

**Model of the *in vivo*
spectral absorption of
algal pigments. Part 1.
Mathematical apparatus***

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Abstract

Existing statistical models of *in vivo* light absorption by phytoplankton (Woźniak & Ostrowska 1990, Bricaud *et al.* 1995, 1998) describe the dependence of the phytoplankton specific spectral absorption coefficient $a_{pl}^*(\lambda)$ on the chlorophyll *a*

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concentration C_a in seawater. However, the models do not take into account the variability in this relationship due to phytoplankton acclimation. The observed variability in the light absorption coefficient and its components due to various pigments with depth and geographical position at sea, requires further accurate modelling in order to improve satellite remote sensing algorithms and interpretation of ocean colour maps.

The aim of this paper is to formulate an improved model of the phytoplankton spectral absorption capacity which takes account of the pigment composition and absorption changes resulting from photo- and chromatic acclimation processes, and the pigment package effect. It is a synthesis of earlier models and the following statistical generalisations: (1) statistical relationships between various pigment group concentrations and light field properties in the sea (described by Majchrowski & Ostrowska 2000, this volume); (2) a model of light absorption by phytoplankton capable of determining the mathematical relationships between the spectral absorption coefficients of the various photosynthetic and photoprotecting pigment groups, and their concentrations in seawater (Woźniak *et al.* 1999); (3) bio-optical models of light propagation in oceanic Case 1 Waters and Baltic Case 2 Waters (Woźniak *et al.* 1992a, b, 1995a, b). The generalised model described in this paper permits the total phytoplankton light absorption coefficient *in vivo* as well as its components related to the various photosynthetic and photoprotecting pigments to be determined using only the surface irradiance $PAR(0^+)$ surface chlorophyll concentration $C_a(0)$ and depth z in the sea as input data.

1. Introduction

An important task of present-day marine bio-optics is the construction of a suitable algorithm to determine the light absorption capacities of marine phytoplankton on the basis of remote sensing optical data, including satellite data. Such an algorithm can be invoked to interpret ocean colour maps and improve methods of remotely monitoring primary production in the sea.

At present, the literature describes two statistical spectral models of phytoplankton light absorption which can be used in such an algorithm (Woźniak & Ostrowska 1990, Bricaud *et al.* 1995, 1998).

The first one, by Woźniak and Ostrowska (1990), enables the phytoplankton light absorption spectra $a_{pl}(\lambda)$ [m^{-1}] to be determined from the chlorophyll *a* concentration in the sea C_a [$\text{mg tot. chl } a \text{ m}^{-3}$]:

$$\left. \begin{aligned} a_{pl}(\lambda) &= a_{pl}^*(\lambda) C_a \\ a_{pl}^*(\lambda) &= (0.0187P_i - 0.011) e^{-0.00012(\lambda-441)^2} + \\ &\quad + 0.00645 e^{-0.00035(\lambda-608)^2} + 0.0233 e^{-0.0014(\lambda-675)^2} \end{aligned} \right\}, \quad (1)$$

where

$a_{pl}^*(\lambda)$ – specific light absorption coefficient of live phytoplankton in seawater [$\text{m}^2 (\text{mg tot. chl } a)^{-1}$],

λ – wavelength [nm],

P_i – pigment index of acetone extracts of phytoplankton, *e.g.* the ratio of absorption for the two principal maxima of light absorption by phytoplankton (430 nm and 663 nm). It is related to the chlorophyll *a* concentration in the following way:

$$P_i = 10^{[0.516 - 0.161 (\log C_a(0)) + 0.0422 (\log C_a(0))^2 - 0.0584 (\log C_a(0))^3 + 0.0360 (\log C_a(0))^4]}. \quad (1a)$$

This model, however, was derived on the basis of sparse experimental data and is thus imprecise. Moreover, it does not take into account the pigment package effect in phytoplankton cells (see *e.g.* van de Hulst 1981, Morel & Bricaud 1981).

