Remote sensing of vertical phytoplankton pigment distributions in the Baltic: new mathematical expressions. Part 1: Total chlorophyll a distribution*

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Abstract

This article is the first in a series of three describing the modelling of the vertical different photosynthetic and photoprotecting phytoplankton pigments concentration distributions in the Baltic and their interrelations described by the so-called non-photosynthetic pigment factor. The model formulas yielded by this research are an integral part of the algorithms used in the remote sensing of the

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Baltic ecosystem. Algorithms of this kind have already been developed by our team from data relating mainly to oceanic Case 1 waters (WC1) and have produced good results for these waters. But their application to Baltic waters, i.e., Case 2 waters, was not so successful. On the basis of empirical data for the Baltic Sea, we therefore derived new mathematical expressions for the spatial distribution of Baltic phytoplankton pigments. They are discussed in this series of articles.

This first article presents a statistical model for determining the total concentration of chlorophyll a (i.e., the sum of chlorophylls a + pheo derived spectrophotometrically) at different depths in the Baltic Sea $C_a(z)$ on the basis of its surface concentration $C_a(0)$, which can be determined by remote sensing. This model accounts for the principal features of the vertical distributions of chlorophyll concentrations characteristic of the Baltic Sea. The model's precision was verified empirically: it was found suitable for application in the efficient monitoring of the Baltic Sea. The modified mathematical descriptions of the concentrations of accessory pigments (photosynthetic and photoprotecting) in Baltic phytoplankton and selected relationships between them are given in the other two articles in this series (Majchrowski et al. 2007, Woźniak et al. 2007b, both in this volume).

1. Introduction

The 'light-marine photosynthesis' models that we have been developing for the remote sensing of marine ecosystems (e.g., Woźniak et al. 2003) require, among other things, the determination of the vertical distributions of the concentrations $C_j(z)$[1] of the various phytoplankton pigments in the sea: the principal plant pigment chlorophyll a, $C_a(z)$, and accessory pigments – photosynthetic pigments like chlorophylls b, $C_b(z)$, chlorophylls c, $C_c(z)$ and phycobilins $C_{phyc}(z)$, photosynthetic carotenoids (PSC), $C_{PSC}(z)$ and photoprotecting carotenoids (PPC), $C_{PPC}(z)$. Knowledge of the vertical distributions $C_j(z)$ of all these pigment groups, and also of their mutual proportions as given by the non-photosynthetic pigment index f_a (Ficek et al. 2000), is essential for estimating, for example, the absorptive properties of phytoplankton in the sea and the quantum yield of photosynthesis at different depths in the sea; from these magnitudes the vertical distributions of the primary production of organic matter in the marine environment can be calculated. The model formulas presented in this series of articles form an integral part of the algorithms permitting the efficient monitoring of the Baltic ecosystem by remote sensing.

In our earlier 'light-marine photosynthesis' model for determining the vertical distributions of pigment concentrations in the ocean $C_j(z)$ (Woźniak et al. 2003, Ficek et al. 2003) we used model formulas derived from empirical research and the modelling of the photo- and chromatic acclimation of

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[1]A list of abbreviations and symbols used in this and the subsequent papers in this series will be found in the Annex.

phytoplankton. These formulas enable the concentrations of pigments at different depths z in the sea $C_j(z)$ to be determined from two remotely measured parameters – the total surface chlorophyll a concentration $C_a(0)$, and the spectral downward irradiance at the sea surface $E_d(\lambda, 0)$. They are as follows:

- $C_a(z) = f(C_a(0))$ – the dependence of the chlorophyll a concentration (C_a) at different depths z in the sea on its surface concentration. We derived this formula for oceanic waters (see Woźniak et al. 1992a,b).

- $C_b(z) = f(C_a, F_b)$, $C_c(z) = f(C_a, F_c)$, $C_{PSC}(z) = f(C_a, F_{PSC})$ – the respective dependences of the concentrations of chlorophylls b, c and of PSC on the chlorophyll a concentration (C_a) spectral fitting functions (F_b, F_c, F_{PSC}), which are determined from known irradiance conditions in the sea and the absorption properties of these pigments. We derived the relationships for the concentrations of these pigments in Case 1 oceanic waters (see Majchrowski & Ostrowska 1999, 2000, Majchrowski 2001, Woźniak et al. 2003).

- $C_{PPC}(z) = f(C_a, PDR^*)$ – the dependence of photoprotecting carotenoids on the chlorophyll a concentration (C_a) Potentially Destructive Radiation (PDR^*), which depends, in turn, on the irradiance conditions in the sea and the specific coefficients of light absorption by chlorophyll a. We established this relationship for oceanic waters (see, e.g., Majchrowski & Ostrowska 1999, 2000, Majchrowski 2001).

