‘IO PAS initial model’ of marine primary production for remote sensing applications*

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Abstract

A model of marine primary production with a set of statistical relationships linking physiological parameters of the phytoplankton with abiotic factors of the sea has been developed. The study is based on empirical data analysed from some 3500 stations in various oceanic regions. The data comes from Polish and Russian expeditions as well as from literature.

1. Introduction

Many authors are now improving the models for estimating the primary production of the Ocean and to control the carbon cycle using remote sensing data. The original models (Antoine and Morel, 1996; Antoine *et al.*, 1996; Dera, 1995; Morel, 1991; Morel *et al.*, 1996; Platt and Sathyendranath, 1988; Platt *et al.*, 1988; Sathyendranath *et al.*, 1989; Woźniak *et al.*, 1992a,b; Woźniak *et al.*, 1995) were based on approximate relationships between primary production P, solar underwater irradiance PAR, temperature T and chlorophyll a concentration C_a in the sea (see the notation in the appendix)

$$P = P^C C_a, \tag{1}$$

where the rate of carbon assimilation per unit of chlorophyll a

$$P^C = \Phi_{\mathrm{real}} PUR^*. \tag{2}$$

The real quantum yield of carbon fixation, which we will also call the quantum yield of photosynthesis,

$$\Phi_{\mathrm{real}} = \Phi_{\max} f(PAR). \tag{3}$$

The Photosynthetically Utilised Radiation per unit of chlorophyll

$$PUR^* = \tilde{a}{}^*_{pl}\ PAR, \tag{4}$$

where

$\Phi_{\max}$ – the maximum quantum yield of photosynthesis under given external environmental conditions, with extremely low irradiance, (not to be confused with the constant absolute quantum yield $\Phi_{\mathrm{MAX}} = 0.125$ atoms C quanta^{-1}),

$\tilde{a}{}^*_{pl}$ – plankton light absorption coefficient – the specific, weighted mean of the PAR spectrum,

PAR – Photosynthetically Available Radiation in the sea.

PAR and $\tilde{a}{}^*_{pl}$ are functions of the chlorophyll a (+ pheophytin) concentration C_a definable from a series of earlier models and bio-optical classifications. (Baker and Smith, 1982; Morel, 1988; Smith and Baker, 1978; Woźniak *et al.*, 1992a,b).

It was found, however, that the absorption coefficient a_{pl} strongly depends on the underwater irradiance spectrum. This results *inter alia* from the adaptive properties of plankton cells and the role of the accessory pigments (Bricaud *et al.*, 1995; Woźniak and Ostrowska, 1990a,b). Many authors are now attempting to establish this relationship (Allali *et al.*, 1997; Babin *et al.*, 1996b; Bidigare *et al.*, 1996; Sadoudi *et al.*, 1996); a preliminary solution to this problem is put forward in the present paper.

$\Phi_{\max}$ also appears to be dependent on a number of environmental factors (Babin *et al.*, 1996a; Kudela and Chavez, 1996; Ondrusek and Bidigare, 1996). An initial version of its rather strong dependence on nutrient concentration and weaker relationship with temperature is established in this paper. It aims to present refined statistical relationships between the physiological properties of the phytoplankton and the three main abiotic environmental factors *i.e.* irradiance $PAR(z)$, temperature $T(z)$, and inorganic nitrogen concentration $\mathrm{N_{inorg}}(z)$ in the sea, the set of elements assumed in the marine primary production model.

The statistical relationships given here are based on empirical data analysed from some 3500 stations in various oceanic regions. The data are derived from Polish and Russian expeditions in 1970–1996 as well as from the literature and cover practically all regions and combinations of environmental factors that can occur in the sea.

2. Structure of the model

The basic equations of the model are derived from modifications of eqs. (1) and (2) written in the following form:

$$P = P^B B_a, \tag{5}$$

$$P^B = \Phi_{\mathrm{real}} PUR^*_{PSP}, \tag{6}$$

where

$$PUR^*_{PSP} = PUR^* - PUR^*_{PPP}. \tag{7}$$

PSP denotes Photosynthetic Pigments (chls *a*, *b*, *c*, phycobilins, selected carotenoids, *e.g.* fucoxanthin, 19′ but-fucoxanthin, 19′ hex fucoxanthin, peridinin, prasinoxanthin, α-carotene).