The second model (Bricaud *et al.* 1995, 1998) was created on the basis of a larger set of experimental material and does account for the above-mentioned package effect. According to this model the absorption coefficients depend on chlorophyll *a* concentrations in seawater in the following manner:

$$\left. \begin{aligned} a_{pl}(\lambda) &= a_{pl}^*(\lambda) C_a \\ a_{pl}^*(\lambda) &= A(\lambda) C_a^{-B(\lambda)} \end{aligned} \right\}, \quad (2)$$

where the coefficients $A(\lambda)$ and $B(\lambda)$ are determined in Bricaud *et al.* (1995, Table 1).

In both of these models the chlorophyll *a* concentration C_a is an indispensable magnitude for determining light absorption coefficients. On the one hand, the surface chlorophyll *a* concentration $C_a(0)$ can be obtained from satellite data (see *e.g.* Gordon & McCluney 1975, Woźniak *et al.* 1995b); on the other, the statistical relationships published in many papers allow the chlorophyll *a* concentration in the water column $C_a(z)$ to be determined from the surface concentration $C_a(0)$ (Lewis *et al.* 1983, Platt *et al.* 1988, Morel & Berthon 1989, Sathyendranath *et al.* 1989, Woźniak *et al.* 1992a and b, 1995a). Thus, both models can formally be used in remote sensing algorithms. But to their disadvantage, neither model takes into consideration the depth-related changes in the coefficient $a_{pl}^*(\lambda)$ caused by variability in the pigment composition, which in turn is due to photo- and chromatic acclimation and the package effect.

The model of phytoplankton absorption properties recently formulated by Woźniak *et al.* (1999) accounts for these acclimation processes and the package effect. It thus enables $a_{pl}^*(\lambda)$ to be calculated from, *inter alia*, known values of particular pigment concentrations. Unfortunately, however, these concentrations cannot be determined directly from satellite data.

Statistical relationships were subsequently found (Majchrowski & Ostrowska 1999 and 2000, this volume) between the composition of

phytoplankton pigments and the spectral irradiance conditions in the sea. From these relationships, various pigment concentrations can be computed from the surface chlorophyll *a* concentration $C_a(0)$, the incoming irradiance $PAR(0^+)$, and the bio-optical model of the sea (Woźniak *et al.* 1992a, b, 1995a). $C_a(0)$ and $PAR(0^+)$ can be determined from satellite observations. Therefore, by combining these two sets of model formulae (by Woźniak *et al.* 1999 and by Majchrowski & Ostrowska 2000, this volume) and taking into consideration further statistical relationships to be discussed below, we can set up a model of light absorption by live phytoplankton that allows us to estimate the phytoplankton light absorption capacities using satellite $C_a(0)$ and $PAR(0^+)$ data. This modelling was the subject of Majchrowski's doctoral dissertation (Majchrowski 2000).

2. Structure and mathematical apparatus of the model

Figure 1 presents a block diagram of the model's algorithm. It consists of three sections:

Section A: specified input data necessary for the computations: surface chlorophyll *a* concentration $C_a(0)$ (block 1), surface irradiance $PAR(0^+)$ (just below the sea surface (index +) (block 3)) and depth z or optical depth τ in the water column (block 2).

Section B: model formulae approximating the relationships between:

- the surface chlorophyll concentration $C_a(0)$ and vertical chlorophyll profiles $C_a(z)$ (block 4);
- the chlorophyll concentration $C_a(z)$ and optical quantities describing the underwater irradiance transmittance (block 5);
- the underwater irradiance characteristics, and chromatic and photoacclimation factors (block 6);
- chromatic and photoacclimation factors and the relative pigment concentrations (block 7);
- phytoplankton pigment concentrations and the specific absorption coefficients of the pigments (block 8).

At the same time, these model relationships are the assumptions on which the present synthesis is based. They are discussed in detail in earlier publications cited in the relevant places in the text.

Section C: optical characteristics of the marine environment and various properties of the phytoplankton which can be determined from the above input data and model formulae, together with the help of other well known formal relationships in biophysics and hydro-optics (blocks 9 to 18).

