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ORIGINAL RESEARCH ARTICLE

Distributions of photosynthetic and photoprotecting pigment concentrations in the water column in the Baltic Sea: an improved mathematical description

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Summary Mathematical formulas are given to describe the changes with depth of concentrations of chlorophylls *b*, *c*, and photosynthetic and photoprotecting carotenoids in Baltic phytoplankton resulting from the adaptation of algal cells to ambient conditions. They take into account the spectral variability and differences in intensity, characteristic of the Baltic, in the irradiance penetrating the water, and also the spectral similarities among the spectra of different groups of phytoplankton pigments. The formulas were derived and validated on the basis of an extensive set of empirical data acquired from different parts of the Baltic Sea in 1999—2016. The standard error factor *x* of these formulas ranges from 1.32 to 1.73. These values are lower than those obtained for formulas derived for ocean waters, in which the influence of allogenic constituents on optical properties is negligibly small: 1.44 and 1.52 respectively in the case of chlorophyll *c*, and 1.32 and 1.47 respectively for photoprotecting carotenoids. With these formulas, overall levels of the main groups of pigments can be calculated from known irradiance conditions and chlorophyll *a* concentrations at any depth in a layer equal to one and a half thicknesses of the euphotic layer (i.e. to an optical depth of τ = 7) in the Baltic. The accuracy of these approximations is close to that of estimates of other bio-optical characteristics in this sea. This was confirmed by a validation based on an independent dataset (*x* from 1.27 to 1.84).

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1. Introduction

Solar radiation in the visible range (VIS) is a major factor governing the photosynthetic production of organic matter in the sea. The intensity and spectral composition of this radiation in different depths in seawater depends on the autogenic and allogenic substances dissolved or suspended in it. Having diverse physicochemical properties, they absorb and scatter solar radiation with varying intensity in different parts of the spectrum, thereby giving rise to a set of optical properties characteristic of a particular basin.

Phytoplankton are an important group of suspended particles absorbing light for primary production. In some types of water, they are estimated to be responsible for more than 90% of the total absorption of visible light (Woźniak and Dera, 2007). Phytoplankton cells contain VIS-absorbing pigment-proteinaceous complexes, i.e. photosynthetic pigments — chlorophylls, carotenoids and phycobilins. Their roles and functions in the mechanisms of marine biophysical processes utilising solar radiation have been analysed in numerous papers (see Babin et al., 1996; Scheer, 1991; Woźniak et al., 1999; Woźniak and Dera, 2007; and the references therein). The composition and mutual proportions of these pigments are unique taxonomic features of the various classes of algae (Jeffrey and Vesk, 1997; Roy et al., 2011; Wright et al., 1991). Nevertheless, under given, often stressful, growing conditions, the amounts and types of pigments in cells can change. These variations make use of the absorption properties of each compound in order to establish a composition and concentration of pigments optimal for a given set of ambient irradiance conditions. Above all, such changes are an adaptation to the intensity and spectral distribution of the underwater irradiance, which varies in accordance with a season and the area where the phytoplankton are growing.

The high intensity of irradiance in the short-wave part of the visible light spectrum, which can cause the photodestruction of the photosynthetic centre, invokes photoprotecting mechanisms in algae that involve the enhanced production of photoprotecting pigments, chiefly carotenoids like diadinoxanthin, lutein, β-carotene, alloxanthin and zeaxanthin (Bricaud et al., 2004; Demmig-Adams, 1990; Henriksen et al., 2002; Schlüter et al., 2000; Staehr et al., 2002; Stramski et al., 2002; Sukenik et al., 1990; Woźniak and Dera, 2007). Having absorption maxima in this spectral range, they enable the safe utilisation of absorbed energy by algae. In contrast, the narrow spectral ranges of the irradiances prevailing in deeper waters do not always coincide with the absorption range of chlorophyll *a*, the basic photosynthetic pigment. This energy is absorbed by pigments additionally synthesised in algal cells (carotenoids: fucoxanthin, echinenone, peridinin and phycobiliproteins) with absorption maxima in the relevant spectral ranges and then transferred to the chlorophyll *a* molecule for subsequent use in the photosynthesis of organic matter.

The processes by which algal cells adapt to ambient irradiance conditions directly affect the vertical distributions of pigment levels in the water column. The concentrations of photoprotecting pigments relative to the chlorophyll *a* level are higher at the sea surface and decrease with depth. Near the sea surface, this is due to the intensity adaptation elicited by high irradiances in the short-wave part of the spectrum. Deeper in the water column, however, the relative concentrations of photosynthetic pigments increase: this results from the chromatic adaptation of algal cells, which, in turn, is due to the variable spectral distributions of irradiance at different depths (Majchrowski and Ostrowska, 2000, 2009; Woźniak et al., 1997b; Uitz et al., 2006, 2015; Trees et al., 2000).

The variability of pigment concentrations with depth in the context of the photo- and chromatic acclimation occurring in phytoplankton cells has been studied for a long time (Babin et al., 1996; Berner et al., 1989; Bricaud et al., 1983; Dera and Woźniak, 2010; Falkowski and LaRoche, 1991; Harrison and Platt, 1986; Hoffmann and Senger, 1988; Mitchell and Kiefer, 1988; Morel et al., 1987; Sathyendranath et al., 1987; Schlüter et al., 2000; Sosik and Mitchell, 1991; Staehr et al., 2002; Stramski et al., 2002; Sukenik et al., 1990; Woźniak et al., 2003; Woźniak and Dera, 2007). This research has yielded relationships describing these processes in the form of a function dependent on the trophic type of waters, a corresponding function of spectral adaptation (in the case of chromatic acclimation) and a function accounting for the amount of photodestructive radiation propagating in the sea (with respect to intensity photo-adaptation) with satisfactory accuracy for ocean waters, in which optical properties are determined solely by the phytoplankton organisms present in them (Majchrowski and Ostrowska, 2000, 2009; Woźniak et al., 2003; Woźniak and Dera, 2007).

In contrast, the optical properties of Baltic Sea waters are governed not only by phytoplankton, but also by other optically significant, allogenic particles and quite frequently by large amounts of CDOM, which can have a major effect on the transmission of irradiance down into the water (Harvey et al., 2015; Kowalczuk et al., 2005; Levin et al., 2013; Meler et al., 2016; Simis et al., 2017; Stedmon et al., 2000). Within such a context, the adaptation and acclimation of phytoplankton cells to the irradiance conditions prevailing in the Baltic are affected by far more factors than in the case of phytoplankton in ocean waters, in which the influence of allogenic constituents on optical properties is negligibly small (Dera, 1995; Mobley, 1994; Prieur and Sathyendranath, 1981; Woźniak et al., 2013). Formulas describing photo- and chromatic acclimation processes in ocean waters, if applied to waters like those in the Baltic Sea, area consequently encumbered with a substantial error (Majchrowski et al., 2007).

Our analyses aimed to find relationships for estimating pigment concentrations at different depths in the Baltic Sea analogous to those for ocean waters. They revealed patterns of vertical distributions of different groups of pigments characteristic of Baltic waters. Even so, we considered the accuracy of those formulas to be less than satisfactory (Majchrowski et al., 2007; Stoń-Egiert et al., 2012). The levels of error of the simplified model for the Baltic, enabling vertical profiles of phytoplankton pigment concentrations to be determined, were acceptable only for the formulas derived separately for summer and winter. The approximations of that model took into account the influence of irradiance conditions in the water on pigment concentrations in phytoplankton via the statistical link with this trophic type of basin, represented by the surface level of chlorophyll *a* (according to Woźniak and Pelevin, 1991) and the optical depth τ (Majchrowski and Ostrowska, 2009; Majchrowski et al., 2007).

There is no relationship describing how the pigment composition varies in response to the irradiance conditions prevailing in the Baltic with an accuracy approaching that of other estimated photosynthetic characteristics in these

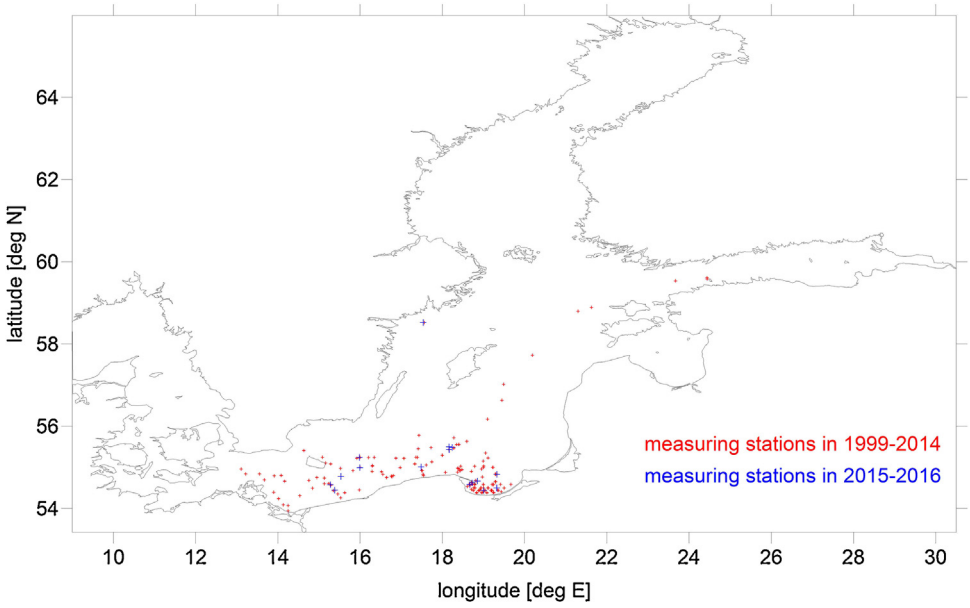

Figure 1 Distributions of stations, at which vertical distributions of pigment concentrations and the relevant characteristics of physical fields were measured in 1999—2016. The red dots indicate the positions of the stations where water samples were taken in 1999—2014 for determining levels of the pigments used for deriving the formulas; the blue dots show the positions of the stations where empirical material was gathered in 2015—2016 and used to validate the formulas.

waters. It was this fact that lay behind the decision to study this aspect of the functioning of Baltic plant communities in greater detail.

The aims of the current analyses were:

1. to extend knowledge on how Baltic plant communities function by analysing the qualitative and quantitative changes in chlorophyll and carotenoid levels taking place as a result of adaptation to the spectrally and intensity variable irradiance conditions obtaining in the Baltic;
2. to derive new model formulas describing how the concentrations of these groups of pigments vary with depth in the Baltic Sea with an accuracy approaching that of the formulas derived for ocean waters.

