DEPENDENCE OF THE PHOTOSYNTHESIS QUANTUM YIELD IN OCEANS ON ENVIRONMENTAL FACTORS

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ABSTRACT

Statistical relationships between quantum yield of photosynthesis and selected environmental factors in the ocean have been studied. The underwater irradiance, nutrient content, water temperature and the water trophicity (i.e. the surface concentration of chlorophyll $C_a(0)$) have been considered, utilizing large empirical data base. Basing on the obtained relationships, a mathematical model of the quantum yield was elaborated. The model makes it possible to determine the quantum yield from the known values of the mentioned environmental factors. Empirical verification of the model gave a positive result.

INTRODUCTION

The phytoplankton quantum yield of photosynthesis Φ is a measure of the photosynthetic efficiency under the environmental conditions obtaining at given depths in the sea. It is defined as the ratio:

$$\Phi = \frac{P^B}{PUR^*} = \frac{P^B}{PAR_0 \cdot \tilde{a}^*_{pl}} \approx \frac{P^B}{1.2 PAR \cdot \tilde{a}^*_{pl}} \qquad (1)$$

where: P^B [mgC (mg tot.chl$a$)$^{-1}$ s^{-1}] - rate of photosynthesis, (also known as the assimilation number), i.e. the production in unit time referred to unit mass of chlorophyll a; PUR^* [Ein (mg tot.chl$a$)$^{-1}$ s^{-1}] - the number of quanta absorbed by phytoplankton pigments in unit time referred to unit mass of chlorophyll a; PAR_0 [Ein m^{-2} s^{-1}] and PAR [Ein m^{-2}s^{-1}] - scalar and downward irradiances by sunlight in the PAR spectral range (400 ÷ 700 nm); $\tilde{a}^*_{pl}$ [m^2 (mg tot.chl$a$)$^{-1}$] – mean specific absorption coefficient for phytoplankton weighted by the downward irradiance spectrum $E_d(\lambda)$, i.e.:

$$\tilde{a}^*_{pl} \approx (PAR_0)^{-1} 1.2 \int_{400nm}^{700nm} E_d(\lambda) a^*_{pl}(\lambda) d\lambda \qquad (2)$$

Though, the least understood aspect of photosynthesis, the quantum yield as defined here, is its most salient characteristic, and must be included in any mathematical model of the process [4, 17, 28, 31]. That is why it has been the subject of empirical study by numerous authors [see e.g. 3, 7, 10, 18, 22, 32] or modeled theoretically and statistically [e.g. 16, 20, 21, 42, 43]. These investigations have shown that the quantum yield of photosynthesis depends on a number of environmental factors, principally the underwater irradiance, the nutrient content, the temperature in the sea, and the trophicity of the waters, i.e. the surface concentration of chlorophyll $C_a(0)$. Owing to the vast differences in the values of these parameters in the World Ocean, quantum yields Φ measured in different seas and at different depths vary over a range of about two orders of magnitude. No one has yet provided a quantitative definition of the relationships between the quantum yield Φ and the environmental parameters that is broad enough to approximate this range of values. Partial solutions to the problem were offered by two simplified mathematical models developed by the teams from Villefranche-sur-Mer [1, 2, 24, 25] and Sopot [9, 38, 39, 40, 41]. However, the accuracy of these models of the quantum yield of photosynthesis is low, because of the numerous simplifications made and the non-recognition of the direct influence of nutrients on the photosynthetic yield.

The aim of this work is to remove these deficiencies in the modeling. In our new model we assumed the quantum yield of photosynthesis Φ in the sea to be a complex function of a set of variable environmental factors, such as underwater irradiance, nutrient content, water temperature and water trophicity. For the sake of simplicity, we took only nitrogenous nutrients into account. This step is justified by the results of numerous researchers, who found nitrogen to be the nutrient limiting photosynthesis in most of the ocean waters [e.g. 3, 5, 6, 19, 25, 45].

EMPIRICAL MATERIAL

The model of the photosynthetic yield was based on the empirical data collected by the authors or available on the Internet. Two important data bases were made use of at various stages of the modelling.

- The bio-optical data base contained around 2500 sets of empirical data collected at some 600 stations in various regions of the World Ocean (see table 1 in Majchrowski and Ostrowska[23]). The most important parameters are: primary production $P(z)$, spectral distributions of the downward irradiance $E_d(\lambda,z)$, spectral coefficients of light absorption by phytoplankton $a_{pl}(\lambda,z)$, chlorophyll *a* concentration $C_a(z)$. Such magnitudes as the mean daily or instantaneous photosynthetic yield $\Phi(z)$ were determined from these *in situ* data with the aid of eq. 1, as were the corresponding $PAR_0(z)$ irradiances and the energies absorbed by all phytoplankton pigments $PUR^*(z)$, and only by photosynthetic pigments $PUR^*_{PSP}(z)$.
- The fluorimetric data base contained over 700 sets of empirical data collected at more than 80 stations in various parts of the World Ocean (see table 1 in Ficek et all [15]). These were the minimal (initial) and maximal *in vivo* induced fluorescences of phytoplankton, respectively denoted F_0 and F_m according to the Kolberg and Falkowski [21] convention; both were measured in the dark-adapted stage, where non-photochemical quenching is at a minimum. These fluorescences were measured *in situ* in water samples containing marine algae with the aid of "pump-probe" fluorimeters using the active stimulated method [21, 26] or the chemical method *in vitro*. In the latter method the fluorescence F_m is measured after the addition of DCMU [see 33].

