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Short-Term Variations of the Bio-Optical Properties of the Ocean in Response to Cloud-Induced Irradiance Fluctuations

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Variations in natural irradiance caused by changing cloud cover were examined as a potential source for the variability of the bio-optical properties in the open ocean. Time series of the scalar irradiance (PAR), beam attenuation coefficient (at 660 nm), stimulated chlorophyll fluorescence, concentration of dissolved oxygen, and water temperature were subject to spectral analysis. These data were acquired in the Sargasso Sea at a depth of 23 m during the Biowatt mooring experiment in 1987. Three cloudy days, on which power spectra of PAR exhibited distinct maxima at periods of about 40 to 100 min, were selected for the analysis. Similar variations occurred in beam attenuation, fluorescence and dissolved oxygen as evidenced by relatively high coherence (> 0.5) between PAR and these variables. This is suggested to be related to rapid photoadaptive responses in the phytoplankton community on time scales of minutes. Possible explanations for these responses include changes in fluorescence yield, photosynthetic rate, cellular absorption, cell size and refractive index. No relationship between PAR and the bio-optical parameters was observed when hydrodynamical factors prevailed over time scales similar to those for cloud-induced irradiance fluctuations. The hydrodynamical effects were successfully traced by water temperature variations which, in further studies, may prove useful for separation of phenomena controlling within-day bio-optical variability in the ocean.

INTRODUCTION

Characterization of the bio-optical properties in the upper ocean is important for studies of primary productivity and relationships between various physical and biological processes. Phytoplankton have been recognized to have a key influence on the optical variability in the open ocean [e.g., *Jerlov*, 1976; *Kirk*, 1975, 1983; *Atlas and Bannister*, 1980]. This variability occurs on many time scales and is forced through conditions limiting phytoplankton growth which include light and nutrient availability, as well as through processes responsible for phytoplankton losses and transport with water masses [*Dickey*, 1990, 1991; *Denman and Gargett*, 1983]. Such bio-optical parameters as stimulated fluorescence of chlorophyll *a*, concentration of dissolved oxygen and beam attenuation coefficient exhibit clear response to diel cycles in processes associated with the planktonic community [*Siegel et al.*, 1989].

The question of how important various physical and biological factors are in controlling bio-optical variability on time scales shorter than a day remains open. It is natural to expect that the radiant flux penetrating into the water is one of the most important physical parameters because it controls the growth and cellular physiology of phytoplankton. In recent years, there have been several attempts to examine phytoplankton responses to within-day variations in natural light regime associated with the passage of clouds [e.g., *Gallegos et al.*, 1977, 1980; *Abbott et al.*, 1982; *Marra and Heinemann*, 1982], 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; *Quéguiner and Legendre*, 1986]. These studies provided the evidence that phytoplankton may respond to rapid changes in irradiance. This includes responses in photosynthetic rate and chlorophyll *a* fluorescence on time scales of tens of seconds to a few hours under intermittent cloud cover [*Abbott et al.*, 1982; *Marra and Heinemann*, 1982].

In this work we report concurrent field measurements of the scalar irradiance (photosynthetically available radiation or PAR), beam attenuation coefficient, stimulated chlorophyll *a* fluorescence, concentration of dissolved oxygen, and water temperature. By performing time series analysis of open ocean mooring data we examine the variability in these parameters at time scales from about 10 to 100 min under weather conditions characterized by changing cloud cover.

MEASUREMENTS AND DATA ANALYSIS

Data were acquired in the Sargasso Sea (34°N, 70°W) between February 28 and May 11, 1987, as a part of the Biowatt II program. Technical details of this project are available elsewhere [*Dickey et al.*, 1990, 1991]; therefore here we limit ourselves to a brief outline relevant to this study. Time series data were obtained with a multivariable moored systems (MVMS) located at a depth of 23.25 m. The configuration of the MVMS included a photosynthetically available radiation sensor with a spherical collector [*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], a pulsed electrode dissolved oxygen sensor [*Langdon*, 1984], and a thermistor for temperature measurements. Symbols and units are listed in Table 1. The sampling was done at 4-min intervals. According to the Nyquist theorem, our analysis is limited to periods longer than 8 min or more conservatively longer than 12 min [*Bendat and Piersol*, 1966]. The most rapid irradiance variations caused by clouds may thus be omitted. Despite this

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TABLE 1. Symbols Used in Text

Symbol	Definition	Unit
PAR	photosynthetically available radiation	10^{21} quanta m^{-2} s^{-1}
c	beam attenuation coefficient at 660nm	m^{-1}
Fluo	stimulated fluorescence	relative units
T	water temperature	°C
O_2	dissolved oxygen content	μM/l
G	power spectral density of PAR	$(10^{21}$ quanta m^{-2} $s^{-1})^2$/cpmin

limitation, our analysis covers a range of time scales which may potentially be important for phytoplankton responses, and consequently for the variabilty of the bio-optical properties of seawater.