The achievement of these aims will enable the relationships obtained to be applied in algorithms for determining a range of characteristics of the marine environment at the level of remotely measurable parameters. In particular, they can be used in existing satellite algorithms derived for the Baltic Sea, such as the DESAMBEM[1] algorithm employed in the SatBałtyk System.[2] This allows a range of characteristics of the Baltic ecosystem, including the magnitude of primary production in the euphotic layer and at other depths, to be determined on the basis of remote sensing data (Darecki et al., 2008; Ostrowska et al., 2015a; Woźniak et al., 2004, 2008, 2011).

2. Material and methods

The formulas in this paper were derived on the basis of the following empirical datasets gathered during measurement campaigns in 1999—2016, mainly in the southern Baltic Sea (Fig. 1):

- total concentrations of groups of phytoplankton pigments [mg m^{-3}] measured using RP-HPLC in seawater sampled from the surface and at different depths: chlorophylls *a* (allomer, epimer, chlorophyllide *a*, div chlorophyll *a*, pheophytin *a*, pheophorbide *a*), chlorophylls *b* and their optical isomers, chlorophylls *c* (chlorophylls *c1* + *c2* and *c3*), photosynthetic carotenoids PSC (fucoxanthin, peridinin, prasinoxanthin, 19′but-fucoxanthin, 19′hex-fucoxanthin, echinenon and α-carotene) and photoprotecting carotenoids PPC (antheraxanthin, alloxanthin, diadinoxanthin, diatoxanthin, lutein, neoxanthin, violaxanthin, β-carotene, myxoxanthophyll and zeaxanthin).
- spectral distributions of underwater irradiance fields measured at specific depths in the sea (using MER2040 irradiance meters [Biospherical Inc., Hyperspectral-Ramses, Trios]), or indirectly using the bio-optical model in the DESAMBEM algorithm (Woźniak et al., 2008).

Methodical details on both parameters are described in the following subsections.

2.1. Sample collection

During the cruises, the water was sampled for pigment content analysis. The samples (0.5—2 dm^3) were taken with an SBE 32 bathometer. The sampling depth was chosen with respect to the shape phytoplankton biomass profiles determined based on fluorimetric indications, usually from three

[1] DESAMBEM — Development of a Satellite Method for Baltic Ecosystem Monitoring.
[2] SatBałtyk — Satellite Environment Monitoring of the Baltic Sea.

to ten depths taking into account the surface layer, the maximum fluorescence depth, and below the euphotic zone and indirect depths. The sea water samples were immediately filtered through Whatman GF/F glass-fibre filters (φ = 25 mm) under a gentle vacuum (<0.4 atm). The filtration time did not exceed one hour. The samples were stored in liquid nitrogen (−196°C) until laboratory analysis to improve extraction efficiency and minimise pigment alterations (Mantoura et al., 1997).

2.2. Extraction of pigments from phytoplankton cells

Extraction of chlorophylls and carotenoids from phytoplankton samples were conducted by use of water solution of 90% acetone (Parsons et al., 1984). Technics of isolation of pigments from algae cells were based on mechanical grinding and sonication (2 min, 20 kHz, Cole Parmer, 4710 Series) in the darkness conditions at 4°C during 2 h. Such prepared extracts were centrifuged (20 min, 5°C, 3210 × *g*, Beckman, GS-6R) to remove the filters and cellular debris and then subjected to the chromatographic analysis.

2.3. Quantification and qualification of pigments during chromatographic analysis

Two types of appropriately calibrated chromatographic systems were used for pigments separations by RP-HPLC in presented data sets: Agilent Technologies HP1050 (in 1999—2010) and HP1200 (2010—2016), equipped with diode array detectors (HP1100 and HP1200 respectively), fluorescence detectors (HP1046 and HP1200 respectively) and type C18 chromatographic columns (LichroCART™ Hypersil ODS — to separate the samples collected in 1999—2001, LichroCART, Lichrospher 100 RP18e — to separate samples collected in 2002—2016) with the same dimensions parameters: 250 × 4 mm, particle size: 5 μm, pore size 100 Å (Merck). Both systems were intercalibrated and comparable results were obtained. Method of pigments isolation and separation was introduced by Mantoura and co-workers (Mantoura and Llewellyn, 1983), adopted and modified in later years by other researchers (Barlow et al., 1993; Stoń and Kosakowska, 2002; Stoń-Egiert and Kosakowska, 2005). The pigments were separated in a gradient mixture of methanol, 1 M ammonium acetate and acetone. Pigment detection was based on absorbance measurements at λ = 440 nm. The fluorescence measurements with extinction at λ_{ex} = 431 nm and emission at λ_{em} = 660 nm were taken parallel during analysis in order to confirm the presence of chloropigments in the sample.

Calibration of chromatographic systems was based on commercially available chlorophylls and carotenoids (The International Agency for 14C Determination DHI Institute for Water and Environment in Denmark). The pigment standards were subjected to chromatographic analysis in order to obtain calibration curves, detection limits and absorption spectra. Qualitative analysis was based on a comparison of the retention times, the absorbance spectra of eluting peaks with those of the standards (Wright and Shearer, 1984) and on individual response factor obtained during calibration procedure conducted for each pigment and parameters obtained during chromatographic resolution of samples. Identification was confirmed by co-injection and on-line diode array spectra. The quantitative characteristics of the pigments occurring in natural samples were based on the external standardisation equation (Mantoura and Repeta, 1997).

The measurement precision was 2.9 ± 1.5% and a recurrence error was 9.7 ± 6.4% (Stoń-Egiert et al., 2010). The chlorophyll *a* concentrations determined with this method stand in agreement with the corresponding concentrations obtained spectrophotometrically in ethanol extracts (Ostrowska et al., 2015b).

The pooled concentrations of pigments included levels of unidentified derivatives and their degradation products estimated on the basis of their similar spectral properties. Their presence in the samples is due mainly to the physiological condition of the phytoplankton, the state of their growth and the degree of development of the plant community, and only minimally to the measurement procedures (Jeffrey, 1997; Louda et al., 1998; Porra et al., 1997; Repeta and Bjørnland, 1997). The highest estimated levels of derivatives and unidentified pigments come from after-bloom periods when the current phytoplankton population consists mainly of ageing and dead cells. The unidentified pigments and derivatives in our database comprise on average from 1 to 7% chlorophylls, 16% PSCs and 10% PPCs. Taking into account the derivatives and degradation products of a specific group of compounds will ensure that the mathematical formulas we shall be deriving are universally applicable in time, regardless of the seasonal cycle of phytoplankton growth and development in the Baltic.

2.4. Spectral distributions of underwater irradiance fields

During the cruise on r/v 'Oceania' the spectral distribution of solar radiation in the water column were measured by spectrophotometer MER 2040 (Biospherical Inc.). The measurements of spectral distribution of light were performed just above, below surface layer and in water column in eight spectral bands (412, 443, 490, 510, 550, 665, 683 and 710 nm). Also, the continous measurements of summarise downward radiation reaching the surface were performed by set of piranometers (Eppley Laboratory Inc.) equipped with Schotta filters (395 and 695 nm). Based on these measurements, using appropriate calculation methods (described in the works of, for example, Woźniak and Montwiłł, 1973, Woźniak et al., 1983), the doses of photosynthetically available radiation PAR (400—700 nm) [Ein m^{-2}] was obtained for selected depth levels (1, 2, 3, 5, 7, 10, 15, 20, 25 and 30 m).

The empirical material acquired in 1999—2016 comprises 339 depth profiles of pigments and their corresponding irradiance distributions. The collected set of data was divided into two sets: data collected in 1999—2014 (313 complete profiles of vertical distributions of pigments and the corresponding irradiances) and data collected in 2015—2016 (26 complete profiles of pigments vertical distributions and the corresponding irradiances). The first more extensive set of data was used to obtain the mathematical relationships presented in this work, while the second set of data was used as independent to validate the relationships obtained. Table 1 lists the characteristics of both sets of empirical pigment concentrations.

The range of variability of chlorophyll *a*, the most important pigment in photosynthesis, recorded in 1999—2014, covered four orders of magnitude (0.068—95.598 mg m^{-3}). This therefore

Table 1 Overall concentrations [mg m^{-3}] of the groups of pigments identified in the analysed database.

Group of pigments	Number of measurements	Concentration [mg m^{-3}]			Median [mg m^{-3}]	Standard deviation [mg m^{-3}]
		Min	Max	Mean		
Measuring years 1999–2014						
Chlorophyll *a* C_a	1372	0.068	95.6	4.30	2.17	7.11
Chlorophyll *b* C_b	1187	0.004	7.63	0.304	0.182	0.481
Chlorophyll *c* C_c	1365	0.005	11.8	0.514	0.208	0.956
Photosynthetic carotenoids C_{PSC}	1368	0.005	28.4	1.02	0.364	2.21
Photoprotecting carotenoids C_{PPC}	1372	0.005	19.5	0.949	0.567	1.441
Measuring years 2015–2016						
Chlorophyll *a* C_a	181	0.069	4.90	2.02	1.86	1.04
Chlorophyll *b* C_b	181	0.008	0.523	0.163	0.140	0.127
Chlorophyll *c* C_c	181	0.005	1.78	0.261	0.184	0.248
Photosynthetic carotenoids C_{PSC}	181	0.015	2.04	0.434	0.385	0.348
Photoprotecting carotenoids C_{PPC}	181	0.030	1.52	0.463	0.435	0.267

embraces 9 trophic types of water[3] (according to the classification of Woźniak and Pelevin, 1991), from oligotrophic (type O2, chlorophyll *a* levels from 0.05 to 0.10 mg m^{-3}) to eutrophic (type E5, concentrations $>$ 20 mg m^{-3}. The 2015–2016 dataset was also gathered from waters with a wide trophic range, i.e. from oligotrophic to eutrophic, except when surface chlorophyll *a* was very high during seasonal increases in phytoplankton biomass.

The content of pigments from different groups was governed by the current state of the growing Baltic phytoplankton, the species composition of which varies seasonally; consequently, the characteristic indicator pigments vary likewise. Levels of accessory pigments were up to 14 times lower than those of chlorophyll *a*, with absolute levels of chlorophyll *b* being the lowest. The relatively high levels of carotenoids were due to the spring blooms of diatoms and dinoflagellates; this is confirmed by numerous studies on the taxonomic composition of Baltic plant communities (Stoń-Egiert et al., 2010; Thamm et al., 2004; Wasmund et al, 1996; Wasmund and Uhlig, 2003).

3. Results

As already mentioned, there are two main groups of pigments (PSC and PPC) absorbing visible solar radiation in phytoplankton cells. The intracellular content of photosynthetic and photoprotecting pigments is governed by the irradiance conditions in the immediate environment of the phytoplankton, as a result of processes adapting them to the intensity and spectral composition of the irradiance. The adaptation to irradiance intensity is controlled above all by the quantitative and qualitative composition of pigments protecting the photosynthetic apparatus from destruction by excessive intensities of short-wave light. On the other hand, chromatic adaptation in phytoplankton establishes the composition of pigments enabling the entire PAR to be utilised in photosynthesis. We therefore performed our analyses separately for pigments directly involved in photosynthesis and for photoprotecting pigments.

