experiments [*Owens et al.*, 1980], have been attributed to changes in the rates of chlorophyll synthesis and degradation, driven by the light:dark cycle. In their study, maximal Chl *a* concentrations were observed before the end of the light period, whereas minimal concentrations occurred at the end of the dark period. Thus the diel variability of cellular Chl *a* content could be in phase with our observations of the daily changes of c_{660}.

We realize that our data set does not allow us to quantify the relative importance of the processes prevailing during our experiment. The coincidence of the high coherence between PAR and c_{660} with the development of the phytoplankton bloom indicates that the growth rate might have been an important factor stimulating the daily cycle of c_{660}. However,

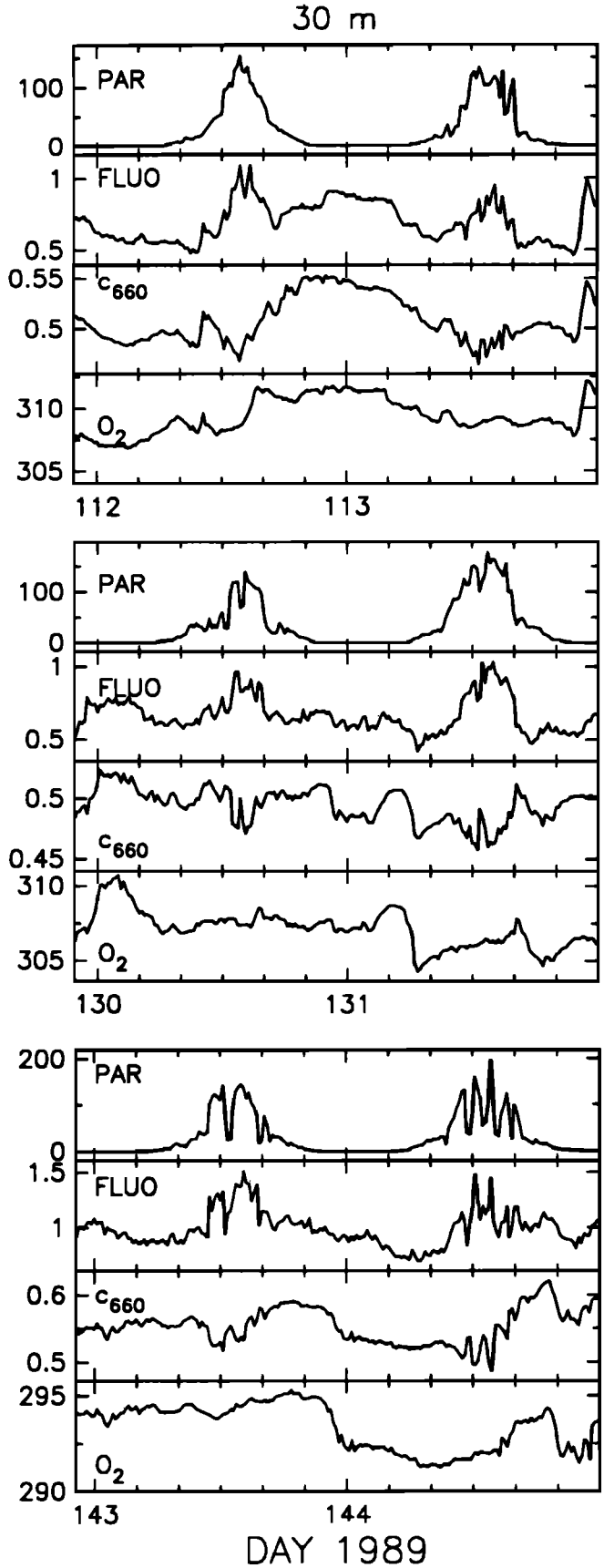

Fig. 15. Examples of daily time courses of bio-optical parameters: PAR, c_{660}, fluorescence, and oxygen as measured at 30-m depth.

