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Chlorophyll natural fluorescence response to upwelling events in the Southern Ocean

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Abstract. Variability of solar-induced (natural) fluorescence and chlorophyll were measured on scales of hours to weeks in the upper layer of a cyclonic eddy located south of the Antarctic Polar Front using a free-floating drifter. The fluorescence signal was analyzed both in terms of chlorophyll concentration and as an indicator of energy distribution in the photosynthetic apparatus. Long-term trends in fluorescence parallel changes in chlorophyll concentration. Considering a significant positive correlation between fluorescence and the relative depth of the eddy upper layer we hypothesize that the observed short-term variations in natural fluorescence are a physiological response of phytoplankton to changes in the supply of limiting nutrients. This interpretation is consistent with the Southern Ocean iron limitation hypothesis.

Introduction

One of the major challenges in the study of carbon fluxes in global marine ecosystems is the estimation of photoautotrophic production. Large areas of the ocean are undersampled, and both spatial and temporal scales of variability are poorly resolved. Between 1979 and 1986, the Nimbus-7 Coastal Zone Color Scanner (CZCS) provided the first satellite data from which global patterns of chlorophyll in the surface of the ocean could be determined [*Gordon et al.*, 1983]. Because these maps were based on the scattering and absorption properties of pigments, they provided an avenue to estimate the amount of light harvested by phytoplankton and proved to be valuable tools in the attempt to develop empirical and mechanistic optical models of ocean primary production [*Perry, 1986*; *Morel and Brethon*, 1989]. However, only a fraction of the energy absorbed by the photosynthetic apparatus, termed the photosynthesis quantum yield (Φ_p), is used in photosynthesis [*Butler*, 1978]. The remaining absorbed energy is released in the form of fluorescence (mostly at 683 nm) and heat. The Φ_p varies with changes in nutrient availability, light intensity and phytoplankton species composition [*Falkowski and Kolber*, 1995]. For this reason estimation of the variability of Φ_p is required to calculate primary productivity using optical models and sea-surface chlorophyll maps.

Three new satellites, scheduled for deployment by NASA (National Aeronautics and Space Administration), NASDA (National Development Agency of Japan), and ESA (European Space Agency) between 1998 and 2000, will have the capability for measuring chlorophyll concentrations in the surface of the ocean as well as chlorophyll natural fluorescence. Apart from solar irradiance, the main source of energy measured at 683 nm in the ocean is chlorophyll [*Gordon*, 1979]. The variation in fluorescence quantum yield (Φ_f), the fraction of absorbed energy emitted as chlorophyll fluorescence during photosynthesis, is a manifestation of changes in the energy distribution within the photosynthetic system [*Krause and Weis*, 1991]. Butler's tripartite model [*Butler*, 1978] of the photochemical apparatus predicts an inverse relationship between Φ_p and Φ_f.

Biological oceanographers have used natural fluorescence to map chlorophyll concentrations by assuming that changes in Φ_f are negligible [*Neville and Gower*, 1977], and to estimate the fraction of absorbed solar energy channeled into photosynthesis by assuming a predictable relation between Φ_f and Φ_p [*Chamberlin et al.*, 1990]. However, the inverse relation between Φ_f and Φ_p is not always straightforward. A third energy path for the de-excitation of chlorophyll is heat dissipation. Under light-saturated conditions, variations in Φ_f can result from changes in photoprotective pigments and heat dissipation (Φ_h), rather than by changes in Φ_p [*Oliazola et al.*, 1994]. A thorough understanding of the physiological basis of Φ_f fluctuations and how they relate to changes in the physical and chemical environment is a necessary pre-requisite for the accurate interpretation of remotely sensed natural fluorescence data.