Apart from these primary magnitudes, a whole range of physical and chemical parameters of the marine environment, including the nitrogenous nutrient content $N_{inorg}(z)$, the concentrations of accessory pigments $C_j(z)$ and the temperature $temp(z)$ in the sea, were measured at all the stations.

RESULTS OF MODELING

Our study makes it possible to express the quantum yield Φ as the product of the theoretical maximum quantum yield Φ_{MAX} = 0.125 atomC quanta^{-1} and six dimensionless factors f_i [36, 37]. Each less than 1 in value, these factors measure the decrease in Φ compared to Φ_{MAX} due to natural (internal) imperfections in the photosynthetic apparatus or to external conditions unfavorable to plant growth. Such an expression is also compatible with the biophysical models of photosynthesis suggested by others [3, 11, 12, 21, 29, 30]. These six dimensionless factors are: f_a - a non-photosynthetic pigment absorption effect factor which describes the decrease in the observed quantum yield in relation to Φ_{MAX} due to the presence in the plant the photo-protecting pigments that do not transfer absorbed energy to the PS2 reaction centers; f_Δ - the inefficiency factor in energy transfer and charge recombination; $f_{c(N)}$ - the factor describing the effect of nutrients on the portion of functional PS2 reaction centers; $f_{c(\tau)}$ - the factor describing the reduction in the portion of functional PS2 reaction centers at large depths; $f_{c(PAR,inh)}$ - the factor describing the reduction in the portion of functional PS2 reaction centers as a result of photoinhibition; $f_{E,t}$ - the classic dependence of photosynthesis on light and temperature [e.g. 9, 13, 24] also known as the light curve of photosynthetic efficiency at a given temperature.

Each of these factors appears to be dependent on one or two environmental factors at most. The quantum yield of photosynthesis can therefore be expressed as [37]:

$$\left.\begin{aligned} &\Phi = \Phi_{MAX} \cdot f_a \cdot f_\Delta \cdot f_{c(N_{inorg})} \cdot f_{c(\tau)} \cdot f_{c(PAR,inh)} \cdot f_{E,t} \\ &\Phi_{MAX} = 0.125 \ [atomC \cdot (quanta)^{-1}] \ or \ [molC \cdot (Ein)^{-1}] \end{aligned}\right\} \quad (3)$$

The magnitude of the separate factors f_i or their dependence on environmental parameters are given in Table 1, together with their range of variability in the World Ocean, estimated from the model. They were obtained by means of the empirical studies, statistical analyses and mathematical modeling, which are described in detail in a number of papers [13, 14, 15, 36, 37]. Here, we shall just give an outline of the most important stages of these investigations.

Analysis of the Factor f_a

The light energy absorbed by the photoprotective carotenoid pigments PPC is not transferred to the photosynthetic centers, and thus not used in photosynthesis. Hence, the true photosynthesis yield Φ_{tr} is the ratio of the rate of photosynthesis to the number of quanta absorbed solely by the photosynthetic pigments PUR^*_{PSP} [Ein (mg tot.chl$a$)$^{-1}$s^{-1}], i.e. $\Phi_{tr}=P^B/PUR^*_{PSP}$, and the observed photosynthesis yield Φ, defined by eq. 1, is smaller than the real figure by a factor $f_a = PUR^*_{PSP}/PUR^*$. Since $PUR^*_{PSP} = PAR_0\ \tilde{a}^*_{pl,PSP}$ and $PUR^* = PAR_0\ \tilde{a}^*_{pl}$, this factor can be described as the ratio of two mean specific absorption coefficients (by phytoplankton $\tilde{a}^*_{pl}$ and by photosynthetic pigments only $\tilde{a}^*_{pl,PSP}$) weighted by the irradiance spectrum – see eq. (1) in Table 1. The factor f_a

can therefore be determined from the model calculations of $\tilde{a}^*_{pl,PSP}$ and $\tilde{a}^*_{pl}$ as the function of the trophicity $C_a(0)$, surface irradiation $PAR(0)$ and optical depth τ (or real z) as input data. To this end, one can also implement an approximate model, less time-consuming than the full set of model calculations, which uses the polynomial functions that we derived earlier – $\tilde{a}^*_{pl,PSP}=f(C_a(0),\tau)$ and $\tilde{a}^*_{pl}=f(C_a(0),\tau,PAR(0))$ – given in Ficek et al.[14]. According to the analysis, the factor f_a varies from 0.33 to 1, the value depending on the trophic type of sea and depth in the water column. The values of f_a are usually the highest in eutrophic waters and decrease as waters become progressively more oligotrophic (cf. examples in Fig. 1). It is also characteristics of f_a that it increases with depth.