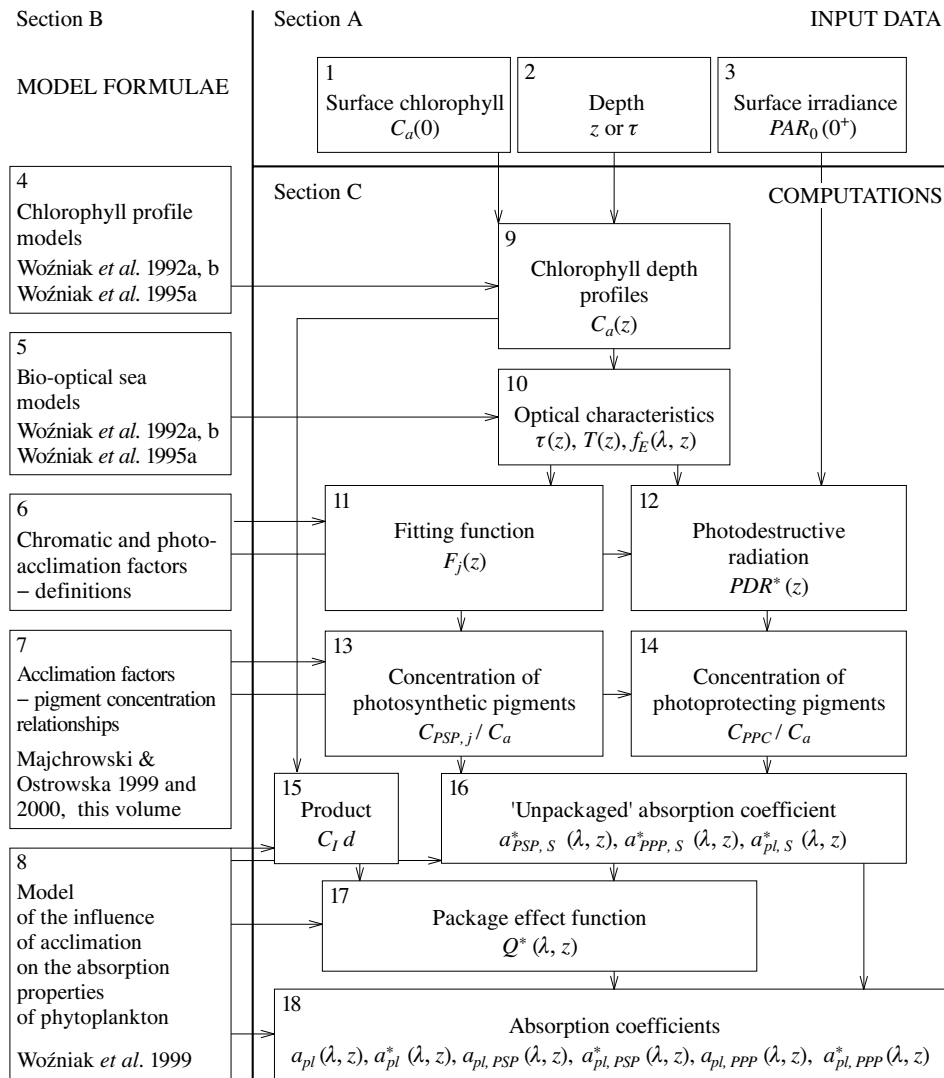


Fig. 1. Block diagram of the model of *in vivo* spectral absorption properties of algal pigments (adapted from Majchrowski 2000)

The mathematical apparatus of the algorithm is given in detail in Table 1. The key model formulae in this algorithm (eqs. (T1)–(T20)) were established by means of statistical analyses of empirical data and semi-empirical modelling. This is described in detail in our earlier papers (Wozniak *et al.* 1992a and b, 1995a, 1997, 1999, Kaczmarek & Wozniak, 1995, Dera 1995, Majchrowski & Ostrowska 1999 and 2000, this volume).

