

## Relationship between the maximum quantum yield of carbon fixation and the minimum quantum yield of chlorophyll *a* in vivo fluorescence in the Gulf of St. Lawrence

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### Abstract

Intensive monitoring of the maximum quantum yield of carbon fixation ( $\phi_{\max}$ ) and of the minimum quantum yield of chlorophyll *a* in vivo fluorescence ( $\phi_{F_0}$ ) was followed along the path of drifting buoys in the estuary and the Gulf of St. Lawrence, Canada. Samples were collected every third hour during two 24-h periods. Over the 170 measurements,  $\phi_{\max}$  varied by a factor of 20 [from 0.004 to 0.08 mol C (mol quanta)<sup>-1</sup>]. As predicted by a model of primary processes in photosystem 2, a significant and positive linear relationship was observed between  $\phi_{\max}$  and  $\phi_{F_0}$ . In the estuary, the covariability of  $\phi_{\max}$  and  $\phi_{F_0}$  seems to be driven by light, because it was observed only during daytime and was characterized by a parallel increase of  $\phi_{\max}$  and  $\phi_{F_0}$  with depth. Examination of the spectral values of  $\phi_{F_0}$  suggests a contribution of photoprotectant carotenoids. In the gulf, because a parallel, although weaker, increase of  $\phi_{\max}$  and  $\phi_{F_0}$  with depth also persisted during nighttime, nutrient deficiency is probably an additional cause of covariation between  $\phi_{\max}$  and  $\phi_{F_0}$ . In both regions, an overall diel cycle was observed for  $\phi_{\max}$  with a maximum at around noon;  $\phi_{F_0}$  did not show a clear diel periodicity. Despite the vertical covariability of  $\phi_{\max}$  and  $\phi_{F_0}$ , the diel cycle of  $\phi_{\max}$  was uncoupled to  $\phi_{F_0}$  and thus to photosystem 2 activity. These results suggest a significant diel variation in the photosynthetic quotient of natural phytoplankton.

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During the last decade, the estimation of marine primary production from remotely sensed data has become a major objective in biological and biogeochemical oceanography. Recent efforts to improve the predictive capacity of models for this task have centered on understanding the natural variability of photosynthetic parameters, namely the maximum rate of carbon fixation ( $P_{\max}^B$ ) and the coefficient of photosynthetic efficiency ( $\alpha^B$ ). In that context, attempts have been made to relate  $P_{\max}^B$  to environmental variables, such as temperature (Balch et al. 1989). Variations in  $\alpha^B$ , on the other hand, have mostly been examined through studies conducted on its two components, i.e. the chlorophyll-specific in vivo absorption coefficient [ $a^*(\lambda)$ ] and the maximum quantum yield of carbon fixation ( $\phi_{\max}$ ). Laboratory experiments have demonstrated that [ $a^*(\lambda)$ ] is highly variable within and among species (see Prézélin and Boczar 1986). Extensive field studies have also quantified this variability for natural communities (see Bricaud et al. 1995). On the other

hand, it is not easy to perform extensive measurements of  $\phi_{\max}$  at sea. The traditional radiocarbon assimilation method is time-consuming and always involves complex handling of samples and long incubation periods, which result in experimental errors. Because of these difficulties, little is known about the extent and the nature of the natural variability of  $\phi_{\max}$ .

Laboratory experiments suggest that the two main factors influencing  $\phi_{\max}$  at sea are exposure to excess light and nutrient deficiency. Excess light induces photoinhibition by inactivating a fraction of the reaction centers (photodamage; Neale 1987) and by dissipating energy into the antenna photoprotectant pigments (Bidigare et al. 1989; Olaizola and Yamamoto 1994). Nutrient deficiency, which leads to the lack of some reaction center proteins, has an effect like photodamage (Greene et al. 1992). In oceanic conditions, Cleveland et al. (1989) found a relationship between  $\phi_{\max}$  variability (a factor of 3) and the distance above the nitracline.

Alternative methods have been used to provide fast measurements of variables directly linked to  $\phi_{\max}$  at sea. For instance, pump-probe fluorometry allowed Kolber et al. (1990) and Falkowski et al. (1991) to relate the photosynthetic energy conversion efficiency of phytoplankton to nitrate concentration in different regions of the world oceans. However, because this variable characterizes only one of the many primary processes that determine the variations of  $\phi_{\max}$ , it can only explain a fraction of the natural variability of  $\phi_{\max}$ .

The excitation spectrum of *in vivo* chlorophyll *a* fluorescence has been used to obtain spectral information on the light absorption capabilities of phytoplankton (Yentsch and Yentsch 1979; Neori et al. 1984; Mitchell and Kiefer 1988). The spectral ratio of fluorescence to absorption has also been used to obtain the spectral values of the relative quantum yield of fluorescence (Neori et al. 1984). If measured with a source weak enough to maintain all reaction centers open, the minimum quantum yield of fluorescence,  $\phi_{F_0}(\lambda)$  [mol quanta (mol quanta)<sup>-1</sup>], can be obtained. Based on the model for primary processes in photosystem 2 of Schatz et al. (1988), Kiefer and Reynolds (1992) expressed  $\phi_{F_0}$  as

$$\phi_{F_0} = \frac{\psi_{F_0}}{1 - \psi_{cso}\psi_{cro}} \quad (1)$$

$\psi_{F_0}$ ,  $\psi_{cso}$ , and  $\psi_{cro}$  are the "single step" probabilities for fluorescence, charge separation, and charge recombination at the level of photosystem 2. The maximum quantum yield of photochemistry,  $\phi_{P_0}$  [mol e<sup>-</sup> (mol quanta)<sup>-1</sup>], can also be expressed as

$$\phi_{P_0} = \frac{\psi_{cso}\psi_{sto}}{1 - \psi_{cso}\psi_{cro}} \quad (2)$$

$\psi_{sto}$  is the probability for charge stabilization at the level of the acceptor *Q*.  $\phi_{\max}$  is related to  $\phi_{P_0}$  through

$$\phi_{\max} = \phi_{P_0}/PQ \quad (3)$$

PQ [mol e<sup>-</sup>(mol C)<sup>-1</sup>] is the photosynthetic quotient, generally expressed as mol O<sub>2</sub> (mol C)<sup>-1</sup>. Alteration of

photosystem 2 activity is often associated with radiationless dissipation (e.g. Krause and Weis 1991). Because, according to Kiefer and Reynolds (1992), radiationless dissipation equally affects  $\psi_{F_0}$  and  $\psi_{cso}$  (the ratio  $\psi_{F_0}:\psi_{cso}$  remains constant), it can be assumed that  $\phi_{F_0}$  covaries with  $\phi_{\max}$ .

Recent developments have made possible the derivation of the spectral values of the absorption coefficient of natural phytoplankton from total particle absorption measurements on filters (Bricaud and Stramski 1990). Therefore,  $\phi_{F_0}(\lambda)$  can now be easily obtained at sea and used to extensively study the natural variability of  $\phi_{\max}$  in terms of its magnitude and wavelength dependency. Fluorescence measurements have the advantages of being nondestructive and rapid. They are also versatile because they can be extended to *in situ* techniques (Chamberlin et al. 1990; Kolber and Falkowski 1994). Emission spectra can already be measured *in situ* with optic fibers (Cowles et al. 1993).

Our objective was to determine the range of natural variations of  $\phi_{\max}$ . To do this, we present the results of an extensive spatial and temporal monitoring of  $\phi_{\max}$  carried out at sea. Simultaneous measurements of  $\phi_{F_0}(\lambda)$  are used to identify the potential environmental factors inducing  $\phi_{\max}$  variability.

## Materials and methods

Measurements were carried out in the estuary (area 1, 7 July 1990) and the Gulf (area 2, 8 July 1990) of St. Lawrence (Fig. 1). During the 2 weeks preceding and including the sampling days, weak winds always prevailed. On the sampling days, the sky was cloudy for the estuary and partially clear for the gulf. In each area, seawater samples were collected every third hour over a period of 24 h at stations located along the path of a drifting buoy (Fig. 1). A rosette sampler equipped with 6-liter Go-Flo bottles, an Applied Microsystems STD-12, and a Seatech *in situ* fluorometer was used to collect water at 10 depths covering the entire euphotic zone. At each sampling station, vertical profiles of temperature, salinity, and *in vivo* fluorescence of Chl *a* were recorded. For each seawater sample, the measurements included concentrations of Chl *a*, *b*, and *c*, carotenoids and pheopigments, *in vivo* absorbance of total particles, *in vivo* fluorescence excitation spectrum of phytoplankton and derivatives, initial slope of the curves of carbon fixation rate vs. available quanta, and phytoplankton composition (light microscopy). The depth of the euphotic zone (1% surface PAR) was determined with an underwater quantum scalar irradiance sensor (Biospherical, QSP-240) and a deck reference collector.