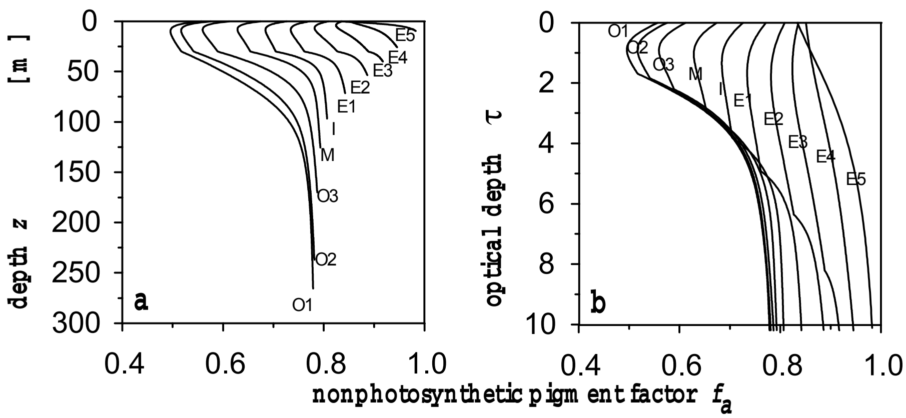

Fig. 1. The modeled vertical distributions of non-photosynthetic pigment factor f_a in different trophic types of sea: dependence on the real depth z [m] (a), dependence on the optical depth τ (b). The symbols of trophic types correspond to the surface chlorophyll a concentration $C_a(0)$ [mg tot.chla·m^{-3}]:* O1 - *0.035;* O2 - *0.07;* O3 - *0.15;* M - *0.3;* I - *0.7;* E1 - *1.5;* E2 - *3;* E3 - *7;* E4 - *15;* E5 - *30.

Analysis of Factors f_Δ and f_c

Further reasons why actual quantum yields of photosynthesis are smaller than the possible maximum, include: 1) the natural inefficiency of the photosynthetic apparatus, due to imperfections in energy transfer and charge recombination, and described by factor f_Δ, and 2) the presence of non-functional PS2 reaction centers. The latter are characterized by factor f_c, the ratio of the number of functional centers to the total number of reaction centers PS2, i.e. both functional and non-functional. As Kolber and Falkowski [21] hinted, the product of f_Δ and f_c is approximately equal to the maximum change in the quantum yield of the phytoplankton chlorophyll variable fluorescence

$$\Delta\Phi_{fl} \approx f_\Delta f_c \,. \quad (4)$$

In turn, the maximum variable fluorescence yield is given by the relation of variable and maximum fluorescence of phytoplankton chlorophyll measured *in vivo* in dark-adapted conditions $(F_m\text{-}F_0)/F_m$). The empirical material in the fluorimetric data base was analyzed in order to establish the magnitude of the factors f_Δ and f_c.

The fluorescence yields $\Delta\Phi_{fl} \approx f_{\Delta} f_c$, determined for various stations and depths, differ widely (see Fig 2a). The vertical profiles $\Delta\Phi_{fl}(z)$, however, display certain characteristic regularities (see Fig 2b). The tendency for $\Delta\Phi_{fl}$ to rise with increasing trophicity is evident: this increase is due to the larger quantity of nutrients in eutrophic waters.

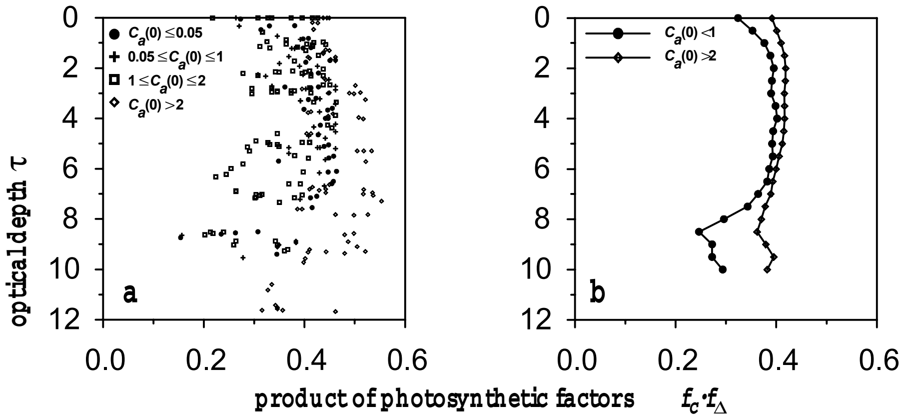

Fig. 2. Exemplary vertical profiles (referred to the optical depth τ) of maximal variable fluorescence yield of phytoplankton chlorophyll in vivo $\Delta\Phi_{fl} = f_{\Delta} f_c$ in various trophic types of sea: measured values (a); mean values in two different groups of seas (b)

This nutrient content exerts a positive effect on a portion of the functional PS2 reaction centers (RC). Furthermore, there is for each type of water, a certain optimal depth at which $\Delta\Phi_{fl}$ is the greatest. On moving either up or down from this optimal depth, we find the value of $\Delta\Phi_{fl}$ decreasing, probably because the factor f_c also falls. All these trends were noted earlier [3, 21]. At present, it seems reasonable to explain the decrease in f_c at the surface by photoinhibition, that is, the destructive activity of excess irradiance. On the other hand, the smaller number of functional PS2 centers at greater depths may be due to insufficient irradiance and diminishing numbers of RC. The quantitative description of these trends, i.e. finding the characteristic values of f_{Δ} and presenting f_c as a function of the underwater irradiance in the sea, the optical depth and the nutrient content in the water, was obtained by means of a statistical analysis of the relations between the chlorophyll variable fluorescence $\Delta\Phi_{fl}$ and these parameters of the marine environment.