Data Acquisition

Free-floating optical drifters provide an opportunity to measure variations in natural fluorescence in the surface layer of the ocean [*Abbott et al.*, 1995] and to relate these variations to changes in biological properties that can also be derived from in situ bio-optical measurements [*Smith et al.*, 1991]. Furthermore, by measuring changes within a water mass, temporal variability may be isolated from horizontal variability [*Niiler et al.*, 1987]. However, temporal variability attributed to bio-optical fluctuations observed in this manner also includes the variability resulting from the vertical movements of the water column [*Abbott et al.*, 1995].

During the 1994-1995 austral summer, and as part of the Palmer-Long Term Ecological Research program (Palmer-LTER, [*Smith et al.*, 1995]), we deployed a METOCEAN Data Systems optical drifter in the southern region of the Drake Passage (62°00'S 62°16'W, Fig 1A). The drifter was equipped with a 7-channel upwelling radiance sensor (412, 443, 490, 510, 555, 670 and 683 nm), a one channel downwelling irradiance sensor (490 nm), temperature and hydrostatic pressure probes. The underwater sensors and probes were located at a depth of approximately 0.3 m. A drogue, centered at 15 m depth, allowed

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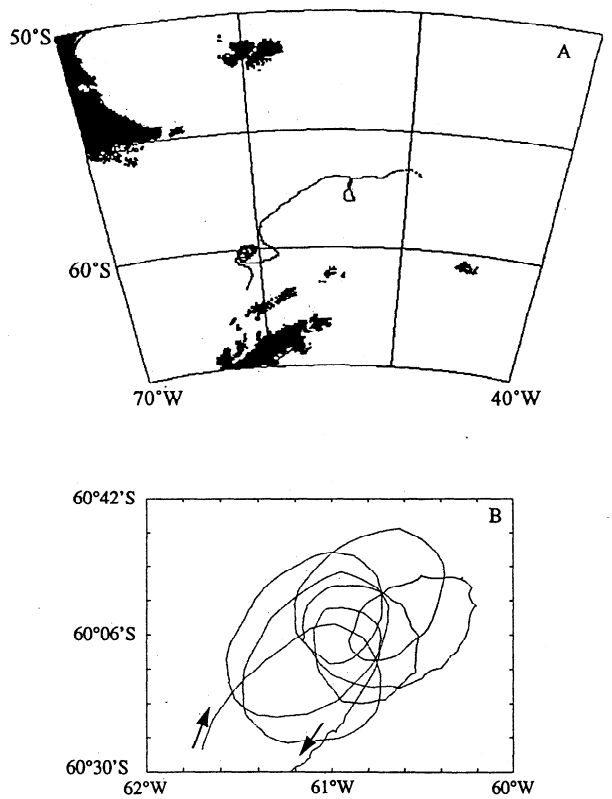


Figure 1. [A] Map displaying the trajectory of the optical drifter. [B] Detail of the trajectory associated with the cyclonic eddy.

the drifter to follow a specific water mass. Data were collected at 90 second intervals. Hourly mean and standard deviation values were transmitted via satellite (Service ARGOS) along with the geographical position of the drifter.

The concentration of chlorophyll (chl) surrounding the drifter was estimated using the ratio between upwelling radiance at 443 and 555 nm [*Clark*, 1981]. Calibration parameters for this ratio were calculated based on samples collected in the study area. Shipboard measurements of upwelling radiance obtained using a Tethered SpectroRadiometer Buoy (TSRB, Satlantic Inc.), which had the same optical resolution characteristics as those of the drifter, where compared to discrete sea surface concentration of chl measured by fluorometry [*Strickland and Parsons*, 1972]. Chlorophyll natural fluorescence was measured at 683 nm and corrected for backscatter by subtracting the upwelling radiance at 670 nm.

Fluorescence quantum yield (Φ_f) is a function of the solar energy absorbed by the photosynthetic apparatus and cannot be estimated directly from the drifter data. However, because our bio-optical estimates of the chlorophyll concentration are derived from the absorption properties of phytoplankton, changes in the amount of fluorescence per unit estimated chlorophyll and per unit downwelling sea-surface irradiance at 490 nm (Ed490) are proportional to changes in Φ_f. In our analysis we have defined an apparent fluorescence quantum yield (Φ_f(Ed490)) as the slope of the regression of fluorescence per unit chlorophyll versus Ed490. The slope was calculated from the data collected over sampling periods averaging 48 hours (Fig. 2). For this reason the effect of diurnal photoadaptative processes in the variability of Φ_f cannot be extracted from Φ_f(Ed490).