Table 1. Mathematical apparatus of the spectral absorption properties of algal pigments: *in vivo* model

<p>Section A</p> <p>The input parameters of the model are the surface chlorophyll concentration $C_a(0)$ [mg tot. chl a m^{-3}] (block 1), depth in the water column – the real depth z [m] or the optical depth τ (block 2) and the dailly mean surface irradiance $PAR(0^+)$ [μEin $m^{-2} s^{-1}$] or scalar irradiance $PAR_0(0^+)$ [μEin $m^{-2} s^{-1}$] (block 3).</p>
<p>Section B</p> <p>The model formulae are:</p> <p>Block 4: relationships between vertical profiles of chlorophyll a concentration $C_a(z)$ and its surface concentration $C_a(0)$:</p> $C_a(z) = C_a(0) \frac{C_{const} + C_m \exp[-(z - z_{max})\sigma_z]^2}{C_{const} + C_m \exp[-(z_{max})\sigma_z]^2}, \quad (T1)$ <p>where</p> <ul style="list-style-type: none"> • for stratified oceanic waters (Woźniak <i>et al.</i> 1992a and b): $C_{const} = 10^{[-0.0437 + 0.8644 (\log C_a(0)) - 0.0888 (\log C_a(0))^2]},$ $C_m = 0.269 + 0.245 (\log C_a(0)) + 1.51 (\log C_a(0))^2 + 2.13 (\log C_a(0))^3 + 0.81 (\log C_a(0))^4,$ $z_{max} = 17.9 - 44.6 (\log C_a(0)) + 38.1 (\log C_a(0))^2 + 1.32 (\log C_a(0))^3 - 10.7 (\log C_a(0))^4,$ $\sigma_z = 0.0408 + 0.0217 (\log C_a(0)) + 0.00239 (\log C_a(0))^2 + 0.00562 (\log C_a(0))^3 + 0.00514 (\log C_a(0))^4;$ <ul style="list-style-type: none"> • for Baltic waters (Woźniak <i>et al.</i> 1995a): $C_{const} = \left[0.77 - 0.13 \cos\left(2\pi \frac{n_d - 74}{365}\right) \right]^{C_a(0)},$ $C_m = \frac{1}{2M} \left[(0.36)^{C_a(0)} + 1 \right] \times \left[M + 1 + (M - 1) \cos\left(2\pi \frac{n_d - 120}{365}\right) \right],$ $M = 2.25(0.765)^{C_a(0)} + 1,$ $z_{max} = 9.18 - 2.43 (\log C_a(0)) + 0.213 (\log C_a(0))^2 - 1.18 (\log C_a(0))^3,$ $\sigma_x = 0.118 - 0.113 (\log C_a(0)) - 0.0139 (\log C_a(0))^2 + 0.112 (\log C_a(0))^3,$ <p>n_d – the day number of the year.</p>

Block 5: bio-optical relationships for estimating the following quantities (according to Woźniak *et al.* 1992a and b, 1995a, Kaczmarek & Woźniak 1995):

- optical depth in the sea:

$$\tau(z) = -\ln T(z); \quad (\text{T2})$$

- spectral distribution of irradiance:

$$f_E(\lambda, z) = f_E(\lambda, 0) \exp \left[-\int_0^z K_d(\lambda, z) dz \right]; \quad (\text{T3})$$

- transmittance of irradiance through the water column:

$$T(z) = \int_{400 \text{ nm}}^{700 \text{ nm}} f_E(\lambda, z) d\lambda, \quad (\text{T4})$$

where

$f_E(\lambda, 0)$ – normalised typical spectral distribution of irradiance PAR entering the sea (see *e.g.* Fig. 4b in Dera 1995):

$$\int_{400 \text{ nm}}^{700 \text{ nm}} f_E(\lambda, 0) d\lambda = 1,$$

$K_d(\lambda, z)$ – downward spectral irradiance diffuse attenuation coefficient.