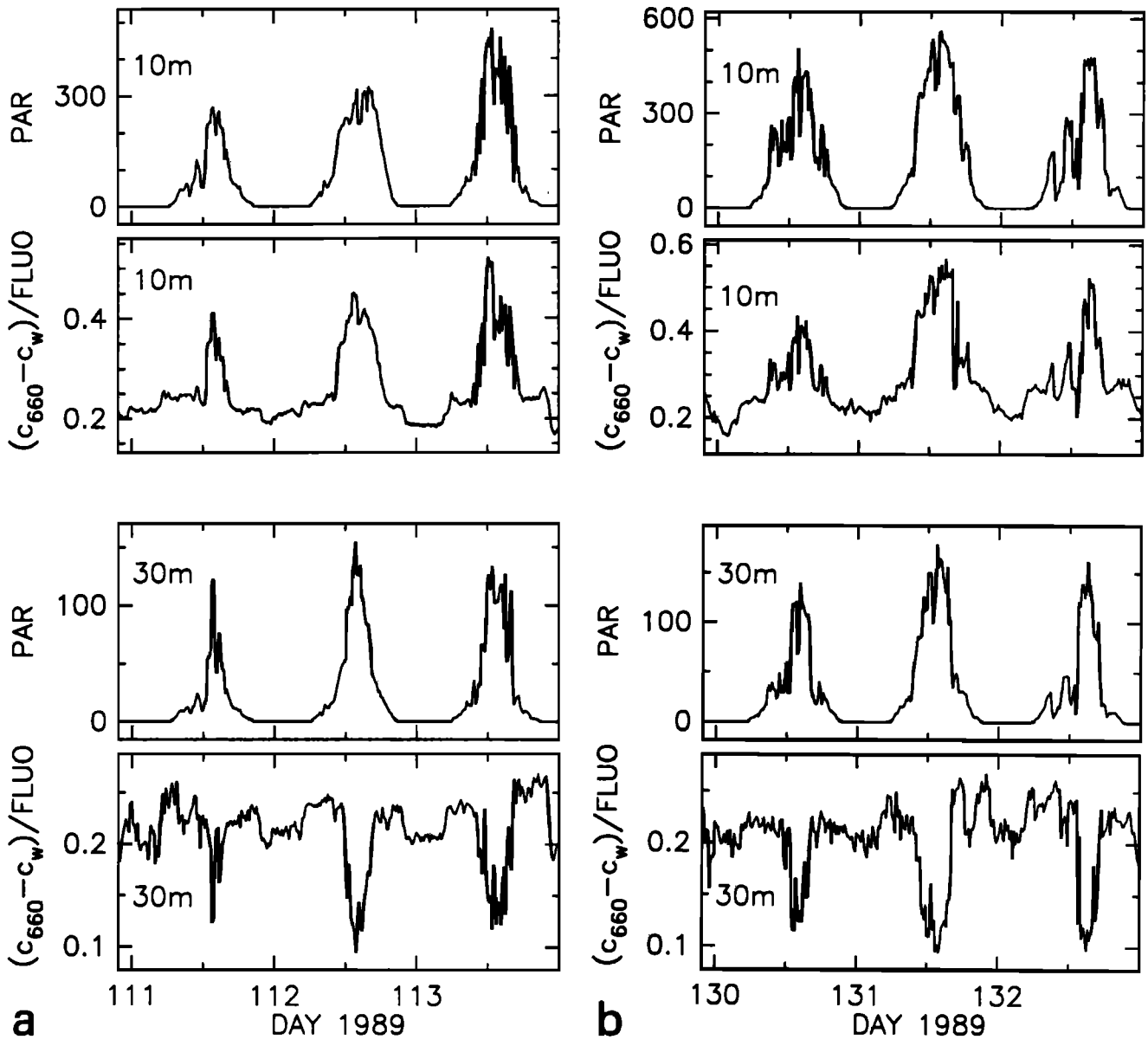

Fig. 16. Examples of the daily cycles in PAR and the $(c_{660}-c_w)$/FLUO ratio at (*a*) 10 and (*b*) 30 m. Note that c_w is the clear water beam attenuation coefficient (0.364 m^{-1}).