3.1. Photosynthetic pigments

Relative levels of photosynthetic pigments increase with depth because chromatic adaptation of phytoplankton cells intensifies the production of pigments with absorption properties that effectively utilise the spectral distributions of irradiances at the depths where the algae are at any given instant. Hence, in the photosynthetic apparatus of phytoplankton, there is an increase in the proportion of those pigments, the light absorption ranges of which include bands present in underwater irradiance fields in which chlorophyll *a* does not absorb (Babin et al., 1996; Woźniak et al., 2003).

How the absorption properties of the individual pigments are matched to the ambient irradiance conditions can be defined by the spectral fitting function $F_j(z)$, also known as the chromatic adaptation factor (Majchrowski and Ostrowska, 1999, 2000; Woźniak et al., 1997a, 1997b, 2003). The spectral fitting functions were determined for three main groups of photosynthetic pigments: chlorophylls *b* and *c* and photosynthetic carotenoids on the basis of their known spectral shape of absorbance coefficients (Ficek et al., 2004) and irradiance at characteristic sampling depths. They are defined by the following equation:

$$F_j(z) = \frac{1}{a^*_{j,max}} \int_{400\,nm}^{700\,nm} \frac{E_d(\lambda, z)}{PAR(z)}\, a^*_j(\lambda)\, d\lambda, \qquad (1)$$

where j – the type of pigment's group: PSC – photosynthetic carotenoids, a – chlorophyll *a*, b – chlorophylls *b* and c – chlorophylls *c*, a^*_j (λ) – specific coefficient of absorption for the jth group of pigments [m^2 (mg pigment)$^{-1}$] (Ficek et al., 2004), $a^*_{j,max}$ – maximum specific absorption coefficient for the jth group of pigments [m^2 (mg pigment)$^{-1}$], $E_d(\lambda,z)$ – spectral distribution of downward irradiance at depth z [Ein m^{-2} s^{-1} nm^{-1}], PAR (z) – photosynthetic available radiation at depth z [Ein m^{-2} s^{-1}].

[3] In accordance with the convention used by our research team, the trophic index (trophicity) is defined as the surface concentration of chlorophyll *a* Ca(0). Depending on the concentration Ca(0) [mg tot. chl m^{-3}], the following trophic types of waters can be distinguished: oligotrophic: O1 –Ca(0) = 0.02–0.05; O2 –Ca(0) = 0.05–0.10; O3 –Ca(0) = 0.10–0.20; mesotrophic: M –Ca(0) = 0.2–0.5; intermediate: I –Ca(0) = 0.5–1.0; eutrophic: E1 –Ca(0) = 1–2; E2 –Ca(0) = 2–5.

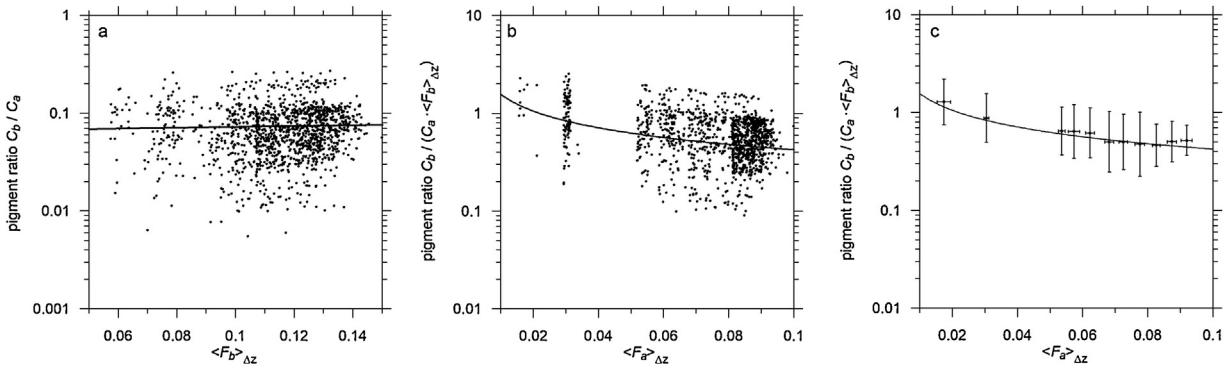

Figure 2 Relationships between the relative concentration of chlorophyll *b* (referred to the concentration of chlorophyll *a*) C_b/C_a and the mean spectral fitting functions of chlorophyll *b* $<F_b>_{\Delta z}$ in the mixing layer (see Eq. (1a)) for empirical data obtained in 1999–2014 (a); the relationship between relative chlorophyll *b* concentrations expressed by the formula $C_b/(C_a<F_b>_{\Delta z})$ and mean spectral fitting functions of chlorophyll *a* $<F_a>_{\Delta z}$ (b) and their averaged values (c).

This function depends mainly on the relative spectral distribution of irradiance in the sea $f(\lambda, z) = E_d(\lambda, z)/PAR(z)$ but only minimally on its absolute values. It can take values from 0 to 1. If the spectral distribution of the absorption coefficient of a given pigment or groups of pigments does not coincide anywhere with the underwater irradiance spectrum, the spectral matching function is 0. If, on the other hand, the spectral distribution of underwater irradiance coincides exactly with the absorption spectrum of a given group of pigments, then the spectral matching function takes the value of 1.

In order to take account of mixing in the water column, the consequent vertical movements of phytoplankton cells, and how the "history" of these movements affect pigment levels, the spectral matching function in a water layer was averaged for the purposes of the statistical analyses. The best results were obtained for water layer thicknesses of $\Delta z = z_2 - z_1$, where:

$$z_2 = z + 15\,\text{m} \text{ and } z_1 = \begin{cases} 0 \text{ if } z < 15\,\text{m} \\ z - 15\,\text{m} \text{ if } z \geq 15\,\text{m} \end{cases}, \quad (1a)$$

This means that the concentration of each pigment at depth *z* has been determined using F_j averaged for a layer of 30 m ($z \pm 15$ m), or less, for depths of 0–15 m.

It is well known that the overall absorption of light by phytoplankton is the superposition of the absorption of all groups of pigments present in phytoplankton cells capable of absorbing light in a given region of the spectrum (Woźniak and Dera, 2007). So, bearing in mind the similarities of the light absorption spectra of the different varieties of chlorophyll with maxima in roughly the same spectral areas, we analysed the statistical dependence of the relative concentrations of chlorophylls *b* and *c* not only on their individual spectral matching functions but also on the spectral matching function of chlorophyll *a* (see Figs. 2 and 3). In this figures are presented the relationships, obtained for empirical data collected in 1999–2014, between the relative concentration of chlorophylls *b* and *c* (referred to the concentration of chlorophyll *a*) and the mean spectral fitting functions of particular photosynthetic chlorophylls group: chlorophyll b $<F_b>_{\Delta z}$ and c $<F_c>_{\Delta z}$ in the 30 m mixing layer (Figs. 2a and 3a). The dependences of these relationships on additional parameters such as the spectral matching function of chlorophyll *a* $<F_a>_{\Delta z}$ are clearly visible in Figs. 2b, c and 3b,c. In the case of PSCs, the analyses covered entire groups of pigments and exhibited a dependence of their relative concentration only on the average matching functions determined for that group, $<F_{PSC}>_{\Delta z}$ (Fig. 4).

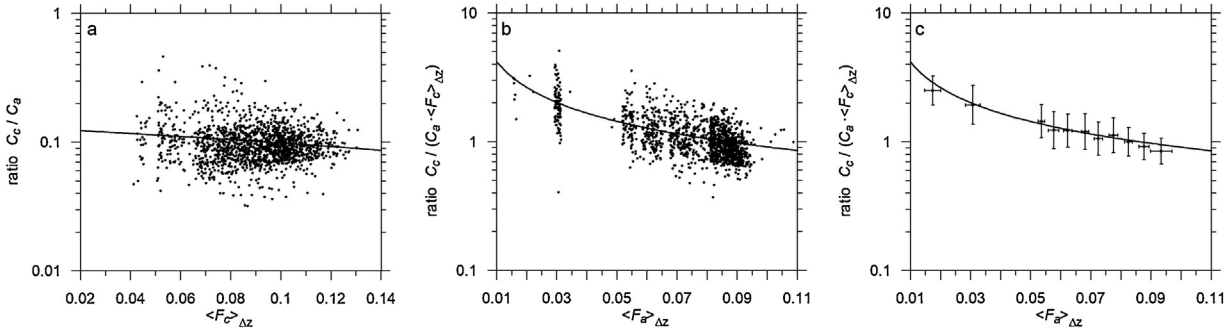

Figure 3 Relationships between the relative concentration of chlorophyll *c* (referred to the chlorophyll *a* concentration) C_c/C_a and the mean spectral fitting functions of chlorophyll *c*, $<F_c>_{\Delta z}$ in the mixing layer (see Eq. 1a) for empirical data (a); the relationship between relative chlorophyll *c* concentrations expressed by the formula $C_c/(C_a<F_c>_{\Delta z})$ and mean spectral fitting functions of chlorophyll *a* $<F_a>_{\Delta z}$ (b) and their averaged values (c).

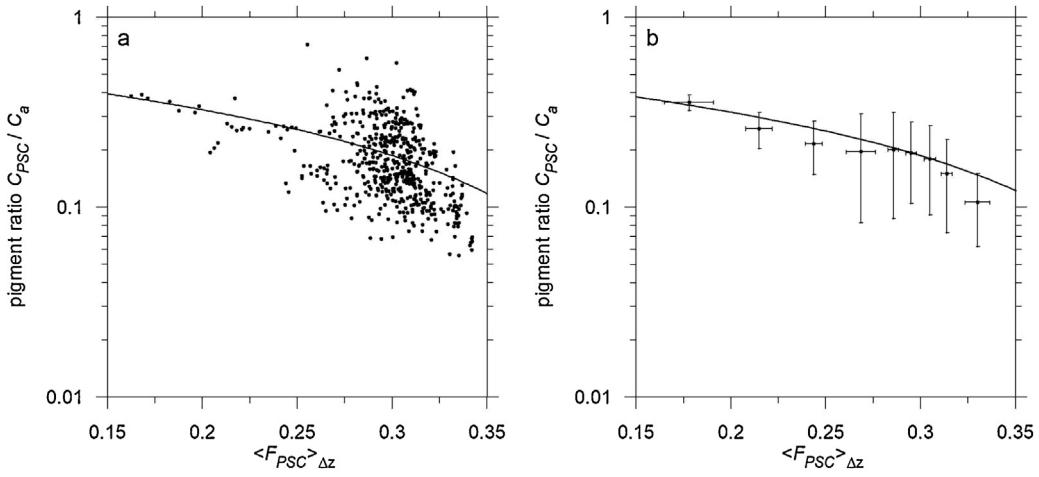

Figure 4 Relationships between the relative concentration of photosynthetic carotenoids (referred to the chlorophyll *a* concentration) C_{PSC}/C_a and their mean spectral fitting functions $<F_{PSC}>_{\Delta z}$ in the mixing layer (see Eq. 1a) for empirical data (a) and their averaged values (b).