The coefficient $K_d(\lambda, z)$ is related to the chlorophyll concentration $C_a(z)$:

$$K_d(\lambda, z) = K_w(\lambda) + C_a(z) \{ C_1(\lambda) \exp[-a_1(\lambda) C_a(z)] + K_{d,i}(\lambda) \} + \Delta K(\lambda), \quad (\text{T5})$$

where

$$\Delta K(\lambda) = \begin{cases} 0 & \text{for oceanic Case 1 Waters,} \\ 0.068 \exp[-0.014(\lambda - 550)] & \text{for Baltic Case 2 Waters.} \end{cases}$$

The constants $C_1(\lambda)$, $a_1(\lambda)$, $K_{d,i}(\lambda)$ and the attenuation of pure water $K_w(\lambda)$ are given in Woźniak *et al.* 1992a and b (*ibid.* Table 2).

Block 6: acclimation factors defined as functions of specific absorption coefficients of various pigment groups of the phytoplankton and selected properties of the underwater light field (according to Woźniak *et al.* 1997):

- chromatic acclimation factor for the j -th group of pigments (or function of spectral fitting):

$$F_j(z) = \frac{1}{a_{j, \max}^*} \int_{400 \text{ nm}}^{700 \text{ nm}} f(\lambda, z) a_j^*(\lambda) d\lambda; \quad (\text{T6})$$

- photoacclimation factor (known as the Potentially Destructive Radiation):

$$PDR^*(z) = \int_{400 \text{ nm}}^{480 \text{ nm}} a_a^*(\lambda) \langle E_0(\lambda, z) \rangle_{\text{day}} d\lambda, \quad (\text{T7})$$

where

$f(\lambda, z) = f_E(\lambda, z)/T(z)$ – spectral distribution of irradiance in the PAR spectral range at depth z :

$a_j^*(\lambda)$ – spectral specific absorption coefficient for the j -th group of ‘unpacked’ pigments (*i.e.* in solvent) (for chlorophyll a – $a_a^*(\lambda)$; for chlorophyll b – $a_b^*(\lambda)$; for chlorophyll c – $a_c^*(\lambda)$; for photosynthetic carotenoids – $a_{PSC}^*(\lambda)$). The numerical values of $a_j^*(\lambda)$ can be determined using the sub-algorithm given by eq. (T13) below;

$a_{j, \max}^*$ – specific absorption coefficient at the maximum absorption spectral range of the j -th ‘unpacked’ pigment;

$\langle E_0(\lambda, z) \rangle_{\text{day}} = PAR_0(0^+) f_E(\lambda, z)$ or $\langle E_0(\lambda, z) \rangle_{\text{day}} \approx \approx 1.2 PAR(0^+) f_E(\lambda, z)$ – daily mean spectral scalar irradiance at depth z :

$PAR_0(0^+)$ – scalar irradiance, $PAR(0^+)$ – irradiance – just below the water surface (index (0^+)) in the PAR spectral range (approximated from 400 to 700 nm).

Block 7: relationships between acclimation factors and pigment concentrations (according to Majchrowski & Ostrowska 1999, 2000, this volume):

- for photosynthetic pigments:

$$\frac{C_{PSC}}{C_a} = 1.348 < F_{PSC} >_{\Delta z} - 0.093, \quad (\text{T8})$$

$$\frac{C_b}{C_a} = 54.07 < F_b >_{\Delta z}^{5.157} + 0.091, \quad (\text{T9})$$

$$\frac{C_c}{C_a} = 0.042 < F_a >_{\Delta z}^{-1.197} < F_c >_{\Delta z}; \quad (\text{T10})$$

- for photoprotecting carotenoids:

$$\frac{C_{PPC}}{C_a} = 0.1758 \langle PDR^* \rangle_{\Delta z} + 0.176, \quad (\text{T11})$$

where

$C_b, C_c, C_{PSC}, C_{PPC}$ [mg pigment m^{-3}] – respective concentrations of chlorophylls b , chlorophylls c , photosynthetic carotenoids PSC and photoprotecting carotenoids PPC ;