After numerous attempts to apply the methods of non-linear regression to a multivariable function, we were able to formulate the following expression describing this function, which gives a good approximation of the empirical data:

$$\Delta\Phi_{fl} \approx f_{\Delta} \cdot f_c = c_1 \cdot \underbrace{\frac{N_{inorg}}{N_{inorg} + c_2}}_{f_c(N_{inorg})} \cdot \underbrace{\exp\left[-c_3 \frac{PAR}{c_4 (c_5)^{temp/10}} \right]}_{f_c(PAR,inh)} \cdot \underbrace{(1 - c_6 \cdot \tau^2)}_{f_c(\tau)} \qquad (5)$$

where the variables are expressed in the following units: N_{inorg} – the concentration of inorganic nitrogen in [µM]; PAR – the downward irradiance in the interval 400 – 700nm [$\mathrm{Ein \cdot m^{-2} \cdot s^{-1}}$]; τ - the optical depth [dimensionless], and the constants take the values: c_1=0,600±0,112[dimensionless]; c_2=0,0585µM; c_3=0,00937[dimensionless]; c_4=3,05·10^{-5} $\mathrm{Ein \cdot m^{-2} \cdot s^{-1}}$; c_5=1,907[dimensionless]; c_6=0,0031[dimensionless]. As it can be seen, the expression for the relation between the product $f_{\Delta} \cdot f_c$ and the environmental parameters given by eq. (5) comprises the product of four dimensionless factors. These could be interpreted as follows:

- The first factor, given by constant c_1, is the factor f_{Δ}, postulated by Kolber and Falkowski [21] describing the "inefficiency" of energy transfer and charge recombination in the photosynthetic apparatus. The value for marine phytoplankton as a whole is typically $f_{\Delta} = 0.600 \pm 0.112$ (see eq. (2) in Table 1). The value is thus somewhat lower than that (f_{Δ} =0.65) given by [21]. Which of these values is closer to the actual one is hard to state at present.