Hence, using the least squares method, statistical dependences were derived enabling depth changes in photosynthetic pigments levels, presented in Fig. 2b, c, 3b, c and 4a as a solid line, in phytoplankton cells to be determined with respect to the ambient irradiance conditions in the form:

$$C_b/C_a = 0.115\langle F_a\rangle_{\Delta z}^{-0.567} \times \langle F_b\rangle_{\Delta z}, \quad (2)$$

$$C_c/C_a = 0.198\langle F_a\rangle_{\Delta z}^{-0.663} \times \langle F_c\rangle_{\Delta z}, \quad (3)$$

$$C_{PSC}/C_a = 0.576 - 1.30\langle F_{PSC}\rangle_{\Delta z}, \quad (4)$$

where $\langle F_j\rangle_{\Delta z}$ – mean chromatic adaptation factor in the 30 m layer for particular groups of pigments, $\langle F_j\rangle_{\Delta z} = 1/z_2 - z_1 \int_{z_1}^{z_2} F_j(z)dz$, j – the type of pigment's group: PSC – photosynthetic carotenoids, a – chlorophyll a, b – chlorophylls b and c – chlorophylls c, C_a, C_b, C_c, C_{PSC} – concentrations of groups of pigments: chlorophylls a, chlorophylls b, chlorophylls c, photosynthetic carotenoids PSC [mg m^{-3}].

Table 2 and Fig. 5 list the errors of these approximations. These errors show the accuracy with the developed formulas describing the analyzed set of empirical data. As one can see, the proposed formulas describe vertical variations in concentrations of photosynthetic pigments in 1999–2014 with satisfactory accuracy. The PCS concentration is encumbered with the highest systematic error with PSC while the best approximation of measured concentrations was obtained for chlorophyll *c*.

3.2. Photoprotecting pigments

The part played by photoprotecting carotenoids PPCs in the surface water layer is crucial: chlorophyll *a*, the fundamental pigment in photosynthesis, is vulnerable to photo-oxidation because of the direct action of excessive quantities of radiation in the 400–480 nm range – this is known as Potentially Destructive Radiation (PDR). This is reflected in the depth profile of averaged relative PPC concentrations. These levels are the highest at the surface, where, as a result of intensity adaptation processes, phytoplankton cells contain pigments in abundance to protect chlorophyll *a* molecules from the excessive absorption of PDR (Majchrowski and Ostrowska, 1999, 2000; Woźniak et al., 1999, 2003).

The presence of PPCs in phytoplankton at a given depth is thus due directly to the intensity of radiation from the shortwave part of the PAR spectrum reaching that depth:

$$PDR^*(z) = \int_{400\,nm}^{480\,nm} a_a^*(\lambda)\langle E_0(\lambda, z)\rangle_{day}\, d\lambda, \quad (5)$$

Table 2 Errors of concentrations of pigment groups estimated using formulas 2–4 based on an analysis of data collected from 1999 to 2014.

Group of pigments	Arithmetic statistics		Logarithmic statistics			
	Systematic error	Statistical error	Systematic error	Standard error factor	Statistical error	
	$<\epsilon>$ [%]	σ_ϵ [%]	$<\epsilon>_g$ [%]	x	σ_- [%]	σ_+ [%]
C_b	12.0	± 76.7	−4.45	1.73	−42.3	73,2
C_c	7.29	± 41.9	0.340	1.44	−30.4	43.8
C_{PSC}	18.1	± 47.44	−9.60	1.50	−33.5	50.4

Where $\epsilon = (C_{i,C} - C_{i,M})/C_{i,M}$ – arithmetic error; $<\epsilon>$ – mean arithmetic error, $\langle\epsilon_g\rangle$ – mean logarithmic error, $\langle\epsilon\rangle_g = 10^{[\langle\log(C_{i,C}/C_{i,M})\rangle]} - 1$, $<\log(C_{i,C}/C_{i,M})>$ – mean of $\log(C_{i,C}/C_{i,M})$, σ_ϵ – standard deviation (statistical error), $\sigma_{\log}$ – standard deviation of $\log(C_{i,C}/C_{i,M})$, $x = 10^{\sigma_{\log}}$ – standard terror factor, $\sigma_+ = x - 1$ i $\sigma_- = \frac{1}{x} - 1$.

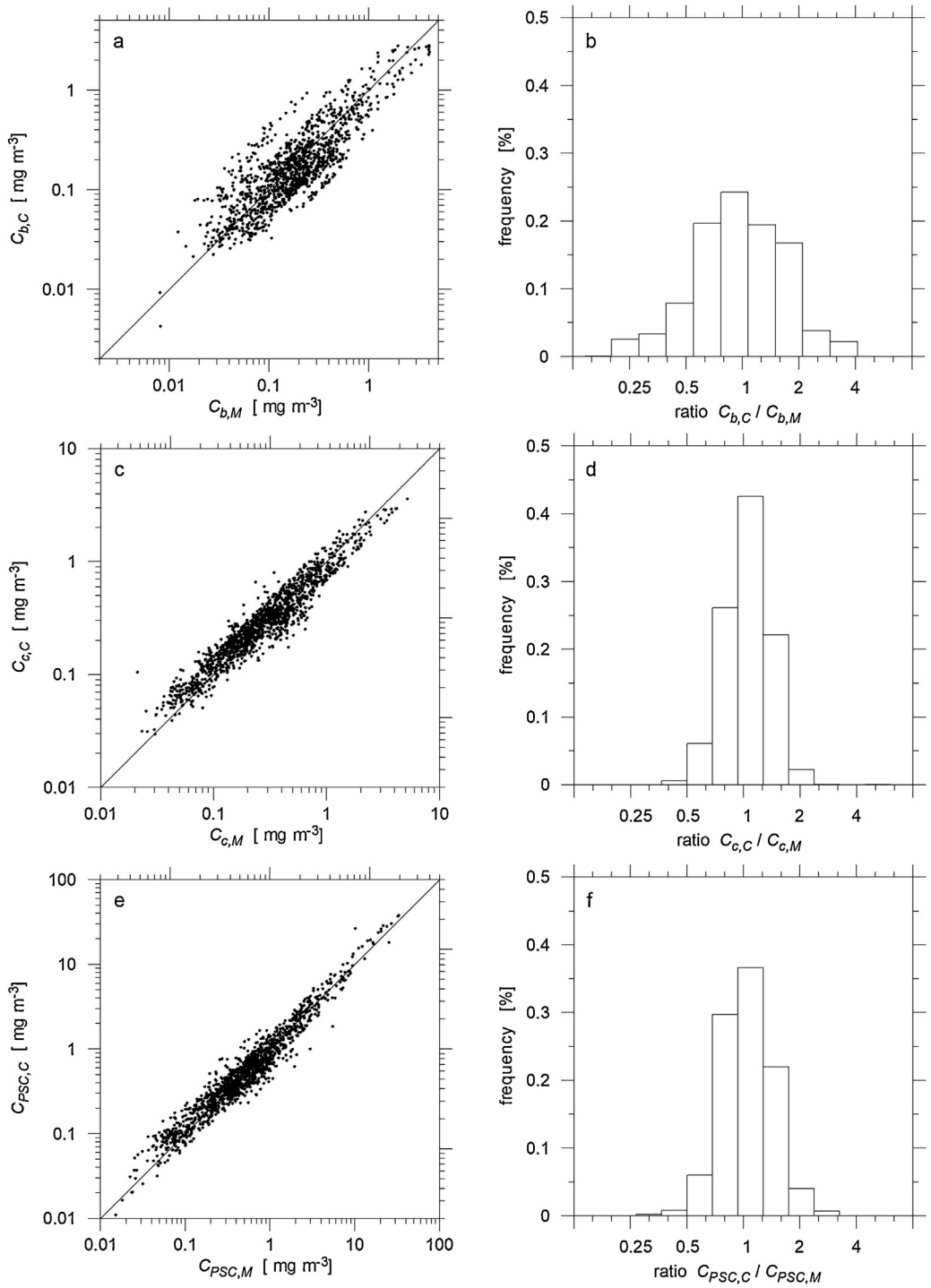

Figure 5 Comparison of concentrations of various groups of pigments C_b (a), C_c (c) and C_{PSC} (e) determined empirically (subscript M) and using formulas 2—4 (subscript C) for a dataset on the basis of which the relationships were derived; histograms of the relative errors in these formulas $C_{b,C}/C_{b,M}$ (b), $C_{c,C}/C_{c,M}$ (d), $C_{PSC,C}/C_{PSC,M}$ (f).

where PDR^* — potentially destructive radiation per unit mass of chlorophyll *a* [μEin (mg chla)$^{-1}$ s^{-1}] (also known as the acclimation factor), $<E_0(\lambda,z)>_{day}$ — mean daily scalar irradiance in the sea at a given depth *z* [Ein m^{-2} s^{-1} nm^{-1}], $a^*_a(\lambda)$ — specific coefficient of light absorption by chlorophyll *a* [m^2 (mg pigment)$^{-1}$].

Using collected database a statistical analysis of the changes in relative PPC concentrations with respect to the irradiance conditions prevailing at different depths in the sea was performed for averaged values of potentially destructive radiation in short part of light spectrum (400—480 nm) per unit mass of chlorophyll *a* PDR* in layers Δ*z*:

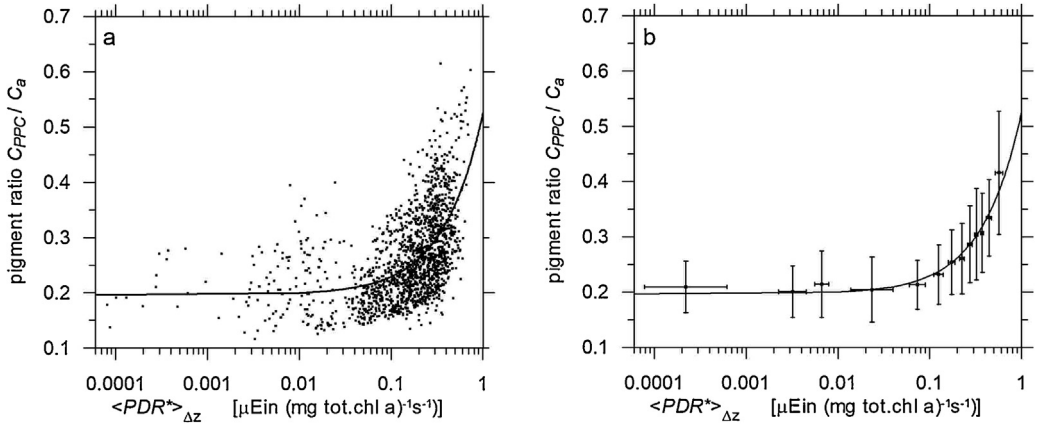

Figure 6 Relationship between the relative concentration of photoprotecting pigments (referred to chlorophyll *a*) C_{PPC}/C_a and the function of Potentially Destructive Radiation PDR* averaged in the 30 m layer $<PDR^*>\Delta_z$ for empirical data (a) and their averaged values (b).

$$\langle PDR^* \rangle_{\Delta z} = \frac{1}{z_2 - z_1} \int_{z_1}^{z_2} PDR^*(z)dz, \tag{6}$$

where z_1 and z_2 are defined in Eq. (1).