our data provide also new evidence that c_{660} cannot always be regarded as a conservative property with respect to within-day photoadaptive responses. A combination of the "modifying" mechanisms was probably of special significance for the variability of c_{660} at 30 m which happened on a time scale shorter than a day [see also Stramska and Dickey, 1992]. The nature of beam attenuation changes in response to varying light clearly needs to be investigated in the future. In addition, interpretation of past and future beam attenuation data needs to be done with care. In particular shipboard profile sampling does not usually resolve the diurnal cycle, and as a consequence these data are likely aliased.

In summary, our study has documented the presence of the strong daily cycles in bio-optical properties of the open ocean. We have shown that the significance of those cycles varies in time throughout the season. The diurnal periodicity of c_{660} and O_2 was especially pronounced during the development of the phytoplankton bloom in late May. The fluorescence signal was dramatically affected by the ambient light intensity. The measurements at depths of 10 and 30 m resolved fluorescence rhythms completely out of phase with each other. The comparison between 10- and 30-m beam attenuation signals suggests that at 30 m c_{660} was more sensitive to within-day PAR variability. Further investigations are needed to quantify the daily variations of bio-optical properties in the ocean, to establish what natural conditions favor this cycling, and to assess the impact of this variability on the procedures for estimating the phytoplankton biomass and production. Finally, as our understanding of the properties of phytoplankton improves, the approach of studying the daily cycles of bio-optical properties can be an effective way of examining phytoplankton populations in their natural oceanic habitat.