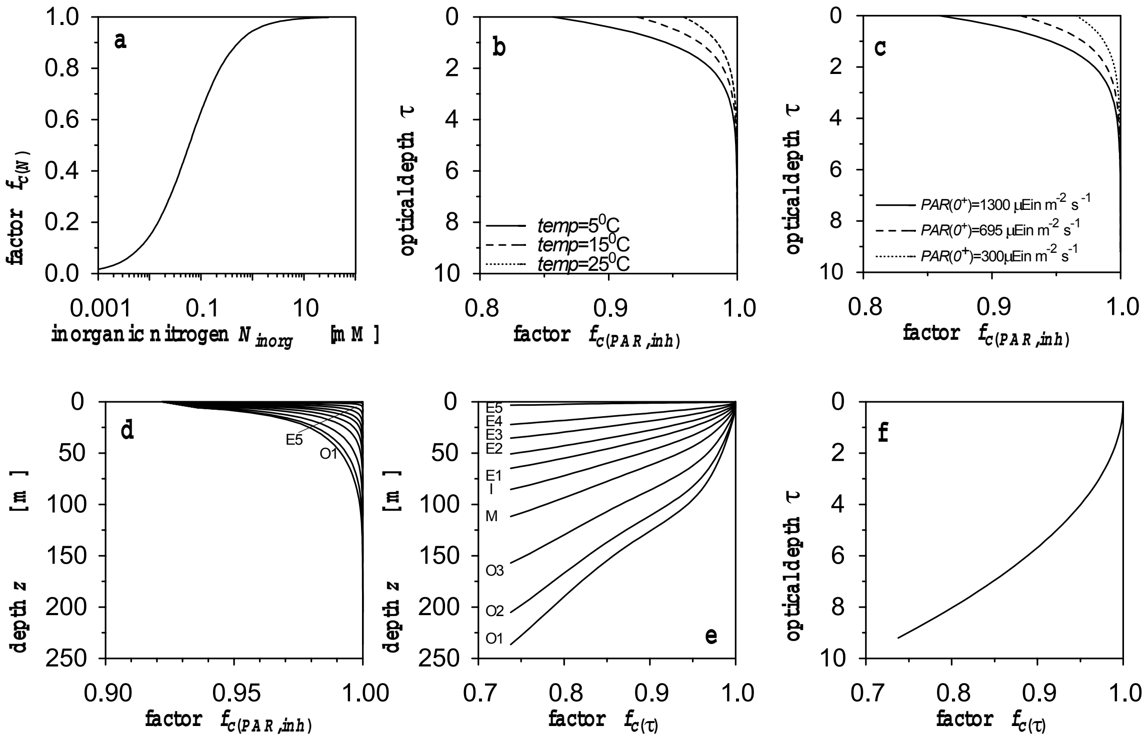

Fig. 3. Influence of abiotic environmental factors on the relative number of functioning photosynthetic RC in marine phytoplankton, estimated on the basis of model relationships (eqs (3)-(5) in Table 1): dependence of the factor $f_{c(N)}$ on the concentration of inorganic nitrogen nutrients in the sea (a);vertical distributions (with respect to the optical depth) of the factor $f_{c(PAR,inh)}$ determined for a surface irradiance of PAR(0^+)=695 µEin $m^{-2}s^{-1}$ and three temperatures: (temp = 5, 15, 25^0C) (b); vertical distributions (with respect to the optical depth) of the factor $f_{c(PAR,inh)}$ determined for the temperature temp=15^0C and three surface irradiances: PAR(0^+) = 300, 695, 1300 µEin·m^{-2}·s^{-1} (c); vertical distributions (with respect to the real depth) of the factor $f_{c(PAR,inh)}$ in different trophic types of sea (see comment in Fig 1), determined for surface irradiance PAR(0^+)=695 µEin $m^{-2}s^{-1}$ and the temperature temp = 15^0C (d); vertical distributions (with respect to the real depth) of the factor $f_{c(\tau)}$ in different trophic types of sea (see comment in Fig 1) (e); vertical distributions (with respect to the optical depth) of the factor $f_{c(\tau)}$.

- The next factor, $f_{c(Ninorg)}$, (see eq. (4) in Table 1) describes the effect of nutrient concentrations on the number of functional RC in the photosynthetic apparatus. The expression resembles equations of the Michaelis-Menten type. The constant c_2=0,0585µM is equivalent to the concentration of nitrogenous nutrients, for which the relative number of functional RC falls to half the maximum number. Bearing in mind the natural variability of the nitrogen concentration in the sea, from ca. 0.003µM to ca. 30µM, the factor $f_{c(Ninorg)}$ can vary in value twenty fold – from ca. 0.05 to ca. 1 (see Fig. 3a).
- The third factor in eq. (5) is $f_{C(PAR,inh)}$, which describes the decrease, due to light inhibition, in the relative number of functional RC in the surface layer. This factor correlates well with the absolute level of PAR_0 irradiance in the sea and is also dependent on the water temperature. It is given by the relationship (5) in Table 1. The existence of such light inhibition has been demonstrated by other authors [27]. This inhibition reduces the photosynthetic yield to only a relatively small extent and affects only surface waters. The value of factor $f_{c(PAR,inh)}$ is generally in excess of 0.85 and increases rapidly with depth – see Fig.3b–d.
- The last factor affecting the relative number of functional RC in the phytoplankton is the optical depth. This is described by the relationship for $f_{C(\tau)}$ given in Table 1 (eq. (3)). Clearly (but see also Figs. 3e and f), at large optical depths in the sea there is a distinct drop in the value of $f_{c,(\tau)}$, from 1 at the surface to ca. 0.73 at depths equal to twice the thickness of the euphotic layer τ_{2ze}≈9.6. At present, the mechanism of this phenomenon is not well understood. Presumably, it is brought about by a light deficit and the "fading" of chlorophyll *a* [35, 44] As a result of such "fading", the photosynthetic reaction centres do not function, even if large concentrations of nutrients and sufficient amounts of photosynthetically useful radiation are present.

Analysis of the Factor $f_{e,t}$

The relation between the photosynthetic yield and the irradiance conditions are described by the so-called "light curves" of the yield, which are equivalent to factor $f_{E,t}$ and are additionally dependent on the sea water temperature. Establishing the relationship between $f_{E,t}$ and the irradiance and temperature for the entire phytoplankton in the World Ocean was the final, but also the most labor-intensive stage of our statistical analysis. Some 2500 sets of empirical data from the bio-optical data bank had to be analyzed, including the mean daily quantum yield $\boldsymbol{\Phi}(z)$ at given depths. From these data and the relevant statistical formulas (see above), the mean daily values of $f_{E,t}(z)$ could be determined for particular depths. According to eq. (3), they were

$$f_{E,t}(z)=\frac{\Phi(z)}{0.125\frac{atomC}{quanta}\cdot f_a\cdot f_\Delta\cdot f_{C,(N_{inorg})}\cdot f_{C,(PAR,inh)}\cdot f_{C,(\tau)}}, \tag{6}$$

where the factors $f_a, f_\Delta, f_{c,(Ninorg)}, f_{c,(PAR,,inh)}, f_{c(\tau)}$ were assumed, or calculated with the aid of the formulas given in Table 1 (eqs. (1) – (5)). The empirical relationship $f_{E,t}(z)$ *versus* $PAR(z)$ (Fig. 4a) displays considerable scatter, due, among other things, to the influence of the temperature on the yield. This is illustrated, for example, in Fig. 4b, which shows