- $f_a(z) = f(a^*_{pl,PPP}, a^*_{pl,PSP}, C_{PPP}, C_{PSP}, PAR(0), \tau)$ – the dependence of the non-photosynthetic pigment factor on the following: a) the irradiance at the sea surface by the photosynthetically available radiation (PAR); b) the total concentration of all photosynthetic pigments (PSP) – C_{PSP} and photoprotecting pigments (PPP) – C_{PPP}, and their specific absorption coefficients in vivo, $a^*_{pl,PSP}$, and $a^*_{pl,PPP}$; c) the optical depth τ in the sea. We derived this relation for oceanic waters (see Ficek et al. 2000, Ficek 2001, Woźniak et al. 2003).

Earlier we had also developed a preliminary model description of the vertical distributions of the chlorophyll a concentration in the Baltic (Woźniak et al. 1995a,b), based on mathematical formulas resembling those for oceanic waters, but which took account of the seasonal changes occurring in the Baltic. Unfortunately, that description failed to live up to expectations.

We also recently attempted to adapt the oceanic 'light-marine photosynthesis' model to the remote sensing of the Baltic ecosystem. Again, the earlier formulas for determining depth profiles of pigment concentrations in the clear, Case 1 waters of the oceans failed to produce results of a similar

quality when applied to the algorithms for remotely sensing primary production in the Baltic. Also, the precision of the formula for calculating the depth profiles of chlorophyll a, modified for the Baltic to allow for its seasonal variations, was poor. The reasons for this are to be sought in the specifics of Baltic waters. These are brackish (Baltic Proper surface waters $\sim 6 - 8$ PSU) and contain considerable amounts of anthropogenic substances – dissolved and suspended yellow substances as well as other optically active substances. Any description of the adaptation and acclimation of algae to the conditions prevailing in these waters therefore appears to be a much more formidable task than for Case 1 waters.

In response to these arguments, our objective was to derive more precise, though not necessarily more complicated, mathematical formulas for determining vertical concentration profiles of chlorophyll a, $C_a(z)$, accessory pigments $C_j(z)$ and the factor f_a in the Baltic. To this end, we accumulated a bank of suitable empirical data from 1978–2005. These data were subjected to statistical analysis: this enabled us to derive new formulas for the Baltic, the utility of which we then tested in satellite algorithms for determining primary production in the Baltic. The subsequent empirical verification of these formulas showed them to be of a far superior precision than the earlier ones, which were mentioned above.

The present paper, the first in a series of thematically linked articles, presents the modified mathematical description of the vertical distributions of the total chlorophyll a concentration in the Baltic. The other two papers in the series will deal with the modified mathematical descriptions of the accessory pigment concentrations in Baltic phytoplankton (part 2, Majchrowski et al. 2007, this volume) and the non-photosynthetic pigment factor f_a characteristic of Baltic waters (part 3, Woźniak et al. 2007b, this volume).

2. Characteristics of the empirical material

Our statistical analysis is based on numerous empirical data sets, systematically collected over many years (1978–2005) and stored in the Oceanographic Data Bank at IO PAS. Most of this work was funded by the Committee for Scientific Research and the Ministry of Scientific Research and Information Technology through project PBZ-KBN 056/P04/2001 (*The study and development of a satellite system for monitoring the Baltic ecosystem*).

Chlorophyll a concentrations were measured at different depths in the sea using the traditional spectrophotometric method (Strickland & Parsons

1968) over very many years (1978–2005) and at all seasons, mainly from r/v 'Oceania', but also from r/v 'Baltica' and other research vessels. For the purposes of our analysis some 5000 vertical profiles of chlorophyll a were gathered, measured in Baltic Sea basins of different trophic index, i.e., in different regions of this sea, but mostly in its southern part. We may therefore make the assumption that the results analysed here are representative of all situations encountered in the southern Baltic, but to a certain extent also in the adjacent regions. Table 1 lists the numbers of vertical profiles of total chlorophyll a concentration, $C_a(z)$, estimated spectrophotometrically in samples of water drawn from different depths in the sea. Each $C_a(z)$ profile specified in Table 1 consists of at least 5 measurement points at particular depths z. The table also shows the number of $C_a(z)$ profiles measured in different trophic types of Baltic water and in each month of the year. In some cruises chlorophyll a concentrations were measured not only spectrophotometrically, but also with an in situ fluorescence technique (see, e.g., Ostrowska et al. 2000a,b, Ostrowska 2001) using a PumpProbe fluorimeter (Ecomonitor, Moscow) calibrated in total chlorophyll a concentration units [mg tot. chl a m^{-3}] (Ostrowska et al. 2000a,b, Ostrowska 2001). Table 2 lists the vertical

Table 1. Number of vertical profiles of the total chlorophyll a concentration, consisting of no less than 5 measurement points at different depths, measured spectrophotometrically in 1978–2005, and classified according to trophic type of water and month of the year (season)