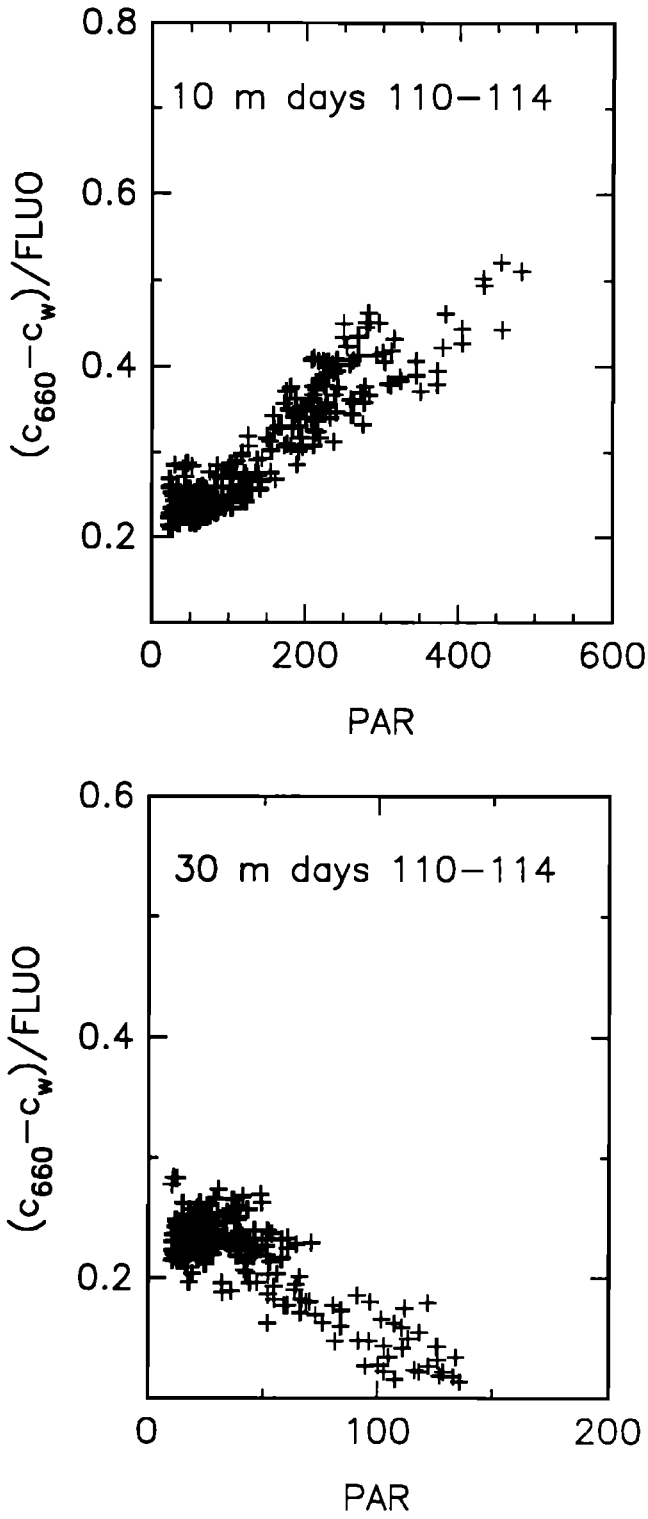

Fig. 17. Example of the $(c_{660}-c_w)$/FLUO relationship on PAR.

Acknowledgments. This research was sponsored by the Office of Naval Research as part of the Marine Light in the Mixed Layer program (contract N00014-89-J-1498). We wish to express our appreciation to John Marra, Chris Langdon, Bob Weller, and Al Plueddemann for sharing portions of the data used for our analysis. We would also like to thank Derek Manov for his excellent technical assistance provided during the experiment. Comments by John Cullen and two anonymous reviewers are gratefully acknowledged.

REFERENCES

Abbott, M. R., P. J. Richerson, and T. M. Powell, In situ response of phytoplankton fluorescence to rapid variations in light, *Limnol. Oceanogr., 27*, 218-225, 1982.

Ackleson, S. G., J. J. Cullen, J. Brown, and M. P. Lesser, Some changes in optical properties of marine phytoplankton in response to high light intensity, in *Ocean Optics 10, Proc. SPIE Int. Soc. Opt. Eng., 1302*, 238-249, 1990.

Baker, E. T., and J. W. Lavelle, The effect of particle size on the light attenuation coefficient of natural suspensions, *J. Geophys. Res., 89*, 8197-8202, 1984.

Bannister, T. T., and G. Rice, Parallel time courses of oxygen evolution and chlorophyll fluorescence, *Biochem. Biophys. Acta, 162*, 555-580, 1968.

Bartz, R., J. R. V. Zaneveld, and H. Pak, A transmissometer for profiling and moored observations in water, in *Ocean Optics 5, Proc. SPIE Int. Soc. Opt. Eng., 160*, 102-108, 1978.

Bartz, R., R. Spinrad, and J. C. Kitchen, A low power, high resolution, *in situ* fluorometer for profiling and moored applications in water, in *Ocean Optics 9, Proc. SPIE Int. Soc. Opt. Eng., 925* 157-170, 1988.

Bendat, J. S., and A. G. Piersol, *Measurement and Analysis of Random Data*, 390 pp., John Wiley, New York, 1966.

Bishop, J. K. B., The correction and suspended particulate matter calibration of Sea Tech transmissometer data, *Deep Sea Res., 33*, 121-134, 1986.

Bloomfield, P., *Fourier Analysis of Time Series: An Introduction*, 258 pp., John Wiley, New York, 1976.

Bonaventura, C., and J. Myers, Fluorescence and oxygen evolution from *Chlorella pyrenoidosa, Biochim. Biophys. Acta, 189*, 366-383, 1969.

Booth, C. R., The design and evaluation of a measurement system for photosynthetically active quantum scalar irradiance, *Limnol. Oceanogr., 19*, 326-335, 1976.

Brand, L. E., Persistent diel rhythms in the chlorophyll fluorescence of marine phytoplankton species, *Mar. Biol., 69*, 253-262, 1982.