**Absorption and pigments**—*In vivo* absorbance measurements were performed on 25-mm Whatman GF/F glass-fiber filters after filtration of 0.5–1.75 liters of seawater samples under low vacuum pressure. The filters (sample and blank) were placed on 25 × 25-mm glass cover slips, saturated with filtered seawater, and set in holders near the photomultiplier tube of a Perkin Elmer Lambda-6

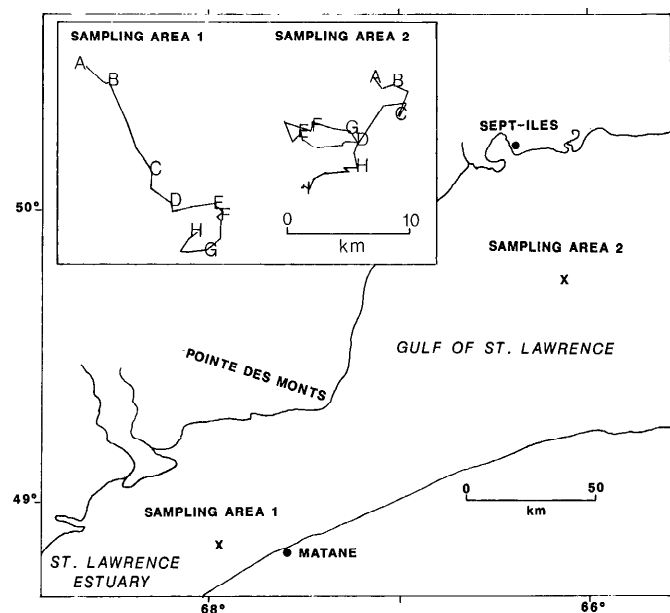


Fig. 1. Location of the two sampling areas in the estuary and the Gulf of St. Lawrence. The location of the sampling stations along the trajectories of drifting buoys shown in insert.

double-beam spectrophotometer. Absorbance was measured between 400 and 700 nm with 1-nm increments and then corrected to account for pathlength amplification related to the use of glass-fiber filters using the algorithm of Bricaud and Stramski (1990). The filters were then immediately immersed in 90% acetone to extract pigments and their concentrations determined spectrophotometrically by the equations of Jeffrey and Humphrey (1975). Previous laboratory tests showed that absorbance measurements do not alter pigment measurements when the sequence is performed within 5 min. The *in vivo* absorption coefficient of phytoplankton [ $a_{ph}(\lambda)$ ] was estimated with the algorithm of Bricaud and Stramski (1990) as modified by Babin et al. (1993). This method assumes that the absorption by nonalgal particles [ $a_d(\lambda)$ ] varies inversely with wavelength according to an exponential function derived from two spectral ratios. The value of  $a_{ph}(\lambda)$  is obtained by subtracting  $a_d(\lambda)$  from the absorption by total particles [ $a_p(\lambda)$ ].

**Fluorescence**—The water samples were collected from two five-bottle casts, and the fluorescence measurements were performed within 15–20 min of collection. For each depth, a 4-liter precleaned and semitransparent glass bottle was filled with seawater. The large volume of the glass bottles prevented significant warming of the samples while their low transparency, combined with the low artificial light of the laboratory, provided a low-light ( $\sim 10 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ) pretreatment. All samples had the same preconditioning, whatever the time of the day and collection depth. For each sample, a quartz cuvette filled with the seawater sample was placed in a LS-50 Perkin Elmer spectrofluorometer, and an excitation scan (emission measured at 685 nm) was performed between 400

and 650 nm, with 0.5-nm increments. The excitation source of the LS-50 was a 9.9-W xenon flash lamp with a half-peak duration of  $\sim 10 \mu\text{s}$ , a flash rate of 60 Hz, and a maximum pulse height of  $115 \text{ W m}^{-2}$ . With such short flashes and low rate, it is most probable that only single turnovers are stimulated because the period between flashes (16.7 ms) is longer than the typical turnover time for carbon fixation (Dubinsky et al. 1986). According to the target theory (see Mauzerall and Greenbaum 1989), as long as the lamp flash does not produce more than one photon per photosystem 2, constant fluorescence ( $F_0$ ) is measured. When an upper limit of  $5 \text{ nm}^2$  is assumed for the effective absorption cross section of photosystem 2 at 440 nm (see Mauzerall and Greenbaum 1989), the maximum irradiance for  $F_0$  measurements is  $\sim 0.3 \mu\text{mol quanta m}^{-2} \text{ flash}^{-1}$ . The xenon lamp used in this study produces flashes of energy equivalent to  $4 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{ flash}^{-1}$  at 440 nm; it can therefore be assumed that we performed true measurements of  $F_0$ .

We performed a relative spectral calibration that used the LS-50 built-in procedure. Such a calibration provides results corrected for the emission spectrum of the xenon lamp (i.e. the lamp spectrum is made flat). Biases caused by variability in the lamp intensity over time and by self-shading of the sample were avoided by monitoring daily the emission of quinone sulfate in 0.1 N perchloric acid.

**Carbon fixation rate**—The quantum yield of carbon fixation was estimated from incubation of subsamples inoculated with  $\text{H}^{14}\text{CO}_3^-$  according to Babin et al. (1994). Each seawater sample was subdivided into ten 50-ml subsamples in tissue culture flasks (Falcon Labware); the flasks were stacked in front of a 250-W arc lamp (Optimarc Super Metal Halide, Duro-Test International Corp.) into incubation chambers that were thermoregulated with flowing water. The irradiance decreased from flask to flask with distance from the lamp, with no significant spectral variations. The flask stacks from each sampling depth were then arranged radially around the arc lamp. Each subsample was inoculated with  $5 \mu\text{Ci}$  of  $\text{H}^{14}\text{CO}_3^-$  and incubated for 60–90 min under constant temperature simulating average *in situ* values. After incubation, the subsamples were filtered onto GF/F glass-fiber filters which were put into scintillation vials, wetted with 0.5 N HCl for 45 min, neutralized with 0.5 N NaOH, and radioassayed by scintillation counting.

The tissue culture flasks have two opposite faces that are optically flat and clear and fit closely to each other. This experimental approach allows incubation under accurately known light conditions, even over a narrow light range, and provides  $P$  vs.  $E_0$  curves with very low scatter. PAR inside the flasks was measured at each position with a laboratory scalar quantum irradiance-meter (Biospherical QSL-100); the irradiance spectrum of the lamp was measured (in relative units) with an underwater spectroradiometer (Focal Technologies OS-1) equipped with a  $4\pi$  collector fixed at the end of a 3-m optic-fiber cable.

**Carbon fixation and fluorescence yields**— $\phi_{\text{max}}$  [ $\text{mol C (mol quanta)}^{-1}$ ] can be expressed as

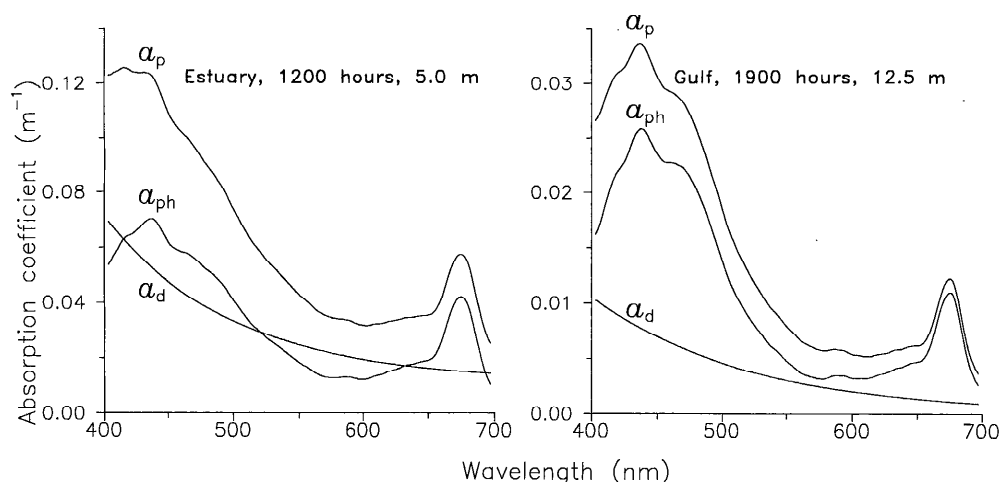


Fig. 2. Typical examples of the decomposition of total particle spectra ( $\alpha_p$ ) into phytoplankton ( $\alpha_{ph}$ ) and nonliving particle ( $\alpha_d$ ) spectra.

$$\phi_{\max} = \frac{12,000 \alpha^B}{\bar{a}^*} \quad (4)$$

$\alpha^B$  [ $\text{mg C (mg Chl } a)^{-1} (\text{mol quanta m}^{-2})^{-1}$ ] is the initial slope of the  $P$  vs.  $Eo$  curve (computed with the model of Jassby and Platt 1976), and  $\bar{a}^*$  [ $\text{m}^2 (\text{mg Chl } a)^{-1}$ ] is the mean chlorophyll-specific absorption coefficient weighted by the irradiance spectrum,  $E(\lambda)$  [ $\text{mol quanta m}^{-2}\text{s}^{-1}\text{nm}^{-1}$ ], of the lamp in the incubator:

$$\bar{a}^* = \frac{\int_{400}^{700} E(\lambda) a_{ph}^* d\lambda}{\int_{400}^{700} E(\lambda) d\lambda} \quad (5)$$

The factor 12,000 in Eq. 4 accounts for the different units used to express the different variables.

