Influence of non-photosynthetic pigments on the measured quantum yield of photosynthesis*

OCEANOLOGIA, 42 (2), 2000.
pp. 231–??.

KEYWORDS
Photosynthesis quantum yield
Non-photosynthetic pigment factor
Bio-optical model

Dariusz Ficek[2]
Roman Majchrowski[2]
Mirosława Ostrowska[1]
Bogdan Woźniak[1,2]

[1] Institute of Oceanology,
Polish Academy of Sciences,
Powstańców Warszawy 55, PL–81–712 Sopot, Poland

[2] Institute of Physics,
Pedagogical University,
Arciszewskiego 22 B, PL–76–200 Słupsk, Poland;
e-mail: darek@wsp.slupsk.pl

Manuscript received 20 March 2000, reviewed 10 April 2000, accepted 19 April 2000.

Abstract

The aim of this work was to assess the effect of non-photosynthetic (photoprotecting) pigments on the measured quantum yield of photosynthesis in the sea. The energy absorbed by these pigments is not utilised during photosynthesis. As a result, the measured yield of this process, *i.e.* the photosynthetic yield referred to the total energy absorbed by all phytoplankton pigments, is less than the actual quantum yield of photosynthesis, *i.e.* the yield referred to the energy absorbed by photosynthetic pigments only. The model of the absorption properties of marine phytoplankton derived by the authors (see Woźniak *et al.* 2000, this volume) was employed to determine the relevant contributions of photosynthetic and non-photosynthetic pigments to the total energy absorbed by phytoplankton

* This paper was presented at the 'Second Workshop on Luminescence and Photosynthesis of Marine Phytoplankton', Sopot–Paraszyno, 11–15 October 1999.

in different trophic types of seas and at different depths in the water column. On this basis the non-photosynthetic pigment absorption factor f_a, which describes the relation between the true and measured quantum yields of photosynthesis, could be characterised. The analysis shows that f_a varies in value from 0.33 to 1, and that it depends on the trophic type of sea and the depth in the water column. The values of this factor are usually highest in eutrophic waters and decrease as waters become progressively more oligotrophic. It is also characteristic of f_a that it increases with increasing depth in the sea.

1. Introduction

Under natural conditions in the sea, phytoplankton produces not only chlorophyll *a*, but also various types of accessory (photoprotecting and photosynthetic) pigments, including photoprotecting carotenoids (PPC), which protect chlorophyll *a* from photo-oxidation (Bidigare *et al.* 1990, Woźniak *et al.* 1997). The energy absorbed by these pigments is not used for photosynthesis (Babin *et al.* 1996a, b, Bidigare *et al.* 1996). This is why the measured (observed) quantum yield of photosynthesis, referred to quanta absorbed by all photoprotecting and photosynthetic phytoplankton pigments, differs from the true quantum yield, referred only to the quanta absorbed by the photosynthetic pigments.

Let Φ_1 [mol C Ein $^{-1}$] be the measured (observed) quantum yield of photosynthesis – the carbon fixation P^B [mol C (mg tot. chl $a)^{-1}$ s^{-1}] divided by the energy PUR^* absorbed by all photoprotecting and photosynthetic phytoplankton pigments [Ein (mg tot. chl $a)^{-1}$ s^{-1}]:

$$\Phi_1 = \frac{P^B}{PUR^*}, \tag{1}$$

and let Φ_2 be the true quantum yield of photosynthesis – the carbon fixation P^B divided by the energy PUR^*_{PSP} absorbed by phytoplankton photosynthetic pigments only [Ein (mg tot. chl $a)^{-1}$ s^{-1}]:

$$\Phi_2 = \frac{P^B}{PUR^*_{PSP}}. \tag{2}$$

The absorbed energies PUR^* and PUR^*_{PSP} can be determined from the following formulae using the respective irradiances and phytoplankton absorption coefficients:

$$PUR^* \approx \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} E_0(\lambda)\; a^*_{pl}(\lambda)\, d\lambda = \tilde{a}^*_{pl}\; PAR_0, \tag{3}$$

$$PUR^*_{PSP} \approx \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} E_0(\lambda)\; a^*_{pl,\,PSP}(\lambda)\, d\lambda = \tilde{a}^*_{pl,\,PSP}\; PAR_0, \tag{4}$$

where

$E_0(\lambda)$ – spectral scalar irradiance,

$a_{pl}(\lambda), a_{pl,\,PSP}(\lambda)$ – respective spectra of absorption coefficients of total phytoplankton pigments and of photosynthetic pigments only,