As in the case of PSCs, the best results were obtained for a water thickness of 30 m.

Fig. 6 illustrates the dependence of PPC concentration referred to chlorophyll *a* on averaged PDR* functions. The evident increase in the relative level of PPCs for values of $<PDR^*>\Delta_z$ greater than 0.1 [µEin (mg tot chl *a*)$^{-1}$ s^{-1})] indicates that their presence in the pigment composition depends strongly on the irradiance conditions in which phytoplankton live.

Eq. (7), derived from statistical analyses, describes the dependence of the relative PPC concentration in a given set of irradiance conditions at any depth in the sea:

$$C_{PPC}/C_a = 0.328\langle PDR^* \rangle_{\Delta z} + 0.196, \tag{7}$$

where $\langle PDR^* \rangle_{\Delta z}$ – mean *PDR** function in the 30 m layer; C_{PPC} – PPC concentration [mg m^{-3}].

The errors encumbering this formula are listed in Table 3 and Fig. 7 compares PPC levels determined (using Eq. 7 presented in Fig. 7 as a solid line) with empirical values. Values of errors indicate that the developed formula corresponds well to the data set on the basis of which it was

Table 3 Errors of concentrations of photoprotecting carotenoids PPC estimated using Eq. (7) based on an analysis of data collected from 1999 to 2014. The errors were determined using the formulas given in Table 2.

Group of pigments	Arithmetic statistics		Logarithmic statistics			
	Systematic error	Statistical error	Systematic error	Standard error factor	Statistical error	
	$<\epsilon>$ [%]	σ_ϵ [%]	$<\epsilon>_g$ [%]	x	σ_- [%]	σ_+ [%]
C_{PPC}	6.58	± 22.9	2.68	1.32	−24.1	31.7

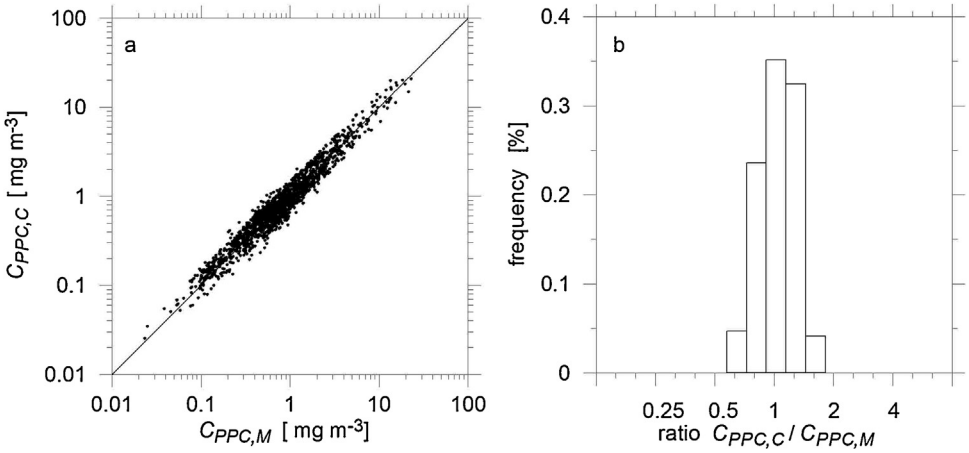

Figure 7 Comparison of concentrations of photoprotecting pigments determined empirically ($C_{PPC,M}$) and based on formula 7 ($C_{PPC,C}$) (a); histograms of the relative errors in this formula (b).

determined. Approximation errors show similar values as in the case of approximations developed for photosynthetic pigments.

4. Discussion

Composition and concentration of phytoplankton pigments, particular in the surface layer of different sea regions have been the subject of investigations by many authors (e.g. Ho et al., 2015; Araujo et al., 2017; Wulff and Wängberg, 2004). This is the base for further analyzing differences in the spatial and seasonal distribution of pigments in different seas (Smith et al., 2010; Wänstrand and Snoeijs, 2006; Zhang et al., 2017) or determining the phytoplankton composition using CHEMTAX (Mendes et al., 2011; Swan et al., 2016).The composition of the pigments can be recognized on the basis of the radiation signal of the sea surface recorded by the satellite radiometer. Global and local satellite algorithms to determine the concentration of chlorophyll in the surface layer of the sea are now widely used (Zheng and DiGiacomo, 2017; Kim et al., 2017) methods for determining other phytoplankton pigments are intensively developed (Pan et al., 2010; Soja-Woźniak et al., 2018). However, the satellite observes only the surface layer, while the pigments compositions and concentrations change with depth. Complete information can only be obtained by knowing the depth profiles of pigments in combination with satellite observations. For this purpose, an accurate mathematical description of the distribution of pigment depth profiles is necessary. The development of mathematical formulas describing such distributions with satisfactory accuracy is complex and requires a comprehensive representative data bank from various regions and seasons in the water body under investigation. In many research teams are developed mathematical descriptions the dependences of bio-optical processes in the sea on environmental conditions in different regions (Cherukuru et al., 2016; Dickey et al., 1993; Strutton et al., 2011). The vertical variation of phytoplankton pigments has been described so far in the clean waters of open oceans (Majchrowski and Ostrowska, 2000), but there are no reports of similar formulas that have been worked and calibrated for shelf seas and coastal areas. Only in the case of the Baltic Sea, the authors attempted to develop such a dependence taking into account the specific optical properties of this basin (Majchrowski et al., 2007; Stoń-Egiert et al., 2012).

This work was inspired by the lack of statistical analyses and physically justified formulas for estimating pigment compositions in phytoplankton cells in the Baltic Sea with an accuracy comparable to that of formulas applicable to ocean waters.

The dependencies used hitherto (see Table 4) enabled pigment concentrations in Baltic waters to be estimated from their statistical dependences on optical depth and surface concentration of chlorophyll *a*, determined separately for summer and winter (Majchrowski et al., 2007), or else did not take into account the mutual influence of pigments with similar absorption properties on their total concentration and relative proportions in the photosynthetic apparatus (Stoń-Egiert et al., 2012). Table 4 also sets out the error factors *x* of all the formulas derived to date: one can thus assess which of the approximations best reflects the modelled dataset.

The formulas derived for ocean waters (Majchrowski and Ostrowska, 2000) yield modelled values closer to measured values than is the case with the formulas so far derived for Baltic waters. As already mentioned, however, absorption properties in open ocean waters are governed mainly by phytoplankton. Therefore, ocean formulas, if applied to the determination of relative pigment concentrations in the optically far more complex waters of the Baltic, are encumbered with major errors (Majchrowski et al., 2007).

By introducing the spectral matching function to the mathematical description of changes in phytoplankton pigment levels with depth (Stoń-Egiert et al., 2012), we were able to derive formulas that retain temporal continuity and are of a form that is independent of the season when analyses are carried out. These formulas thus fulfil the requirements for continuous, long-term observations of changes in plant communities. However, there is no statistically significant improvement in the accuracy of estimates, and in the case of chlorophyll *b*, the error factor *x* actually increased from 1.77 to 2.34 with respect to the statistical relationships.

Our analyses show that a mathematical description of the adaptation of photosynthetic pigments: chlorophyll *c* and *b* to ambient conditions must take into account the presence of other groups of pigments with similar spectral features. The formulas derived in accordance with this assumption give far better estimates of a dataset than the statistical relationships derived earlier. The error factors *x* are then approximately the same as those obtained for ocean waters. The results of our analyses can thus be deemed satisfactory, particularly in the case of chlorophyll *c* (where error factors *x* are 1.44 for the Baltic and 1.52 for ocean waters) and PPCs (1.32 and 1.47 respectively).

The estimation accuracy of depth profiles of pigments in the Baltic Sea using new formulas was analysed on the basis of independent dataset collected in the years 2015—2016 not used for deriving any of these new relationships (see Table 1). The errors are presented in Table 5 section 1. A compelling argument justifying the use of formulas based on physical premises instead of purely statistical relationships is provided by the comparison (see Table 5 section 2) of errors in determining pigment concentrations using statistical formulas (Majchrowski et al., 2007), so far encumbered with the smallest error, and the new formulas derived in this paper. Those errors were determined for the same independent set of data gathered in 2015—2016. Table 5 shows that the inclusion in the mathematical description of the concentrations of chlorophylls *b* and *c* $<F_a>$ improved the accuracy of determining these pigments: this is confirmed by the magnitudes of both the systematic errors $<\epsilon>_g$ and the standard error factor *x*. In the case of both PSCs and PPCs, the accuracy is similar to or only slightly less than in the case of the statistical formulas. Since, however, the relationships used to date required an arbitrary separation into two seasons, the result can be regarded as satisfactory. It is worth noting that the accuracy of these formulas approaches that of similar statistical relationships for estimating other characteristics describing the state and functioning of Baltic plant communities (Stramska and Zuzewicz, 2013; Meler et al., 2017).

These dependencies make it possible at the euphotic zone to track changes with depth of the relative concentrations of

Table 4 Comparison of statistical formulas describing the vertical distributions of relative pigment concentrations in samples of the Baltic Sea and ocean waters.