Variations in the vertical velocity of the water column were estimated from the conservation of potential vorticity equation [*Flierl*, 1979], and the drifter's measured horizontal displacement velocities. Calculations of vertical velocities using the conservation of mass equation [*Pond and Pickard*, 1978] provided a similar pattern of upwelling and downwelling events.

Results

Approximately one week after deployment, the drifter was trapped within a cyclonic eddy centered at approximately (60°10'S, 61°00'W). It remained in the eddy for the next 50 days describing a circular trajectory with an average radius of 19 km (Fig. 1B). During this period we observed regular short-term (days) oscillations in the fluorescence signal, Φ_f(Ed490), and in the relative depth of the eddy's upper layer (h ho^{-1}, Fig. 3) [*Flierl*, 1979]. Neither the temperature data, chlorophyll concentrations nor downwelling irradiance measured at 490 nm provide any evidence of short-term fluctuations of the magnitude and frequency necessary to explain the observed fluorescence oscillations. A long-term increasing trend observed in the natural fluorescence was also evident in the chlorophyll signal (Fig. 3).

Interpretation and Discussion

There are several potential explanations for the positive correlation between Φ_f(Ed490) and h ho^{-1} ($\alpha < 0.001$, maximum cross correlation = 0.472 and standard error = 0.045 when Φ_f(Ed490) lags 0.87 days) if we acknowledge that Φ_f can vary in response to changes in mixed-layer light regime, nutrient availability and the taxonomic composition of the phytoplankton population. Alterations in the mixed-layer light regime may trigger changes in the per cell concentration of photosynthetic pigments or in the ratio of accessory photosynthetic pigments to chl *a* (Prézelin, 1981). These changes could modify the absorption of radiation at 443 nm in the upper water column and affect our estimation of chl *a*. Changing the mixed-layer light regime may also induce photoinhibition and photoprotection of the photosystem [*Falkowski and Kolber*, 1995]. However, the lack of a strong negative correlation between Ed490 and Φ_f(Ed490) (Fig. 3) suggests that the short-term variability observed in Φ_f(Ed490) may be caused by other factors.

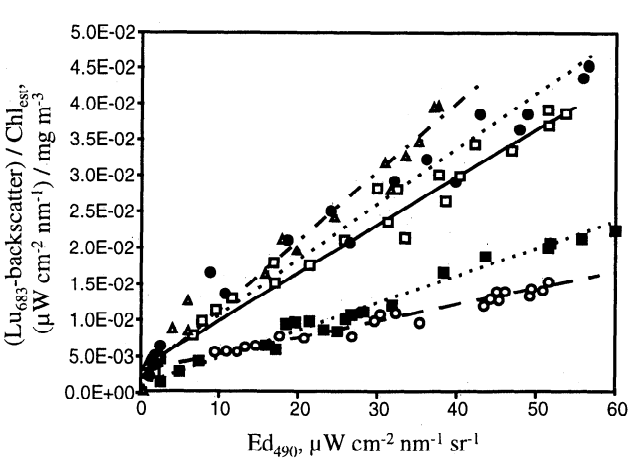


Figure 2. Natural fluorescence per unit chlorophyll plotted versus sea-surface solar irradiance measured at 490 nm (Ed490). Regression slopes (Φ_f(Ed490), see figure 3C for values) were calculated based on data collected over 48 hours intervals (open circle: January 17-18; open squares: Jan 23-24; closed squares: Jan 28-29; closed circles: Feb. 11-12; open triangles: Feb 19-20).