Campbell L., and E. J. Carpenter, Diel patterns of cell division in marine *Synechococcus* spp. (Cyanobacteria): Use of the frequency of dividing cells technique to measure growth rate, *Mar. Ecol. Prog. Ser., 32*, 139-148, 1986.

Chisholm, S. W., and J. C. Costello, Influence of environmental factors and population composition on timing of cell division in *Thalassiosira Fluviatilis* (bacillariophyceae) grown on light/dark cycles, *J. Phycol., 16*, 375-383, 1980.

Chisholm, S. W., F. Azam, and R. W. Eppley, Silicic acid incorporation in marine diatoms on light:dark cycles, Use as an assay for phased cell division, *Limnol. Oceanogr., 23*, 518-529, 1978.

Colebrook, J. M., Continuous plankton records: Seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea, *Mar. Biol., 51*, 23-32, 1979.

Cosper, E., Influence of light intensity on diel variations in rates of growth, respiration and organic release of marine diatom: Comparison of diurnally constant and fluctuating light, *J. Plankton Res., 4*, 705-724, 1982.

Côté, B., and T. Platt, Day-to-day variations in the spring-summer photosynthetic parameters of coastal marine phytoplankton, *Limnol. Oceanogr., 28*, 320-344, 1983.

Cullen, J. J., C. S. Yentsch, T. L. Cucci, and H. L. MacIntyre, Autofluorescence and other optical properties as tools in biological oceanography, in *Ocean Optics 9, Proc. SPIE Int. Soc. Opt. Eng., 925*, 149-156, 1988.

Cullen, J. J., M. R. Lewis, C. O. Davis, and R. T. Barber, Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the equatorial Pacific, *J. Geophys. Res., 97*, 639-654, 1992.

Cushing, D. H., A difference in structure between ecosystems in strongly stratified waters and those that are only weakly stratified, *J. Plankton Res.*, *11*, 1-13, 1989.

Daro, M. H., Migratory and grazing behavior of copepods and vertical distribution of phytoplankton, *Bull. Mar. Sci.*, *43*, 710-729, 1988.

Denman, K. L., Covariability of chlorophyll and temperature in the sea, *Deep Sea Res.*, *23*, 539-550, 1976.

Denman, K. L., and A. E. Gargett, Multiple thermoclines are barriers to vertical exchange in the subarctic Pacific during SUPER, May 1984, *J. Mar. Res.*, *46*, 77-103, 1988.

Denman, K. L., and T. Platt, Coherences in the horizontal distributions of phytoplankton and temperature in the upper ocean, *Mem. Soc. R. Sci. Liege*, 6th Ser., *7*, 19-30, 1975.

Dickey, T. D., The emergence of concurrent high-resolution physical and bio-optical measurements in the upper ocean and their applications, *Rev. Geophys.*, *29*, 383-413, 1991.

Dickey, T. D., J. Marra, T. Granata, C. Langdon, M. Hamilton, J. Wiggert, D. Siegel, and A. Bratkovich, Concurrent high resolution bio-optical and physical time series observation in the Sargasso Sea during the spring of 1987, *J. Geophys. Res.*, *96*, 8643-8664, 1991.

Doty, M. S., and M. Oguri, Evidence for a photosynthetic daily periodicity, *Limnol. Oceanogr.*, *2*, 37-40, 1957.

Eppley, R.W., J. N. Rogers, J. J. McCarthy, and A. Sournia, Light:dark periodicity in nitrogen assimilation of the marine phytoplankters *Skeletonema costatum* and *Coccolithus huxleyi* in N-limited chemostat culture, *J. Phycol.*, *7*, 150-154, 1971.

Erga, S. R., and B. R. Heimdal, Ecological studies on the phytoplankton of Korsfjorden, western Norway, The dynamics of a spring bloom seen in relation to hydrographical conditions and light regime, *J. Plankton Res.*, *6*, 67-90, 1984.

Erga, S. R., and H. R. Skjoldal, Diel variations in photosynthetic activity of summer phytoplankton in Lindåspollene, western Norway, *Mar. Ecol. Prog. Ser.*, *65*, 73-85, 1990.