We will consider here only sunrise-to-sunset data on selected days in which irradiance was highly variable owing to cloudy weather. Each time series record consisted of a total number, N, of 178 digital data points. Prior to basic statistical calculations, certain preprocessing of raw time series data was needed because the short-term fluctuations in the measured variables are usually superimposed on long-term trends (e.g., strong diurnal cycle). Accordingly, to remove slowly varying trends and assure a zero mean value of time series, the data were transformed by a first-order difference filter [*Jenkins and Watts*, 1968]. We then estimated the power spectral density functions for single time series records as well as phase and coherence functions to describe joint properties of records from two random processes. The calculations were made using the conventional Blackman-Tukey algorithms [e.g., *Bendat and Piersol*, 1966]. We applied the Parzen lag weighting function to the correlation functions in order to maintain the coherence function within the theoretical range $\gamma^2 \leq 1$. The spectra were calculated with the maximum time lag M of 35, so the frequency resolution bandwidth was 1.2×10^{-4} Hz. The maximum time lag was a little beyond the number usually recommended for calculating the

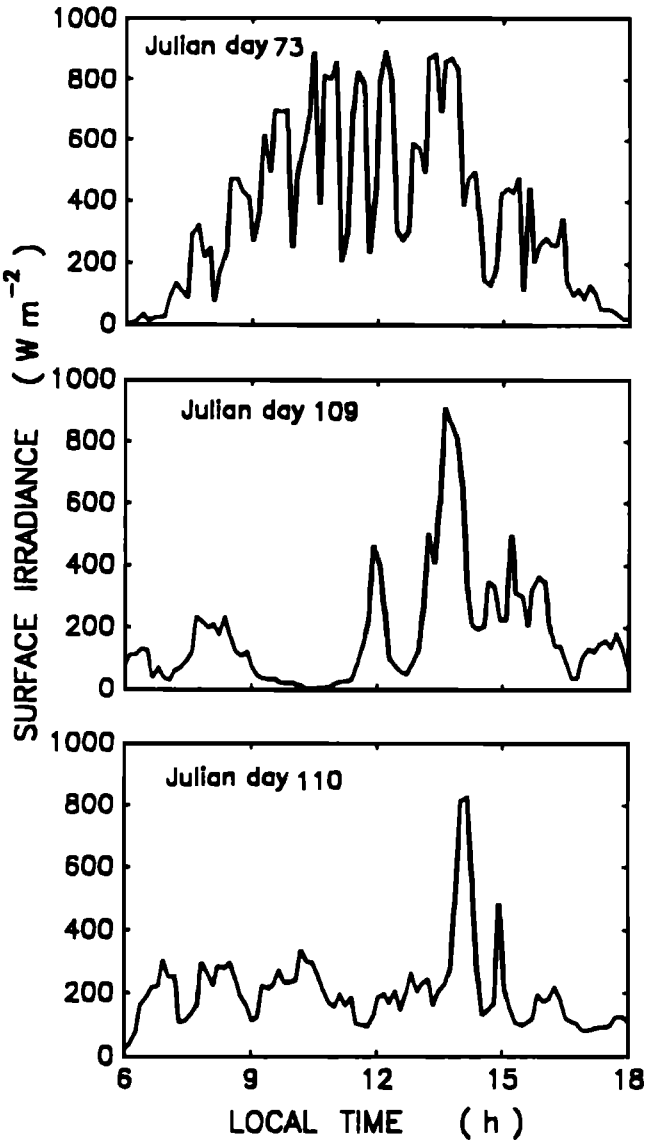

Fig. 1*a*. Time series of the surface irradiance measured during Biowatt 1987 experiment (for Julian days 73, 109, and 110). These data were collected on a WHOI meteorological buoy and are 7.5-min averages.

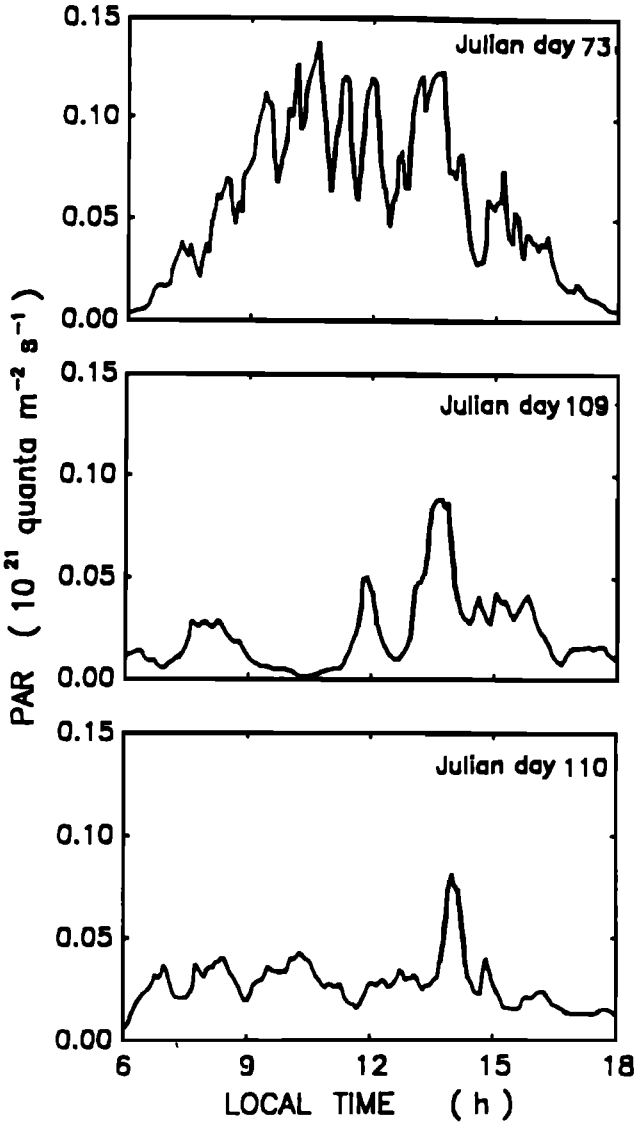

Fig. 1*b*. Time series of PAR, collected at 23.25 m depth.

spectra ($M = 0.1\,N$), but this higher lag number increased the frequency resolution of our analysis. Test calculations with gradually increasing M indicated that the spectra changed smoothly at $M \leq 35$, so the maximum time lag of 35 is acceptable.