Considering the spectral correction performed on the fluorescence spectra and the constant excitation energy between measurements, the minimum quantum yield of fluorescence ( $\phi_{Fo}$ ) was simply computed, in relative units, as the fluorescence integrated between 400 and 650 nm, divided by the absorption coefficient averaged over the same spectral range. The spectral values of the minimum quantum yield of fluorescence were obtained by dividing  $Fo(\lambda)$  by  $a_{ph}(\lambda)$ .

## Results and discussion

The St. Lawrence estuary is strongly influenced by two major rivers on its north shore (Therriault and Levasseur 1985). In this region, the buoy drifted over a long distance (Fig. 1), and, as seen by examination of vertical profiles of temperature and salinity, water masses changed between stations F and G while entering the Gaspé current along the south shore of the estuary. In the gulf, the buoy drifted over a shorter distance within the relatively spatially homogeneous Anticosti gyre (Levasseur et al. 1990),

and it remained in the same water mass during the entire 24-h sampling period. In both areas, the low winds preceding the sampling period allowed the water column to be strongly stratified. Depth of the surface mixed layer was  $\sim 7$  m in the estuary and 18 m in the gulf, and that of the euphotic zone was  $\sim 10$  m in the estuary and 25 m in the gulf. In the two areas, a deep chlorophyll maximum was observed at the depth of  $\sim 1\%$  surface irradiance, although it was less pronounced in the estuary. The vertical profiles of salinity, temperature, and in situ fluorescence remained the same during both 24-h cycles, except at stations G and H in the estuary.

The estuary is in a region of the St. Lawrence River that is very productive because of the advection of lower salinity waters containing high nutrient concentrations year-round (Therriault and Levasseur 1985). During the sampling period, an average Chl  $a$  concentration of  $4.6 \text{ mg m}^{-3}$  was observed in the estuary. The gulf station was in the Anticosti gyre, which experiences acute nutrient limitation in summer. Levasseur et al. (1990) reported for this same region at the same time of year undetectable nitrate concentrations in the surface layer and a nitracline at 20-m depth. The average Chl  $a$  concentration in the gulf was  $0.5 \text{ mg m}^{-3}$ .

Figure 2 shows typical examples of the decomposition of the total particle absorption spectrum into absorption spectra by phytoplankton and nonalgal particles, using the method of Bricaud and Stramski (1990). Figure 3 shows the spectral distribution of the average and the standard deviation values of the chlorophyll-specific absorption coefficient for phytoplankton in the estuary and the gulf. These spectra have a shape typical of diatoms and dinoflagellates, for which Chl  $c$  and carotenoids are important light-harvesting pigments (Prézelin and Boczar 1986). In fact, although nanoflagellates numerically dominated in the two sampling areas (64–85%), dinoflagellates and diatoms, because of their much larger volumes (8–5,000 times the volume of nanoflagellates in the St. Lawrence estuary), probably accounted for the bulk of the

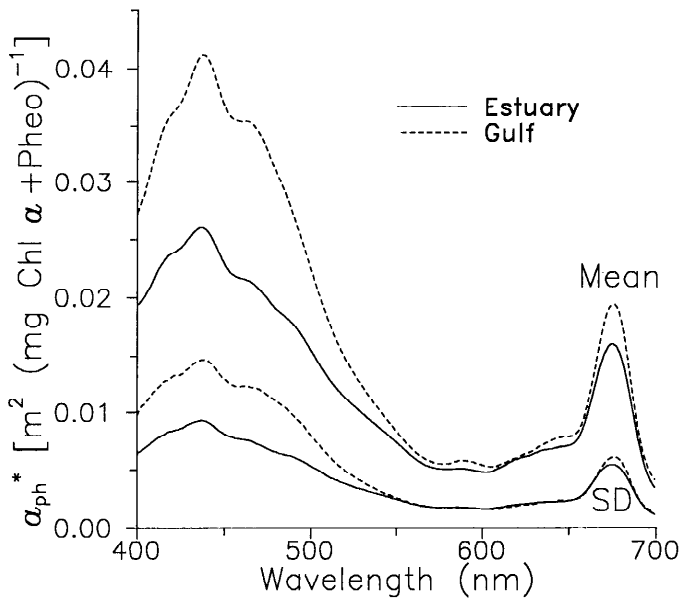


Fig. 3. Spectral distribution of the mean and standard deviation of the chlorophyll-specific absorption coefficients ( $a_{ph}^*$ ), for the estuary ( $n = 80$ ) and the gulf ( $n = 90$ ).

absorption. The average value of  $\bar{a}^*$  is  $0.016 \text{ m}^2 (\text{mg Chl})^{-1}$  in the estuary and  $0.023$  in the gulf, and the coefficient of variation (C.V.) is 32% for both areas.

Figure 4 shows representative excitation spectra for the two sampling areas. Between 400 and 600 nm, the general shape of each excitation spectrum is similar to its respective absorption spectrum (on the same figure). Each exhibits a distinct excitation minimum at  $\sim 450$  nm and another at  $\sim 500$  nm. Although the latter one was somewhat hidden in the background noise, it was almost systematically observed on all excitation spectra. These min-

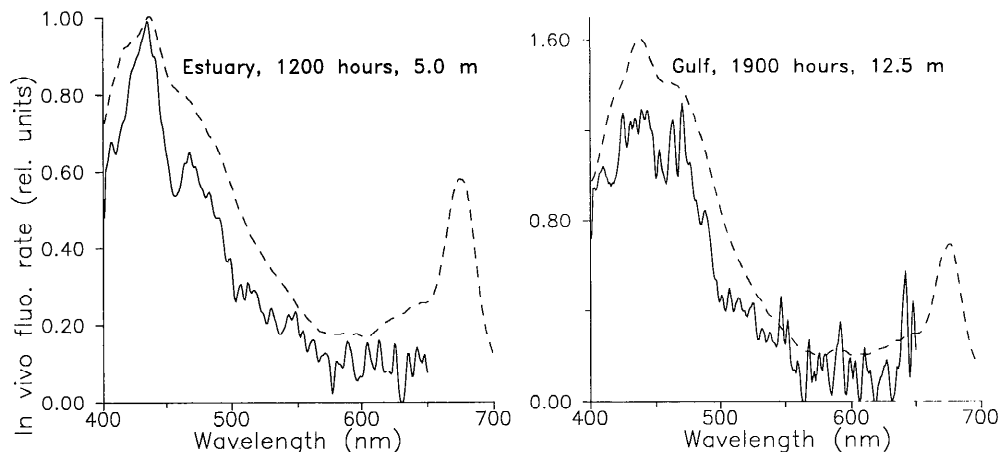


Fig. 4. Examples of in vivo excitation spectra of Chl *a* fluorescence in the estuary and the gulf (emission at 685 nm). The corresponding spectra of  $a_{ph}(\lambda)$  are plotted (dashed lines) in relative units.

ima correspond to the absorption maxima of carotenoids that do not transfer energy to Chl *a* (see figure 12.1 of Rabinowitch and Govindjee 1969) but instead dissipate absorbed quanta as heat (see Demmig-Adams 1990). A photoprotective function has been ascribed to such pigments (Bilger and Bjorkman 1990). In the case of diatoms and dinoflagellates, diatoxanthin is the xanthophyll that would fulfill this function (Olaizola and Yamamoto 1994). Because there is always a time lag between sample collection and shipboard measurements and because the preconditioning of the sample is critical during this time lag, the results never exactly reflect what actually happens in situ. Of special interest is photoinhibition, which involves processes of both fast ( $t_{1/2} = 15$  min) and slow decay ( $t_{1/2} = 3$  h). The recovery rates depend very much, however, on the preconditioning (Krause and Weis 1991). The fast component appears to be correlated with the xanthophyll cycle, although radiationless energy dissipation related to this cycle has been observed to persist for minutes, hours, or even a day in some cases (Demmig-Adams 1990). Given the shape of the excitation spectra shown in Fig. 4 and the results presented below, we believe that we tracked at least some of this component (photoprotectant pigments).