Falkowski, P. G., Light-shade adaptation in marine phytoplankton, in *Primary Productivity in the Sea*, edited by P. G. Falkowski, pp. 99-119, Plenum, New York, 1980.

Falkowski, P. G., Physiological responses of phytoplankton to natural light regimes, *J. Plankton Res.*, *6*, 295-307, 1984.

Falkowski, P. G., and D. A. Kiefer, Chlorophyll *a* fluorescence in phytoplankton, Relationship to photosynthesis and biomass, *J. Plankton Res.*, *7*, 715-731, 1985.

Fuhrman, J. A., R. W. Eppley, Å. Hagström, and F. Azam, Diel variations in bacterioplankton, phytoplankton and related parameters in the Southern California Bight, *Mar. Ecol. Prog. Ser.*, *27*, 9-20, 1985.

Glover, H. E., and A. E. Smith, Diel patterns of carbon incorporation into biochemical constituents of *Synechococcus* spp. and larger algae in the northwest Atlantic Ocean, *Mar. Biol.*, *97*, 259-267, 1988.

Hamilton, M., T. Granata, T. Dickey, J. Wiggert, D. Siegel, J. Marra, and C. Langdon, Diel variations of bio-optical properties in the Sargasso Sea, in *Ocean Optics 10, Proc. SPIE Int. Soc. Opt. Eng.*, *1302*, 214-224, 1990.

Harding, L. W., Jr., and J. F. Heinbokel, Periodicities of photosynthesis and cell division: Behavior of phase-lagged replicate cultures of *Ditylum brightwellii* in a diurnally varying photic regime, *Mar. Ecol. Prog. Ser. 15*, 225-232, 1984.

Harding, L. W., Jr., B. W. Meeson, B. B. Prézelin, and B. M. Sweeney, Diel periodicity of photosynthesis in marine phytoplankton, *Mar. Biol.*, *61*, 95-105, 1981*a*.

Harding, L. W., Jr., B. B. Prézelin, B. M. Sweeney, and J. L. Cox, Diel oscillations in the photosynthesis-irradiance relationship of a planktonic marine diatom, *J. Phycol.*, *17*, 389-394, 1981*b*.

Harding, L. W., Jr., B. B. Prézelin, B. M. Sweeney, and J. L. Cox, Diel oscillations of the photosynthesis-irradiance (P-I) relationship in natural assemblages of phytoplankton, *Mar. Biol.*, *67*, 167-178, 1982*a*.

Harding, L. W., Jr., B. B. Prézelin, B. M. Sweeney, and J. L. Cox, Primary production as influenced by diel periodicity of phytoplankton photosynthesis, *Mar. Biol.*, *67*, 179-186, 1982*b*.

Hitchcock, G. L., Diel variation in chlorophyll *a*, carbohydrate and protein content of the marine diatom *Skeletonema costatum*, *Mar. Biol.*, *57*, 271-278, 1980.

Jerlov, N. G., *Marine Optics*, Elsevier, New York, 1976.

Jørgensen, E. G., Photosynthetic activity during the life cycle of synchronous *Skeletonema* cells, *Physiol. Plant*, *19*, 789-799, 1966.

Kiefer, D. A., Fluorescence properties of natural phytoplankton populations, *Mar. Biol.*, *22*, 263-269, 1973*a*.

Kiefer, D. A., Chlorophyll *a* fluorescence in marine centric diatoms: Response of chloroplasts to light and nutrient stress, *Mar. Biol.*, *23*, 39-46, 1973b.

Kirk, J. T. O., *Light and Photosynthesis in Aquatic Ecosystems*, Cambridge University Press, New York, 1983.

Kitchen, J. C., J. R. V. Zaneveld, and H. Pak, Effect of particle size distribution and chlorophyll content on beam attenuation spectra, *Appl. Opt.*, *21*, 3913-3918, 1982.