RESULTS

Time series of shortwave insolation during 3 days when the sky was partly cloudly are shown in Figure 1*a*. The different patterns in these records apparently reflect differences in magnitude and type of cloudiness. The largest fluctuations in insolation are observed on Julian day 73 and are presumably related to the passage of cumuliform clouds. We note that all major features of light variations above the sea surface as shown in Figure 1*a* were also present in time series records of PAR taken simultaneously at a depth of 23.25 m (Figure 1*b*). This indicates that the observed variations in underwater irradiance were associated with changes in atmospheric conditions. Figure 2 shows an example of concurrent time series of the scalar irradiance, beam attenuation (c), stimulated fluorescence (Fluo), dissolved oxygen (O_2), and water temperature (T). These data series were collected on Julian day 73. From the visual inspection of time series it is difficult to decide if there were any resonant high-frequency components in the series, because they account for only a small part of total variance. To assess the high-frequency properties, we needed to separate different components, and for that purpose spectral analysis was used.

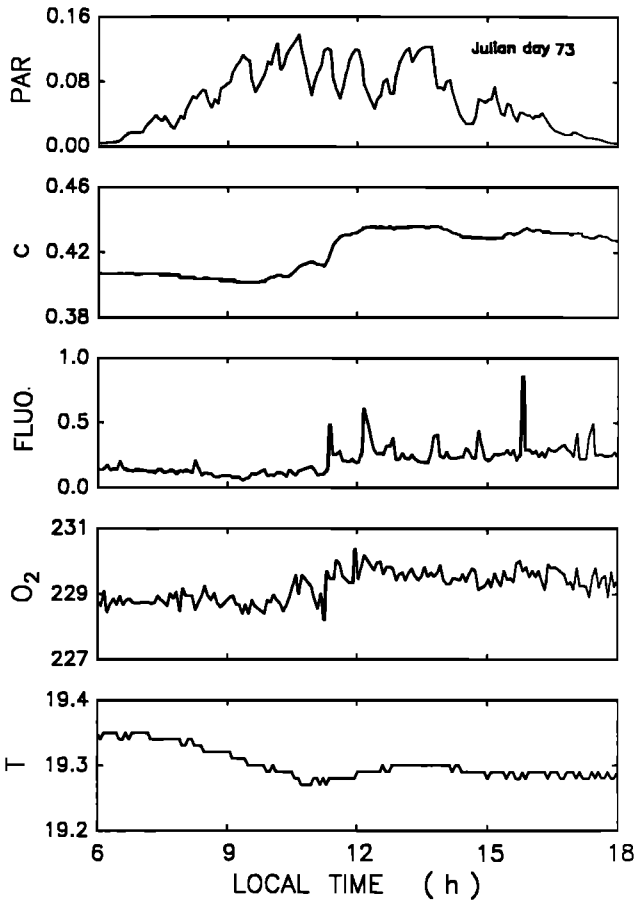

Fig. 2. Time series of PAR, c, stimulated fluorescence, dissolved oxygen and water temperature at 23.25 m for Julian day 73.See Table 1 for explanations and units.

The power spectra of PAR records exhibit a distinct maximum which suggests that the major contribution to fluctuations is concentrated within a more or less broad band of frequencies (Figure 3). On different days the maxima are located at different frequencies. While the dominant oscillations on Julian day 73 have periods of about 40 min, twofold longer periods are most significant on Julian day 109. The longer periods are presumably related to less patchy or more stratiform type clouds.

Figure 4 summarizes the cross-spectral analysis between PAR on the one hand, and the beam attenuation (c), chlorophyll a fluorescence (Fluo), and dissolved oxygen (O_2) on the other hand, on Julian day 73. Figure 4*a* shows the squared coherence functions (solid line) with 90% confidence intervals (dashed line) and cutoff value (dotted), calculated as described, for example, by *Bendat and Piersol* [1969] and *Bloomfield* [1976].