No	Authors	Group of pigments	Equations	Standard error factor x
1	obtained in this work – for the Baltic Sea	chl *b*	$C_b/C_a = 0.1146\langle F_a\rangle_{\Delta z}^{-0.5673} \times \langle F_b\rangle_{\Delta z}$	1.73
		chl *c*	$C_c/C_a = 0.1976\langle F_a\rangle_{\Delta z}^{-0.6627} \times \langle F_c\rangle_{\Delta z}$	1.44
		PSC	$C_{PSC}/C_a = 0.5760 - 1.2961\langle F_{PSC}\rangle_{\Delta z}$	1.50
		PPC	$C_{PPC}/C_a = 0.3279\langle PDR^*\rangle_{\Delta z} + 0.1962$	1.32
2	Majchrowski et al. (2007) – for the Baltic Sea	chl *b*	winter $x = \log(Ca(0))$	1.77
			$C_b/C_a = 10^{-1.0703-0.1599\tau+0.04312\tau^2-0.30871x-0.040076x\tau-0.074687x^2}$ summer	
			$C_b/C_a = 10^{-0.8808+0.075078\tau-0.023728\tau^2-0.54886x+0.046307x\tau+0.20785x^2}$	
		chl *c*	winter $x = \log(Ca(0))$	1.64
			$C_c/C_a = 10^{-1.2314+0.14836\tau-0.031219\tau^2+0.051019x-0.0093837x\tau+0.053311x^2}$ summer	
			$C_c/C_a = 10^{-1.1330+0.1146\tau-0.020600\tau^2-0.011478x+0.0037213x\tau-0.0082814x^2}$	
		PSC	winter $x = \log(Ca(0))$	1.82
			$C_{PSC}/C_a = 10^{-1.1436+0.064027\tau-0.0054346\tau^2+0.29550x-0.0065549x\tau+0.015895x^2}$ summer	
			$C_{PSC}/C_a = 10^{-0.82451+0.072685\tau-0.014871\tau^2+0.016015x-0.010256x\tau+0.029283x^2}$	
		PPC	$C_{PPC}/C_a = 0.164\langle PDR^*\rangle_{\Delta z} + 0.164$	1.73
3	Stoń-Egiert et al. (2012) – for the Baltic Sea	chl *b*	$C_b/C_a = 90.01\langle F_b\rangle_{\Delta z}^{4.2825} + 0.0751$	2.34
		chl *c*	$C_c/C_a = -0.2024\langle F_c\rangle_{\Delta z} + 0.1110$	1.53
		PSC	$C_{PSC}/C_a = -0.4810\langle F_{PSC}\rangle_{\Delta z} + 0.3175$	1.83
		PPC	$C_{PPC}/C_a = 0.0623\langle PDR^*\rangle_{\Delta z} + 0.2251$	1.62
4	Majchrowski and Ostrowska (2000) – for ocean waters	chl *b*	$C_b/C_a = 54.068\langle F_b\rangle_{\Delta z}^{5.157} + 0.091$	1.68
		chl *c*	$C_c/C_a = 0.0424\langle F_c\rangle_{\Delta z}\langle F_a\rangle_{\Delta z}^{-1.197}$	1.52
		PSC	$C_{PSC}/C_a = 1.348\langle F_{PSC}\rangle_{\Delta z} - 0,093$	1.32
		PPC	$C_{PPC}/C_a = 0.1758\langle PDR^*\rangle_{\Delta z} + 0.176$	1.47

the main pigment groups in Baltic waters over the whole range of irradiances and trophic conditions prevailing in this sea. Columns 1 and 2 in Fig. 8 exemplify model profiles of relative pigment concentrations (to the concentration of chlorophyll *a* at given depth) determined using these relationships for an irradiance of 500 μEin m^{-2} s^{-1}. They cover a layer of about 1.5 euphotic zones for trophic types from meso- to eutrophic (for surface chlorophyll *a* levels from 0.2 to >50 mg m^{-3}). The modelled vertical changes in relative concentrations of the various groups of pigments are shown for both the real depth z (column 1) and the optical depth τ (column 2) characterising the changes in irradiance conditions with depth in the water. Column 3 in this figure shows some empirical profiles for trophic type E1, with surface chlorophyll levels from 1 to 2 mg m^{-3}.

Table 5 Systematic errors $<\epsilon>_g$ [%] and error factors x, determined for an independent dataset from 2015 to 2016, defining the accuracy of pigment concentrations calculated using the formulas obtained in this work and also those applied hitherto in models describing the optical properties of the Baltic Sea.

No	Authors	Group of pigments	Systematic error $<\epsilon>_g$ [%]	Standard error factor x
1	obtained in this work – for the Baltic Sea	chl *b*	2.19	1.84
		chl *c*	−3.82	1.46
		PSC	1.87	1.54
		PPC	13.3	1.26
2	Majchrowski et al., 2007 – for the Baltic Sea	chl *b*	49.6	2.12
		chl *c*	−30.4	1.60
		PSC	−27.1	1.59
		PPC	−9.4	1.24

With respect to each group of pigments, these formulas take into account the spectral and intensity differentiation in irradiance in waters of different trophic types; they also characterise well the course of chromatic and intensity adaptation in phytoplankton In the case of all trophic types, the changes in the relative levels all pigment groups with depth in the Baltic differ in comparison with such changes in open ocean waters (Majchrowski and Ostrowska, 2000). As already mentioned, this is due to the presence in these waters of allogenic suspended particulate matter and dissolved substances, which give rise to spectral and intensity distributions of irradiance in ocean waters different from

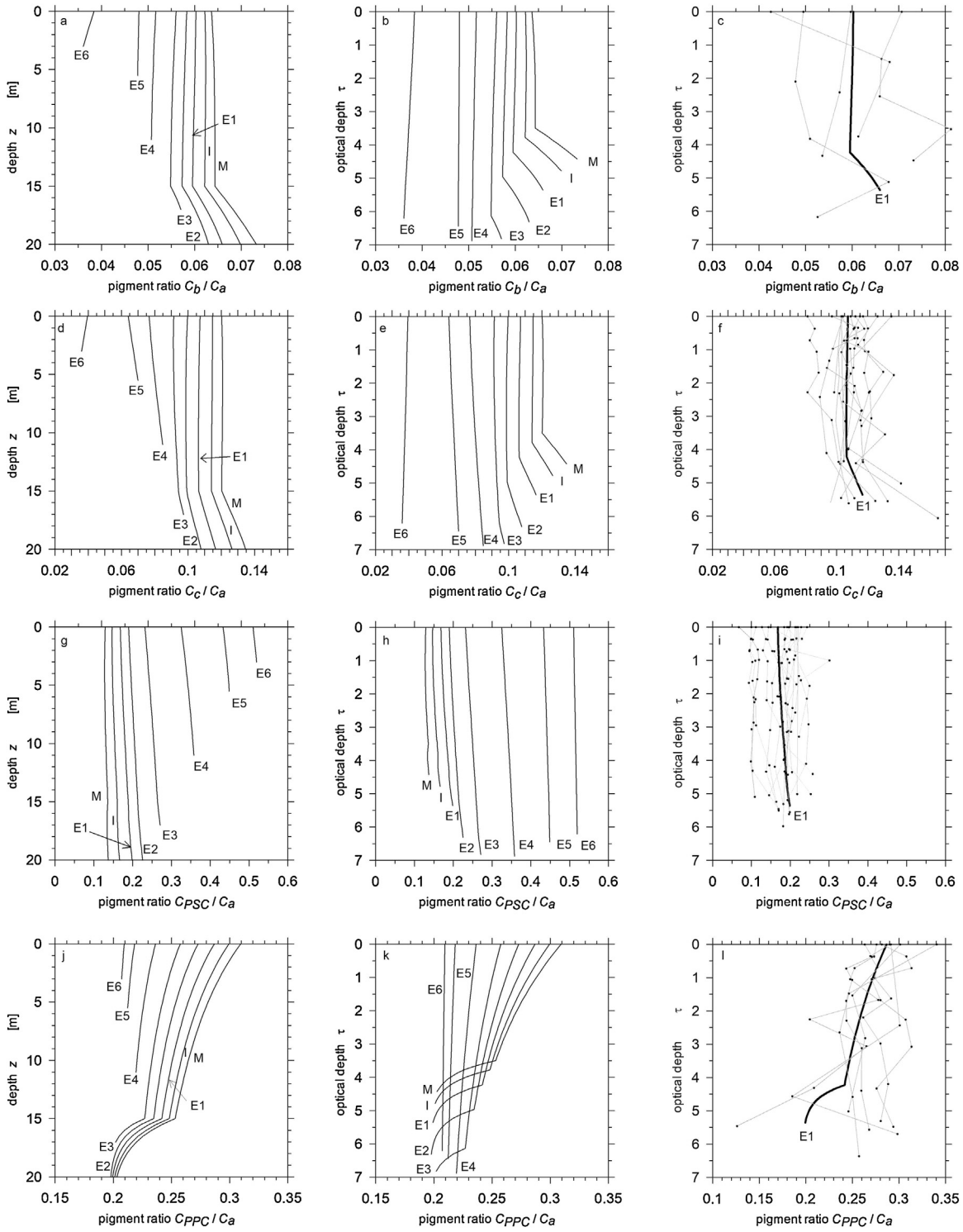

Figure 8 Vertical profiles of relative accessory pigment concentrations to a depth of 1.5 euphotic zone (i.e. optical depth = 7) in different trophic type of waters: modelled according to formulas 2, 3, 4, 7 with respect to the real depth z (column 1) and the optical depth τ (column 2); comparison of profiles — empirical (grey) and modelled (black) — in waters with a surface chlorophyll concentration from 1 to 2 mg m^{-3} (column 3). The modelled profiles are for an irradiance 500 μEin m^{-2} s^{-1} and characteristic trophic types of Baltic waters defined on the basis of the surface concentration of chlorophyll a. The symbols denote the trophic type according to the classification of Woźniak and Pelevin (1991).

those in shelf waters and enclosed seas (Dera, 1995; Woźniak and Dera, 2007).

Column 3 in Fig. 8 exemplifies profiles of the relative contents of the pigment groups within a particular range of chlorophyll *a* concentrations together with the modelled profile corresponding to these conditions. Clearly, the formulas described in this work quantitatively and qualitatively fit into the range of variability of the relative pigment levels

recorded in the Baltic Sea. Any discrepancies are the greatest in the case of the relationship describing changes in chlorophyll *b*, the concentrations of which are lower than those of the other accessory pigments. In addition, this pigment is present mainly in cells of algae from the classes chlorophytes, prasinophytes and euglenophytes, which make up just a small percentage (from 0.01 to 3.40%) of the phytoplankton biomass and no more than 30% during blooms (Stoń-Egiert et al., 2010).

5. Summary

The formulas presented in this work enable changes with depth in concentrations of chlorophylls *b* and *c*, PSCs and PPCs to be determined in the Baltic Sea on the basis of known irradiance characteristics and the concentration of chlorophyll *a*, the principal photosynthetic pigment, with an accuracy no worse than that of formulas derived for ocean waters. The errors ensuing from applying these formulas for calculating chlorophyll, PSC and PPC levels are in all cases smaller than with the formulas used to date.

The achieved accuracy of estimation is sufficient for assessing the spatial variability of pigment concentrations on the basis of remote measurements made during research cruises or by satellite. This will considerably speed up the accumulation of information on the environment; it will also enable water sampling sites and areas to be selected on a continuous basis and detailed laboratory analyses to be carried out in line with research objectives.