PPP denotes Photoprotecting Pigments (selected carotenoids, *e.g.* diadinoxanthin, alloxanthin, zeaxanthin, diatoxanthin, lutein, antheraxanthin and β-carotene). P^B is the rate of carbon fixation per unit of active chlorophyll *a*

$$P^B = \frac{P}{B_a} = P^C \rho^{-1} \qquad \text{and} \qquad \rho = \frac{B_a}{C_a}, \tag{8}$$

Φ_{real} in eq. (6), given earlier in eq. (3) is modified as follows:

$$\Phi_{\mathrm{real}} = \Phi_{\max}(\mathrm{N_{inorg}}, T)\, f(PUR^*_{PSP}), \tag{9}$$

where $f(PUR^*_{PSP}) = LF$ is a dimensionless light factor.

Also the PUR^*_{PSP} given in eq. (6) according to the eq. (7) has been modified as follows:

$$PUR^*_{PSP} \equiv \tilde{a}^*_{PSP}\ PAR, \tag{10}$$

where

$$\tilde{a}^*_{PSP} = Q\,\frac{\int_{\lambda=400}^{700} a^*_{PSP,\,S}(\lambda) E(\lambda) d\lambda}{PAR}, \tag{11}$$

and $Q = \tilde{a}^*_{pl}\ /\ \tilde{a}^*_{pl,\,S}$ is a correction factor due to the package effect and because phycobilin has been neglected;

$$\tilde{a}^*_{pl,\,S} = \frac{\int_{\lambda=400}^{700} a^*_{pl,\,S}(\lambda) E(\lambda) d\lambda}{PAR} \tag{12}$$

describes the mean specific absorption coefficient of light of the plankton in solution, where the package effect does not exist. $\tilde{a}^*_{pl}$, is the coefficient in its natural state. Furthermore,

$$\begin{aligned} a^*_{PSP,\,S}(\lambda) \approx \frac{1}{C_a}[&C_a\, a^*_a(\lambda) + C_{PSC}\, a^*_{PSC}(\lambda) + C_b\, a^*_b(\lambda) + \\ &+ C_c\, a^*_c(\lambda)], \end{aligned} \tag{13}$$

$$\begin{aligned} a^*_{pl,\,S}(\lambda) \approx \frac{1}{C_a}[&C_a\, a^*_a(\lambda) + C_{PSC}\, a^*_{PSC}(\lambda) + C_b\, a^*_b(\lambda) + \\ &+ C_c\, a^*_c(\lambda) + C_{PPC}\, a^*_{PPC}(\lambda)]. \end{aligned} \tag{14}$$

3. Material and methods

The following quantities existing in the set of eqs. (5) to (14) are initially established by means of statistical analysis of the empirical data:

$\rho = f[C_a(0), \tau]$ – see eq. (15),

$\Phi_{\max} = f(\mathrm{N_{inorg}}, T)$ – see eq. (16),

$Q = f(C_a)$ – see eq. (17),

$C_{PSC} = f(C_a, SOPS)$ – see eqs. (18) and (19),

$C_b = f(C_a, SOPS)$ – see eq. (20),

$C_c = f(C_a)$ – see eq. (21),

$C_{PPC} = f[C_a, SOPS, PAR(0)]$ – see eqs. (22) to (24),

$LF \equiv \frac{\Phi_{\mathrm{real}}}{\Phi_{\max}} = f(PUR^*_{PSP})$ – see eqs. (25) and (26).

Some of these formulas result from an approximation of the empirical data set with the aid of well-founded physical functions *e.g.* the Michaelis–Menten expression, the Arrhenius low and others (eqs.: (16), (19), (19a), (23), (25) and (26)). The other formulas are approximations of the empirical data set by polynomials or other functions describing only statistical relationships (eqs. (25), (17), (18) and others).

The empirical material enabling these relationships to be established was obtained during numerous cruises to different regions of the World Ocean on the research vessels of the P. P. Shirshov Institute of Oceanology of the Russian Academy of Sciences in Moscow and of the Institute of Oceanology of the Polish Academy of Sciences in Sopot. Data from about 3500 open sea stations were analysed (see chart in Fig. 1 and Tab. 1).