Trophic type	Range $C_a(0)$ [mg m^{-3}]	January	February	March	April	May	June	July	August	September	October	November	December	Total
1	2	3	4	5	6	7	8	9	10	11	12	13	14	**15**
O1	$C_a < 0.05$	0	1	0	0	1	0	0	0	0	0	4	0	**6**
O2	$0.05 < C_a <= 0.1$	0	1	1	0	8	0	1	0	0	0	0	0	**11**
O3	$0.1 < C_a <= 0.2$	1	0	2	5	16	5	0	2	0	0	4	3	**38**
M	$0.2 < C_a <= 0.5$	41	32	60	10	42	65	2	4	0	3	20	1	**280**
I	$0.5 < C_a <= 1$	112	69	67	101	95	40	26	33	4	33	130	19	**729**
E1	$1 < C_a <= 2$	16	9	46	101	263	96	84	111	94	71	196	9	**1096**
E2	$2 < C_a <= 5$	1	8	64	291	604	128	129	162	241	89	117	6	**1840**
E3	$5 < C_a <= 10$	7	3	35	296	166	11	24	13	21	11	9	5	**601**
E4	$10 < C_a <= 20$	0	0	34	83	33	0	1	0	1	0	0	4	**156**
E5	$20 < C_a <= 50$	0	0	21	17	3	1	0	0	9	0	0	0	**51**
E6	$50 < C_a$	0	0	0	6	3	0	0	0	0	0	0	0	**9**
Total		**178**	**123**	**330**	**910**	**1234**	**346**	**267**	**325**	**370**	**207**	**480**	**47**	**4817**

Table 2. Number of vertical profiles of the total chlorophyll a concentration in the Baltic, measured fluorimetrically in 1997–2001 during 11 cruises of r/v 'Oceania'; classification as in Table 1

Trophic type	Range $C_a(0)$ [mg m^{-3}]	January	February	March	April	May	June	July	August	September	October	November	December	Total
1	2	3	4	5	6	7	8	9	10	11	12	13	14	**15**
O1	$Ca < 0.05$	0	0	0	0	0	0	0	0	0	0	0	0	**0**
O2	$0.05 < C_a <= 0.1$	0	0	0	0	1	0	0	0	0	0	0	0	**1**
O3	$0.1 < C_a <= 0.2$	0	0	0	0	0	0	0	0	1	0	0	0	**1**
M	$0.2 < C_a <= 0.5$	0	0	13	0	3	0	0	0	1	1	0	0	**18**
I	$0.5 < C_a <= 1$	0	0	27	16	0	0	0	0	0	0	0	0	**43**
E1	$1 < C_a <= 2$	0	0	24	9	47	0	0	0	0	11	11	0	**102**
E2	$2 < C_a <= 5$	0	8	31	0	25	0	0	0	71	15	21	0	**171**
E3	$5 < C_a <= 10$	0	1	7	0	12	0	0	0	7	4	0	0	**31**
E4	$10 < C_a <= 20$	0	1	9	0	4	0	0	0	5	0	0	0	**19**
E5	$20 < C_a <= 50$	0	0	4	0	0	2	0	0	5	0	0	0	**11**
E6	$50 < C_a$	0	1	0	0	7	0	0	0	0	0	0	0	**8**
Total		**0**	**11**	**115**	**25**	**99**	**2**	**0**	**0**	**90**	**31**	**32**	**0**	**405**

chlorophyll a concentration profiles in the Baltic obtained with the latter method. The fluorescence techniques have a number of advantages over the traditional methods of determining chlorophyll a from discrete water samples and are commonly used to determine in situ vertical distributions of this pigment in the water column. In the present work, we use PumpProbe fluorimeter data from 11 cruises on r/v 'Oceania' in 1997–2001. These data are not used for the derivation of our statistical model, but to assess the performance of the model. We have at our disposal some 400 depth profiles of chlorophyll a concentration estimated fluorimetrically. The fluorescence was measured with a vertical resolution of approximately 0.3 m. More information about these data is given in Table 2.

3. Methods and results of statistical analyses

Modelling the vertical distributions of chlorophyll a in the sea has a long history. Many authors have analysed such distributions from various standpoints (Smith 1981, Richardson et al. 2002, Stramska & Stramski 2005, Uitz et al. 2006) and derived statistical formulas describing these profiles (Lewis et al. 1983, Platt et al. 1988, Morel & Berthon 1989, Sathyendranath et al. 1989, Woźniak et al. 1992a,b, 1995a,b, Kameda & Matsumura 1998). In most cases, these formulas consist of the sum of two independent