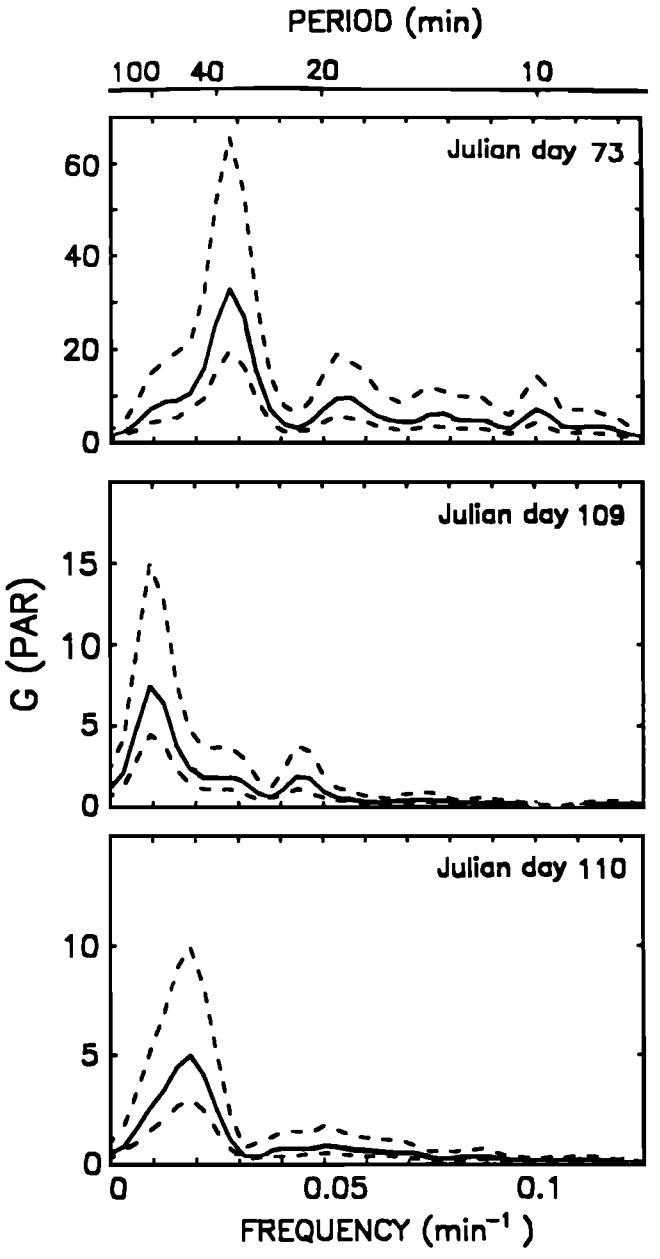

Fig. 3. Power spectral density of PAR (solid line), calculated for time series shown in Figure 1*b*. Dashed lines indicate 90% confidence intervals. See text for details.

The confidence intervals can be used only if the coherence function is greater then the cutoff value (significantly different from 0). One can see that the coherence function between PAR and the bio-physical variables peaks at frequencies around 0.025 min^{-1} assuming values of about 0.6 (Figure 4*a*). In the same band, the power spectrum of PAR has a maximum (see Figure 3, top panel). The negative values of phase (Figure 4*b*) indicate that the PAR signal leads all other variables. The phase spectra vary smoothly within this frequency band, which is usually indicative of good correlation between two random variables. This supports a conjecture that the variations in beam attenuation, fluorescence and dissolved oxygen are correlated with PAR. To a first approximation, one can interpret our problem as a single input - single output physical system where PAR is the input and *c*, Fluo, and O_2 are the outputs. It appears that all three output signals respond to the variability of PAR dominated by 40-min oscillations. We note that for the ideal case of a linear system, the coherence function would be unity. Our realistic systems have the coherence less than unity which can result from the nonlinear response of the output signals to PAR or the presence of other inputs that contribute to the outputs.

Another example (Julian day 110) which supports the hypothesis that the bio-optical properties in the upper layers of the ocean may respond to the cloud-induced fluctuations in PAR is shown in Figure 5. In this case the magnitude of PAR