An important aspect of these relationships is that they are independent of season. This will ensure continuity in the estimates of depth profiles of pigment concentrations for analyses and monitoring of their annual and seasonal variabilities. Reliable information on the quantitative and qualitative composition of pigments in phytoplankton cells at any depth obtained on the basis of known levels of chlorophyll *a* and the spectral distribution of irradiance in the water may underpin a range of analyses for assessing the state and functioning of Baltic plant communities. Of no mean significance, moreover, is the fact that the data essential for calculating these concentrations can be measured remotely without time-consuming and often costly laboratory studies having to be performed; this will substantially accelerate the acquisition of the relevant data.

With remote sensing techniques for measuring surface chlorophyll *a* and the irradiance conditions, one can also quite quickly determine phytoplankton pigments levels in a whole basin, and even, if the necessary satellite data are available, for the whole Baltic Sea. The formulas presented in this paper describe vertical distributions of pigments in the water column, so analyses can cover the entire euphotic zone.

These mathematical physically justified formulas have been incorporated into the DESAMBEM multi-component light-marine photosynthesis model used in the SatBałtyk system. They further improve the accuracy of the SatBałtyk spatial and depth profiles of various characteristics describing the Baltic ecosystem and the photosynthesis of organic matter in its waters, such as the absorption of solar radiation by phytoplankton, quantum yields of photosynthesis and chlorophyll *a* fluorescence, either global or estimated at various levels of primary productivity, to name but a few.

Acknowledgements

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References

Araujo, M.L.V., Mendes, C.R.B., Tavano, V.M., Garcia, C.A.E., Baringer, M.O., 2017. Contrasting patterns of phytoplankton pigments and chemotaxonomic groups along 30°S in the subtropical South Atlantic Ocean. Deep-Sea Res. Pt. I 120, 112—121, http://dx.doi.org/10.1016/j.dsr.2016.12.004.

Babin, M., Sadoudi, N., Lazzara, L., Gostan, J., Partensky, F., Bricaud, A., Veldhuis, M., Morel, A., Falkowski, P.G., 1996. Photoacclimation strategy of *Prochlorococcus* sp. and consequences on large scale variations of photosynthetic parameters, Ocean Optics 13. Proc. SPIE 2963, 314—319, http://dx.doi.org/10.1117/12.266462.

Barlow, R.G., Mantoura, R.F.C., Gough, M.A., Fileman, T.W., 1993. Pigment signatures of the phytoplankton composition in the northeastern Atlantic during the 1990 spring bloom. Deep-Sea Res. Pt. II 40 (1/2), 459—477.

Berner, T., Dubinsky, Z., Wyman, K., Falkowski, P.G., 1989. Photoadaptation and the 'package effect' in *Dunaliella tertiolecta* (Chlorophyceae). J. Phycol. 25 (1), 70—78, http://dx.doi.org/10.1111/j.0022-3646.1989.00070.x.

Bricaud, A., Morel, A., Prieur, L., 1983. Optical efficiency factors of some phytoplankters. Limnol. Oceanogr. 28 (5), 816—832, http://dx.doi.org/10.4319/lo.1983.28.5.0816.

Bricaud, A., Claustre, H., Ras, J., Oubelkheir, K., 2004. Natural variability of phytoplanktonic absorption in oceanic waters: influence of the size structure of algal populations. J. Geophys. Res. 109, C11010, http://dx.doi.org/10.1029/2004JC002419.

Cherukuru, N., Davies, P.L., Brando, V.E., Anstee, J.M., Baird, M.E., Clementson, L.A., Doblin, M.A., 2016. Physical oceanographic processes influence bio-optical properties in the Tasman Sea. J. Sea Res. 110, 1—7, http://dx.doi.org/10.1016/j.seares.2016.01.008.

Darecki, M., Ficek, D., Krężel, A., Ostrowska, M., Majchrowski, R., Woźniak, S.B., Bradtke, K., Dera, J., Woźniak, B., 2008. Algorithms for the remote sensing of the Baltic ekosystem (DESAMBEM). Part 2: Empirical validation. Oceanologia 50 (4), 509—538.

Demmig-Adams, B., 1990. Carotenoids and photoprotection in plants: a role of xanthophyll zeaxanthin. Biochim. Biophys. Acta 1020 (1), 1—24, http://dx.doi.org/10.1016/0005-2728(90)90088-L.

Dera, J., 1995. Underwater irradiance as a factor affecting primary production. Diss. and monogr, 7. IO PAN, Sopot, 110 pp.

Dera, J., Woźniak, B., 2010. Solar radiation in the Baltic Sea. Oceanologia 52 (4), 533—582, http://dx.doi.org/10.5697/oc.52-4.533.

Dickey, T., Granata, T., Marra, J., Langdon, C., Wiggert, J., Chai-Jochner, Z., Hamilton, M., Vazquez, J., Stramska, M., Bidigare, R., Siegel, D., 1993. Seasonal variability of bio-optical and physical properties in the Sargasso Sea. J. Geoph. Res. Oceans 98 (C1), 865—898, http://dx.doi.org/10.1029/92JC01830.

Falkowski, P.G., LaRoche, J., 1991. Acclimation to spectral irradiance in algae. J. Phycol. 27 (1), 8—14, http://dx.doi.org/10.1111/j.0022-3646.1991.00008.x.

Ficek, D., Kaczmarek, S., Stoń-Egiert, J., Woźniak, B., Majchrowski, R., Dera, J., 2004. Spectra of light absorption by phytoplankton pigments in the Baltic; conclusions to be drawn from a Gaussian analysis of empirical data. Oceanologia 46 (4), 533—555.

Harrison, W.G., Platt, T., 1986. Photosynthesis-irradiance relationships in polar and temperate phytoplankton populations. Polar Biol. 5 (3), 153—164, http://dx.doi.org/10.1007/BF00441695.

Harvey, E.T., Kratzer, S., Andersson, A., 2015. Relationships between colored dissolved organic matter and dissolved organic carbon in different coastal gradients of the Baltic Sea. AMBIO 44 (Suppl. 3), S392—S401, http://dx.doi.org/10.1007/s13280-015-0658-4.

Henriksen, P., Riemann, B., Kaas, H., Sorensen, H.M., Sorensen, H.L., 2002. Effects of nutrient-limitation and irradince on marine phytoplankton pigments. J. Plankton Res. 24 (9), 835—858, http://dx.doi.org/10.1093/plankt/24.9.835.

Ho, T.-Y., Pan, X., Yang, H.-H., Wong, G.T.F., Shiah, F.-K., 2015. Controls on temporal and spatial variations of phytoplankton pigment distribution in the Northern South China Sea. Deep Sea Res. II 117, 65—85, http://dx.doi.org/10.1016/j.dsr2.2015.05.015.

Hoffmann, B., Senger, H., 1988. Kinetics of photosynthesis apparatus adaptation in *Scenedesmus obliquus* to change in irradiance and light quality. Photochem. Photobiol. 47 (5), 737—739, http://dx.doi.org/10.1111/j.1751-1097.1988.tb02773.x.

Jeffrey, S.W., 1997. Structural relationships between algal chlorophylls. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods, UNESCO Publishing, Paris. 566—571.

Jeffrey, S.W., Vesk, M., 1997. Introduction to marine phytoplankton and their pigment signatures. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO Publishing, Paris, 37—84.

Kim, H.-C., Son, S., Kim, Y.H., Khim, J.S., Nam, J., Chang, W.K., Lee, J.-H., Ryu, J., 2017. Remote sensing and water quality indicators in the Korean West coast: Spatio-temporal structures of MODIS-derived chlorophyll-a and total suspended solids. Mar. Pollution Bull. 121, 425—434, http://dx.doi.org/10.1016/j.marpolbul.2017.05.026.

Kowalczuk, P., Olszewski, J., Darecki, M., Kaczmarek, S., 2005. Empirical relationships between coloured dissolved organic matter (CDOM) absorption and apparent optical properties in Baltic Sea waters. Int. J. Remote Sens. 26 (2), 345—370, http://dx.doi.org/10.1080/01431160410001720270.

Levin, I., Darecki, M., Sagan, S., Radomyslskaya, T., 2013. Relationships between inherent optical properties in the Baltic Sea for application to the underwater imaging problem. Oceanologia 55 (1), 11—26, http://dx.doi.org/10.5697/oc.55-1.011.

Louda, J.W., Li, J., Liu, L., Winfree, M.N., Baker, E.W., 1998. Chlorophyll-a degradation during senescence and death. Org. Geochem. 29 (5—7), 1233—1251, http://dx.doi.org/10.1016/j.orggeochem.2011.03.018.

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.

Majchrowski, R., Ostrowska, M., 2009. Mathematical description of vertical algal accessory pigment distributions in oceans — a brief presentation. Oceanologia 51 (4), 561—580, http://dx.doi.org/10.5697/oc.51-4.561.

Majchrowski, R., Stoń-Egiert, J., Ostrowska, M., Woźniak, B., Ficek, D., Lednicka, B., Dera, J., 2007. Remote sensing of vertical phytoplankton pigment distributions in the Baltic: new mathematical expressions. Part 2: Accessory pigment distribution. Oceanologia 49 (4), 491—511.

Mantoura, R.F.C., Llewellyn, C.A., 1983. The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. Anal. Chim. Acta 151, 297—314.

Mantoura, R.F.C., Repeta, D.J., 1997. Calibration methods for HPLC. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO Publ., Paris, 407—428.

Mantoura, R.F.C., Wright, S.W., Jeffrey, S.W., Barlow, R.G., Cummings, D.E., 1997. Filtration and storage of pigments from microalgae. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO Publ., Paris, 283—305.

Meler, J., Kowalczuk, P., Ostrowska, M., Ficek, D., Zabłocka, M., Zdun, A., 2016. Parameterization of the light absorption properties of chromophoric dissolved organic matter in the Baltic Sea and Pomeranian lakes. Ocean Sci. 12, 1013—1032, http://dx.doi.org/10.5194/os-12-1013-2016.

Meler, J., Ostrowska, M., Stoń-Egiert, J., Zabłocka, M., 2017. Seasonal and spatial variability of light absorption by suspended particles in the southern Baltic: A mathematical description. J. Mar. Sys. 170, 68—87, http://dx.doi.org/10.1016/j.jmarsys.2016.10.011.

Mendes, C.R., Sá, C., Vitorino, J., Borges, C., Garcia, V.M.T., Brotas, V., 2011. Spatial distribution of phytoplankton assemblages in the Nazaré submarine canyon region (Portugal): HPLC-CHEMTAX approach. J. Mar. Sys. 87, 90—101, http://dx.doi.org/10.1016/j.jmarsys.2016.10.011.

Mitchell, B.G., Kiefer, D.A., 1988. Chlorophyll a specific absorption and fluorescence excitation spectra for light-limited phytoplankton. Deep-Sea Res. 35, 639—663, http://dx.doi.org/10.1016/0198-0149(88)90024-6.

Mobley, C.D., 1994. Light and Water, Radiative Transfer in Natural Waters. Acad. Press, San Diego, USA, 592 pp.

