# Variability of the portion of functional PS2 reaction centres in the light of a fluorometric study*

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**KEYWORDS**
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**Abstract**

The paper contains a preliminary analysis of the links between the portion $f_c$ of functional PS2 reaction centres in the photosynthetic apparatus of marine phytoplankton and environmental factors. The analysis is based *inter alia* on fluorometric measurements of $f_c$ (see Kolber & Falkowski 1993) in water sampled from different depths and trophic types of sea. From the statistical generalisations was derived an analytical form of the relationship between $f_c$, and the optical

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depth and trophic type of sea (the trophicity index was taken to be the surface concentration of chlorophyll $a$). According to this relationship, $f_c$ rises as the trophicity of the sea does so. Moreover, there is a certain optimal optical depth for each type of water at which the number of functional PS2 reaction centres reaches a maximum. Above or below this depth the value of $f_c$ falls. At the present stage of investigations it seems reasonable to assume that this drop in the number of functional PS2 reaction centres close to the surface is due to the destructive effect of excessive irradiance. On the other hand, their reduced number at greater depths, below the $f_c$ maximum, can be attributed to the deficit of light and the consequent destruction of reaction centres.

## 1. Introduction

The quantum yield of marine phytoplankton photosynthesis does not achieve the maximal theoretical value 0.125 molC Ein$^{-1}$ (Clayton 1980, see also Woźniak & Dera 2000, this volume) and does not usually exceed 0.085 molC Ein$^{-1}$ (Babin *et al.* 1996 and papers cited therein). The reason for this is that in nature, growth conditions are usually far from optimal (lack or excess of light, lack of nutrients, non-photosynthetic pigment effect, *etc.*). Some environmental conditions cause the photosynthetic rate at functional PS2 reaction centres to decrease, others lead to a reduction in the portion of PS2 reaction centres in the total number of such centres. This paper is a study of the ratio $f_c$ of functional to all PS2 reaction centres.

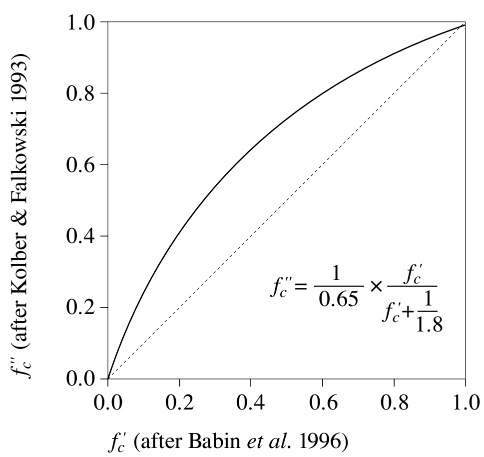


**Fig. 1.** Relationship between the values of $f_c$ (the portion of functional PS2 reaction centres) determined from the expressions given by Kolber & Falkowski (1993) ($f_c$ – see eq. (1)) and by Babin *et al.* (1996) ($f_c$ – see eq. (2))

The factor $f_c$ can be determined on the basis of Pump Probe pulse fluorometer measurements carried out on dark-adapted phytoplankton samples (Babin *et al.* 1996, Kolber & Falkowski 1993). Two expressions exist that enable $f_c$ to be determined with fluorometric methods:

- the one put forward by Kolber & Falkowski (1993):

$$f_c = \frac{1}{0.65} \frac{F_0 - F_m}{F_m}, \tag{1}$$

- that suggested by Babin *et al.* (1996):

$$f_c = \frac{1}{1.8} \frac{F_m - F_0}{F_0}, \tag{2}$$

where

$F_0$ and $F_m$ – *in vivo* induced fluorescences: minimal (initial) and maximal (both measured in the dark-adapted stage where non-photochemical quenching is at a minimum).

The value of $f_c$ varies under different environment conditions. Many authors have shown that the portion of functional reaction centres active in different water regions depends closely on trophicity and depth in the sea (Babin *et al.* 1996, Kolber & Falkowski 1993). The present work aims to derive a preliminary quantitative description of these relationships, that is, to find mathematical formulae for the function $f_c = \mathrm{f}\,(C_a(0), \tau)$, where $C_a(0)$ – surface concentration of chlorophyll $a$ (index of the trophic type of sea), $\tau$ – optical depth in the sea.

## 2. Material and methods

Empirical data from different areas of the World Ocean obtained by ourselves and other authors were used. Our data set includes

- data collected by Pogosyan and the Sopot team in the Indian Ocean and Black Sea cruise of r/v 'Vityaz' (see Vedernikov *et al.* 1990),
- Baltic data collected by the authors during cruises of r/v 'Oceania' in 1997–99 (unpublished).