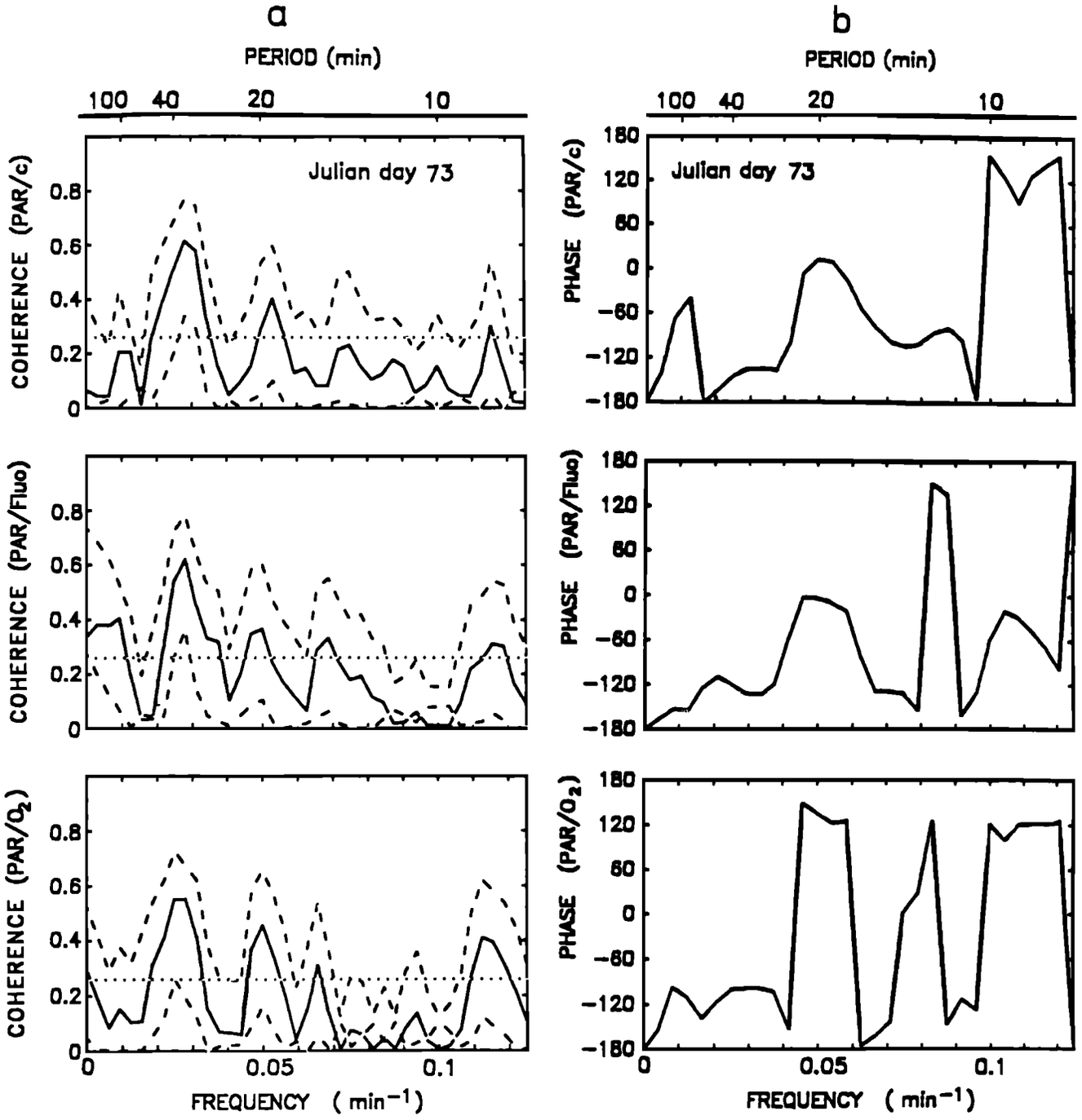

Fig. 4. (*a*) Squared coherence and (*b*) phase functions estimated for day 73 of the year. Dashed lines are 90% confidence intervals; dotted lines, coherence cutoff value.

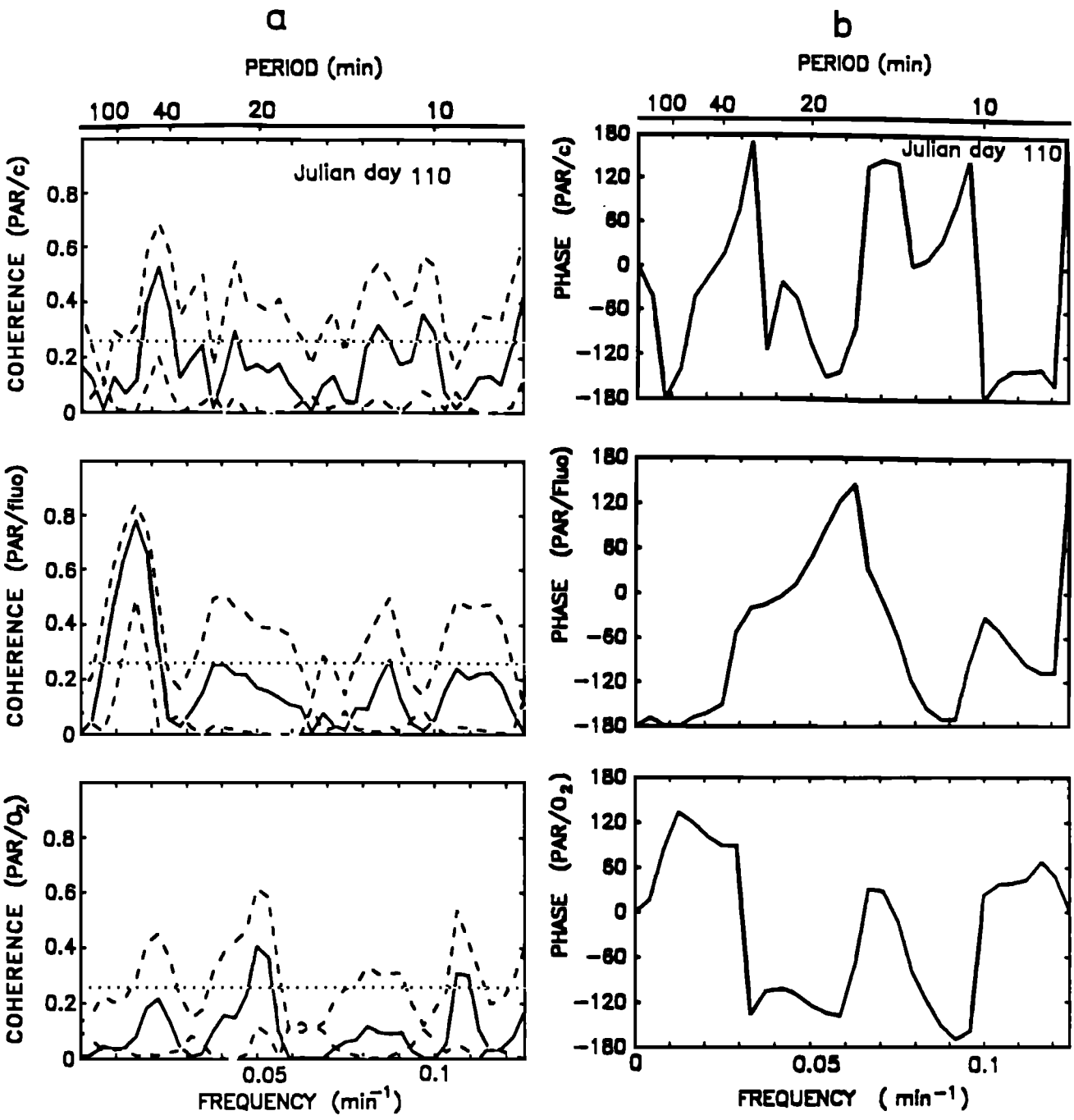

Fig. 5. As Figure 4, but for day 110.

fluctuations (see bottom panel of Figure 1*b*) is not as large as on the previous example, and the dominant oscillations are characterized by somewhat longer periods (about 50 min). We observe that while the coherence between PAR and fluorescence is very high (~0.8), there is no significant relationship between PAR and oxygen signals at ≈0.02 cpm (Figure 5*a*). PAR and beam attenuation still show a quite significant coherence of about 0.5.