PAR_0 – total scalar irradiance in the 400–700 nm range:

$$PAR_0 = \int_{400\,\text{nm}}^{700\,\text{nm}} E_0(\lambda)\, d\lambda;$$

$\tilde{a}^*_{pl}$, $\tilde{a}^*_{pl,\,PSP}$ – respective mean specific absorption coefficients weighted by the irradiance spectrum in the 400–700 nm range for all phytoplankton pigments and for photosynthetic phytoplankton pigments only:

$$\tilde{a}^*_{pl} = \frac{1}{PAR_0} \int_{400\,\text{nm}}^{700\,\text{nm}} E_0(\lambda)\; a^*_{pl}(\lambda)\, d\lambda, \tag{5}$$

$$\tilde{a}^*_{pl,\,PSP} = \frac{1}{PAR_0} \int_{400\,\text{nm}}^{700\,\text{nm}} E_0(\lambda)\; a^*_{pl,\,PSP}(\lambda)\, d\lambda. \tag{6}$$

In extreme cases, when no photoprotecting pigments are present in phytoplankton cells, both these energies are equal. In other cases PUR^*_{PSP} is always less than PUR^* ($PUR^* \geq PUR^*_{PSP}$), so the measured (observed) quantum yield of photosynthesis Φ_1 is always lower than or at most equal to the true quantum yield of photosynthesis $\Phi_2 (\Phi_1 \leq \Phi_2)$.

The aim of this paper is to evaluate by mathematical modelling the degree to which these two quantum yields differ from each other in different types of seas and under different conditions. To do this we used the model relationships discussed earlier (Majchrowski & Ostrowska 1999 and 2000, this volume) between the concentrations of particular photosynthetic or non-photosynthetic pigments and light conditions in the sea, as well as the model of light absorption capacities of marine phytoplankton developed by Woźniak *et al.* (2000, this volume).

2. Methods of calculating the non-photosynthetic pigment absorption factor

The difference between the measured (apparent) Φ_1 and the true quantum yield of photosynthesis Φ_2 can be described by the ratio f_a:

$$f_a = \frac{\Phi_1}{\Phi_2}, \tag{7}$$

which we call the non-photosynthetic pigment absorption factor f_a.

Values of f_a vary from 0 to 1, which shows that the quantum yield of photosynthesis decreases owing to the presence of photoprotecting pigments.

If we determine f_a using eqs. (1)–(4), it becomes the ratio of the two mean specific absorption coefficients $\tilde{a}^*_{pl,\,PSP}$ and $\tilde{a}^*_{pl}$, averaged with the weight of the irradiance spectrum:

$$f_a = \frac{\tilde{a}^*_{pl,\,PSP}}{\tilde{a}^*_{pl}}. \qquad (8)$$

According to the definitions of these absorption coefficients (eqs. (5) and (6)), it is possible to determine them, provided we have the following data:

- the spectrum of scalar irradiance $E_0(\lambda,\, z)$ and the total scalar irradiance in the 400–700 nm spectral range $PAR_0(z)$ at various depths in the sea (or the vector irradiance $PAR\,(z)$, as there is a simple link between them: $PAR_0 \approx 1.2\,PAR$),
- the spectrum of the total absorption coefficients for all phytoplankton pigments $a_{pl}(\lambda,\, z)$ and for photosynthetic pigments $a_{pl}PSP\,(\lambda,\, z)$, but only at the same depths as $E_0(\lambda,\, z)$.