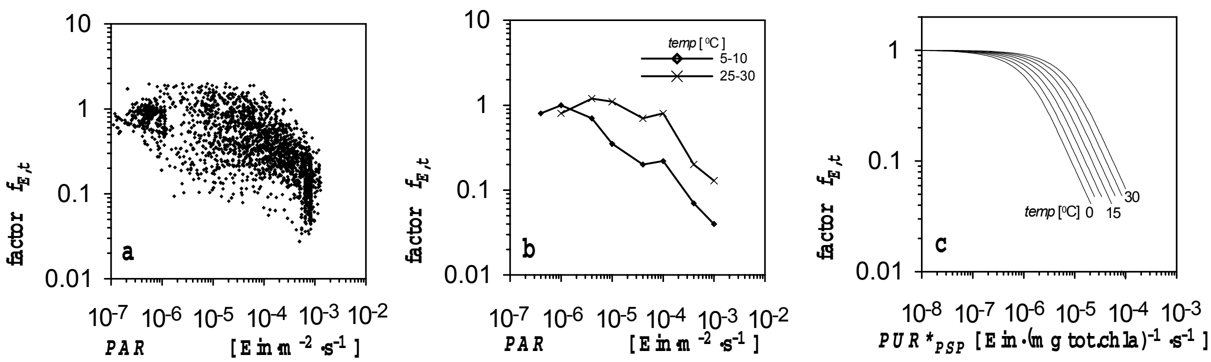

Fig. 4. Observed dependence of mean daily values of the factor $f_{E,t}(z)$ at different depths in the sea on the underwater irradiance PAR or absorbed energy PUR^*_{PSP}: for all the points collected in the „bio-optical data bank" (a); averaged for two exemplary temperature intervals 5-10 °C and 25-30 °C (b); modeled dependence of $f_{E,t}$ on the energy PUR^*_{PSP} for various temperatures (according to eq. (6) in Table 1) (c).

that the plots of the relation $f_{E,t}(z)$ *versus* $PAR(z)$ are positioned differently for different temperatures. Hence, it is imperative to take account of the effect of temperature on the "light curve" parameters of the photosynthetic yield.

The following expression for the light curves of the photosynthetic efficiency at different temperatures was used for performing the approximations on the entire data bank [34]:

$$f_{E,t} = \left[1 - \exp\left(-\frac{PUR^*_{PSP}}{KPUR^*_{PSP}(temp)}\right)\right]\frac{KPUR^*_{PSP}(temp)}{PUR^*_{PSP}}, \qquad (7)$$

where $KPUR^*_{PSP}(temp)$ depends on the temperature *temp* [^{0}C] in accordance with the Arrhenius law:

$$KPUR^*_{PSP}(temp) = KPUR^*_{PSP,0} \cdot Q_{10}^{\,temp/10^0C}, \qquad (8)$$

where $KPUR^*_{PSP,0}$ is the "saturation irradiance" at $temp=0^0$C, and Q_{10} is a parameter indicating the multiplication factor of the increase in saturation irradiance due to a temperature rise of $\Delta temp=10^0$C.

Using these formulas together, non-linear regression methods applied to two variables (described in detail in [13]) yielded the following results for the approximations:

$$KPUR^*_{PSP,0} = 8{,}545 \cdot 10^{-7} \quad \left[Ein(mg\ tot\ chla)^{-1} \cdot s^{-1}\right]$$
$$Q_{10} = 1.874 \qquad (9)$$

This magnitude was assigned to the model developed in the present work (see eq. (6) in Table 1). Plots of $f_{E,t}$ *versus* PUR^*_{PSP} for selected temperatures *temp* modeled with the aid of this relationship are shown in Fig. 4c.

CONCLUSIONS AND PRACTICAL COMMENTS

As it can be seen from Table 1, the quantum yield Φ typically varies under different marine conditions by about 100 times, i.e. two orders of magnitude. This is less than the product of typical variability of the all six dimensionless factors f_i in formula 3, which can reach a figure of 400. This means that the activities of some of these factors cancel each other out. Light and temperature have the greatest impact on the variability of the natural quantum yield Φ (range about 20 times). Of somewhat less significance is the nutrient content, which may affect the quantum yield by a factor of 4. Finally, threefold variations may occur as a result of variability in non-photosynthetic pigments f_a. The other factors affect the variability in Φ to a much lesser extent.

Table 1. The photosynthesis quantum yield determining factors f_i (see eq. (49)) expressed through mathematical formulae describing their dependence on abiotic environmental factors, the sea trophicity index $C_a(0)$, and optical depth τ.

No of eq.	Mathematical description of the dependence	Typical magnitude of variability in the World Ocean
1	$f_a = \frac{\tilde{a}^*_{pl,PSP}}{\tilde{a}^*_{pl}}$, where: $a^*_{pl} = f(C_a(0), \tau, PAR(0^+))$, $a^*_{pl,PSP} = f(C_a(0), \tau)$	0.33÷1 (about 3 times)
2	$f_\Delta \approx 0.600 \pm 0.112$	nearly constant
3	$f_{c(\tau)} = 1 - 0.00310\tau^2$	0.72÷1 (about 1.4 times)
4	$f_{c(N_{inorg})} = \frac{N_{inorg}}{N_{inorg} + 0.0585}$	0.25÷1 (about 4 times)
5	$f_{c(PAR,inh)} = \exp\left(-0.00937\frac{PAR}{3.049\cdot10^{-5}\cdot1.907^{\frac{temp}{10}}}\right)$	0.85÷1 (less than 1.2 times)
6	$f_{E,t} = \left[1 - \exp\left(-\frac{PUR^*_{PSP}}{8.545\cdot10^{-7}\cdot1.874^{\frac{temp}{10}}}\right)\right]\frac{8.545\cdot10^{-7}\cdot1.874^{\frac{temp}{10}}}{PUR^*_{PSP}}$	0.05÷1 (about 20 times)
	Φ - as the product, altogether	0.0002÷0.075 (about 400 times)
	Φ - as observed values	0.001÷0.075 (about 100 times)