In contrast to Julian days 73 and 110, no consistent pattern emerges from the analysis of data collected on Julian day 109 (Figure 6). The coherence values are very low, which indicates that none of the variables in question responds clearly to the PAR fluctuations.

As mentioned previously one of the possible explanations for the coherence values much less than unity is the contribution of inputs other than PAR to the signals of c, Fluo, or O_2. We tested the possibility that dynamical processes of water motion are responsible for the lack of coherence on Julian day 109. The water temperature was assumed to be a passive tracer of water mass. In Figure 7 (middle panel) there is a very high coherence extending to 0.9 between the water temperature and beam attenuation signals. This indicates that the water movements rather than light fluctuations could have had a dominant effect on the observed variability of bio-optical properties and dissolved oxygen on that date. In contrast, this is not the case on Julian days 73 and 110. No significant

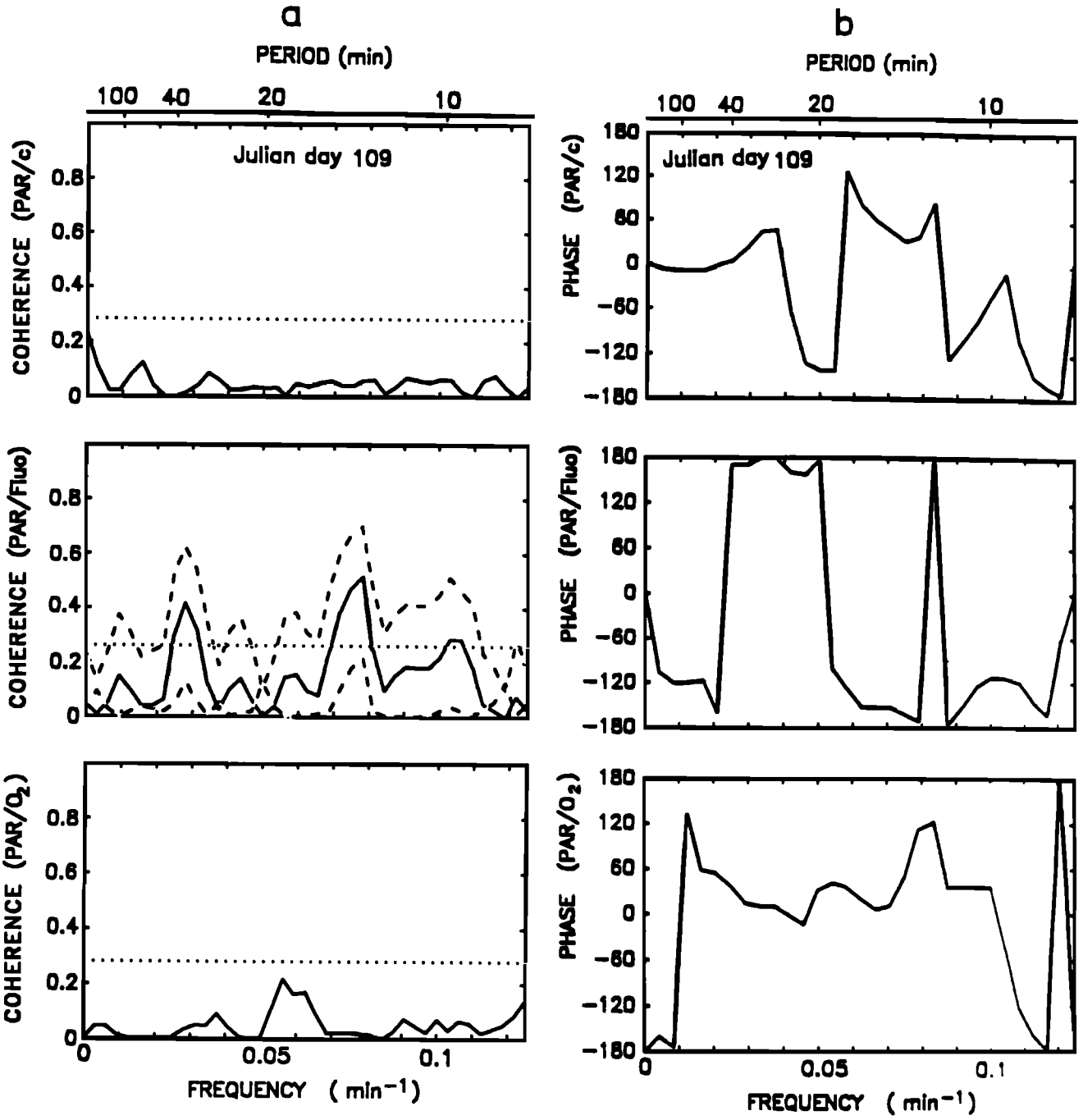

Fig. 6. As Figure 4, but for day 109.

coherence between water temperature and beam attenuation is observed for these dates and frequency bands considered earlier (Figure 7, top and bottom panels) which again supports our conclusion that irradiance fluctuations played a dominant role in stimulating bio-optical responses.