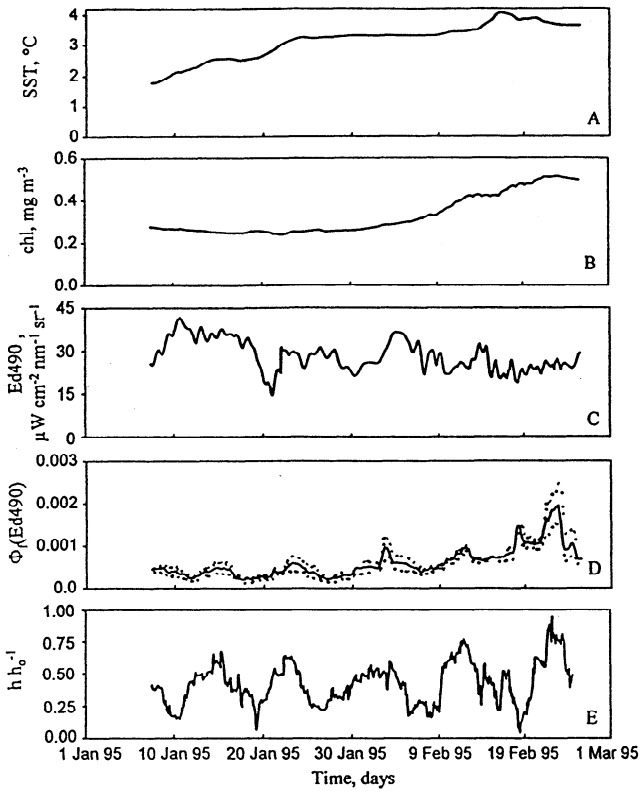


Figure 3. Temporal variability of [A] sea surface temperature, [B] chlorophyll concentration, [C] Ed490, [D] Φ_f(Ed490), and [E] relative depth of the upper layer of the water column sampled by the drifter within the cyclonic eddy. Dotted lines in panel C show the 95% confidence interval of Φ_f(Ed490).

It is not possible with the data available to eliminate completely the possibility that the fluctuations observed in Φ_f are the result of changes in phytoplankton community structure. However, if we consider that the drifter is following a specific mixed-layer water mass, with a net slippage relative to the water mass of less than 1 km d^{-1} [*Niiler et al.*, 1987], then the Φ_f signal pattern would imply that the ecosystem sampled has two distinct communities with spatial distribution of approximately 5 km. These communities would be associated not only with different regions of the eddy but also with a different upper water layer depth (h ho^{-1}). However, the lag period of 1 day between Φ_f and h ho^{-1} and the relative constancy in the chlorophyll concentration argue against this interpretation.

We hypothesize that the observed patterns in Φ_f are a result of nutrient-induced changes in the distribution of energy in the photochemical apparatus. Decreases and increases in h ho^{-1} are correlated, respectively, with positive and negative water column vertical velocities as derived from the mass balance equation. These oscillations are an indication of upwelling events. The lack of a temperature signal in these events is the result of the relatively small vertical thermal gradient in the surface waters of the Southern Ocean compared to the resolution of the thermistor in the optical buoy (0.16°C).

The Southern Ocean is considered to be a region with high inorganic nutrient concentrations and low phytoplankton biomass [El-Sayed, 1987]. Evidence suggests [*Martin et al.*, 1990] that phytoplankton productivity is iron-limited in the Drake Passage (60°46'S, 63°26'W). In this calculation it was assumed that the upwelling rate was 0.25 m d^{-1} and therefore the iron input into the euphotic zone from these upwelling processes could sustain a phytoplankton new production rate of at most 3 mmol C m^{-2} d^{-1}[*Martin et al.*, 1990]. Maximum upwelling rates (positive vertical velocities) derived from the drifter trajectory within the eddy range between 20-60 m d^{-1}, assuming a constant divergence in a homogeneous surface layer 30 m deep. These rates are two orders of magnitude greater than those used by Martin et al., a result that is consistent with upwelling rates previously observed in small meanders along fronts [*Pollard and Regier*, 1992]. According to our observations and interpretations, nutrient stress may be significantly relaxed in the upper euphotic zone during eddy induced upwelling events. Under these conditions, a larger fraction of the energy captured by the photosynthetic apparatus could be directed towards photochemistry decreasing the amount of energy released in the form of heat and fluorescence [*Kiefer and Reynolds*, 1992; *Behrenfeld et al.*, 1996]. When upwelling relaxes, the decrease in nutrient flux would reverse the trend, decreasing phytoplankton photosynthesis, and increasing the release of energy as heat and fluorescence. Because cyclonic eddies appear to be common features associated with the Polar Front in the Drake Passage [*Hofmann and Whitworth III*, 1985], they may represent an important, although erratic, source of iron upwelling in this region of the world ocean.