Kondo, J., Y. Sasano, and T. Ishii, On wind driven current and temperature profiles with diurnal period in the oceanic planetary boundary layer, *J. Phys. Oceanogr.*, *9*, 360-32, 1979.

Lande, R., and A. M. Wood, Suspension times of particles in the upper ocean, *Deep Sea Res.*, *34*, 61-72, 1987.

Langdon, C., Dissolved oxygen monitoring system using a pulsed electrode: Design, performance and evaluation, *Deep Sea Res.*, *31*, 1357-1367, 1984.

Litaker, W., C. S. Duke, B. E. Kenny, and J. Ramus, Diel Chl *a* and phaeopigment cycles in a shallow tidal estuary: Potential role of microzooplankton grazing, *Mar. Ecol. Prog. Ser.*, *47*, 259-270, 1988.

Loftus, M. E., and H. H. Seliger, Some limitations of the in vivo fluorescence technique, *Chesapeake Sci.*, *16*, 79-92, 1975.

Longhurst, A. R., and R. Williams, Materials for plankton modelling: Vertical disttribution of Atlantic zooplankton in summer, *J. Plankton Res.*, *1*, 1-28, 1979.

Lorenzen, C. J., Diurnal variation in photosynthetic activity of natural phytoplankton populations, *Limnol. Oceanogr.*, *8*, 56-62, 1963.

Malone, T. C., Diurnal rhythms in netplankton and nannoplankton assimilation ratios, *Mar. Biol.*, *10*, 285-289, 1971.

Mann, K. H. and J. R. N. Lazier, *Dynamics of Marine Ecosystem*, 466 pp., Blackwell Scientific, Boston, Mass., 1991.

Marra, J., and K. Heinemann, Photosynthesis response by phytoplankton to sunlight variability, *Limnol. Oceanogr.*, *27*, 1141-1153, 1982.

Morales, C. E., A. Bedo, R. P. Harris, and P. R. T. Tranter, Grazing of copepod assemblages in the north-east Atlantic: The importance of the small size fraction, *J. Plankton Res.*, *13*, 455-472, 1991.

Morel, A., and A. Bricaud, Inherent optical properties of algal cells including picoplankton: Theoretical and experimental results, in Photosynthetic Picoplankton, edited by T. Platt and W. K. W. Li, *Can. Bull. Fish. Aquat. Sci.*, *214*, 521-559, 1986.

Nelson, D. M., and L. E. Brand, Cell division periodicity in 13 species of marine phytoplankton on a light:dark cycle, *J. Phycol.*, *15*, 67-75, 1979.

Nielsen, T. K., K. Richardson, Food chain structure of the North Sea plankton communities: Seasonal variations of the role of

the microbial loop, *Mar. Ecol. Prog. Ser.*, *56*, 75-87, 1989.

Olson, R. J., S.W. Chisholm, E. R. Zettler, and E. V. Armbrust, Pigments, size, and distribution of *Synechococcus* in the North Atlantic and Pacific oceans, *Limnol. Oceanogr.*, *35*, 45-58, 1990.

Owens, T. G., P. G. Falkowski, and T. E. Whitledge, Diel periodicity in cellular chlorophyll content in marine diatoms, *Mar. Biol.*, *59*, 71-77, 1980.

Prézelin, B. B., and H. E. Glover, Variability in time/space estimates of phytoplankton, biomass and productivity in the Sargasso Sea, *J. Plankton Res.*, *13*, suppl., 45-67, 1991.

Prézelin, B. B., and A. C. Ley, Photosynthesis and chlorophyll *a* fluorescence rhythms in marine phytoplankton, *Mar. Biol.*, *55*, 295-307, 1980.

Prézelin, B. B., and B. M. Sweeney, Characterization of photosynthetic rhythms in marine dinoflagellates, I, Pigmentation, photosynthetic capacity, and respiration, *Plant. Physiol.*, *60*, 384-387, 1977.