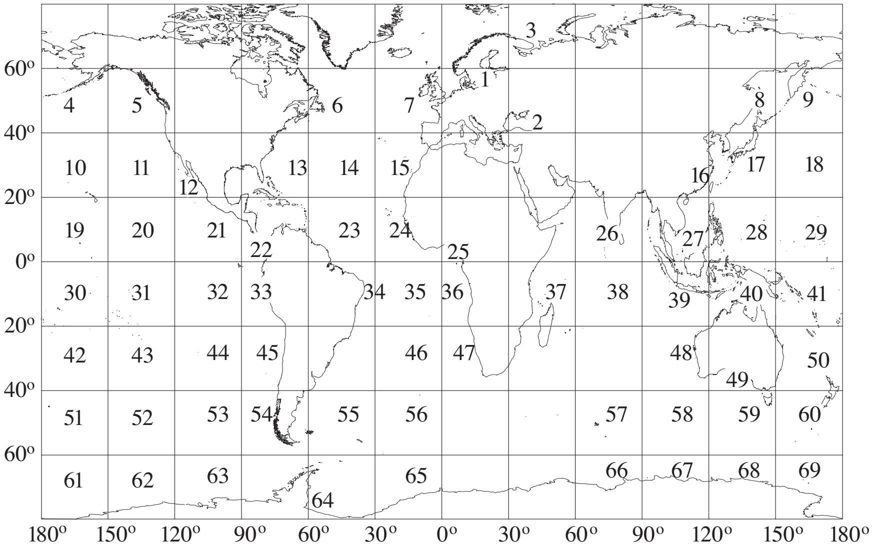

Fig. 1. Locations of data collection regions. The numbers refer to areas delimited by geographical grid lines. The respective numbers of the various regions are used in Tab. 1

Note that the measurements were performed by different methods and with variable precision (Bekasova *et al.*, 1990; Bojanowski, 1984; Hapter *et al.*, 1984; Karabashev *et al.*, 1990; Koblentz-Mishke *et al.*, 1985; Koblentz -Mishke, 1987; Konovalov *et al.*, 1990; Moroshkin, 1973; Olszewski, 1984; Ooms, 1996; Ponomareva and Pasternak, 1985; Semina, 1981, 1985; Vinogradov, 1971, 1980; Vinogradov and Ozmidov, 1986; Witek and Allikas, 1990; Woźniak *et al.*, 1984; Zvalinsky *et al.*, 1990). Moreover, the data sets were often incomplete, as can be seen from Tab. 1.

Table 1. Numbers of stations at which the vertical profile data were analysed. The numbers of the regions are shown on the map in Fig. 1

Region	Number of stations			
number	$C_a(z)^{1)}$	$N(z)$, $T(z)^{2)}$	$P(z)^{3)}$	$OPS(z)^{4)}$
1	910	800	220	761
2	251	200	71	103
3	10	10	9	
4	24	24	10	
5	22	21	14	
6	27	10	9	30
7	10	10	10	
8	13	5	13	
9	21	16	12	
10	1	1		
11	7	7		
12	3	2	3	
13	7	7	7	
14	48	22	18	40
15	140	87	78	
16	3			
17	26	9	16	
18	5		5	
19	14	14	9	
20	4	4	2	
21	17	7	17	
22	34	28	34	
23	41	41		
24	288	291	35	
25	4	4		
26	12	3	3	9
27	32	32		
28	35	8	31	
29	42	24	19	
30	21		16	
31	28			
32	13		12	
33	89		78	
34	50	49		
35	198	204	13	
36	58	55	36	
37	10	6	6	10
38	11	1	2	4
39	78		60	

Table 1. (continued)

Region number	Number of stations $C_a(z)$ 1)	$N(z)$, $T(z)$ 2)	$P(z)$ 3)	$OPS(z)$ 4)
40	19		19	
41	119	4	42	9
42	15		15	
43	36		14	
44	7		7	
45	37		35	
46	4	4	4	2
47	14	14	14	6
48	70		69	
49	4		2	
50	145		71	
51	14		14	
52	57		57	
53	22		18	
54	12		8	
55	5			10
56	8		4	10
57	3		1	
58	12		9	
59	19		17	
60	57		51	
61	11		3	
62	14		13	
63	10		10	
64	58	48	23	44
65	6			
66	3			
67	4		1	
68	6		4	
69	31		24	
Total	3429	2072	1038	1037

Comments:

1) Vertical distributions of chlorophyll a + pheo. concentration and other pigments in some cases.
2) Vertical distributions of nutrient concentrations and temperatures in the euphotic layer.
3) Vertical distributions of primary production.
4) Vertical distributions of irradiance PAR and/or irradiance spectrum and various optical properties of seawater.