On the other hand, values of $E_0\,(\lambda,\, z)$, $PAR_0\,(z)$ and $a_{pl}\,(\lambda,\, z)$, $a_{pl,\,PSP}\,(\lambda,\, z)$ can be determined based on a knowledge of the irradiance just below the sea surface $PAR_0\,(0^+)$ and the trophicity (*i.e.* surface chlorophyll *a* concentration $C_a(0)$) using the following two models:

- the bio-optical model of optical properties of the sea, with which typical scalar and vector irradiances for various trophic types of sea and at different depths in the water column can be determined. A number of similar bio-optical models are described in various papers (Smith & Baker 1978, Baker & Smith 1982, Morel 1988, Woźniak *et al.* 1992a, b, 1995). In this paper we used Woźniak's bio-optical classification of oceanic waters;
- the model of phytoplankton absorption, which allows us to determine spectra of the total absorption coefficients for all phytoplankton pigments and the absorption coefficient for photosynthetic phytoplankton pigments only (Woźniak *et al.* 1999 and Majchrowski & Ostrowska 1999, 2000, this volume).

The results of calculating the factor f_a are now given.

3. Results

Examples of the non-photosynthetic pigment absorption factor f_a determined according to the method described in this paper are given in Fig. 1 (see also Appendix). The calculations were made for the irradiance just below the sea surface $PAR_0(0^+) = 695$ μEin m^{-2} s^{-1}. This is a typical value of the daily mean irradiance at mean latitudes. As one can see in Fig. 1, f_a varies for different depths and different trophic types of seas;

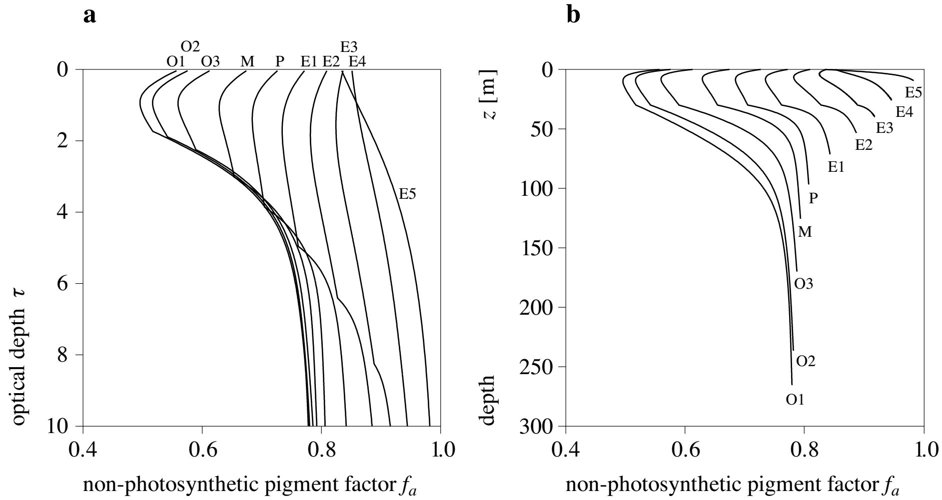

Fig. 1. The modelled vertical distribution of the non-photosynthetic pigment factor f_a in different trophic types of sea: dependence on optical depth τ (a), dependence on real depth z [m] (b). The symbols of trophic types correspond to the surface chlorophyll a concentration $C_a(0)$: O1 – $C_a(0) = 0.035$ mg tot. chl a m^{-3}; O2 – $C_a(0) = 0.07$ mg tot. chl a m^{-3}; O3 – $C_a(0) = 0.15$ mg tot. chl a m^{-3}; M – $C_a(0) = 0.35$ mg tot. chl a m^{-3}; P – $C_a(0) = 0.7$ mg tot. chl a m^{-3}; E1 – $C_a(0) = 1.5$ mg tot. chl a m^{-3}; E2 – $C_a(0) = 3.5$ mg tot. chl a m^{-3}; E3 – $C_a(0) = 7$ mg tot. chl a m^{-3}; E4 – $C_a(0) = 15$ mg tot. chl a m^{-3}; E5 – $C_a(0) = 35$ mg tot. chl a m^{-3}