In the estuary,  $\phi_{max}$  ranged from 0.004 to 0.040 mol C (mol quanta) $^{-1}$ , with an average of 0.012 (C.V. = 55%). In the gulf,  $\phi_{max}$  ranged from 0.005 to 0.076 mol C (mol quanta) $^{-1}$ , with an average of 0.018 (C.V. = 71%). These values are lower than the ones reported by Cleveland et al. (1989) [0.033–0.102 mol C (mol quanta) $^{-1}$ ,  $n = 14$ ] and even lower than those reported by SooHoo et al. (1987) for total particles.

Our  $\phi_{max}$  values could be underestimates caused by overestimated absorption values, which may happen if absorption by phytoplankton is not effectively discriminated from absorption by detrital particles. The absorption spectra (Figs. 2 and 3), however, do not exhibit the

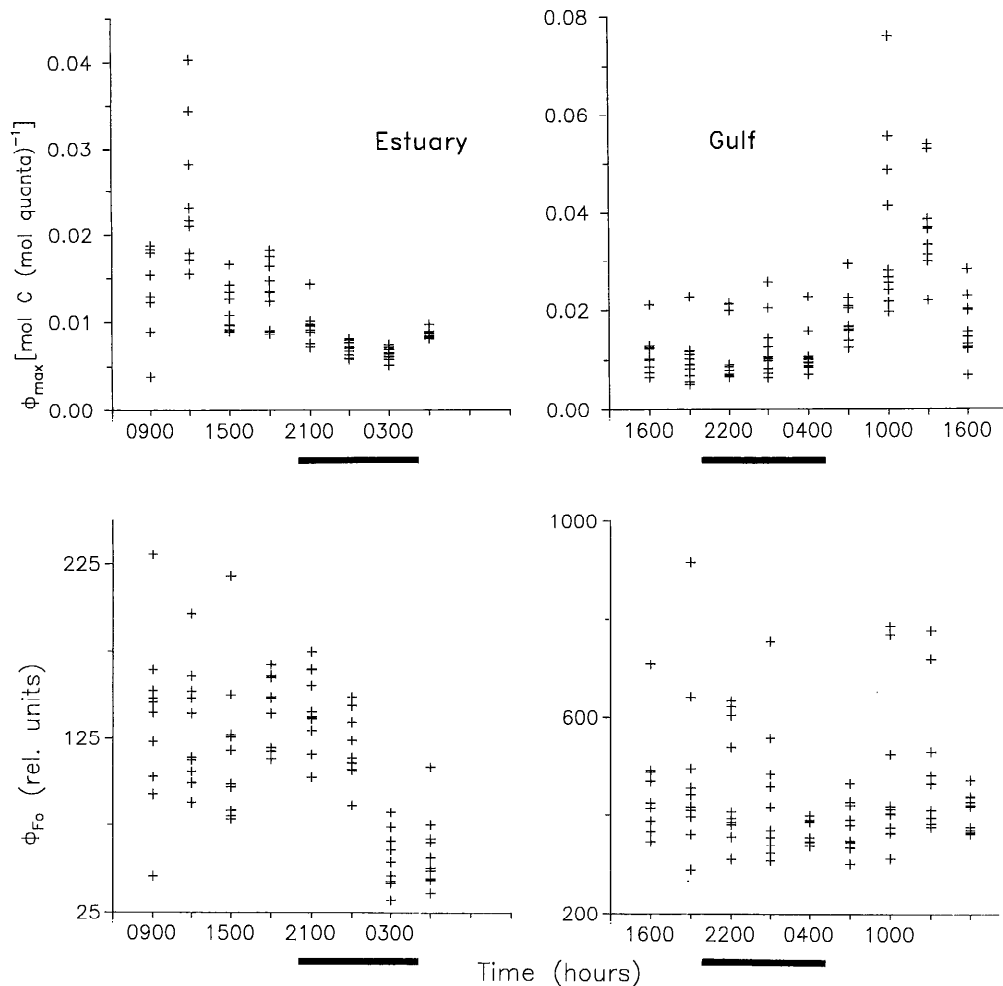


Fig. 5. Diel variations of the maximum quantum yield of photosynthesis ( $\phi_{\max}$ ) and of the minimum quantum yield of in vivo fluorescence ( $\phi_{F_0}$ ) for all depths pooled in the estuary and the gulf. Observations at 0300 and 0600 hours in the estuary correspond to stations G and H, respectively. Black bars indicate dark periods.

apparent increase toward shorter wavelengths that would support this possibility. Besides, no significant covariation was observed between  $\phi_{\max}$  and the ratio of pheopigments to pheopigments + Chl *a* (see Cleveland et al. 1989). Nevertheless, because the average level of the latter was significant (averaging  $0.26 \pm 0.1$ ), it may have led to an underestimation of  $\phi_{\max}$  by  $\sim 35\%$ , assuming the chlorophyll-specific absorption coefficient of pheopigment is similar to that of Chl *a*. The average  $\phi_{F_0}$  in relative units was 112.1 in the estuary and 459.9 in the gulf, with a C.V. of 40 and 38%, respectively.

Figure 5 shows the temporal variations in  $\phi_{\max}$  and  $\phi_{F_0}$ . The main conclusions reached from examination of this figure are that  $\phi_{\max}$  seems to follow a diel cycle in the two sampling areas, with higher values observed during the day, while  $\phi_{F_0}$  does not show any apparent diel periodicity; that in the estuary, both  $\phi_{\max}$  and  $\phi_{F_0}$  have a higher C.V. during the day (see Table 1), while no such trend is distinctly observed in the gulf; and that the values of  $\phi_{F_0}$

at stations G and H in the estuary (0300 and 0600 hours) seem to stand apart. There is a significant overall relationship ( $P < 0.05$ ; Fig. 6) between  $\phi_{\max}$  and  $\phi_{F_0}$  in the two regions, although the coefficients of determination are low (0.22 in the estuary and 0.13 in the gulf). Figure 7 illustrates this relationship as a function of time. In the estuary, a highly significant relationship exists from 0600 to 1500 hours, but not at night (see Table 1). In the gulf, a significant relationship is observed from 1000 to 0100 hours (except at 2200), but not from 0400 to 0700 hours. In both areas, there is an apparent diel periodicity in the slope of the relationship (Table 1), with greater values during the day and lesser values at night.

Mean vertical profiles of  $\phi_{\max}$  and  $\phi_{F_0}$  for daytime and nighttime are shown in Fig. 8 for the estuary and the gulf. In both areas, there is a clear 2–2.5-fold increase of the two variables toward the bottom of the euphotic zone. At night,  $\phi_{\max}$  values are low over the entire water column and a weak increase with depth persists, especially in the

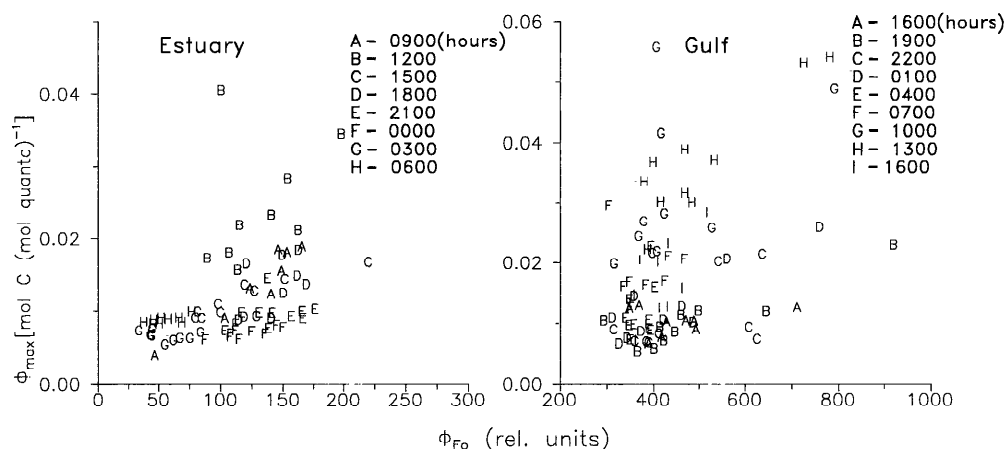


Fig. 6. Relationship between the maximum quantum yield of photosynthesis ( $\phi_{\max}$ ) and the minimum quantum yield of in vivo fluorescence ( $\phi_{F_0}$ ) in the estuary and the gulf using all available data.

gulf. A flattening of the vertical profile is also observed for  $\phi_{F_0}$  in both areas, showing weak increase with depth. The general decrease of  $\phi_{F_0}$  values by night in the estuary is due to the inclusion of stations G and H in the mean profile.