The spectra of the specific light absorption coefficient of the phytoplankton pigments ($a^*_a(\lambda)$, $a^*_b(\lambda)$, $a^*_c(\lambda)$, $a^*_{PPC}(\lambda)$ and $a^*_{PSC}(\lambda)$) were taken from Bidigare *et al.* (1996).

A complete set of data from the 23rd expedition of the r/v 'Vityaz' to the North Atlantic and the Black Sea in 1991 was used for the preliminary validation of the model.

4. Results of the modelling

The relationships established in our study as well as some of their graphical representations are presented here below. There is no detailed discussion of the errors of particular model formulas owing to the limited space in this paper, but the results of testing the whole model are given.

The pigment ratio $\rho = B_a \,/\, C_a$ in eq. (8), *i.e.* the fraction of living chlorophyll a, is determined by the polynomial

$$\rho[\log C_a(0),\, \tau] = \sum_{i=0}^{2} \left[\sum_{j=0}^{2} a_{i,\,j} (\log C_a(0))^j \right] \tau^i, \tag{15}$$

where $\tau = K_{PAR}\, z$ – optical depth in the sea. The $a_{i,\,j}$ values are given in Tab. 2.

Table 2. Values of $a_{i,\,j}$ in eq. (15)

$_j\backslash\, i$	0	1	2
0	0.7027	0.01497	–0.004769
1	0.2008	–0.06439	0.003730
2	0.1634	–0.07041	0.004410

The pigment ratio is shown graphically in Fig. 2.

The maximum quantum yield of carbon fixation is given by

$$\begin{aligned}\Phi_{\max}(\mathrm{N_{inorg}},\, T) \;&=\; 0.086 \left[\frac{\text{atoms C}}{\text{quanta}}\right] \frac{\mathrm{N_{inorg}}}{\mathrm{N_{inorg}} + 1.175(0.1084)^{T/10}} \times \\ &\times\; \exp[-8.87\times 10^{-4}\, \mathrm{N_{inorg}} (T+273)^{0.247}],\end{aligned} \tag{16}$$

where $\mathrm{N_{inorg}}$ is the concentration of inorganic nitrogen compounds (nitrate, nitrite, ammonia) in [μM dm^{-3}], T [°C] – temperature *in situ*.

Fig. 3 gives a graphical representation of $\Phi_{\max}$ according to eq. (16).

The package correction factor Q in eq. (11) depends on the chlorophyll a concentration C_a and the dependence is approximated here as follows:

$$\log Q = 0.9089 (\log C_a)^{-0.1752}. \tag{17}$$

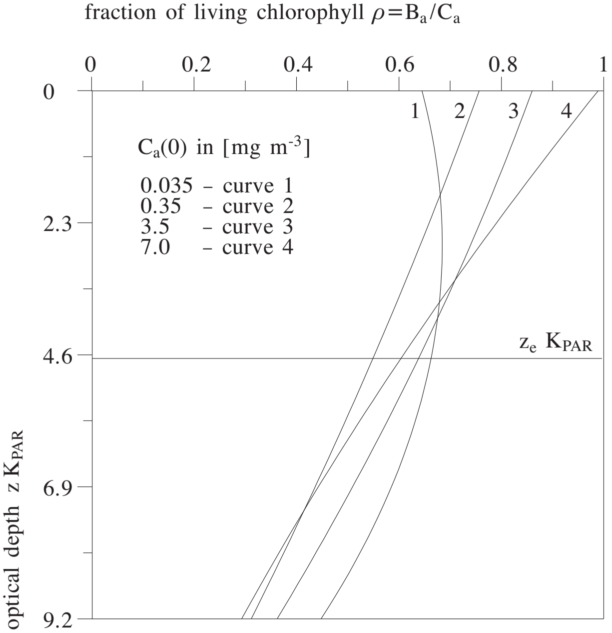

Fig. 2. Mean vertical distributions of the fraction of living chlorophyll *a* for various trophic types of waters determined by eq. (15). $C_a(0)$ – chlorophyll *a* + pheo. concentration in surface water, $z_e\ K_{PAR}$ – optical depths of the lower limit of the euphotic zone (1% of surface PAR)