components – a constant one, independent of depth z in the sea, and a depth-variable one, usually described by a Gaussian function. These models provide a good description of the vertical distributions of the chlorophyll a concentration in stratified Case 1 waters, with a distinctive maximum of this concentration at a certain depth; the depth and distinctiveness of this maximum depend largely on the trophic type of the basin in question (see Figure 1a).
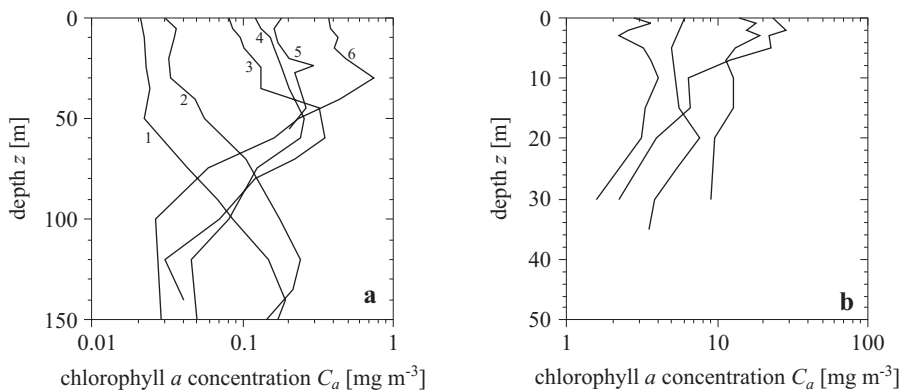
Figure 1. Examples of empirical vertical profiles of the total chlorophyll a concentration $C_a(z)$: for different oceanic regions (Case 1 waters) (1–3 Indian Ocean, 4–6 Atlantic) (a); for Baltic waters (Case 2 waters) – based on empirical data from the IO PAS Sopot data bank (b)

Unfortunately, a whole range of external factors affects the content of the various components of Case 2 waters. They give rise to changes in the fine structure of the depth profiles of chlorophyll concentration and determine the magnitude (distinctiveness) and depth at which the maximum concentration of this pigment occurs. This is usually quite close to the surface and is usually less distinctive than in the profiles of clear oceanic waters (see Figures 1a,b).

In order to keep the model simple and easy to operate, we attempted to find a link between the vertical profiles of chlorophyll a, $C_a(z)$, and the surface concentration of this pigment $C_a(0)$ only. Often serving as the trophic index of a basin (see Tables 1 and 2, columns 1 and 2), this latter concentration supplies a wealth of information about its properties. Given a sufficiently large data bank, it has been shown possible to construct a statistical model of the vertical distributions of the chlorophyll concentration for Baltic waters with satisfactory precision. Statistical analysis of the empirical material using non-linear regression yielded the following mathematical description of the vertical distributions of

chlorophyll a concentrations in the Baltic: it is the sum of two components – one is constant with depth; the other is depth-variable and described by a Gaussian function:

$$C_a(z) + C_a(0)\frac{A + B\exp[-(z - z_m)^2\,\sigma]}{A + B\exp[-(z_m)^2\,\sigma]}, \tag{1}$$

where
$A = 10^{(1.38\log(C_a(0))+0.0883)}$,
$B = 10^{(0.714\log(C_a(0))+0.0233)}$,
$z_m = -4.61\log(C_a(0)) + 8.86$,
$\sigma = 0.0052$.

Figure 2 illustrates profiles of the relative concentrations of the total chlorophyll a for waters of different trophic index, determined on the basis of model formula (1). Figure 3a shows examples of model profiles of absolute chlorophyll a concentrations for the Baltic determined using formula (1); for comparison, Figure 3b shows the corresponding profiles for stratified oceanic waters determined using the earlier oceanic model (Woźniak et al. 1992a). Comparison of the plots in Figures 1, 2 and 3 shows that the model profiles are a good reflection of trends in nature: the maximum concentration of chlorophyll a occurs closer and closer to the surface, becoming less and less distinctive as its surface concentration increases. Comparison of the model profiles for the Baltic and for stratified Case 1 waters (see Fig. 3) shows that the 'Baltic' model takes account of the empirically observed, less distinctive shape of the profile in Case 2 waters, and also of the fact that the maximum lies much closer to the surface in waters of the same trophic index.
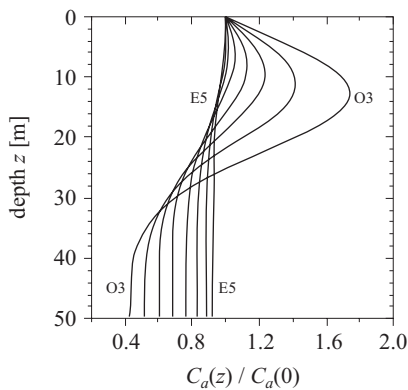
Figure 2. Relative vertical distributions of the total chlorophyll a concentration $C_a(z)/C_a(0)$ in Baltic waters of different trophic index, determined with the model formula (1). The symbols on the figure denote the various trophic types of water in accordance with the classification in Tables 1 and 2, columns 1 and 2
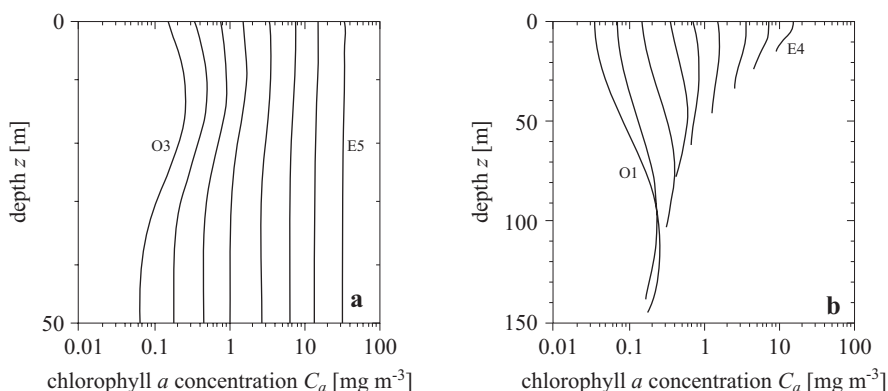
Figure 3. Examples of model profiles of the total chlorophyll a concentration $C_a(z)$ for waters of different trophic index: for Baltic waters, determined using model formula (1) (a); for stratified waters, determined using the oceanic model (Woźniak et al. 1992a) (b). The symbols on the figure denote the various trophic types of water in accordance with the classification in Tables 1 and 2, columns 1 and 2