*Coupled and uncoupled variability of carbon fixation and fluorescence*—The above results suggest that three cases can be observed for the temporal and vertical variations of  $\phi_{\max}$  and  $\phi_{F_0}$ :  $\phi_{\max}$  and  $\phi_{F_0}$  may covary;  $\phi_{\max}$  may vary according to a distinct pattern, while  $\phi_{F_0}$  does not show any trend; and  $\phi_{F_0}$  may vary while  $\phi_{\max}$  does not.

Covariation between  $\phi_{\max}$  and  $\phi_{F_0}$  is predicted from the model of Schatz et al. (1988) (see also Kiefer and Reynolds 1992) as long as the activity of photosystem 2 is the sole source of variation. Factors suspected to influence the activity of photosystem 2 are the presence of photoprotectant pigments, nutrient deficiency, and photodamage due to excess light. All these factors may have an influence on both  $\phi_{\max}$  and  $\phi_{F_0}$  through an increase in the rate constant for radiationless dissipation (see Kiefer and Reyn-

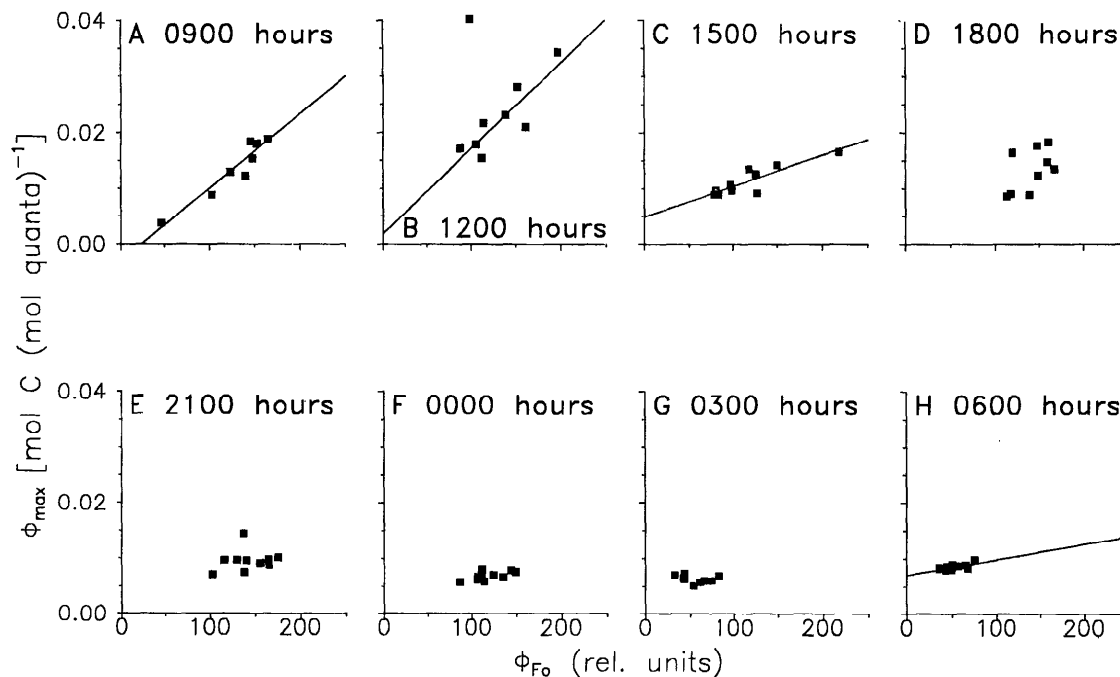
olds 1992). They are often called “nonphotochemical quenching” factors.

Variations of  $\phi_{\max}$  uncoupled with  $\phi_{F_0}$  are not related to photosystem 2 activity, so other factors should be considered to explain them. On the one hand, the weak sensitivity of  $\alpha^B$  to temperature (see Davison 1991) suggests that the enzyme-driven Calvin cycle (dark reactions) is not a source of variability in  $\phi_{\max}$ . On the other hand, a significant fraction of the reductant produced by the light reaction of photosynthesis can be used for tasks other than carbon fixation—nitrate reduction probably being the main one (see Turpin 1991). As a result, the photosynthetic quotient [PQ; mol O<sub>2</sub> (mol C)<sup>-1</sup>] can be higher than unity, depending on the redox level of available nutrients and the C:N ratio (Laws 1991). PQ variations may therefore induce inverse variations in  $\phi_{\max}$  without affecting  $\phi_{F_0}$ . PQ can also increase through losses of reductant by respiration or exudation (Geider 1992) because techniques used to measure carbon assimilation generally do not provide true gross photosynthesis values. However, respiration losses and exudation are not likely to be important factors for incubations lasting 60–90 min.

Table 1. Coefficients of variation of  $\phi_{\max}$  and  $\phi_{F_0}$  and slopes (model 2 linear regression; Fig. 7) and coefficients of determination for the relationship between  $\phi_{\max}$  and  $\phi_{F_0}$  at different times of the day (different stations) in the estuary and the gulf. Asterisks: \*— $P < 0.05$ .

Estuary					Gulf				
Time	C.V. (%)		Slope ( $\times 10^{-3}$ )	$R^2$	Time	C.V. (%)		Slope ( $\times 10^{-3}$ )	$R^2$
	$\phi_{\max}$	$\phi_{F_0}$				$\phi_{\max}$	$\phi_{F_0}$		
0900	40	36	0.138*	0.899	1600	36	61	0.012*	0.729
1200	34	26	0.177*	0.759	1900	49	37	0.028*	0.774
1500	24	36	0.063*	0.761	2200	56	26	0.053	0.120
1800	27	15	0.184	0.280	0100	48	31	0.045*	0.779
2100	20	16	0.043	0.282	0400	41	7	0.104	0.194
0000	11	16	0.041	0.369	0700	27	13	0.099	0.026
0300	11	30	0.041	0.086	1000	50	35	0.110*	0.511
0600	6	35	0.041*	0.441	1300	27	28	0.072*	0.800
					1600	37	13	0.117*	0.403

### Estuary



### Gulf

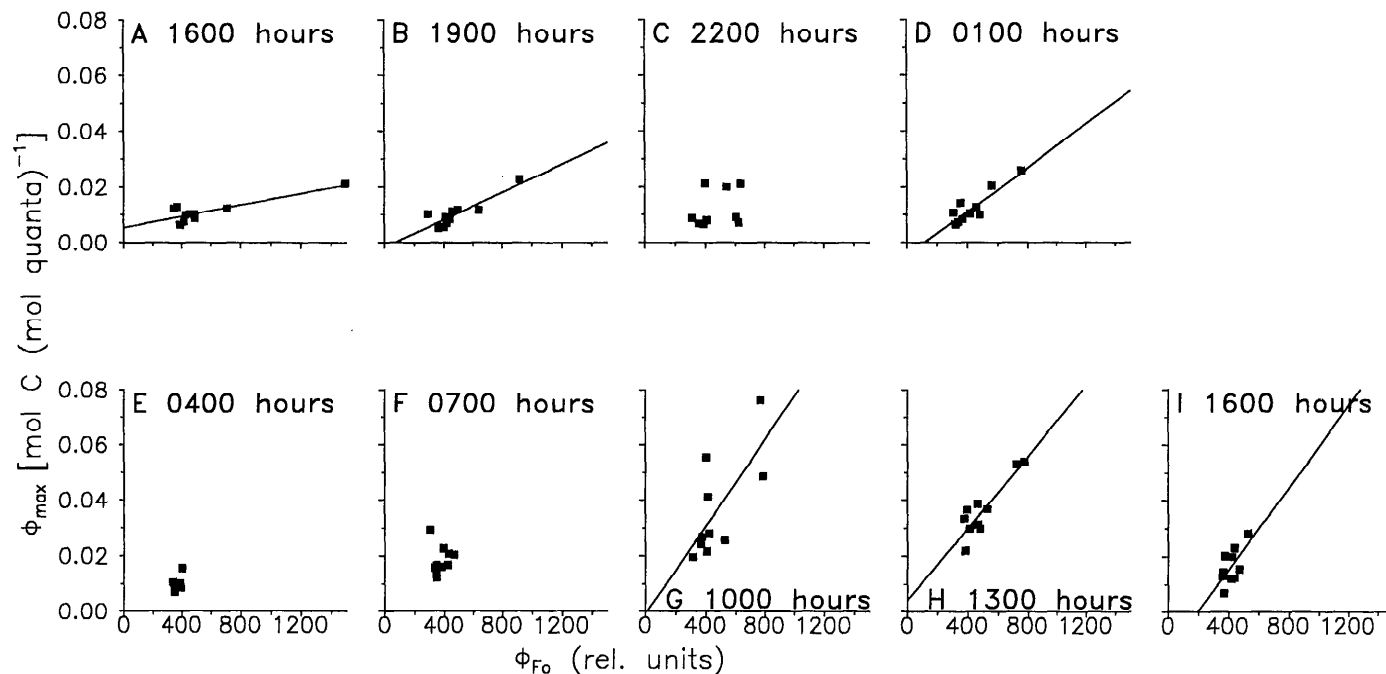


Fig. 7. Relationship between the maximum quantum yield of photosynthesis ( $\phi_{\max}$ ) and the minimum quantum yield of in vivo fluorescence ( $\phi_{F_0}$ ), at different times of day for the estuary and the gulf (see Table 1).