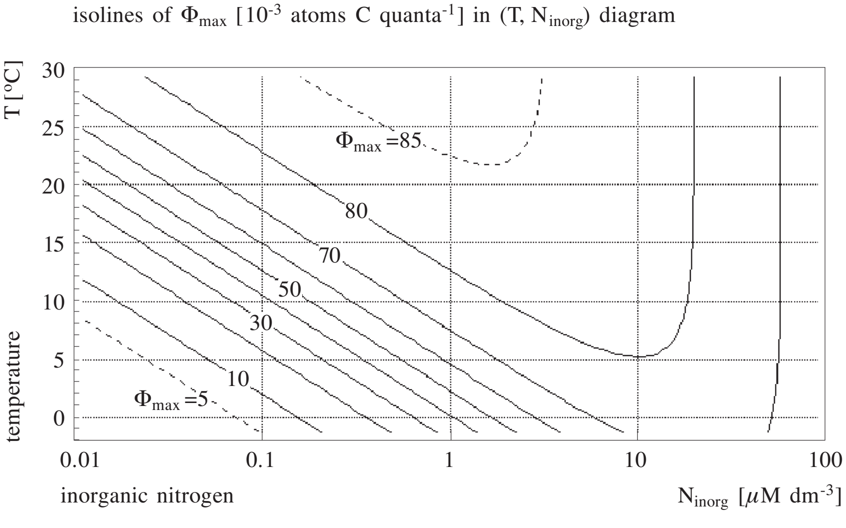

Fig. 3. The $\Phi_{\max}$ quantum yield of carbon fixation dependence on temperature and inorganic nitrogen concentration (determined by eq. (16))

The concentration of photosynthetic carotenoids C_{PSC} in eq. (13) and eq. (14) is given by

$$C_{PSC} = \left(3.890\, F_{PSC}^{9.969} + 0.4601\right) C_a, \tag{18}$$

where the F_{PSC} function, which we call the chromatic adaptation factor, is a function of the spectral fitting of the photosynthetic carotenoids, defined by

$$F_{PSC} = \frac{1}{a^*_{PSC,\,\max}} \int_{400}^{700} f(\lambda)\, a^*_{PSC}(\lambda)\, d\lambda, \tag{19}$$

where $f(\lambda) = \frac{E(\lambda)}{PAR}$ is the spectral distribution of irradiance in the PAR spectrum range (assumed here from 400 to 700 nm) measured in $[\mathrm{nm}^{-1}]$.

The concentration C_{PSC} as a function of the chromatic adaptation factor F_{PSC} is shown on the diagrams in Fig. 4a. Fig. 4b gives some idea of the accuracy of the calculation.

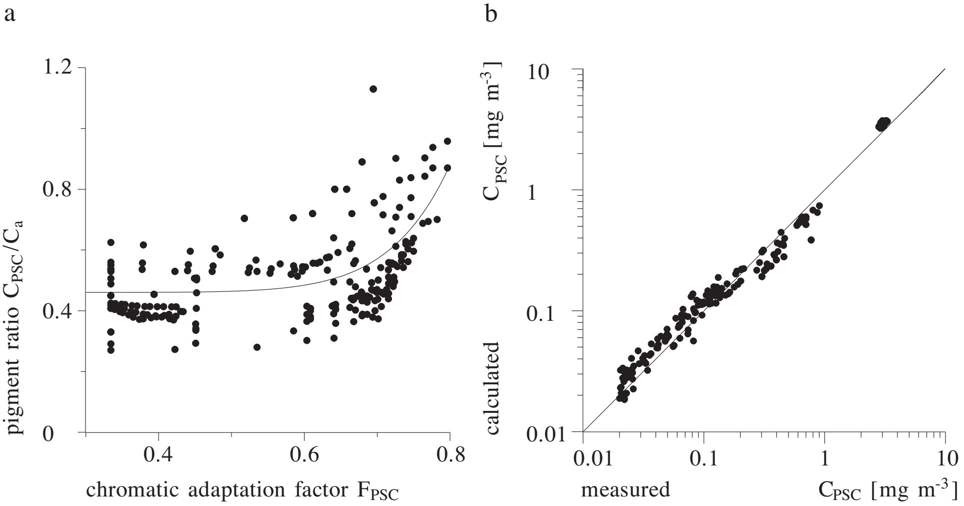

Fig. 4. Statistical dependence of the photosynthetic carotenoids C_{PSC} to chlorophyll C_a concentration ratio on the chromatic adaptation factor for photosynthetic carotenoids F_{PSC} (dots – measured, line – approximated by eq. (18)) (a); Comparison of calculated (eq. (18)) and measured photosynthetic carotenoid concentrations (b)

The formula for the chlorophyll *b* concentration is similar to that for carotenoids:

$$C_b = \left(62853\, F_b^{14.14} + 0.1655\right) C_a, \tag{20}$$

where a similar chromatic adaptation factor

$$F_b = \frac{1}{a^*_{b,\,\max}} \int_{400}^{700} f(\lambda)\, a^*_b(\lambda)\, d\lambda \tag{19a}$$

is introduced for chlorophyll b with the above spectral distribution of irradiance $f(\lambda)$.