the trophicity is given by the surface chlorophyll a concentration index $C_a(0)$. The non-photosynthetic pigment absorption factor f_a increases with chlorophyll a concentration – it is smallest in oligotrophic waters, where the concentration of photoprotecting pigments is relatively high. In contrast, the largest value of f_a should be recorded in eutrophic waters, where the photosynthetic pigment concentration is relatively high. As regards variability with depth, we can say that f_a usually increases with depth. This is because of the fall in the number of quanta of high-energy radiation from the short-wave range of visible light which can photo-oxidise chlorophyll a. Hence, the relative quantity of photoprotecting carotenoids produced by phytoplankton also falls. In the extreme cases of super-eutrophic seas, even if these are shallow, only photosynthetic pigments are present $\tilde{a}^*_{pl,\,PSP} \approx \tilde{a}^*_{pl}$ and the factor f_a approaches 1.

For the case presented in Fig. 1, f_a varies over the range 0.5–1. This result was obtained for a mean irradiance $PAR_0\,(0^+) = 695$ μEin m^{-2} s^{-1}. If we take a larger irradiance into consideration, for example $PAR_0\,(0^+) = 1300$ μEin m^{-2} s^{-1}, which is typical of equatorial waters, we obtain a minimal value of $f_a = ca$ 0.32, not 0.5. The natural variability of recorded values of the non-photosynthetic pigment absorption factor f_a thus lies between 0.32 and 1, depending on the trophic type of sea and the depth. Therefore, as a result of variations in the ratio of photosynthetic pigments to all pigments, the measured quantum yield of photosynthesis can vary by a factor of three.

In conclusion, it has to be said that values of f_a had to be calculated from a complicated model. To make the calculation easier we derived an alternative, polynomial method of determining the mean absorption coefficients $\tilde{a}^*_{pl}$, $\tilde{a}^*_{pl,\,PSP}$, and then f_a (from eq. (8)), on the basis of the surface chlorophyll a concentration $C_a(0)$, the optical depth τ and sea surface irradiance $PAR_0\,(0^+)$. To do this we approximated by means of a polynomial the values of $\tilde{a}^*_{pl}$, $\tilde{a}^*_{pl,\,PSP}$ and f_a obtained from computations using the complete mathematical apparatus of earlier models. The relevant values of $\tilde{a}^*_{pl}$ and $\tilde{a}^*_{pl,\,PSP}$ can be determined with the aid of polynomials (9) and (10). The values of the coefficients $A_{m,\,n}$, $B_{m,\,n}$ and $C_{m,\,n}$, are given in Tables 1–3. On the other hand, f_a was obtained according to eq. (8) by dividing the following polynomials:

$$\begin{aligned}\tilde{a}^*_{pl} &= \sum_{m=0}^{4}\left[\sum_{n=0}^{4} A_{m,\,n}\,(\log C_a(0))^n\right]\tau^m + \\ &+ \sum_{m=0}^{4}\left[\sum_{n=0}^{4} B_{m,\,n}\,(\log C_a(0))^n\right]\tau^m + \\ &+ PAR\,(0^+)\sum_{m=0}^{4}\left[\sum_{n=0}^{4} C_{m,\,n}\,(\log C_a(0))^n\right]\tau^m, \end{aligned} \tag{9}$$

$$\tilde{a}^*_{pl,\,PSP} = \sum_{m=0}^{4}\left[\sum_{n=0}^{4} A_{m,\,n}(\log C_a(0))^n\right]\tau^m. \tag{10}$$

Table 1. Values of $A_{m,\,n}$ in eqs. (9) and (10)

a) for $0.035 < C_a(0) < 1.5$

n / m	0	1	2	3	4
0	1.382×10^{-2}	-6.329×10^{-3}	-9.281×10^{-3}	-5.333×10^{-3}	-1.195×10^{-3}
1	4.717×10^{-4}	-2.980×10^{-3}	1.460×10^{-2}	1.269×10^{-2}	3.641×10^{-3}
2	-8.151×10^{-5}	7.691×10^{-4}	-5.625×10^{-3}	-6.276×10^{-3}	-2.265×10^{-3}
3	3.254×10^{-5}	-1.270×10^{-4}	6.555×10^{-4}	8.225×10^{-4}	3.218×10^{-4}
4	-2.272×10^{-6}	6.099×10^{-6}	-2.156×10^{-5}	-2.871×10^{-5}	-1.206×10^{-5}