DISCUSSION

As yet, a detailed interpretation of our results is hindered by limited understanding of a mechanistic basis which controls the bio-optical variability on the considered time scales. Numerous studies in the past [*Falkowski*, 1984, and references therein] demonstrated that light-shade adaptive changes in phytoplankton cellular components or processes in response to variations in irradiance occur on time scales of a few hours to a few days. These scales are generally significantly longer than those associated with cloud-induced variability in natural irradiance. The first-order rate constants describing the kinetics of light-shade adaptation in phytoplankton exposed to transitions from low to high (L-H) or from high to low (H-L) irradiance range from about 10^{-2} to 6×10^{-2} h^{-1} [*Falkowski*, 1980, 1984]. This indicates that the final physiological steady state is established within tens of hours following the change in irradiance. It is unknown to what extent, if any, the kinetics of this relatively slow transition process between the two physiological states influences our observations of in situ variability of Chl *a* fluorescence, beam attenuation and oxygen

in response to the L-H and H-L changes in irradiance due to passage of clouds.

It is also known that algae have evolved mechanisms of fast response to light changes on time scales from tens of seconds to a few minutes [e.g., *Bannister and Rice*, 1968; *Bonaventura and Myers*, 1969; *Harris*, 1980; *Vincent*, 1979]. Specifically, a sudden exposure of cells to bright light causes the fluorescence induction change, the initial phase of which lasts for a few seconds and is characterized by a distinct peak. This peak is then followed by a decline which requires minutes for completion. These induction changes are attributed to the redox state of the primary acceptor of photosystem II, redistribution of absorbed energy between two photosystems, and regulation of electron transport, as well as changes in chloroplasts. Complementary response in photosynthetic oxygen evolution was shown to accompany these rapid fluorescence changes. Such simultaneous variations are expected because photosynthesis and fluorescence can be viewed as processes competing for the absorbed energy.

Changes in cellular fluorescence over slightly longer time intervals were investigated by *Kiefer* [1973]. He identified two components of fluorescence decay after exposure to intense light. A fast component, involving chloroplast contraction, occurred within 2 min, and a slow component required 30 to 60 min for completion. Fluorescence decay in this second phase was related to increase in chloroplast aggregation, and was accompanied by a decrease in cellular absorption.

Our data from the Sargasso Sea, specifically those collected on Julian days 73 and 110, support the fact that in situ phytoplankton are capable of responding rapidly to changing irradiance. The fastest induction phenomena cannot be resolved in our time series data because the sampling interval was 4 min. The statistical properties of fluorescence fluctuations are, however, likely related to slower components of the induction effects described by *Kiefer* [1973]. We observed that the magnitude of fluorescence can change as much as fivefold within 20 min. Such a change in fluorescence would hypothetically be equivalent to a change in chlorophyll *a* concentration of about 0.4 mg m^{-3}. It appears, however, that the concentration of chlorophyll *a* is not responsible for the observed short-term variability in fluorescence. This is because physiological changes in cellular pigment content seem to take at least several hours [*Falkowski*, 1984]. Our observations likely reflect short-term in situ variations in absorption capability per unit pigment concentration and/or fluorescence yield, that is the ratio of quanta emitted by fluorescence to quanta absorbed [*Falkowski and Kiefer*, 1985]. Similar variability in natural phytoplankton fluorescence interpreted in terms of induction phenomena has been observed in lakes [*Vincent*, 1979; *Abbott et al.*, 1982].

The concentration of dissolved oxygen in the Sargasso Sea on cloudy and variable days also exhibited rapid changes, reaching as much as 0.8% within 20 min. Much smaller changes on the same time scale, usually less than 0.05%, were observed on sunny days with no significant influence of dynamical processes. The short-term changes in O_2 concentration are apparently related to changes in photosynthetic rate. We estimated that there is relatively high coherence (> 0.5) between oxygen and fluorescence signals on time scales of 10 to 50 min for Julian day 73, which indicates that both processes are coupled through physiological responses of the phytoplankton population. Photosynthetic oxygen evolution in phytoplankton cultures was previously