The spectra of chlorophylls c and a are similar, thus the ratio C_c/C_a is assumed constant and the chlorophylls c concentration can simply be given by

$$C_c = 0.1807\, C_a. \tag{21}$$

It is evident from eqs. (18) to (21) that the relative concentration of photosynthetic pigments does not in practice depend on the absolute irradiance level but only on the irradiance spectrum. By contrast, the behaviour of photoprotecting pigments is more complicated: they depend on the irradiance intensity in the spectral range, which could cause photooxidation of the chlorophyll a.

The concentration of photoprotecting carotenoids C_{PPC} is initially established by the formula

$$C_{PPC} = \left(0.5077\, \overline{PDR^*}^{\,0.3669}\right) C_a, \tag{22}$$

where PDR^* is the Potentially Destructive Radiation (the asterisk means that this is the PDR per unit of chlorophyll mass), which appears to be a light intensity acclimatisation factor. We have defined it as follows:

$$PDR^* = \int_{400}^{480} a^*_a(\lambda) < E(\lambda) >_{\text{day}}\, d\lambda, \tag{23}$$

where $E(\lambda)$ is the typical scalar irradiance level in the medium – its daily mean value $< E(\lambda) >_{\text{day}}$ in this paper.

The mean $\overline{PDR^*}$ is the mean value in a water layer $\Delta z + \Delta z'$

$$\overline{PDR^*} = \frac{1}{\Delta z + \Delta z'} \int_{z-\Delta z'}^{z+\Delta z} PDR^*(z)\, dz. \tag{24}$$

In this way we take the influence of water mixing into account.
In our calculation

$$\Delta z = 10 \text{ m} \quad \text{and} \quad \Delta z' = \begin{cases} z & \text{if} \quad z < 10 \text{ m} \\ 10 \text{ m} & \text{if} \quad z \geq 10 \text{ m}. \end{cases}$$

The pigment ratio C_{PPC}/C_a is presented in Figs. 5a and 5b.

The light factor $LF = f(PUR^*_{PSP})$ in eq. (9) is approximated in the Michaelis–Menten form as follows:

$$LF = \frac{PUR^*_{PSP,\,1/2}}{PUR^*_{PSP} + PUR^*_{PSP,\,1/2}}, \tag{25}$$

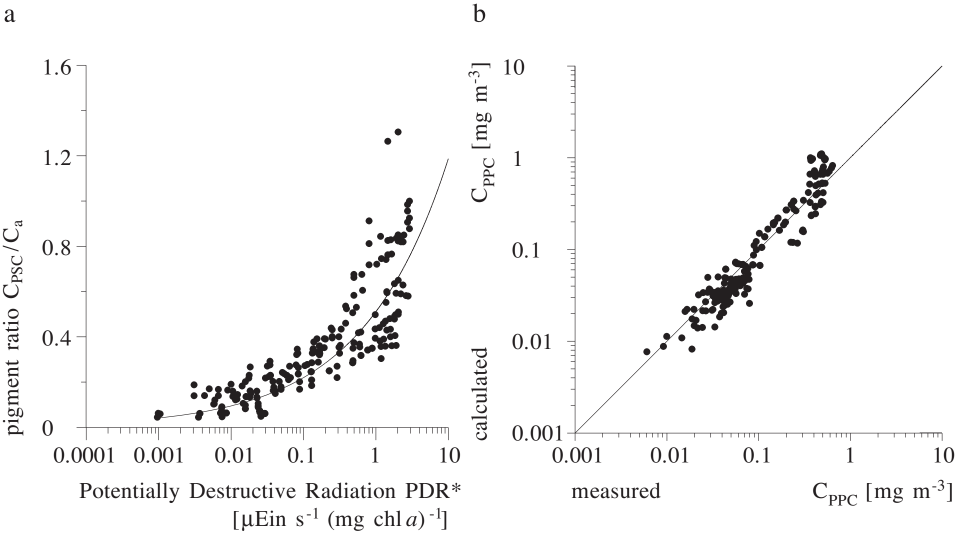

Fig. 5. Statistical dependence of photoprotecting carotenoids C_{PPC} to chlorophyll a + pheo. C_a concentration ratio on the Potentially Destructive Radiation PDR^* (dots – measured, line – calculated by eqs. (22) to (24)) (a); Comparison of calculated (eqs. (22)–(24)) and measured photoprotecting carotenoid concentrations (b)