Table 1. (continued)

b) for $1.5 \leq C_a(0) < 70$

n / m	0	1	2	3	4
0	1.359×10^{-2}	-6.661×10^{-3}	-1.754×10^{-3}	1.293×10^{-3}	-1.661×10^{-4}
1	9.238×10^{-4}	-2.283×10^{-3}	-4.078×10^{-4}	2.144×10^{-3}	-7.524×10^{-4}
2	-2.708×10^{-4}	4.368×10^{-4}	8.568×10^{-4}	-1.295×10^{-3}	4.043×10^{-4}
3	5.401×10^{-5}	-7.769×10^{-5}	-1.056×10^{-4}	1.735×10^{-4}	-5.546×10^{-5}
4	-2.979×10^{-6}	3.940×10^{-6}	5.061×10^{-6}	-8.404×10^{-6}	2.708×10^{-6}

Table 2. Values of $B_{m,n}$ in eq. (9)

a) for $0.035 < C_a(0) < 1.5$

n / m	0	1	2	3	4
0	2.536×10^{-3}	-1.639×10^{-3}	-1.651×10^{-3}	-7.143×10^{-4}	-9.046×10^{-5}
1	8.931×10^{-4}	-1.608×10^{-5}	3.912×10^{-3}	3.449×10^{-3}	8.775×10^{-4}
2	-2.102×10^{-4}	3.960×10^{-4}	-1.610×10^{-3}	-1.823×10^{-3}	-6.203×10^{-4}
3	2.463×10^{-5}	-5.496×10^{-5}	1.993×10^{-4}	2.480×10^{-4}	8.994×10^{-5}
4	-1.058×10^{-6}	2.419×10^{-6}	-7.358×10^{-6}	-9.231×10^{-6}	-3.403×10^{-6}

b) for $1.5 \leq C_a(0) < 70$

n / m	0	1	2	3	4
0	2.499×10^{-3}	-1.723×10^{-3}	-1.826×10^{-4}	4.156×10^{-4}	-6.549×10^{-5}
1	9.413×10^{-4}	-1.010×10^{-3}	-5.527×10^{-4}	8.603×10^{-4}	-2.390×10^{-4}
2	-2.556×10^{-4}	3.013×10^{-4}	5.962×10^{-5}	-1.741×10^{-4}	5.277×10^{-5}
3	3.117×10^{-5}	-5.173×10^{-5}	2.531×10^{-5}	-9.859×10^{-7}	-1.458×10^{-6}
4	-1.335×10^{-6}	2.609×10^{-6}	-1.975×10^{-6}	6.795×10^{-7}	-8.609×10^{-8}

Table 3. Values of $C_{m,n}$ in eq. (9)

a) for $\tau < \tau_{z=30\,\mathrm{m}}$

n / m	0	1	2	3	4
0	-5.484	-7.703×10^{-1}	-3.168×10^{-1}	-5.333×10^{-3}	3.498×10^{-2}
1	8.595×10^{-2}	-3.253×10^{-1}	1.815×10^{-1}	4.791×10^{-2}	-4.652×10^{-2}
2	-6.055×10^{-3}	1.522×10^{-1}	-1.618×10^{-1}	-3.010×10^{-3}	2.477×10^{-2}
3	-1.955×10^{-2}	7.841×10^{-3}	2.382×10^{-2}	-1.459×10^{-2}	1.453×10^{-3}
4	3.529×10^{-3}	-7.324×10^{-3}	5.537×10^{-3}	-2.024×10^{-3}	3.284×10^{-4}

Table 3. (continued)

b) for $\tau \geq \tau_{z=30\,\mathrm{m}}$

n / m	0	1	2	3	4
0	−3.071	8.855	16.99	12.05	2.894
1	-7.338×10^{-1}	−4.255	−8.369	−5.812	−1.319
2	7.143×10^{-2}	8.335×10^{-1}	1.634	1.070	2.167×10^{-1}
3	-1.065×10^{-2}	-7.695×10^{-2}	-1.399×10^{-1}	-8.100×10^{-2}	-1.273×10^{-2}
4	5.096×10^{-4}	2.674×10^{-3}	4.366×10^{-3}	2.066×10^{-3}	1.525×10^{-4}

Estimates of the errors of approximation are given in Table 4. In all cases the errors are relatively small (usually < 2.5%). This means that polynomial approximations are practicable, especially as they reduce the time needed to calculate f_a.