4. Empirical verification of the model

The precision of this model formula was tested with the aid of chlorophyll concentrations measured by fluorimetry (see Table 2). This technique is considered more accurate than the traditional spectrophotometric one, because measurements are made in situ and the study material is not exposed to the changes in conditions that samples in the traditional method are subject to. Moreover, the measured depth profiles are practically continuous.

Chlorophyll concentrations estimated with the 'new Baltic model' – formula (1) for Baltic Case 2 waters – were compared with empirical concentrations obtained by fluorimetry. The results of this verification for the whole bank of empirical data (Table 2) from different depths within the surface layer (thickness = about twice that of the euphotic zone z_e) are illustrated in Figure 4, and the calculated errors referred to different depth within the layers of different thicknesses ($0 - 1z_e$, $0 - 1.5z_e$, $0 - 2z_e$) are listed in Table 3 (items 8, 9, 10). For comparison, this table also gives the errors in similar empirical verifications of previous models of the vertical distributions of chlorophyll concentrations for oceanic Case 1 waters (Woźniak et al. 1992a,b) and for Baltic Case 2 waters (old Baltic) (Woźniak et al. 1995a,b):

(item 1) errors of the model developed for Case 1 waters, determined on the basis of the data bank containing chlorophyll a concentrations in the Baltic measured fluorimetrically (Table 2) for a layer of thickness $0 - 1z_e$;

(item 2) errors of the model developed for Case 1 waters, determined on the basis of the data bank containing chlorophyll a concentrations in the Baltic measured fluorimetrically (Table 2) for a layer of thickness $0 - 1.5z_e$;

(item 3) errors of the model developed for Case 1 waters, determined on the basis of the data bank containing chlorophyll a concentrations in the Baltic measured fluorimetrically (Table 2) for a layer of thickness $0 - 2z_e$;

(item 4) errors of the model developed for Case 1 waters, determined for the ocean (layer of thickness $0 - 1z_e$) and cited after Woźniak et al. (1992a,b);

(item 5) errors of the model developed for Case 2 waters, determined on the basis of the data bank containing chlorophyll a concentrations in the Baltic measured fluorimetrically (Table 2) for a layer of thickness $0 - 1z_e$;

(item 6) errors of the model developed for Case 2 waters, determined on the basis of the data bank containing chlorophyll a concentrations in the Baltic measured fluorimetrically (Table 2) for a layer of thickness $0 - 1.5z_e$;

(item 7) errors of the model developed for Case 2 waters, determined on the basis of the data bank containing chlorophyll a concentrations in the Baltic measured fluorimetrically (Table 2) for a layer of thickness $0 - 2z_e$.
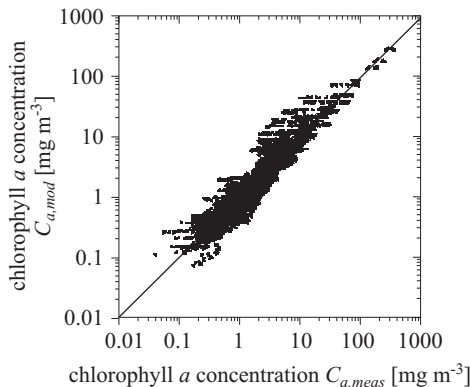
Figure 4. Comparison of total chlorophyll a concentrations measured ($C_{a,\,meas}$) and calculated using the model ($C_{a,\,mod}$) for an independent set of empirical data (with measurements performed fluorimetrically – Table 2) for different depth within a surface layer of water of thickness $2z_e$

As expected, the errors in calculating chlorophyll concentrations with the present model are much smaller than with the earlier models. Confirmation of this is provided by the better precision of the new mathematical description of vertical chlorophyll a concentrations in the Baltic. The errors of the new model (Table 3 – items 8, 9 10) are comparable with those of