Variations of  $\phi_{F_0}$  uncoupled with  $\phi_{\max}$  are, as in the previous case, not related to the activity of photosystem 2 (not to be confused with uncoupling of fluorescence and photosynthesis at excessive irradiances). One possible ex-

planation is internal reabsorption of fluorescence (Collins et al. 1985). The significance of this phenomenon is, however, not known for natural environments.

In the following sections, the above-mentioned pro-

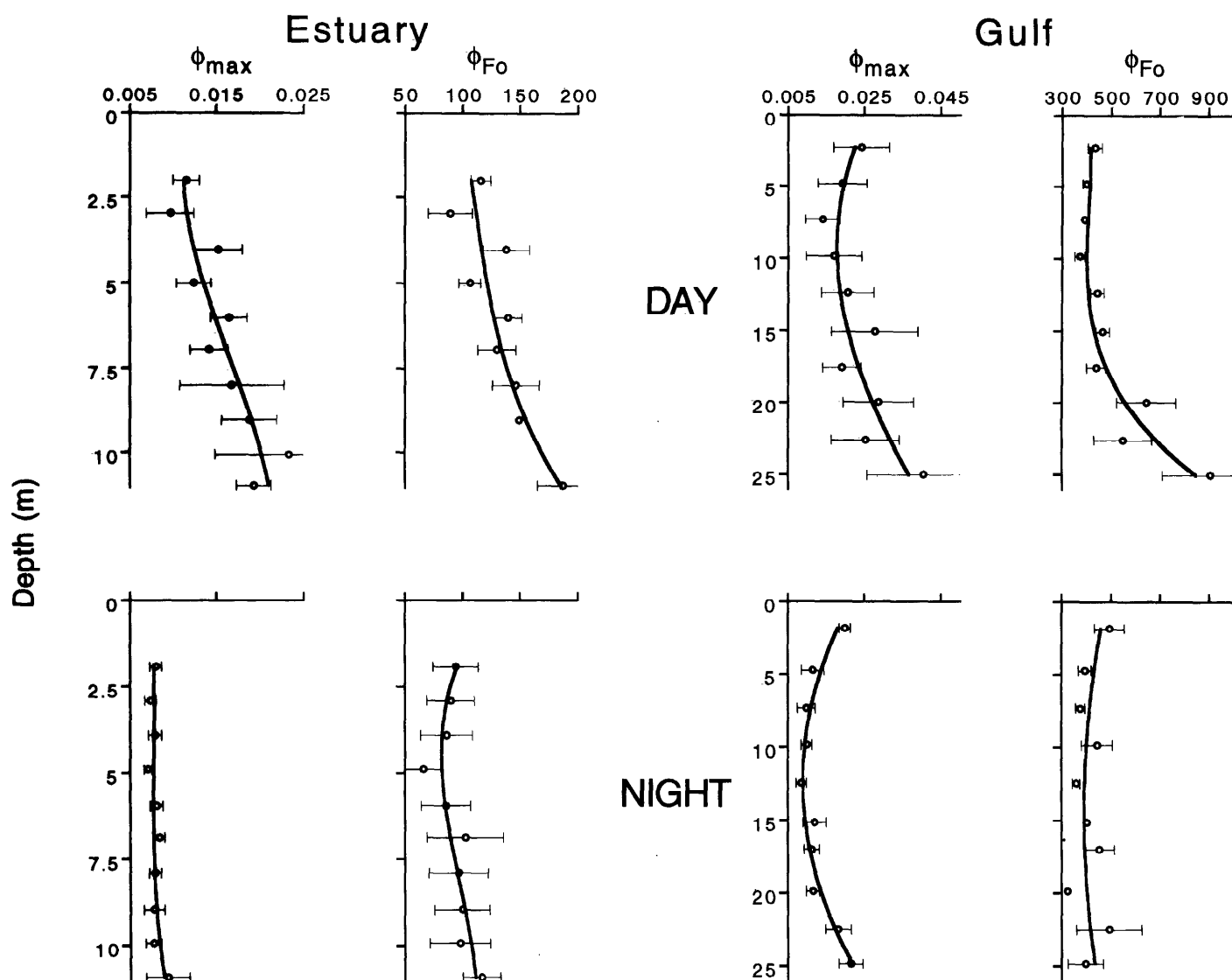


Fig. 8. Mean vertical profiles of  $\phi_{\max}$  and  $\phi_{Fo}$  during the day (0900–1800 and 1000–1900 hours) and at night (2100–0600 and 2200–0700 hours) in the estuary and the gulf, respectively.

cesses are discussed in turn, with specific reference to our results.

*Nonphotochemical quenching*—In the estuary, the C.V. of  $\phi_{\max}$  and  $\phi_{Fo}$  shows high values during the day and low values at night (Table 1). The correlation between  $\phi_{\max}$  and  $\phi_{Fo}$  is highly significant during the day, but no significant correlation exists at night (Fig. 7), which suggests that the relationship between  $\phi_{\max}$  and  $\phi_{Fo}$  is induced by light. A strong nutrient effect was not expected in this eutrophic region of the St. Lawrence estuary. A light-induced relationship implies either a photoprotection or a photodamage effect.

Photoprotectant pigments can be detected in three ways: by monitoring their concentration, by examining the shape of the absorption or excitation spectra, or by looking at the relationship between  $\phi_{\max}$  and the spectral values of  $\phi_{Fo}$  in the region of the spectrum where photoprotectant

pigments absorb light. It is difficult to measure the concentration of diatoxanthin at sea unless the concentration of phytoplankton is high, as in the study of Olaizola et al. (1992). Variability in the concentration of diatoxanthin relative to other photosynthetic pigments can hardly be detected on the absorption or excitation spectra because several other carotenoids (fucoxanthin, peridinin, . . .) absorb in the same spectral region and are often negatively correlated with diatoxanthin. In our study, it was possible to detect the effect of diatoxanthin in the estuary by looking at the relationship between  $\phi_{\max}$  and  $\phi_{Fo}(\lambda)$  between 400 and 550 nm during the day.

The spectral values of the slope and of the coefficient of determination ( $R^2$ ) of the simple linear regression of  $\phi_{\max}$  on  $\phi_{Fo}(\lambda)$  have been plotted in Fig. 9 for the data collected between 0900 and 1500 hours in the estuary. The figure shows a spectral dependency in the range of 430–515 nm, with two maxima at  $\sim 450$  and 500 nm.

Although the *in vivo* absorption spectrum of diatoxanthin is not well known, changes in absorbance at  $\sim 505$  nm co-occurred with variations in the relative concentration of this pigment (Olaizola and Yamamoto 1994). Moreover, fluorescence minima were systematically observed at  $\sim 450$  and  $500$  nm in our excitation spectra (Fig. 4). Because photodamage does not induce a spectral dependency between photosynthesis and fluorescence, photoprotectant pigments are thought to be responsible for the relationship between  $\phi_{\max}$  and  $\phi_{F_0}$  observed in the estuary. The lack of evidence for photodamage in the estuary is consistent with the cloudy conditions that prevailed during sampling.