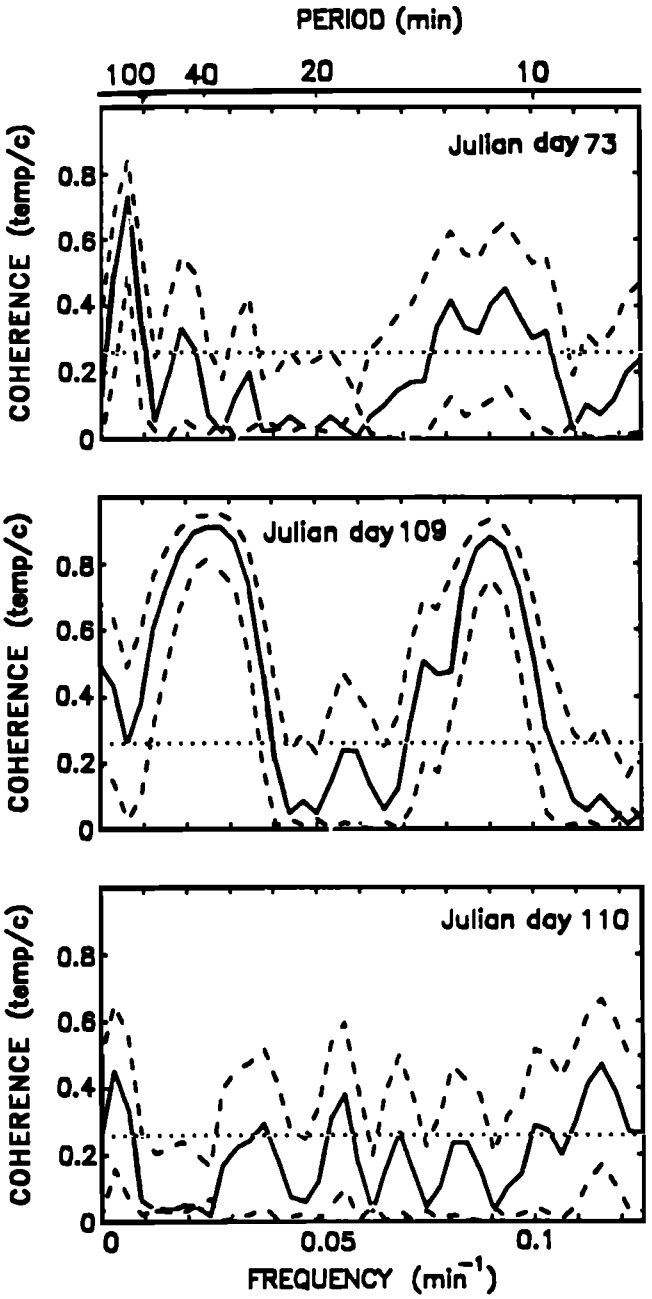

Fig. 7. Coherence function between beam *c* and water temperature *T* for days 73, 109, and 110.

shown to track changes in natural light due to cloud cover, and this was suggested to be associated with noncyclic photosynthetic electron transport [*Marra and Heinemann*, 1982].

The beam attenuation coefficient, c, is an additive bulk property representing absorption and scattering by pure seawater itself, particulate matter, and dissolved substances. The variability in *c* at 660 nm in the open ocean is generally thought to be associated with suspended particle concentration [*Baker and Lavelle*, 1984; *Bishop*, 1986; *Spinrad et al.*, 1989; *Siegel et al.*, 1989]. Diurnal variation in *c* was suggested to reflect the cycle in photosynthetic production of phytoplankton and their losses through microzooplankton grazing [*Siegel et al.*, 1989]. For the present case on time scales of tens of minutes, however, no significant changes in particle

abundance are expected if one excludes the possibility of hydrodynamical effects. The rapid variations of the beam attenuation observed in this work on Julian days 73 and 110 might have been caused by corresponding changes in phytoplankton physiology. The composite value of the attenuation coefficient due to entire phytoplankton population can be expressed using the relationship between the bulk optical properties and individual particle properties [e.g., *Bricaud et al.*, 1981; *Morel and Bricaud*, 1986]:

$$c(\lambda) = \int_{D_{min}}^{D_{max}} Q_C(\lambda,m,D)\, G(D)\, N(D)\, dD$$

where D is the cell size, D_{max} and D_{min} are the limits of the optically significant sizes, Q_C is the attenuation efficiency factor of a single cell (which for a fixed light wavelength λ is a function of refractive index of cell, m, and cell size D), $G(D)$ is the projected area of the cell having size D, and $N(D)dD$ is the number of cells per unit volume in the size range $(D, D+dD)$. This equation indicates that the beam attenuation can change due to variations in cell refractive index and size even though the total concentration of cells remains constant.

Recently, laboratory studies with cultures have shown that living cells respond on time scales of minutes to hours to changes in the light environment by varying their sizes and refractive indices [*Ackleson et al.*, 1990]. Generally, cell swelling accompanied by a decrease in the real part of refractive index characterized the phytoplankton response to increased light intensity. These changes were evident within the first hour following the change of irradiance, and a reciprocal pattern was also observed. *Ackleson et al.* [1990, p. 248] concluded that "the interpretation of bulk optical properties, such as c, must extend beyond particle concentration to include cell refractive index and size." Our mooring data collected on cloudy and variable days provide perhaps the first in situ evidence supporting the above conclusion. The amplitude of variations of the beam attenuation was usually < 0.003 m^{-1} over 30-min intervals. This is significantly less than that reported previously for diurnal variations in the North Pacific Ocean (0.01 m^{-1} [*Siegel et al.*, 1989]). Our relative variation over 30 min ($\Delta c/c \approx 0.007$) is, however, similar to the lower limit estimated from *Ackleson et al.* [1990], which is favorable agreement because laboratory experiments can exaggerate the natural responses. Except for the effects of varying size and real part of the refractive index, a rapid change in absorption associated with intracellular pigment packaging [*Kiefer*, 1973] is another potential source for the observed variability of the beam attenuation.

A better understanding of the short-term variability of the bio-optical properties in the upper ocean and its potential significance needs further, specially designed experiments, which can now be accomplished with mooring systems. Presently we are doing MVMS measurements with sampling at 1-min intervals. The results discussed in this paper suggest that the separation of hydrodynamical effects, which were traced by water temperature, is of critical importance when studying bio-optical responses to within-day variations in natural light regime.

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