Table 3. Relative errors in the determination of the total chlorophyll a concentration in layers of thicknesses $0-1z_e$, $0-1.5z_e$ and $0-2z_e$ for three different models: (Oceanic) developed for oceanic Case 1 waters (Woźniak et al. 1992a,b) (items 1–4); (old Baltic) developed earlier for Baltic Case 2 waters (Woźniak et al. 1995a,b) (items 5–7); (new Baltic) developed in the present work as formula (1) for Baltic Case 2 waters (items 8–10)

Item	Model	Data	Arithmetic statistics		Logarithmic statistics			
			systematic error $<\varepsilon>$ [%]	statistical error σ_ε [%]	systematic error $<\varepsilon>_g$ [%]	standard error factor x	statistical error σ_+ [%]	σ_- [%]
1	Oceanic	Baltic $0-1z_e$	−5.10	±27.45	−7.95	1.27	27.15	−21.35
2		Baltic $0-1.5z_e$	−1.10	±32.43	−4.77	1.30	30.15	−23.17
3		Baltic $0-2z_e$	4.86	±41.42	−0.43	1.35	35.25	−26.06
4		Ocean $0-1z_e$	1.0	±28.3			mean for layer $0-1z_e$ (Woźniak et al. 1992a,b)	
5	old Baltic	Baltic $0-1z_e$	13.85	±37.37	9.81	1.34	34.09	−25.42
6		Baltic $0-1.5z_e$	11.83	±39.97	6.75	1.44	43.86	−30.49
7		Baltic $0-2z_e$	10.22	±41.60	4.15	1.53	53.16	−34.71
8	new Baltic	Baltic $0-1z_e$	−1.06	±28.38	−3.86	1.26	25.94	−20.60
9		Baltic $0-1.5z_e$	−0.18	±32.54	−3.72	1.29	29.24	−22.62
10		Baltic $0-2z_e$	1.78	±37.44	−2.61	1.32	32.24	−24.38

where

$\varepsilon = (C_{a,mod} - C_{a,meas})/C_{a,meas}$ – relative error,

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

σ_ε – standard deviation of errors (statistical error),

$<\varepsilon>_g = 10^{[<\log(C_{a,mod}/C_{a,meas})>]} - 1$ – logarithmic mean of errors,

$<\log(C_{a,mod}/C_{a,meas})>$ – mean of $\log(C_{a,mod}/C_{a,meas})$,

$\sigma_{\log}$ – standard deviation of $\log(C_{a,mod}/C_{a,meas})$,

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

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

chlorophyll a concentrations in the ocean estimated with the oceanic model (item 4). We can therefore regard our objective as having been achieved and the precision of the model as satisfactory for the time being. In the future, however, we shall be striving to improve this description further.

5. Final remarks

The model formula presented in this paper for approximating the vertical distributions of total chlorophyll a in the Baltic takes into consideration the principal features of these distributions, not only those occurring in all sea waters, but also those specific to the Baltic. It reflects the presence of the maximum of this concentration at the depth where the two main limiting factors – the intensity of the irradiance penetrating from the surface and the concentration of nutrients in the water – create optimum conditions for photosynthesis. Nonetheless, both the distinctiveness and the depth of occurrence of this maximum are affected by a variety of environmental factors, very many of which complicate the pigment concentration profiles in Case 2 waters, such as those of the Baltic. As the surface concentration $C_a(0)$ can be determined by remote sensing (Ruddick et al. 2000, Sathyendranath et al. 2001), and the precision of chlorophyll a concentrations estimated according to the method presented here is high, it can be applied in remote sensing algorithms for the efficient and reliable monitoring of the Baltic Sea.

Of course, model formula (1) does not have universal application. The coefficients it contains – determined by statistical analysis – link the general, universal shape of vertical chlorophyll concentration profiles with the environmental conditions prevailing in the Baltic. In order to obtain a similarly straightforward model of such profiles for some other marine basin, one would first have to carry out a statistical analysis of the model for the largest possible number of empirical data gathered in the basin in question and then establish new coefficients, specific to that basin.

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Annex

List of the abbreviations and symbols used in this and the two other articles in this series (Majchrowski et al. 2007, Woźniak et al. 2007b, this volume), and also in the article on modelling the quantum yield of photosynthesis in the Baltic (Woźniak et al. 2007a, this volume)