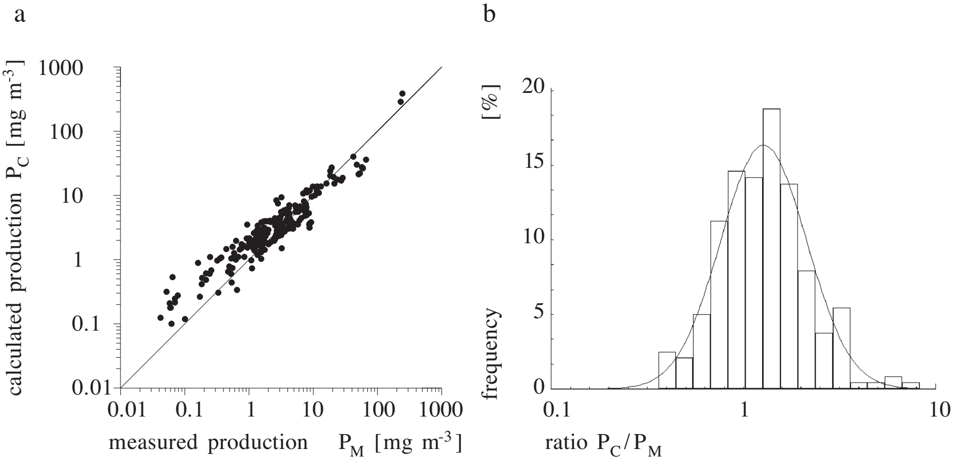

Fig. 6. Comparison of daily primary productions (calculated using the model, and measured) at various stations and depths in the North Atlantic and Black Sea (a); Frequency distribution of the ratio P_C/P_M (b)

where

$$PUR^{*}_{PSP,1/2} = 1.105 \left[\frac{\mu\text{Ein}}{(\text{mg chl}\,a\ + \text{pheo.})\,s}\right] (1.387)^{T/10}, \tag{26}$$

and T – temperature in [°C].

A kind of preliminary validation of the whole model is given in Figs. 6a and 6b. The daily primary production, calculated from eq. (5) using all the above formulas, is compared with the set of empirical data from the 23rd cruise of r/v 'Vityaz' (1991, North Atlantic and the Black Sea). About 170 points on diagram 6a cover the data set from various depths, stations and times.

The statistical distribution of the calculated to measured primary production ratio is presented in Fig. 6b and the error estimation is given in Tab. 3.

Table 3. The relative errors in estimating daily primary productions at different depths in the sea from the model

Arithmetic statistics		Logarithmic statistics			
systematic $<\varepsilon>$ [%]	statistical σ_ε [%]	systematic $<\varepsilon>_g$ [%]	range of variability σ_- [%]	σ_+ [%]	variability factor x
+43.6	±61.7	+26.2	–18.8	+96.3	1.55

where

$\varepsilon = (P_C - P_M)/P_M$ – errors;

$<\varepsilon>$ – arithmetic mean of errors;

σ_ε – standard deviation of errors (statistical error);

$<\varepsilon>_g$ – geometric mean of errors, $<\varepsilon>_g = 10^{<\log P_C/P_M>} - 1$;

$\sigma_- = 10^{[<\log(P_C/P_M)>-\sigma_{\log}]} - 1$ and $\sigma_+ = 10^{[<\log(P_C/P_M)>+\sigma_{\log}]} - 1$;

x – variability factor, $x = 10^{\sigma_{\log}}$;

$<\log(P_C/P_M)>$ – mean of $\log(P_C/P_M)$;

$\sigma_{\log}$ – standard deviation of $\log(P_C/P_M)$.

5. Conclusions

The empirical validation of the present model of marine primary production clearly shows that the errors of the calculations of the primary production in practice do not exceed the usual experimental errors (see Tab. 3). This confirms that our modelling procedure was correct.