All groups of data contain values of the portion of functional reaction centres $f_c$ measured fluorometrically, surface chlorophyll $a$ concentrations $C_a(0)$ and optical depth $\tau$ in the sea. $F_m$ and $F_0$ were measured with different methods in different groups of data. During the 'Oceania' cruises, active stimulated fluorescence techniques were used (Babin *et al.* 1996, Kolber & Falkowski 1993). By contrast, the maximum fluorescence in the Indian Ocean and Black Sea was measured not after the pump flash as in the Pump Probe method but chemically, following the addition of DCMU (see Vedernikov *et al.* 1990). Values of $f_c$ were obtained from eq. (1). The concentrations of chlorophyll $a$ in seawater were determined with standard methods ($C_a$ = chl $a$ + pheo) (Strickland & Parsons 1968). The relevant optical depths from which the water samples for fluorometric analysis were taken were determined optically *in situ*. Such methods were described by Woźniak & Montwiłł (1973), and Woźniak *et al.* (1983).

The number of stations and measured data sets are given in Table 1.

**Table 1.** Experimental data sets

| Experiment | Number of stations | Number of data sets | Location |
|---|---|---|---|
| r/v 'Vityaz' (1988) | 8 | 131 | Indian Ocean |
| r/v 'Vityaz' (1988) | 22 | 154 | Black Sea |
| r/v 'Oceania'(1994–98) | 53 | 448 | Baltic Sea |
| total | 83 | 733 | |

## 3. Results

Figure 2a shows examples of measured $f_c$ values *versus* optical depth. The points from different trophic types of water are denoted by various symbols. In general these points are independent of depth, but if waters of

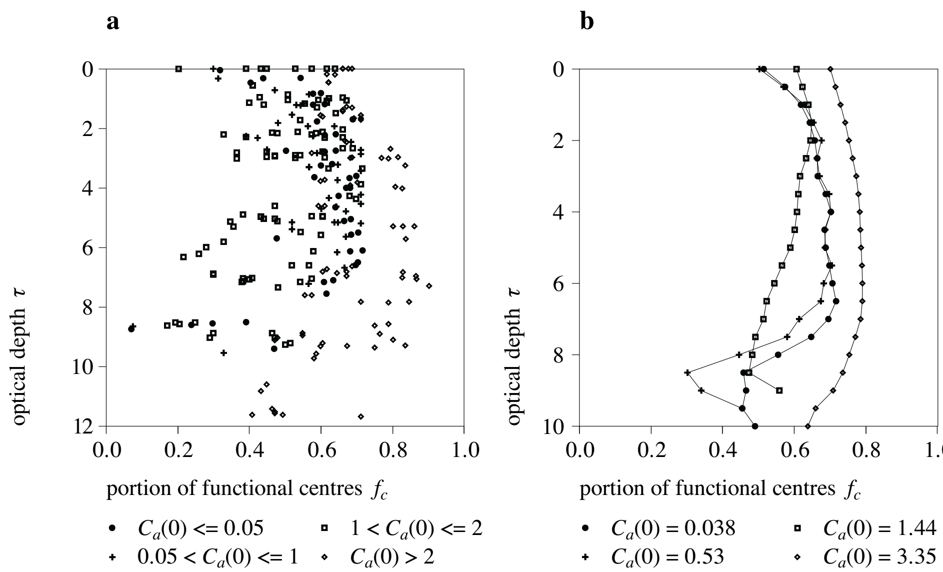


**Fig. 2.** Vertical distribution of the portion of functional reaction centres $f_c$ in different trophic types of sea. The surface concentration of chlorophyll $a$ ($C_a(0)$ [mg tot. chl $a$ m$^{-3}$]) is assumed to be the index of trophic types of sea: example of experimental points (a), averaged for different trophic types of sea (b)

different trophicity are scrutinised this dependence becomes apparent. This is clear from Fig. 2b, which shows the mean value for each trophicity range of $f_c$ profiles.

To examine the relationship between $f_c$, optical depth and trophic type of water (assumed to be the surface chlorophyll $a$ concentration), we approximated the ratio $F_0/F_m$ in eq. (1) with a polynomial. As a result we obtained the 2nd degree polynomial:

$$\frac{F_0}{F_m} = \sum_{m=0}^{2} \left[ \sum_{n=0}^{2} A_{m,\,n} \, (\log C_a(0))^n \right] \tau^m, \tag{3}$$

where

$\tau$ – [dimensionless],

$C_a(0)$ – expressed in [mg tot. chl $a$ m$^{-3}$].

The values of $A_{m,\,n}$ are given in Table 2.

**Table 2.** Values of $A_{m,\,n}$ in eq. (3)

| n / m | 0 | 1 | 2 |
|---|---|---|---|
| 0 | 0.6958 | −0.08513 | 0.009619 |
| 1 | −0.1295 | 0.03742 | −0.005846 |
| 2 | −0.09065 | 0.02902 | −0.004215 |