Symbol	Denotes	Units
1	2	3
a_{pl}	Coefficient of light absorption by phytoplankton	m^{-1}
$a_{pl,\,PSP}$	Coefficient of light absorption by photosynthetic pigments	m^{-1}
a_{pl-UP}	Model coefficient of light absorption by all phytoplankton pigments except the so-called unrecorded pigment	m^{-1}
$a_{pl-UP,\,s}$	Model coefficient of light absorption by all phytoplankton pigments except the so-called unrecorded pigment in the unpackaged (solvent) state	m^{-1}
a^*	Mass-specific coefficient of light absorption	$m^2\ g^{-1}$
a^*_{pl}	Mass-specific coefficient of light absorption by all phytoplankton pigments	$m^2(mg\ tot.\ chl\ a)^{-1}$
$a^*_{pl,\,PPP}$	Mass-specific coefficient of light absorption by photoprotecting pigments	$m^2(mg\ tot.\ chl\ a)^{-1}$
$a^*_{pl,\,PSP}$	Mass-specific coefficient of light absorption by photosynthetic pigments	$m^2(mg\ tot.\ chl\ a)^{-1}$
a^*_j	Mass-specific, model coefficient of light absorption by recorded pigments	$m^2(mg\ pigment)^{-1}$
a^*_a	Mass-specific coefficient of light absorption by chlorophyll a	$m^2(mg\ tot.\ chl\ a)^{-1}$
a^*_b	Mass-specific coefficient of light absorption by chlorophylls b	$m^2(mg\ chl\ b)^{-1}$
a^*_c	Mass-specific coefficient of light absorption by chlorophylls c	$m^2(mg\ chl\ c)^{-1}$
a^*_{phyc}	Mass-specific coefficient of light absorption by phycobilins	$m^2(mg\ phyc)^{-1}$
a^*_{PSC}	Mass-specific coefficient of light absorption by photosynthetic carotenoids	$m^2(mg\ PSC)^{-1}$
a^*_{UP}	Mass-specific, model coefficient of light absorption by unrecorded pigments	$m^2(mg\ UP)^{-1}$
$\widetilde{a}^*_{pl}$	Mean mass-specific absorption coefficient for all pigments weighted by the irradiance spectrum	$m^2(mg\ tot.\ chl\ a)^{-1}$
$a^*_{a,\,max},$ $a^*_{b,\,max},$ $a^*_{c,\,max},$ $a^*_{PSC,\,max}$	Mass-specific coefficients of light absorption in bands of maximum absorption for chlorophyll a, chlorophyll b, chlorophyll c and PSC	$m^2(mg\ pigment)^{-1}$

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1	2	3
$\widetilde{a}^{*}_{pl,\,PSP}$	Mean mass-specific absorption coefficient of photosynthetic pigments weighted by the irradiance spectrum	$\mathrm{m}^2(\mathrm{mg\ tot.\ chl}\,a)^{-1}$
$C_a(0)$	Surface concentration of total chlorophyll a (i.e., sum of chlorophylls a + pheo derived spectrophotometrically)	$\mathrm{mg\ tot.\ chl}\,a\ \mathrm{m}^{-3}$
C_j	Concentrations of the jth group of pigments (including chlorophyll a)	$\mathrm{mg\ of\ the}\ j^{\text{th}}\ \mathrm{pigment\ m}^{-3}$
C_a	Concentration of chlorophyll a	$\mathrm{mg\ tot.\ chl}\,a\ \mathrm{m}^{-3}$
C_b	Concentration of chlorophyll b	$\mathrm{mg\ chl}\,b\ \mathrm{m}^{-3}$
C_c	Concentration of chlorophyll c	$\mathrm{mg\ chl}\,c\ \mathrm{m}^{-3}$
C_{phyc}	Concentration of phycobilins	$\mathrm{mg}\ phyc\ \mathrm{m}^{-3}$
C_{PSC}	Concentration of photosynthetic carotenoids	$\mathrm{mg\ PSC\ m}^{-3}$
C_{PPC}	Concentration of photoprotecting carotenoids	$\mathrm{mg\ PPC\ m}^{-3}$
C_{UP}	Concentration of unrecorded pigments	$\mathrm{mg\ UP\ m}^{-3}$
E_d	Downward irradiance spectra in the PAR spectral range (400–700 nm)	$\mu\mathrm{Ein\ m}^{-2}\ \mathrm{s}^{-1}\ \mathrm{nm}^{-1}$
$E_0(\lambda)$	Scalar irradiance spectra in the PAR spectral range (400–700 nm)	$\mu\mathrm{Ein\ m}^{-2}\ \mathrm{s}^{-1}\ \mathrm{nm}^{-1}$
F_j	Spectral fitting function of the jth group of pigments	dimensionless
F_a	Spectral fitting function of chlorophylls a	dimensionless
F_b	Spectral fitting function of chlorophylls b	dimensionless
F_c	Spectral fitting function of chlorophylls c	dimensionless
F_{PSC}	Spectral fitting function of photosynthetic carotenoids	dimensionless
$<F_j>_{\Delta z}$	Mean values of F_j in water layer Δz	dimensionless
$<F_{PSC}>_{\Delta z}$	Mean values of F_{PSC} in water layer Δz	dimensionless
$<F_b>_{\Delta z}$	Mean values of F_b in water layer Δz	dimensionless
$<F_c>_{\Delta z}$	Mean values of F_c in water layer Δz	dimensionless
$<F_a>_{\Delta z}$	Mean values of F_a in water layer Δz	dimensionless
$f(\lambda)$	Spectral function of the distribution downward irradiance in the PAR range	nm^{-1}
f_a	Non-photosynthetic pigment absorption factor	dimensionless