The model improves definitions and mathematical descriptions of photoacclimatisation. It introduces *e.g.* a chromatic adaptation factor for the photosynthetic pigment composition (eqs. (19) and (19a)) and the light intensity acclimatisation factor for the photoprotecting pigment content (eqs. (23) and (24)).

The empirical constants given in the model formulas should be treated as an approximation, though not necessarily the best one. This comment applies in particular to the mathematical approximation of the maximum quantum yield of carbon fixation $\Phi_{\max}$ (eq. (16)) and the parameter $PUR^{*}_{PSP,\,1/2}$ of the light factor (eq. (26)). This is due to the indirect determination of the approximations by means of non-linear regressions of thousands of empirical data sets of P^B, PAR, $\mathrm{N_{inorg}}$ and T, which leads to ambiguous results.

Further improvement of this model is advisable in order to make it applicable to the remote sensing of primary production.

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Appendix

Notation

Symbol	Description	Units
a	light absorption coefficient:	m^{-1}
a_{pl}	– of phytoplankton	m^{-1}
$a_{pl,S}$	– of phytoplankton pigments in solvent	m^{-1}
a_a, a_b, a_c	– of chlorophylls a, b, c	m^{-1}
a_{PPC}	– of photoprotecting carotenoids	m^{-1}
a_{PPP}	– of photoprotecting pigments	m^{-1}
a_{PSC}	– of photosynthetic carotenoids	m^{-1}
a_{PSP}	– of photosynthetic pigments	m^{-1}
a^*_m	specific absorption coefficient of mth pigment in solvent	m^2 (mg pigment)$^{-1}$
$\tilde{a}^*$	mean specific absorption coefficient weighted by the irradiance spectrum	m^2 (mg chl a +pheo.)$^{-1}$
B_a	concentration of living chlorophyll a	mg m^{-3}
C_a	sum of chlorophyll a + pheo. concentrations	mg m^{-3}
$C_a(0)$	sum of chlorophyll a + pheo. concentrations in the surface water	mg m^{-3}
C_b, C_c, C_{PPC}, C_{PSC}	concentrations of chl b, chl c, photoprotecting carotenoids, photosynthetic carotenoids	mg m^{-3}
$f(\lambda)$	spectral distribution of irradiance	nm^{-1}
F_b, F_{PSC}	chromatic adaptation factors for chl b, for photosynthetic carotenoids	dimensionless
$E(\lambda)$	spectral scalar irradiance	μEin m^{-2} s^{-1} nm^{-1}
K_{PAR}	PAR irradiance attenuation coefficient	m^{-1}
LF	light factor	dimensionless
N_{inorg}	concentration of inorganic nitrogen	μM dm^{-3}
P	primary production	atoms C m^{-3} s^{-1}
P_M, P_C	daily primary production: measured, calculated	mg C m^{-3}

Notation (continued)

Symbol	Description	Units
P^C	carbon fixation rate (per unit mass of chlorophyll a + pheo.)	atoms C (mg chl a +pheo.)$^{-1}$ s^{-1}
P^B	carbon fixation rate (per unit mass of living chlorophyll a)	atoms C (mg chl a)$^{-1}$ s^{-1}
PAR	photosynthetically available (scalar irradiance)	radiation μEin m^{-2} s^{-1}
$PAR(0)$	photosynthetically available radiation at the surface	μEin m^{-2} s^{-1}
PDR^*	potentially destructive radiation (per unit of chlorophyll a mass)	μEin (mg chl a)$^{-1}$ s^{-1}
PUR^*	photosynthetically utilised radiation (per unit of chlorophyll a mass)	μEin (mg chl a +pheo.)$^{-1}$ s^{-1}
PUR^*_{PSP}, PUR^*_{PPP}	parts of PUR^* of photosynthetic and photoprotecting pigments	μEin (mg chl a +pheo.)$^{-1}$ s^{-1}
$SOPS$	spectral optical properties of the sea	–
Q	correction factor to phytoplankton light absorption coefficient due to the package effect and neglect of phycobilins	dimensionless
T	temperature	°C
z	depth in the sea	m
z_e	depth of euphotic zone (level of 1% of the surface PAR irradiance)	m
$\Phi_{\max}$	maximum quantum yield of carbon fixation	atoms C quanta^{-1}
Φ_{real}	real quantum yield of carbon fixation	atoms C quanta^{-1}
λ	light wavelength	nm
ρ	pigment ratio B_a/C_a	dimensionless
τ	optical depth in the sea	dimensionless