$\langle F_a \rangle_{\Delta z}, \langle F_b \rangle_{\Delta z}, \langle F_c \rangle_{\Delta z}, \langle F_{PSC} \rangle_{\Delta z}, \langle PDR^* \rangle_{\Delta z}$ – mean values of chromatic acclimation factors and photoacclimation factor, in a water layer $\Delta z = z_2 - z_1$:

$$\langle F_j \rangle_{\Delta z} = \frac{1}{z_2 - z_1} \int_{z_1}^{z_2} F_j(z) dz,$$

$$\langle PDR^* \rangle_{\Delta z} = \frac{1}{z_2 - z_1} \int_{z_1}^{z_2} PDR(z)^* dz,$$

where

j – pigment group index (a, b, c or PSC),

$z_1 = z - 30$ m if $z \geq 30$ m and $z_1 = 0$, if $z < 30$ m, $z_2 = z + 30$ m.

The mean values in water layer Δz have been taken in order to include the influence of water mixing.

Block 8: model relationships between pigment concentrations and different optical capacities of marine phytoplankton (according to Woźniak *et al.* 1999):

- relationship between the product $C_I d$ and the chlorophyll concentration C_a :

$$C_I d = 24.65 C_a^{0.75}, \quad (\text{T12})$$

where

C_I [mg tot. chl a m^{-3}] – intercellular chlorophyll a concentration,

d [m] – cell diameter, (C_a value given in [mg tot. chl a m^{-3}]);

- relationships between the specific absorption coefficient of ‘unpacked’ pigments (*i.e.* in solvent) and chlorophyll a concentration:

(i) for the j -th pigment group:

$$a_j^*(\lambda) = \sum_i a_{\max,i}^* e^{-\frac{1}{2} \left(\frac{\lambda - \lambda_{\max,i}}{\sigma_i} \right)^2}, \quad (\text{T13})$$

where

$\lambda_{\max,i}$ [nm] – centre of the spectral maximum band [nm],

σ_i – dispersion of the band,

$a_{\max,i}^*$ [m^2 (mg pigment) $^{-1}$] – specific absorption coefficient in the spectral maximum band,

where i – Gaussian band numbers of major groups of phytoplankton pigments (*e.g.* chlorophylls a , chlorophylls b , chlorophylls c , photosynthetic carotenoids PSC and photoprotecting carotenoids PPC). The values of $\lambda_{\max,i}$, σ_i and $a_{\max,i}^*$ are given in Table 3 in Woźniak *et al.* 1999.

(ii) for photosynthetic pigments PSP
(in solvent – index S):

$$a_{PSP,S}^*(\lambda) = \frac{1}{C_a} [C_a a_a^*(\lambda) + C_b a_b^*(\lambda) + C_c a_c^*(\lambda) + C_{PSC} a_{PSC}^*(\lambda)], \quad (\text{T14})$$

(iii) for photoprotecting pigments PPP
(in solvent – index S):

$$a_{PPP,S}^*(\lambda) = \frac{1}{C_a} [C_{PPC} a_{PPC}^*(\lambda)], \quad (\text{T15})$$

(iv) for all the phytoplankton pigments
(in solvent – index S):

$$a_{pl,S}^*(\lambda) = a_{PSP,S}^*(\lambda) + a_{PPP,S}^*(\lambda); \quad (\text{T16})$$

- the relationship between the package effect spectral function, $Q^*(\lambda)$ the product $C_I d$ and the ‘unpacked’ absorption coefficient $a_{pl,S}^*$:

$$Q^*(\lambda) = \frac{3}{2\rho'(\lambda)} \left[1 + \frac{2e^{-\rho'(\lambda)}}{\rho'(\lambda)} + 2\frac{e^{-\rho'(\lambda)} - 1}{\rho'^2(\lambda)} \right], \quad (\text{T17})$$

where

$\rho' = a_{pl,S}^* C_I d$ (the so-called optical parameter of cell size);

- the relationships between *in vivo* absorption coefficients, ‘unpacked’ absorption coefficients (index S) and the package effect function:

(i) total for all phytoplankton pigments:

$$\left. \begin{aligned} a_{pl}(\lambda) &= C_a a_{pl}^*(\lambda) \\ a_{pl}^*(\lambda) &= Q^*(\lambda) a_{pl,S}^*(\lambda) \end{aligned} \right\}, \quad (\text{T18})$$

(ii) for photosynthetic pigments PSP :

$$\left. \begin{aligned} a_{pl,PSP}(\lambda) &= C_a a_{pl,PSP}^*(\lambda) \\ a_{pl,PSP}^*(\lambda) &= Q^*(\lambda) a_{PSP,S}^*(\lambda) \end{aligned} \right\}, \quad (\text{T19})$$

(iii) for photoprotecting pigments:

$$\left. \begin{aligned} a_{pl,PPP}(\lambda) &= C_a a_{PPP}^*(\lambda) \\ a_{pl,PPP}^*(\lambda) &= Q^*(\lambda) a_{PPP,S}^*(\lambda) \end{aligned} \right\}. \quad (\text{T20})$$

Section C

- The principles of the computations are:

Block 9: vertical profiles of chlorophyll $C_a(z)$ can be calculated from input data $C_a(0)$ using eq. (T1).

Block 10: vertical profiles of optical depth $\tau(z)$, spectral distribution of irradiance $f_E(\lambda, z)$ and the irradiance transmittance $T(z)$ can be calculated from their relationships with $C_a(z)$ (block 9) using eqs. (T2)–(T5).

Block 11: vertical profiles of the chromatic acclimation factor $F_j(z)$ can be calculated from $f_E(\lambda, z)$ and $T(z)$ (block 10) using eq. (T6).

Block 12: vertical profiles of the photoacclimation factor $PDR^*(z)$ can be calculated from its relationships with $f_E(\lambda, z)$ (block 10) and the surface irradiance $PAR_0(0^+)$ or $PAR(0^+)$ (input data) using eq. (T7).

Block 13: vertical profiles of the relative concentrations of particular photosynthetic pigments $C_{PSP,j}/C_a$ can be determined from $F_j(z)$ (block 11) using eqs. (T8)–(T10).

Block 14: vertical profiles of the relative concentration of photoprotecting carotenoids C_{PPC}/C_a can be determined from $PDR^*(z)$ (block 12) using eq. (T11).

Block 15: vertical profiles of products $C_I d$ can be calculated from $C_a(z)$ (block 9) using eq. (T12).

Block 16: vertical profiles of specific absorption coefficients for ‘unpackaged’ photosynthetic pigments $a_{PSP,S}^*(\lambda, z)$, photoprotecting pigments $a_{PPP,S}^*(\lambda, z)$, and all pigments $a_{pl,S}^*(\lambda, z)$ can be determined from $C_{PSP,j}/C_a$, (block 13) and C_{PPC}/C_a (block 14) using eqs. (T13)–(T16).

Block 17: the vertical distribution of the package effect spectral function $Q^*(\lambda, z)$ can be determined from the product $C_I d$ (block 15) and $a_{pl,S}^*(\lambda, z)$ (block 16) using eq. (T17).

Block 18: vertical profiles of the marine phytoplankton total spectral absorption coefficient and its components can be determined from basic ‘unpackaged’ absorption coefficients (block 16), the package effect function (block 17) and chlorophyll concentrations (block 9) using eqs. (T18)–(T20).

Related to both oceanic and Baltic waters, the algorithm can be used to estimate phytoplankton light absorption coefficients for both Oceanic Case 1 Waters and Baltic Case 2 Waters, according to the Morel & Prieur (1977) water classification.

3. Conclusions

This is the first nontrivial model of the absorption capacities of phytoplankton which takes phytoplankton acclimation processes, pigment package effects and environmental factors into consideration. It enables the absorption capacities to be computed from remote sensing data (surface chlorophyll a concentration and solar irradiance at the sea surface). The insight of the model consists in taking into consideration the acclimation processes in phytoplankton (photo- and chromatic acclimation and package effect), which up to now have not been taken into account in remote sensing models. Moreover, this model can be used to estimate the diversity of phytoplankton absorption capacities with trophic type of water and depth in the sea.