Table 4. The relative errors of polynomial approximation estimated from the models

	Arithmetic statistics		Logarithmic statistics			
	systematic $\langle\varepsilon\rangle$ [%]	statistical σ_ε [%]	systematic $\langle\varepsilon\rangle_\mathrm{g}$ [%]	standard error factor x	statistical σ_- [%]	σ_+ [%]
$\tilde{a}^*_{pl}$	0.0704	± 2.28	0.0729	1.023	−2.25	2.28
$\tilde{a}^*_{pl,\,PSP}$	0.0571	± 1.15	0.0507	1.011	−1.08	1.15
f_a	0.0228	± 1.39	0.0130	1.01	−0.99	1.0

where

$\varepsilon = \frac{(y_C - y_M)}{y_M}$ – errors,

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

σ_ε – standard deviation of errors (statistical error),

$\langle\varepsilon\rangle_\mathrm{g} = 10^{[\langle\log(y_C/y_M)\rangle]} - 1$ – geometric mean of errors,

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

$\sigma_{\log}$ – standard deviation of $\log(y_C/y_M)$,

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

$\sigma_+ = x - 1$.

Note:

y_C, y_M – respectively calculated using eqs. (8)–(10), and measured on the basis of the full model values of $\tilde{a}^*_{pl}$, $\tilde{a}^*_{pl,\,PSP}$ and f.

4. Conclusion

The effect of non-photosynthetic pigments on the observed quantum yield of photosynthesis in the sea has been analysed. To this end, f_a – the non-photosynthetic pigment absorption factor (eq. (7)) – was defined, and a mathematical form of the relationship between this factor, and the trophic type of sea (given by the surface concentration of chlorophyll a) and the optical depth in the sea was derived (see eqs. (8)–(10)).

The analysis has shown that under natural conditions f_a varies by a factor of *ca* 3 (from 0.33 to 1). Its values are dependent on, *inter alia*, the trophic type of sea, increasing from eutrophic to oligotrophic waters, and on depth, usually rising with increasing depth (Fig. 1).

References

Babin M., Morel A., Claustre H., Bricaud A., Kolber Z., Falkowski P. G., 1996a, *Nitrogen- and irradiance-dependent variations of the maximum quantum yield of carbon fixation in eutrophic, mesotrophic and oligotrophic marine systems*, Deep-Sea Res., 43, 1241–1272.

Babin M., Sadoudi N., Lazzara L., Gostan J., Partensky F., Bricaud A., Veldhuis M., Morel A., Falkowski P. G., 1996b, *Photoacclimation strategy of Prochlorococcus sp. and consequences on large scale variations of photosynthetic parameters*, Ocean Optics 13, Proc. SPIE, 2963, 314–319.

Baker K. S., Smith R. C., 1982, *Bio-optical classification and model of natural waters 2*, Limnol. Oceanogr., 27 (3), 500–509.

Bidigare R., Latasa M., Johnson Z., Barber R. T., Trees C. C., Balch W. M., 1996, *Observations of a Synechococcus-dominated cyclonic eddy in open-oceanic water of the Arabian Sea*, Ocean Optics 13, Proc. SPIE, 2963, 260–265.

Bidigare R., Ondrusek M. E., Morrow J. H., Kiefer D. A., 1990, *'In vivo' absorption properties of algal pigments*, Ocean Optics 10, Proc. SPIE, 1302, 290–302.

Majchrowski R., Ostrowska M., 1999, *Modified relationships between the occurrence of photoprotecting carotenoids of phytoplankton and Potentially Destructive Radiation in the sea*, Oceanologia, 41 (4), 589–599.