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1	2	3
f_Δ	Inefficiency factor in energy transfer and charge recombination	dimensionless
f_c	Factor describing the total effect of different factors on the portion of functional PS2 RC	dimensionless
$f_{c(Ca(0))}$	Factor describing the effect of surface chlorophyll a concentration on the portion of functional PS2 RC	dimentionless
$f_{c(N_{inorg})}$	Factor describing the effect of nutrients on the portion of functional PS2 RC	dimensionless
$f_{c(\tau)}$	Factor describing the reduction in the portion of functional PS2 RC at large depths	dimensionless
$f_{c(PAR_{inh})}$	Factor describing the reduction in the portion of functional PS2 RC as a result of photoinhibition	dimensionless
$f_{E,t}$	Classic dependence of photosynthesis on light and temperature, also known as the light curve of photosynthesis efficiency at a given temperature	dimensionless
HPLC	High Performance Liquid Chromatography	
λ	Wavelength of the light	nm
$KPUR^*_{PSP}$	Saturation irradiance	Ein (mg tot. chl a)$^{-1}$ s^{-1}
$KPUR^*_{PSP,0}$	Saturation irradiance at $temp = 0°C$	Ein (mg tot. chl a)$^{-1}$ s^{-1}
MCM	Multi-Component 'light-photosynthesis' model	
P^B	Rate of photosynthesis, (also known as the assimilation number)	molC (mg tot. chl a)$^{-1}$ s^{-1}
PS2 RC	Reaction Centre in photosynthetic apparatus	
PSC	Photosynthetic carotenoids	
PPC	Photoprotecting carotenoids	
PSP	Photosynthetic pigments	
PPP	Photoprotecting pigments	
PDR	Potentially Destructive Radiation	μEin m^{-2} s^{-1}
PDR^*	Potentially Destructive Radiation per unit of the chlorophyll a mass	μEin (mg tot. chl a)$^{-1}$ s^{-1}

List of the abbreviations and symbols used in this and the two other articles in this series (Majchrowski et al. 2007, Woźniak et al. 2007b, this volume), and also in the article on modelling the quantum yield of photosynthesis in the Baltic (Woźniak et al. 2007a, this volume) (*continued*)

1	2	3
$< PDR^* >_{\Delta z}$	Mean value of PDR^* in water layer Δz	μEin $(\text{mg tot. chl } a)^{-1}$ s^{-1}
PAR	Photosynthetically Available Radiation	
PAR	Downward irradiance in the PAR spectral range (400–700 nm)	μEin m^{-2} s^{-1}
PAR_0	Scalar irradiance in the PAR spectral range (400–700 nm)	μEin m^{-2} s^{-1}
PUR	Photosynthetically Usable Radiation	
PUR	Photosynthetically Usable Radiation by all pigments	μEin m^{-2} s^{-1}
PUR_{PSP}	Photosynthetically Usable Radiation absorbed by photosynthetic pigments	μEin m^{-2} s^{-1}
PUR_{PPP}	Photosynthetically Usable Radiation absorbed by photoprotecting pigments	μEin m^{-2} s^{-1}
$PUR^* \equiv PUR_{pl}^*$	Number of quanta absorbed by all phytoplankton pigments in unit time referred to unit mass of chlorophyll a	Ein $(\text{mg tot. chl } a)^{-1}$ s^{-1}
PUR_{PSP}^*	Number of quanta absorbed by photosynthetic pigments in unit time referred to unit mass of chlorophyll a	Ein $(\text{mg tot. chl } a)^{-1}$ s^{-1}
Q_{10}	Parameter indicating the multiplication factor of the increase in saturation irradiance due to a temperature rise of $\Delta temp = 10^{\circ}$C	dimensionless
$Q^*(\lambda)$	Absorption deficiency function due to the pigment packaging effect	dimensionless
$\tau \equiv \tau_{PAR}$	Optical depth in the sea	dimensionless
$temp$	Ambient water temperature	$^{\circ}$C
$temp(0)$	Sea surface temperature	$^{\circ}$C
	Trophic type symbols:	
O	– oligotrophic	
M	– mesotrophic	
I	– intermediate	
E	– eutrophic	
Δz	Thickness of water layer	m
z	Real depth in the sea	m
z_e	Depth of euphotic zone	m

List of the abbreviations and symbols used in this and the two other articles in this series (Majchrowski et al. 2007, Woźniak et al. 2007b, this volume), and also in the article on modelling the quantum yield of photosynthesis in the Baltic (Woźniak et al. 2007a, this volume) (*continued*)

1	2	3
Φ	Measured (observed) quantum yield of photosynthesis, referred to quanta absorbed by all photoprotecting and photosynthetic phytoplankton pigments	atomC quantum^{-1} or molC Ein^{-1}
Φ_{tr}	True quantum yield of photosynthesis	atomC quantum^{-1} or molC Ein^{-1}
Φ_{MAX}	Theoretical maximum quantum yield of photosynthesis	atomC quantum^{-1} or molC Ein^{-1}
$\Delta\Phi_{fl}$	Maximum change in the quantum yield of the variable fluorescence	dimensionless