Prézelin, B. B., M. Putt, and H. E. Glover, Diurnal patterns in photosynthetic capacity and depth-dependent photosynthesis-irradiance relationships in *Synechococcus* spp. and larger phytoplankton in three water masses in the northwest Atlantic Ocean, *Mar. Biol.*, *91*, 205-217, 1986.

Price, J. F., R. A. Weller, and R. Pinkel, Diurnal cycling: Observations and models of the upper ocean response to diurnal heating, cooling, and wind mixing, *J. Geophys. Res.*, *91*, 8411-8427, 1986.

Putt, M., and B. B. Prézelin, Observations of diel patterns of photosynthesis in cyanobacteria and nanoplankton in the Santa Barbara Channel during 'el Nino', *J. Plankton Res.*, *7*, 779-790, 1985.

Putt, M., R. B. Rivkin, and B. B. Prézelin, Effects of altered photic regimes on diel patterns of species-specific photosynthesis, I, Comparison of polar and temperate phytoplankton, *Mar. Biol.*, *97*, 435-443, 1988.

Setser, P. J., N. L. Guinasso, and D. R. Schink, Daily patterns of fluorescence in vivo in the central equatorial Pacific, *J. Mar. Res.*, *40*, 453-471, 1982.

Siegel, D. A., T. D. Dickey, L. Washburn, M. K. Hamilton, and B. G. Mitchell, Optical determination of particulate abundance and production, *Deep Sea Res.*, *36*, 211-222, 1989.

Skjoldal, H. R., and C. Lannergren, The spring phytoplankton bloom in Lindaspollene, a land-locked Norwegian fjord, II, Biomass and activity of net- and nanoplankton, *Mar. Biol.*, *47*, 313-323, 1978.

Spinrad, R, W., H. Glover, B. W. Ward, L. A. Codispoti, and G. Kullenberg, Suspended particle and bacterial maxima in Peruvian coastal waters during a cold water anomaly, *Deep Sea Res.*, *36*, 715-733, 1989.

Star, J. L., and J. J. Cullen, Spectral analysis: A caveat, *Deep Sea Res.*, *28*, 93-97, 1981.

Stramska, M., and T. D. Dickey, Short-term variations of the bio-optical properties of the ocean in response to cloud-induced irradiance fluctuations, *J. Geophys. Res.*, *97*, 5713-5721, 1992.

Stramski D., and D. A. Kiefer, Light scattering by microorganisms in the open ocean, *Prog. Oceanogr.*, *28*, 343-383, 1991.

Vincent, W., Mechanism of rapid photosynthetic adaptation in natural phytoplankton communities, I, Redistribution of excitation energy between photosystems I and II, *J. Phycol.*, *15*, 429-434, 1979.

Weller, R. A., and R. E. Davis, A vector measuring current meter, *Deep Sea Res.*, *27*, 565-582, 1980.

Welschmeyer, N. A., and C. J. Lorenzen, Chlorophyll budgets: Zooplankton grazing and phytoplankton growth in a temperate fjord and the central Pacific gyres, *Limnol. Oceanogr.*, *30*, 1-21, 1985.

Williams, R., Sampling at ocean weather station India, *Ann. Biol. Copenhagen*, *32*, 62-64, 1975.

Woods, J. D., and W. Barkmann, The response of the upper ocean to solar heating, I, The mixed layer, *Q. J. R. Meteorol. Soc.*, *112*, 1-27, 1986.

Woods, J. D., and R. Onken, Diurnal variation and primary production in the ocean - Preliminary results of a Lagrangian ensemble model, *J. Plankton Res.*, *4*, 735-756, 1982.

Yentsch, C. S., and R. F. Scagel, Diurnal study of phytoplankton pigments, An in situ study in East Sound, Washington, *J. Mar. Res.*, *17*, 567-584, 1958.

T. D. Dickey and M. Stramska, Ocean Physics Group, Department of Geological Sciences, University of Southern California, Los Angeles, CA 90089-0740.

(Received March 17, 1992;
revised July 2, 1992;
accepted July 6, 1992.)