Majchrowski R., Ostrowska M., 2000, *Influence of photo- and chromatic acclimation on pigment composition in the sea*, Oceanologia, 42 (2), 157–175.

Morel A., 1988, *Optical modeling of the upper ocean in relation to its biogenous matter content (case 1 waters)*, J. Geophys. Res., 93, 10.749–10.768.

Smith R. C., Baker K. S., 1978, *Optical classification of natural water*, Limnol. Oceanogr., 23 (2), 260–267.

Woźniak B., Dera J., Ficek D., Majchrowski R., Kaczmarek S., Ostrowska M., Koblentz-Mishke O. I., 2000, *Model of the 'in vivo' spectral absorption of algal pigments. Part 1. Mathematical apparatus*, Oceanologia, 42 (2), 177–190.

Woźniak B., Dera J., Ficek D., Majchrowski R., Kaczmarek S., Ostrowska M., Koblentz-Mishke O. I., 1999, *Modelling the influence of acclimation on the absorption properties of marine phytoplankton*, Oceanologia, 41 (2), 187–210.

Woźniak B., Dera J., Koblentz-Mishke O. I., 1992a, *Bio-optical relationships for estimating primary production in the Ocean*, Oceanologia, 33, 5–38.

Woźniak B., Dera J., Koblentz-Mishke O. I., 1992b, *Modelling the relationship between primary production, optical properties, and nutrients in the sea*, Ocean Optics 11, Proc. SPIE, 1750, 246–275.

Woźniak B., Dera J., Majchrowski R., Ficek D., Koblentz-Mishke O. I., Darecki M., 1997, *'IO PAS initial model' of marine primary production for remote sensing applications*, Oceanologia, 39 (4), 377–395.

Woźniak B., Dera J., Semovski S., Hapter R., Ostrowska M., Kaczmarek S., 1995, *Algorithm for estimating primary production in the Baltic by remote sensing*, Stud. i Mater. Oceanol., 68, 91–123.

Appendix

Table 5. Optical depth profiles of the non-photosynthetic pigment factor f_a computed from the compilation model (eq. (8)), for surface irradiance $PAR_0\,(0^+) = 695$ μEin m^{-2} s^{-1} and different trophic types represented by surface chlorophyll a

Optical depth τ	Surface chlorophyll a concentrations $C_a(0)$ [mg tot. chl a m^{-3}]										
	0.035	0.07	0.15	0.35	0.7	1.5	3.5	7	15	35	70
0	0.557	0.576	0.612	0.674	0.726	0.772	0.809	0.836	0.851	0.834	0.734
0.2	0.530	0.549	0.588	0.659	0.713	0.763	0.802	0.833	0.853	0.840	0.745
0.4	0.514	0.534	0.577	0.644	0.703	0.754	0.798	0.831	0.854	0.845	0.755
0.6	0.503	0.523	0.565	0.635	0.695	0.748	0.793	0.829	0.856	0.852	0.766
0.8	0.496	0.517	0.560	0.630	0.689	0.743	0.789	0.827	0.858	0.856	0.777
1	0.496	0.518	0.560	0.628	0.686	0.738	0.786	0.826	0.860	0.863	0.794
1.2	0.500	0.521	0.563	0.629	0.684	0.736	0.784	0.825	0.862	0.866	0.804
1.4	0.506	0.527	0.568	0.631	0.684	0.735	0.783	0.824	0.864	0.873	0.815
1.6	0.514	0.533	0.573	0.634	0.685	0.734	0.782	0.824	0.866	0.880	0.825
1.8	0.531	0.540	0.579	0.637	0.686	0.734	0.781	0.825	0.869	0.883	0.839
2	0.556	0.560	0.584	0.641	0.687	0.735	0.782	0.825	0.871	0.889	0.847
2.2	0.578	0.585	0.589	0.643	0.689	0.736	0.782	0.826	0.874	0.895	0.860
2.4	0.601	0.607	0.613	0.646	0.691	0.737	0.784	0.828	0.876	0.901	0.868
2.6	0.621	0.626	0.631	0.649	0.693	0.739	0.785	0.829	0.879	0.907	0.875
2.8	0.640	0.645	0.650	0.652	0.695	0.741	0.786	0.831	0.882	0.909	0.885
3	0.656	0.661	0.667	0.658	0.697	0.742	0.788	0.833	0.884	0.914	0.894
3.2	0.671	0.676	0.681	0.675	0.699	0.744	0.791	0.835	0.886	0.919	0.900
3.4	0.683	0.687	0.693	0.692	0.701	0.746	0.793	0.837	0.889	0.923	0.908
3.6	0.695	0.699	0.704	0.705	0.702	0.748	0.795	0.840	0.892	0.927	0.913
3.8	0.705	0.709	0.714	0.716	0.704	0.750	0.797	0.842	0.894	0.931	0.920
4	0.714	0.717	0.722	0.728	0.721	0.752	0.800	0.844	0.897	0.933	0.924
4.2	0.721	0.724	0.730	0.736	0.734	0.754	0.802	0.847	0.899	0.937	0.929