where: $C_a(0)$ – surface chlorophyll a concentration [mg tot.chla·m^{-3}], τ - optical depth in the sea (dimensionless), N_{inorg} – inorganic forms of nitrogen (N=N(NO2)+N(NO3)+N(NH4)) [µM], PAR,inh – scalar irradiance in the PAR spectrum range [Ein·m^{-2}·s^{-1}], PUR^*_{PSP} – radiation flux absorbed by photosynthetic pigments [Ein·(mg tot.chla)$^{-1}$·s^{-1}], temp – ambient water temperature [°C].

The modeled description of photosynthetic yield developed in this section was now subjected to empirical validation in order to assess its accuracy. Magnitudes of the quantum yield Φ_C calculated using the model (eq. (3) and Table 1) were compared with empirical magnitudes of the yield Φ_M extracted from the bio-optical data base. The results of this validation, presented in Fig. 5 and Table 2, show that the errors are relatively small. They are much smaller than those encumbering our earlier model [38], which took only the relations between Φ, the trophicity of the water $C_a(0)$ and the underwater irradiance *PAR* into consideration. For instance, the statistical error in the present model σ is about 42%, whereas in Woźniak's earlier model it was as much as 74%.

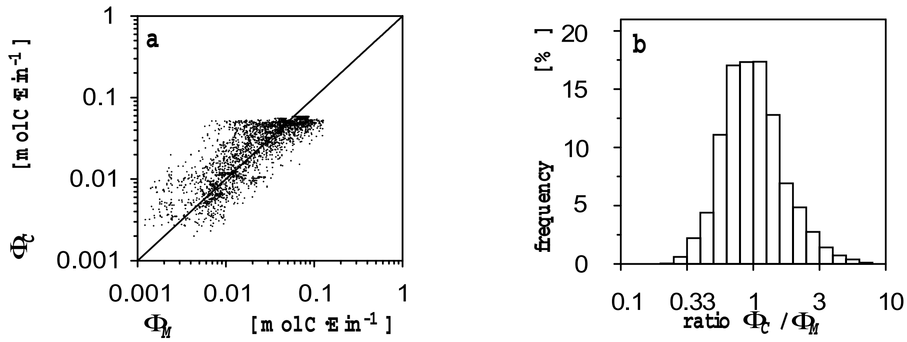

Fig. 5. Comparison of the measured Φ_M and the modelled Φ_C quantum yields (a) and the histogram of the ratio Φ_C/Φ_M (b) at different stations and at various depths in the sea, determined according to the model of yields presented in this paper (eq. (3) in Table 1)

Table 2. Errors of the estimation of the quantum yield of photosynthesis Φ determined using the described model

Arithmetic statistics		Logarithmic statistics			
systematic	statistical	systematic	standard error factor	statistical	
$\langle \varepsilon \rangle$ [%]	σ_ε [%]	$\langle \varepsilon \rangle_g$ [%]	x	σ_- [%]	σ_+ [%]
6.0	±42.5	-1.4	1.53	-34.6	53.1

where:

$\varepsilon = (\Phi_C - \Phi_M)/\Phi_M$ - errors,

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

σ_ε - standard deviation of errors (statistical error),

$\langle \varepsilon \rangle_g = 10^{[\langle \log(\Phi_C/\Phi_M) \rangle]} - 1$ - logarithmic mean of errors

$\langle \log(\Phi_C/\Phi_M) \rangle$ - mean of $\log(\Phi_C/\Phi_M)$,

$\sigma_{\log}$ - standard deviation of $\log(\Phi_C/\Phi_C)$,

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

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

REFERENCES

1. Antoine D., Andre J. M., Morel A., 1996, Global Biogeochemical Cycles. 10, 56-69.
2. Antoine D., Morel A., 1996. Global Biogeochemical Cycles. 10, 42-55.
3. Babin M., Morel A., Claustre H., Bricaud A., Kolber Z., Falkowski P. G., 1996, Deep-Sea Res., 43, 1241-1272.