Examples of the practical application of the new model, an analysis of its utility and estimation errors are given in part 2 of this paper (by Majchrowski *et al.* 2000, this volume) and in the subsequent papers in this volume.

References

- Bricaud A., Babin M., Morel A., Claustre H., 1995, *Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: analysis and parameterisation*, J. Geophys. Res., 100, 13321–13332.
- Bricaud A., Morel A., Babin M., Allali K., Claustre H., 1998, *Variations of light absorption by suspended particles with chlorophyll a concentration in oceanic (case 1) waters: analysis and implications for bio-optical models*, J. Geophys. Res., 103, 31033–31044.
- Dera J., 1995, *Underwater irradiance as a factor affecting primary production*, Diss. and monogr., Inst. Oceanol. PAS, Sopot, 7, 110 pp.
- Gordon H.R., McCluney W.R., 1975, *Estimation of the depth of sunlight penetration in the sea for remote sensing*, Appl. Opt., 14, 413–417.
- Hulst van de H.C., 1981, *Light scattering by small particles*, Dover Pub. Inc., New York, 470 pp.
- Kaczmarek S., Woźniak B., 1995, *The application of the optical classification of waters in the Baltic Sea (Case 2 Waters)*, Oceanologia, 37 (2), 285–297.
- Lewis M.R., Cullen J.J., Platt T., 1983, *Phytoplankton and thermal structure in the upper ocean: consequences of non-uniformity in the chlorophyll profile*, J. Geophys. Res., 88, 2565–2570.
- Majchrowski R., 2000, *Influence of irradiance on the light absorption characteristics of marine phytoplankton*, Ph. D. thesis, Inst. Oceanol. PAN, Sopot, (in Polish).
- Majchrowski R., Ostrowska M., 2000, *Influence of photo- and chromatic acclimation on pigment composition in the sea*, Oceanologia, 42 (2), 157–175.
- 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., Woźniak B., Dera J., Ficek D., Kaczmarek S., Ostrowska M., Koblentz-Mishke O.I., 2000, *Model of the 'in vivo' spectral absorption of algal pigments. Part 2. Practical applications of the model*, Oceanologia, 42 (2), 191–202.
- Morel A., Berthon J.F., 1989, *Surface pigments, algal biomass profiles and potential production of the euphotic layer: relationships re-investigated in view of remote sensing applications*, Limnol. Oceanogr., 34 (8), 1545–1562.
- Morel A., Bricaud A., 1981, *Theoretical results concerning light absorption in a discrete medium and application to specific absorption of phytoplankton*, Deep-Sea Res., 28, 1375–1393.
- Morel A., Prieur L., 1977, *Analysis of variations in ocean color*, Limnol. Oceanogr., 22 (4), 709–722.
- Platt T., Sathyendranath S., Cavarhill C.M., Lewis M.R., 1988, *Ocean primary production and available light: further algorithms for remote sensing*, Deep-Sea Res., 35 (6), 855–879.

- Sathyendranath S., Platt T., Cavarhill C. M., Warnock R. E., Lewis M. R., 1989, *Remote sensing of oceanic primary production: computations using a spectral model*, Deep-Sea Res., 36 (3), 431–453.
- 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 application*, Oceanologia, 39 (4), 377–395.
- Woźniak B., Dera J., Semovski S., Hapter R., Ostrowska M., Kaczmarek S., 1995a, *Algorithm for estimating primary production in the Baltic by remote sensing*, Stud. i Mater. Oceanol., 68, 91–123.
- Woźniak B., Ostrowska M., 1990, *Optical absorption properties of phytoplankton in various seas*, Oceanologia, 29, 117–146.
- Woźniak B., Smekot-Wensierski W., Darecki M., 1995b, *Semi-empirical modelling of backscattering and light reflection coefficients in WC1 seas*, Stud. i Mater. Oceanol., 68, 61–90.