In the gulf, although no distinct diel periodicity was observed in the C.V. of  $\phi_{\max}$  and  $\phi_{F_0}$  (Table 1), higher and lower C.V. were observed at 1000 hours and between 0400 and 0700 hours, respectively, for both variables. No significant spectral dependency could be found for the relationship between  $\phi_{\max}$  and  $\phi_{F_0}$ . Also, a near-surface depression of  $\phi_{\max}$  and  $\phi_{F_0}$ , which would suggest photodamage was not observed (Fig. 8). Therefore, the relationship between these variables could not be clearly attributed to light. As mentioned before, the gulf is characterized by extremely low nutrient levels in surface waters during summer. In the same region and at the same period, Levasseur et al. (1990) also found a strong nitracline at  $\sim 20$  m, which corresponds to the maximum thickness of the mixed layer we observed in the gulf. The vertical profiles of  $\phi_{\max}$  and  $\phi_{F_0}$  (Fig. 8) show a significant increase at about the same depth during the day. Such increases near the bottom of the euphotic zone persisted at night for  $\phi_{\max}$ , whereas the vertical variations of  $\phi_{F_0}$  at night were confounded with the noise. These observations suggest that the relationship between  $\phi_{\max}$  and  $\phi_{F_0}$  in the gulf could be in part related to surface-water nutrient deficiency. The high C.V. for both  $\phi_{\max}$  and  $\phi_{F_0}$  at midday (1000 hours) indicates that light also plays a role.

**Losses of reductant**—The  $\phi_{\max}$  values reported here [ $0.004$ – $0.076$  mol C (mol quanta) $^{-1}$ ] are low compared to those of Cleveland et al. (1989) [ $0.033$ – $0.102$  mol C (mol quanta) $^{-1}$ ]. These values are nevertheless realistic when the expected natural variability of the photosynthetic quotient is considered. Laws (1991) reported that PQ should average  $1.4 \pm 0.1$  mol O<sub>2</sub> (mol C) $^{-1}$  for algae growing on nitrate. If we take the minimum quantum requirement as  $9.1$  mol quanta (mol O<sub>2</sub>) $^{-1}$  (Dubinsky et al. 1986),  $\phi_{\max}$  should average  $0.078 \pm 0.005$  mol C (mol quanta) $^{-1}$  without nonphotochemical quenching. In a vertical profile, the maximum  $\phi_{\max}$  value is expected to occur at the bottom of the euphotic zone (or close to the nitracline), where nutrients are abundant and nonphotochemical quenching is minimum. Because the bottom of the euphotic zone is where nitrate is generally the main source of nitrogen, the maximum  $\phi_{\max}$  value in the marine environment should typically be  $0.078 \pm 0.005$  mol C (mol quanta) $^{-1}$  (see Bannister and Weidemann 1984), which corresponds to the highest values we observed. We believe that  $\phi_{\max}$  values close to the maximum quantum

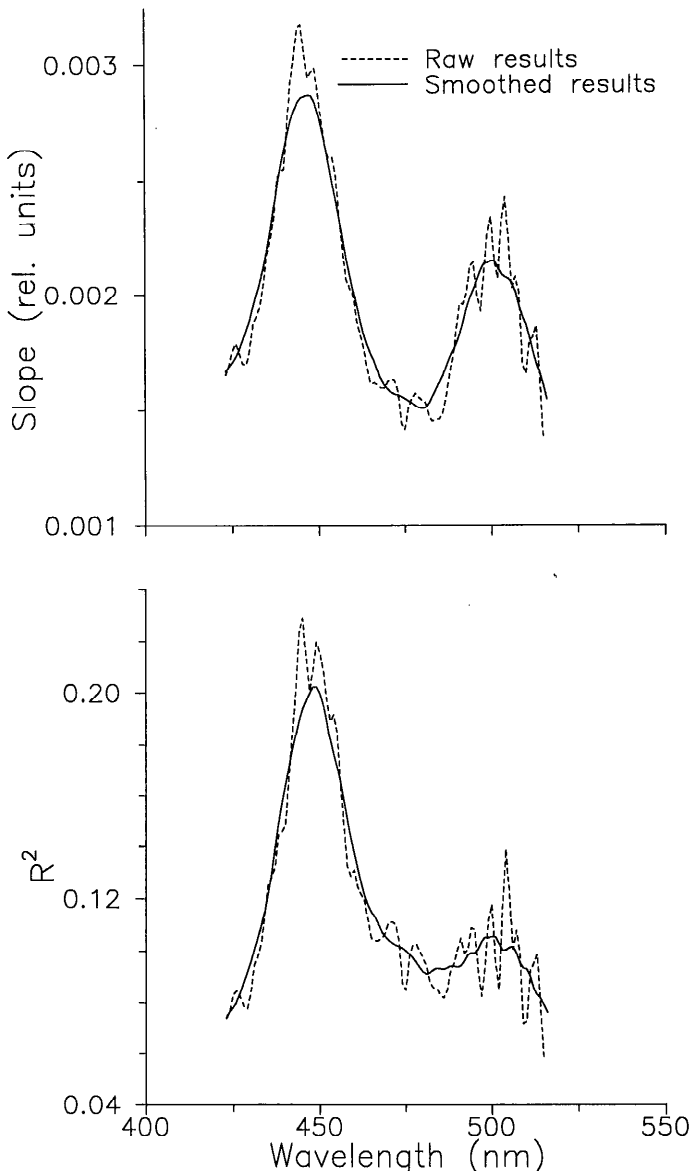


Fig. 9. Spectral values of the slope and of the coefficient of determination ( $R^2$ ) of the linear regression of  $\phi_{\max}$  on  $\phi_{F_0}(\lambda)$  in the estuary between 0900 and 1500 hours. The values are significant between 430 and 515 nm ( $P < 0.1$ ). The smoothed lines are adjusted to the raw data.

yield for oxygen evolution, as reported by Cleveland et al. (1989), are nontypical in the marine environment.

A diel cycle in  $\phi_{\max}$  has not yet been reported for phytoplankton in the laboratory or at sea. However, diel measurements of *in vivo* fluorescence per Chl *a* performed by Kiefer (1973) showed much lower values around noon. Also, Vincent et al. (1984) reported an important drop in the maximum variable fluorescence at midday. These decreases when irradiance is maximal result from photodamage by nonphotochemical quenching. We observed no clear diel cycle for  $\phi_{F_0}$ . Moreover, instead of a minimum around noon, which would be expected if the cycle was driven by photodamage or photoprotection,

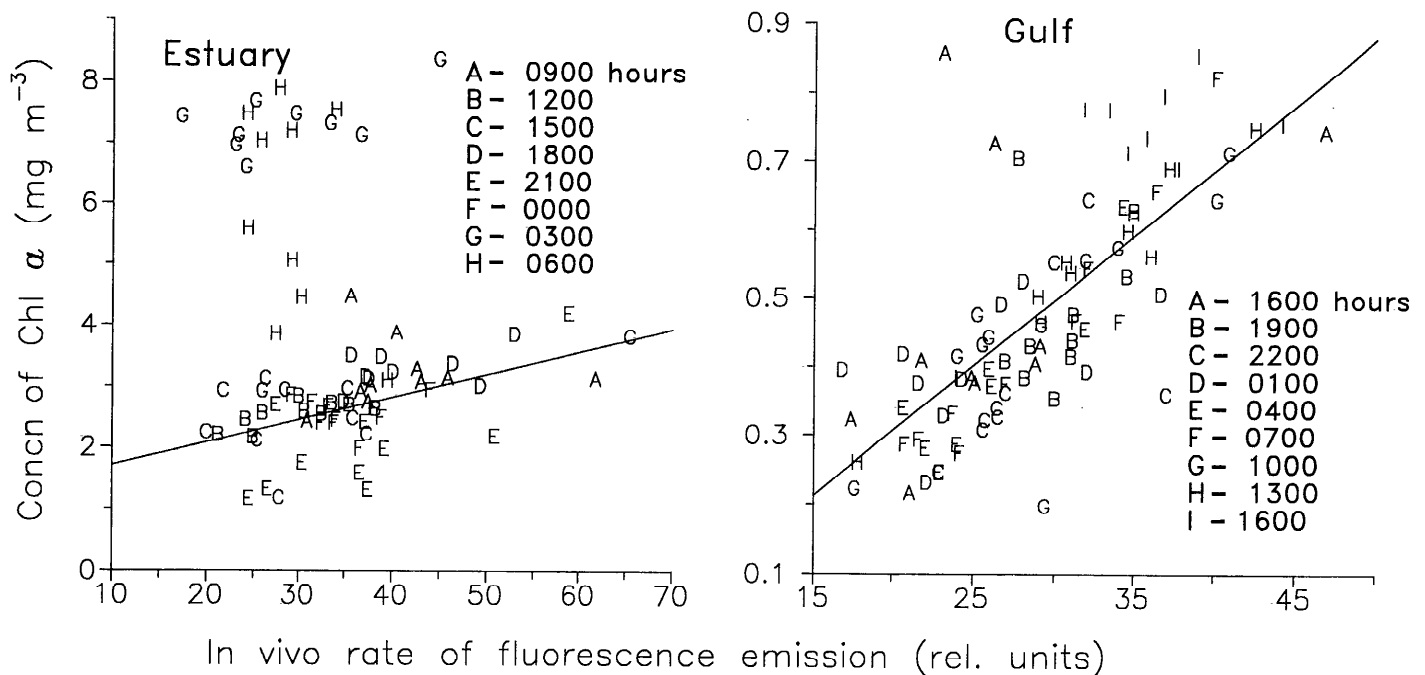


Fig. 10. Relationship between extracted Chl  $a$  and in vivo fluorescence for the estuary and the gulf. Stations G and H for the estuary were not included in the regression analysis (explanations given in the text;  $R^2 = 0.26$  and  $0.55$ , respectively;  $P < 0.05$ ).

we observed the minimum  $\phi_{\max}$  value at night, as did several investigators who monitored  $\alpha^B$  (Vanderveelde et al. 1989).