4. Bannister T. T., 1979, Limnol. Oceanogr., v. 24, 76-96.
5. Belayev V.I., 1987, Naukova Dumka, Kiev, (in Russian).
6. Bougis P., 1976, North-Holland, Amsterdam etc.
7. Cleveland J. S., Perry M. J., Kiefer D. A., Talbot M. C., 1989, J. Mar. Res., 47 (4), 869-886.
8. Dera J., 1992, Marine Physics, Elsevier, Amsterdam-Oxford-New York-Tokyo, 516 pp.
9. Dera J., 1995, Dissertations and Monographs, IO PAS, Sopot, No 7, 110 pp.
10. Eppley R. W., Sharp J. H., 1975, Limnol. Oceanogr., 20, 981-987.
11. Falkowski P. G., Kiefer D. A., 1985, J. Plankton Res., 7, 715-731.
12. Falkowski P. G., Wyman K., Ley A. C., Mauzerall D., 1986, Biochim. Biophys. Acta, 829, 183-192.
13. Ficek D., 2001, Dissertations and Monographs, IO PAS, Sopot, 224 pp (in Polish).
14. Ficek D., Woźniak B., Majchrowski R., Ostrowska M., 2000a, Oceanologia, 42(2), 231-242.
15. Ficek D., Ostrowska M., Kuzio M., Pogosyan S. I., 2000b, Oceanologia, 42(2), 243-249.
16. Geider R. J., Greene R. M., Kolber Z., MacIntyre H. L., Falkowski P. G., 1993, Deep-Sea Res., 40 (6), 1205-1224.
17. Kiefer D. A., Mitchell B. G., 1983, Limnol. Oceanogr., 28, 770-776.
18. Koblentz-Mishke O. I., Woźniak B., Ochakovskiy Yu. E., 1985, Izd. Inst. Okeanol. AN SSSR, Moskva, 336, (in Russian).
19. Koblentz-Mishke O. J., Vedernikov V. I., 1977, [in:] Vinogradov M. E. (ed.), 1977, vol.2, 183-208.Kolber Z., Falkowski P. G., 1993, Limnol. Oceanogr., 38(8), 1646-1665.
20. Kolber Z., Falkowski P. G., 1992, Proc. of Ocean 92 Conference, Newport, Rhode Island.
21. Kolber Z., Falkowski P. G., 1993, Limnol. Oceanogr., 38(8), 1646-1665.
22. Ley A. C., Mauzerall D., 1982, Biochimica Biophysica Acta, 680, 95-106.
23. Majchrowski R., Ostrowska M., 2000, Oceanologia, 42 (2), 157 – 175.
24. Morel A., 1991, Prog. Oceanogr., 26, 263-306.
25. Morel A., Antoine D., Babin M., Dandonneau Y., 1996, Deep-Sea Res., 43, 1273-1304.
26. Ostrowska M., 2001, Dissertations and Monographs, IO PAS, Sopot, 194 pp, (in Polish).
27. Platt T., Gallegos C.L., Harrison W.G., 1980, J. Mar. Res., 38, 687 – 701.

28. Platt T., Sathyendranath S., Ulloa O., Harrison W. G., Hoepffner N., Goes J., 1992, Nature, 356, 229-231.

29. Rubin A. B., 1995, OHTI PHC RAN, Moskva, 33, 38, (in Russian).

30. Rubin A. B., Kononenko A. A., Shaitan K. V., Paschenko V. Z., Riznichenko G. Yu., 1994, Biophysics, 39 (2), 173-195.

31. Smith R. C., Prezelin B. B., Bridigare R. R., Baker K. S., 1989, Limnol. Oceanogr., 34 (8), 1524-1544.

32. Steemann Nielsen E., 1975, Marine Photosynthesis., Elsevier, Amsterdam-New York, 141 pp.

33. Vedernikov V. I., Vshyntsev V. S., Demidov A. A., Pogosyan S. I., Sukhanova I. N., Fadeyev V. V., Chekaluk A. M., 1990, Okeanologiya, 30, 848-854, (in Russian).

34. Webb W. L., Newton M., Starr R. C., 1974, Ecologia, 17, 281-291.

35. Wolken J. J., 1975, Photoprocesses, Photoreceptors and Evolution, Academic Press New York, San Francisco, London, 317 pp.

36. Woźniak B., Dera J., 2000, Oceanologia, 42 (2), 137-156.

37. Woźniak B., Dera J., 2001, Proc. Int. Conf. "Current problems in optics of natural waters" (ONW-2001, St. Petersburg), September 25-28, 2001, 39-49.

38. Woźniak B., Dera J., Koblentz-Mishke O. I., 1992a, Oceanologia, 33, 5-38.

39. Woźniak B., Dera J., Koblentz-Mishke O. I., 1992b, Ocean Optics 11, SPIE, 1750, 246-275.

40. Woźniak B., Dera J., Semovski S., Hapter R., Ostrowska M., Kaczmarek S., 1995a, Stud. i Mater. Oceanol., PAS, Sopot, 68, 91-123.

41. Woźniak B., Smekot-Wensierski W., Darecki M., 1995b, Stud. i Mater. Oceanol., PAS, Sopot, 68, 61-90.

42. Woźniak B., Dera J., Majchrowski R., Ficek D., Koblenz-Mishke O. J., Darecki M., 1997a, Oceanologia 39 (4), 377-395.

43. Woźniak B., Dera J., Majchrowski R., Ficek D., Koblentz-Mishke O.J., Darecki M., 1997b, SPIE vol 3222, 516-528.

44. Woźniak B., Ostrowska M., 1990, Oceanologia 29, 91 – 115.

45. Wróblewski J. S., 1989, Limnol. Oceanogr., 34 (8), 1563 – 1571.