Recent field studies provided additional support to the hypothesis that iron injections stimulates phytoplankton growth rates in surface waters of the Drake Passage south of the Polar Front [*Buma et al.*, 1991; *de Baar et al.*, 1995] and in other pelagic environments with high nutrient and low chlorophyll concentrations [*Behrenfeld et al.*, 1996]. Furthermore, Geider and co-workers [*Geider et al.*, 1993] have shown that iron limitation strongly enhances chlorophyll fluorescence in the diatom *Phaeodactylum tricornutum* and that the physiological response to iron limitation as well as iron addition is manifested in a matter of hours. The implied short-term increase in Φ_p in natural assemblages resulting from iron injection has been observed during two large-scale iron enrichment experiments conducted in the eastern equatorial Pacific [*van Scoy and Coale*, 1994; *Behrenfeld et al.*, 1996].

Conclusions

Considering the above observations, we hypothesize that nutrient inputs into the upper euphotic zone as a result of upwelling events may be responsible for the decreases in Φ_f(Ed490) detected in our field experiment (Fig. 3). If this interpretation is correct, our observation would suggest that nutrient availability is not only limiting the carrying capacity of the system but also algal photosynthesis [*Falkowski et al.*, 1992]. Because the inherent time-scales for changes in algal biomass and physiological responses are in the order of days and hours, respectively, the study of the temporal variability of natural fluorescence in conjunction with chlorophyll concentrations may prove valuable when trying to understand nutrient limitation of phytoplankton productivity. Being able to measure the spatial and temporal variability in Φ_f may help to define scales of variability for the photosynthesis quantum yield.

Our results have two important consequences for the interpretation of remotely sensed chlorophyll natural fluorescence. First, when changes in chlorophyll concentrations are of the same order of magnitude as changes in the fluorescence quantum yield, natural fluorescence cannot be used to estimate chlorophyll concentration (Fig. 3). Spatial and temporal scales are critical in this analysis because variations in natural fluorescence are driven by short-term physiological responses as

well as long term-changes in phytoplankton pigment biomass. Second, the variation in Φ_f may prove to be a useful indicator of changes in the nutritional status of phytoplankton. To date, the only remote sensing evidence for nutrient injections into the upper euphotic zone remains the increase in surface chlorophyll concentration and the decrease in sea surface temperature [*Dugdale et al.*, 1989]. However, in ecosystems where an increase in photoautotrophic production is transferred directly to higher trophic levels, an increase in phytoplankton biomass will not occur. Furthermore, in high latitude pelagic environments where water column stratification is mainly controlled by salinity rather than temperature, upwelling events may not display a strong sea surface temperature signature. Although it is still not apparent how the absolute magnitude of the fluorescence quantum yield per se in light saturated environments can be translated into Φ_p, relative changes in Φ_f in nutrient-limited environments may provide a mechanism to monitor the relaxation of nutrient limitation as a result of deep mixing, upwelling or atmospheric dust deposition events. However, in situ experiments including the measurement of natural fluorescence, photosynthesis, and nutrient availability will be required before we can unambiguously attribute temporal changes in Φ_f to changes in nutrient availability.

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