The diel periodicity of  $\phi_{\max}$  we observed is thus not linked to photosystem 2 activity. It could be related to the presence of nonactive chlorophyll (which fluoresces but does not have any photosynthetic activity), to variations in PQ, or to losses of fixed carbon through exudation and filtration. There is no technique to determine the presence of nonactive pigments, and a significant effect of such pigments has not yet been reported. Exudation and respiration would rather depress  $\phi_{\max}$  during the day, since they covary with light (Geider 1992). Variation in the photosynthetic quotient is thus the only likely factor that could explain variations in  $\phi_{\max}$  uncoupled to  $\phi_{Fo}$ . It is known that carbon accumulation is favored over protein synthesis during the day (Cuhel et al. 1984), which causes the C : N ratio to increase. By night, the C : N ratio decreases with carbon consumption, while protein synthesis is favored. Nutrients, including nitrogen, would be assimilated proportionally with protein synthesis (Cuhel et al. 1984). If protein synthesis and nutrient assimilation were actually favored over carbon assimilation by night, algae growing on nitrate should exhibit a night decrease of PQ. This scenario provides a potential explanation for the observed diel cycle in  $\phi_{\max}$ .

This diel cycle in  $\phi_{\max}$  accounts for the diel variations in the slope of the relationship between  $\phi_{\max}$  and  $\phi_{Fo}$  (Fig. 7, Table 1). The large difference in slopes measured at 1600 hours in the gulf on two consecutive days cannot be interpreted based on the present data set. The level of reproducibility from day to day in such diel cycle is not

known. It may be highly sensitive to variations in irradiance conditions (e.g. cloud cover).

*Intracellular reabsorption of fluorescence*—Very low  $\phi_{Fo}$  values were observed for stations G and H in the estuary. Figure 10 shows the regression between the concentration of Chl  $a$  and the rate of fluorescence. The linear relationship is significant in both cases ( $P < 0.05$ ) for the estuary, when stations G and H are excluded. Stations G and H stand completely apart, with low fluorescence : Chl ratios. At these two stations, the number of large dinoflagellate cells (*Alexandrium tamarense*) was twice as high as at stations A–F. The chlorophyll-specific absorption coefficients at 435 nm at stations G and H were consistently among the lowest measured in the estuary (Fig. 11). Therefore, reabsorption of Chl  $a$  fluorescence resulting from pigment packaging could be responsible for the low  $\phi_{Fo}$  values observed at stations G and H.

An increase in bulk Chl  $a$  concentration is often linked to an increase in the intracellular pigment concentration or the cell volume, with little or no increase in the cell numbers. This link is supported by the fact that an increase in Chl  $a$  is generally paralleled by a decrease in the chlorophyll-specific absorption coefficient (Mitchell and Kiefer 1988; Yentsch and Phinney 1989; Bricaud and Stramski 1990; Babin et al. 1993), thus reflecting a packaging effect. In both sampling areas, a significant positive relationship was observed between  $a_{ph}^*(435)$  and  $[\exp(-\text{Chl})]$  ( $R^2 = 0.76$  and  $0.31$  in the estuary and the gulf,  $P < 0.0001$ ; see Fig. 11 for the estuary). The latter function is consistent with the mathematical expression of the package effect (Morel and Bricaud 1981). Interest-

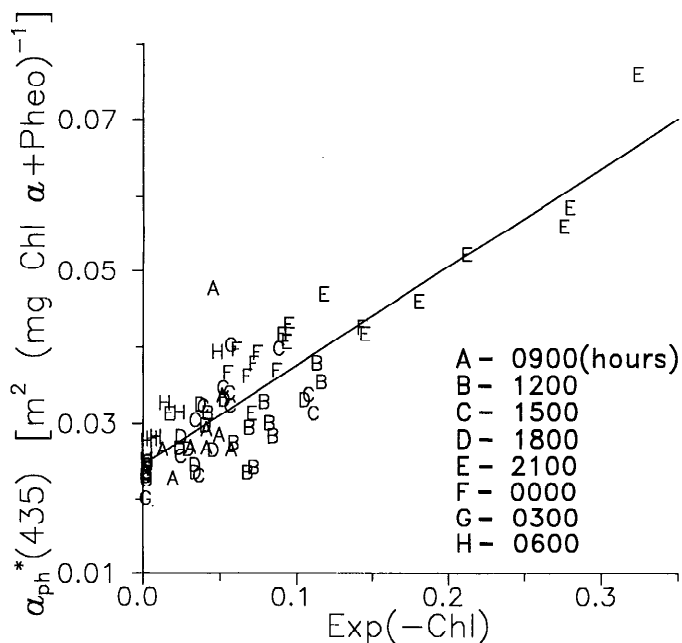


Fig. 11. Relationship between the chlorophyll-specific absorption coefficient of phytoplankton ( $\alpha_{ph}^*$ ) measured at 435 nm and the concentration of Chl *a* + Pheo ( $\text{mg Chl } a + \text{Pheo m}^{-3}$ ) expressed as  $\exp(-\text{Chl})$  ( $R^2 = 0.76$ ,  $P < 0.0001$ ) in the estuary.

ingly, stations G and H fit this relationship nicely (Fig. 10). These observations are consistent with the hypothesis that the packaging effect and the related self reabsorption of Chl *a* fluorescence may be responsible for the low  $\phi_{Fo}$  at stations G and H. Because Chl *a* concentration was 7.5-fold higher in the estuary, we believe that reabsorption is also responsible for the 4-fold higher average  $\phi_{Fo}$  in the gulf.

## Conclusion

In the present study, we sometimes observed a significant, positive relationship between  $\phi_{max}$  and  $\phi_{Fo}$ , as predicted by the model of Schatz et al. (1988). Topliss and Platt (1986) reported a negative relationship between  $\alpha^B$  and the quantum yield of solar-induced fluorescence for data collected in the high Arctic and on the Grand Banks. They argued that this relationship originates from the competition for absorbed quanta between photosynthesis and fluorescence. In fact, the relationship they reported seems to be circumstantial rather than causal; an increase of  $\alpha^B$  with depth is typical and a decrease of the quantum yield of solar-induced fluorescence is expected as the fraction of open reaction centers increases with depth (Kiefer and Reynolds 1992). Theoretically, no causal link can be established between  $\alpha^B$  and the quantum yield of solar-induced fluorescence because only the second factor depends on the fraction of open reaction centers.

If photoprotectant pigments were responsible for the covariability between  $\phi_{max}$  and  $\phi_{Fo}$  in the estuary, one would expect a diel cycle in both variables, with lower values at midday. Instead, we observed the inverse cycle

for  $\phi_{max}$  and no distinct diel periodicity for  $\phi_{Fo}$ . The cycles may have been obscured by PQ, in the first case and by reabsorption in the second case (not considering stations G and H). Because none of the processes mentioned were studied at sea, we cannot say whether the extent of their natural variability can explain the variations observed in  $\phi_{max}$  and  $\phi_{Fo}$ . These uncertainties represent the main limitation of our interpretation. In spite of these uncertainties, our study allowed two important facts to be established:  $\phi_{max}$  is highly variable at sea, both with depth and in time (a factor of up to 20), and there may be a significant uncoupling between variations of  $\phi_{max}$  (for carbon fixation) and photosystem 2 activity. Diel variations (and related processes) certainly accounted for the largest part of  $\phi_{max}$  variations (Fig. 5). Photoprotectant pigments induced  $\phi_{max}$  vertical variations in both sampling areas, while nutrient availability contributed to some of this variability only in the gulf. These results confirm the importance of considering  $\phi_{max}$  as a variable in primary production models. It also emphasizes the relevance of variables such as PQ when fluorescence techniques are used to estimate carbon fixation at sea.

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