Table 5. (continued)

Optical depth τ	Surface chlorophyll a concentrations $C_a(0)$ [mg tot. ch a m^{-3}]										
4.4	0.728	0.731	0.735	0.745	0.747	0.756	0.804	0.849	0.901	0.940	0.935
4.6	0.733	0.736	0.741	0.751	0.757	0.758	0.807	0.851	0.904	0.943	0.938
4.8	0.738	0.741	0.746	0.756	0.765	0.760	0.809	0.854	0.906	0.946	0.942
5	0.743	0.745	0.751	0.761	0.772	0.769	0.812	0.856	0.908	0.949	0.946
5.2	0.746	0.749	0.754	0.765	0.777	0.782	0.814	0.858	0.910	0.951	0.949
5.4	0.749	0.752	0.757	0.769	0.782	0.790	0.816	0.861	0.912	0.954	0.952
5.6	0.752	0.755	0.760	0.772	0.785	0.799	0.818	0.863	0.914	0.956	0.954
5.8	0.755	0.757	0.762	0.774	0.788	0.806	0.821	0.865	0.916	0.958	0.957
6	0.757	0.759	0.765	0.777	0.791	0.811	0.823	0.867	0.918	0.960	0.960
6.2	0.759	0.761	0.766	0.779	0.793	0.815	0.825	0.869	0.919	0.962	0.963
6.4	0.761	0.763	0.768	0.780	0.795	0.819	0.830	0.872	0.921	0.963	0.964
6.6	0.763	0.764	0.770	0.782	0.796	0.822	0.840	0.874	0.923	0.965	0.966
6.8	0.764	0.766	0.771	0.783	0.798	0.824	0.848	0.875	0.924	0.967	0.968
7	0.766	0.767	0.772	0.784	0.799	0.826	0.854	0.878	0.926	0.968	0.970
7.2	0.767	0.768	0.774	0.785	0.799	0.828	0.858	0.879	0.927	0.969	0.971
7.4	0.769	0.770	0.775	0.785	0.800	0.830	0.862	0.881	0.929	0.971	0.973
7.6	0.769	0.771	0.776	0.786	0.801	0.831	0.865	0.883	0.930	0.972	0.974
7.8	0.771	0.772	0.777	0.787	0.802	0.832	0.868	0.885	0.931	0.973	0.975
8	0.772	0.773	0.778	0.787	0.802	0.834	0.870	0.887	0.933	0.974	0.977
8.2	0.773	0.774	0.779	0.788	0.803	0.835	0.873	0.889	0.934	0.975	0.978
8.4	0.774	0.775	0.780	0.788	0.803	0.836	0.874	0.895	0.935	0.976	0.979
8.6	0.774	0.776	0.781	0.789	0.804	0.837	0.876	0.900	0.937	0.977	0.980
8.8	0.775	0.776	0.781	0.790	0.804	0.838	0.878	0.904	0.938	0.978	0.981
9	0.776	0.777	0.782	0.790	0.804	0.838	0.879	0.907	0.939	0.979	0.982
9.2	0.776	0.778	0.783	0.790	0.805	0.839	0.881	0.909	0.940	0.979	0.983