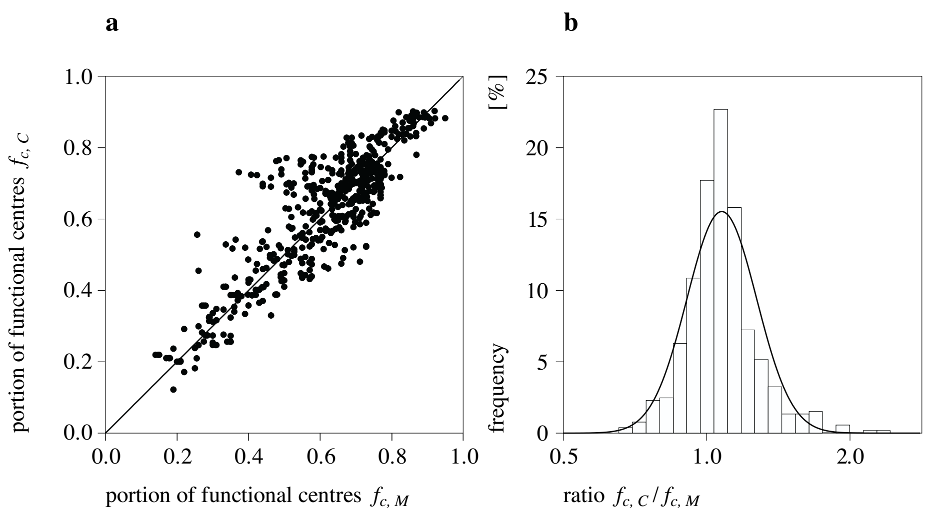


**Fig. 3.** Comparison between the portion of modelled functional centres $f_{c,\,C}$ and that of measured functional centres $f_{c,\,M}$ (a), and frequency distribution of the ratio $f_{c,\,C}/f_{c,\,M}$ (b)

The errors of approximation were also estimated. For this purpose we compared the values of $f_{c,C}$ determined by eqs. (1) and (3), and measured values of $f_{c,M}$ (see Fig. 3). The errors are given in Table 3. Clearly, the results of approximating $f_c$ by eqs. (1) and (3) are quite satisfactory (for example, the statistical error $\sigma_+ \approx 17\%$).

**Table 3.** The relative errors in $f_c$ approximations

| Arithmetic statistics | | Logarithmic statistics | | | |
|---|---|---|---|---|---|
| systematic | statistical | systematic | standard error factor | statistical | |
| $\langle\varepsilon\rangle$ [%] | $\sigma_\varepsilon$ [%] | $\langle\varepsilon\rangle_g$ [%] | $x$ | $\sigma_-$ [%] | $\sigma_+$ [%] |
| 3.12 | ± 17.5 | 1.81 | 1.17 | −14.5 | 17.3 |

where

$\varepsilon = (f_{c,C} - f_{c,M})/f_{c,M}$ – errors,

$\langle\varepsilon\rangle$ – arithmetic mean of errors,

$\sigma_\varepsilon$ – standard deviation of errors (statistical error),

$\langle\varepsilon\rangle_g = 10^{[\langle\log(f_{c,C}/f_{c,M})\rangle]} - 1$ – logarithmic mean of errors,

$\langle\log(f_{c,C}/f_{c,M})\rangle$ – mean of $\log(f_{c,C}/f_{c,M})$,

$\sigma_{\log}$ – standard deviation of $\log(f_{c,C}/f_{c,M})$,

$x = 10^{\sigma_{\log}}$ – standard error factor,

$\sigma_- = \frac{1}{x} - 1$ and

$\sigma_+ = x - 1$.

## 4. Final remarks and conclusion

Vertical profiles of the portion of functional PS2 reaction centres $f_c$ for different trophic types of water are readily determined with eqs. (1) and (3) (see Fig. 4). The tendency for $f_c$ to rise with increasing trophicity is evident: it is related to the larger quantity of nutrients in eutrophic waters. This had been postulated earlier by Babin *et al.* (1996). Moreover, for each type of water there is an optimal depth where $f_c$ achieves a maximum. The values of $f_c$ decrease towards the surface or bottom. Similar trends were noticed earlier by Babin *et al.* (1996), Kolber & Falkowski (1993).

Given the present state of research, the hypothesis that $f_c$ decreases near the surface owing to the destructive influence of excessive irradiance (an inhibition factor) and near the bottom for lack of light and disappearance of PS2 reaction centres seems to be correct.

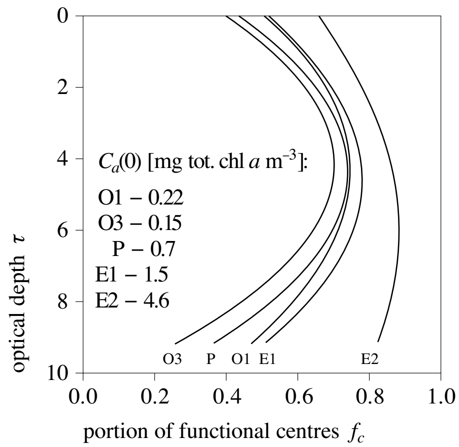


**Fig. 4.** Modelled vertical distributions of the portion of functional PS2 reaction centres $f_c$ for various trophic types of waters

The quantitative description of these trends (*i.e.* $f_c$ as a function of underwater irradiance, optical depth and nutrient concentration in seawater) is being developed further by the authors and will be published in the future.

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