Morel, A., Lazzara, L., Gostan, G., 1987. Growth rate and quantum yield time response for a diatom to changing irradiances (energy and color). Limnol. Oceanogr. 32 (5), 1066—1084, http://dx.doi.org/10.4319/lo.1987.32.5.1066.

Ostrowska, M., Darecki, M., Krężel, A., Ficek, D., Furmańczyk, K., 2015a. Practical applicability and preliminary results of the Baltic environmental satellite remote sensing system (SatBałtyk). Polish Mart. Res. 3 (22), 43—49, http://dx.doi.org/10.1515/pomr-2015-0055.

Ostrowska, M., Stoń-Egiert, J., Woźniak, B., 2015b. Modified methods for defining the chlorophyll concentration in the sea using submersible fluorimeters — Theoretical and quantitative analysis. Cont. Shelf Res. 109, 46—54, http://dx.doi.org/10.1016/j.csr.2015.09.009.

Pan, X., Mannino, A., Russ, M.E., Hooker, S.B., Harding Jr., S.B., 2010. Remote sensing of phytoplankton pigment distribution in the United States northeast coast. Remote Sens. Environ. 114, 2403—2416, http://dx.doi.org/10.1016/j.rse.2010.05.015.

Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, Oxford, 173 pp.

Porra, R.J., Pfündel, E.E., Engel, N., 1997. Metabolism and function of photosynthetic pigments. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO Publ., Paris, 85—126.

Prieur, L., Sathyendranath, S., 1981. An optical classification of coastal and oceanic waters based on the specific spectral absorption curves of phytoplankton pigments, dissolved organic matter, and other particulate materials. Limnol. Oceanogr 26 (4), 671—689, http://dx.doi.org/10.4319/lo.1981.26.4.0671.

Repeta, D.J., Bjørnland, T., 1997. Preparation of carotenoids standards. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO Publ., Paris, 239—260.

Roy, S., Llewellyn, C.A., Egeland, E.S., Johnsen, G., 2011. Phytoplankton Pigments, Characterization, Chemotaxonomy and Applications in Oceanography. Cambridge Univ. Press, 845 pp.

Sathyendranath, S., Lazzara, L., Prieur, L., 1987. Variations in the spectral values of specific absorption of phytoplankton. Limnol. Oceanogr. 32 (2), 403—415, http://dx.doi.org/10.4319/lo.1987.32.2.0403.

Scheer, H., 1991. Structure and occurrence of chlorophylls. In: Scheer, H. (Ed.), Chlorophylls. CRC Press, Boca Raton, 3—30.

Schlüter, L., Mohlenberg, F., Havskum, H., Larsen, S., 2000. The use of phytoplankton pigments for identifying phytoplankton groups in coastal areas: testing the influence of light and nutrients on pigment/chlorophyll *a* ratios. Mar. Ecol.-Prog. Ser. 192, 49—63, http://dx.doi.org/10.3354/meps192049.

Simis, S.G.H., Ylöstalo, P., Kallio, K.Y., Spilling, K., Kutser, T., 2017. Contrasting seasonality in optical-biogeochemical properties of the Baltic Sea. PLoS ONE 12 (4), e0173357, http://dx.doi.org/10.1371/journal.pone.0173357.

Smith Jr., W.O., Dinniman, M.S., Tozzi, S., DiTullio, G.R., Mangoni, O., Modigh, M., Saggiomo, V., 2010. Phytoplankton photosynthetic pigments in the Ross Sea: Patterns and relationships among functional groups. J. Mar. Sys. 82, 177—185.

Soja-Woźniak, M., Darecki, M., Wojtasiewicz, B., Bradtke, K., 2018. Laboratory measurements of remote sensing reflectance of selected phytoplankton species from the Baltic Sea. Oceanologia 60 (1), 86—96, http://dx.doi.org/10.1016/j.oceano.2017.08.001.

Sosik, H.M., Mitchell, B.G., 1991. Absorption, fluorescence, and quantum yield for growth in nitrogen-limited *Dunaliella tertiolecta*. Limnol. Oceanogr. 36 (5), 910—921, http://dx.doi.org/10.4319/lo.1991.36.5.0910.

Staehr, P.A., Henriksen, P., Markager, S., 2002. Photoacclimation of four marine phytoplankton species to irradiance and nutrient availability. Mar. Ecol. Prog. Ser. 238, 47—59, http://dx.doi.org/10.3354/meps238047.

Stedmon, C.A., Markager, S., Kaas, H., 2000. Optical properties and signatures of chromophoric dissolved organic matter (CDOM) in Danish coastal waters. Est. Coast. Shelf Sci. 51, 267—278, http://dx.doi.org/10.1006/ecss.2000.0645.

Stoń, J., Kosakowska, A., 2002. Phytoplankton pigments designation — an application of RP-HPLC in qualitative and quantitative analysis. J. Appl. Phycol. 14 (3), 205—210, http://dx.doi.org/10.1023/A:1019928411436.

Stoń-Egiert, J., Kosakowska, A., 2005. RP-HPLC determination of phytoplankton pigments — comparison of calibration results for two columns. Mar. Biol. 147 (1), 251—260, http://dx.doi.org/10.1007/s00227-004-1551-z.

Stoń-Egiert, J., Łotocka, M., Ostrowska, M., Kosakowska, A., 2010. The influence of biotic factors on phytoplankton pigment composition and resources in Baltic ecosystems: new analytical results. Oceanologia 52 (1), 101—125, http://dx.doi.org/10.5697/oc.52-1.101.

Stoń-Egiert, J., Majchrowski, R., Darecki, M., Kosakowska, A., Ostrowska, M., 2012. Influence of underwater light fields on pigment characteristics in the Baltic Sea — results of statistical analysis. Oceanologia 54 (1), 7—27, http://dx.doi.org/10.5697/oc.54-1.007.

Stramska, M., Zuzewicz, A., 2013. Comparison of primary productivity estimates in the Baltic Sea based on the DESAMBEM algorithm with estimates based on other similar algorithms. Oceanologia 55 (1), 77—100, http://dx.doi.org/10.5697/oc.55-1.077.

Stramski, D., Sciandra, A., Claustre, H., 2002. Effects of temperature, nitrogen, and light limitation on the optical properties of the marine diatom Thalassiosira pseudonana. Limnol. Oceanogr. 47 (2), 392—403, http://dx.doi.org/10.4319/lo.2002.47.2.0392.

Strutton, P.G., Martz, T.D., DeGrandpre, M.D., McGillis, W.R., Drennan, W.M., Boss, E., 2011. Bio-optical observations of the 2004 Labrador Sea phytoplankton bloom. J. Geoph. Res. 116, C11037.

Sukenik, A., Bennett, J., Mortain-Bertrand, A., Falkowski, P.G., 1990. Adaptation of photosynthetic apparatus to irradiance in *Dunaliella tertiolecta*. Plant Physiol. 92 (4), 891—898, http://dx.doi.org/10.1104/pp.92.4.891.

Swan, C.M., Vogt, M., Gruber, N., Laufkoetter, C., 2016. A global seasonal surface ocean climatology of phytoplankton types based on CHEMTAX analysis of HPLC pigments. Deep-Sea Res. Pt. I, 109, 137—156, http://dx.doi.org/10.1016/j.dsr.2015.12.002.

Thamm, R., Schernewski, G., Wasmund, N., Neumann, T., 2004. Spatial phytoplankton pattern in the Baltic Sea. In: Schernewski, G., Wielgat, S. (Eds.), Baltic Sea Typology Coastline Reports 4, Warnemünde, 85—109.

Trees, C.C., Clark, R.D.K., Bidigare, R., Ondrusek, M.E., Mueller, J. L., 2000. Accessory pigments versus chlorophyll A concentrations within the euphotic zone: A ubiquitous relationship. Limnol. Oceanogr. 45 (5), 1130—1143, http://dx.doi.org/10.4319/lo.2000.45.5.1130.

Uitz, J., Claustre, H., Morel, A., Hooker, S.B., 2006. Vertical distribution of phytoplankton communities in open ocean: an assessment based on surface chlorophyll. J. Geophys. Res. 111 (C8), C08005, http://dx.doi.org/10.1029/2005JC003207.

Uitz, J., Stramski, D., Reynolds, R.A., Dubranna, J., 2015. Assessing phytoplankton community composition from hyperspectral measurements of phytoplankton absorption coefficient and remote-sensing reflectance in open-ocean environments,. Remote Sens. Environ. 171, 58—74, http://dx.doi.org/10.1016/j.rse.2015.09.027.

Wasmund, N., Breuel, G., Edler, L., Kuosa, H., Olsonen, R., Schultz, H., Pys-Wolska, M., Wrzołek, L., 1996. Pelagic biology. In: Third periodic assessment of the state of marine environment of the Baltic Sea, 1989—93, Balt. Sea Environ. Proc. No. 64B, HELCOM Background doc. 89—93.

Wasmund, N., Uhlig, S., 2003. Phytoplankton in large river plumes in the Baltic Sea,. ICES J. Mar. Sci. 56, 23—32.

Wänstrand, I., Snoeijs, P., 2006. Phytoplankton community dynamics assessed by ships-of-opportunity sampling in the northern Baltic Sea: A comparison of HPLC pigment analysis and cell counts. Est. Coast. Shelf Sci. 66 (1—2), 135—146, http://dx.doi.org/10.1016/j.ecss.2005.08.003.

Woźniak, B., Bradtke, K., Darecki, M., Dera, J., Dudzińska-Nowak, J., Dzierzbicka-Głowacka, L., Ficek, D., Furmańczyk, K., Kowalewski, M., Krężel, A., Majchrowski, R., Ostrowska, M., Paszkuta, M., Stoń-Egiert, J., Stramska, M., Zapadka, T., 2011. SatBałtyk — A Baltic environmental satellite remote sensing system — an ongoing project in Poland. Part 1: Assumptions, scope and operating range. Oceanologia 53 (4), 897—924, http://dx.doi.org/10.5697/oc.53-4.897.

Woźniak, B., Dera, J., 2007. Light Absorption in Sea Water. Springer, New York, 454 pp.

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

Woźniak, B., Dera, J., Ficek, D., Majchrowski, R., Ostrowska, M., Kaczmarek, S., 2003. Modelling light and photosynthesis in the marine environment. Oceanologia 45 (2), 171—245.

Woźniak, B., Dera, J., Majchrowski, R., Ficek, D., Koblenz-Mishke, O. J., Darecki, M., 1997a. 'IOPAS initial model' of marine primary production for remote sensing application. Oceanologia 39 (4), 377—395.

Woźniak, B., Dera, J., Majchrowski, R., Ficek, D., Koblentz-Mishke, O.J., Darecki, M., 1997b. Statistical relationships between photosynthesis and abiotic conditions in the ocean — the IO PAS initial model for remote sensing application. SPIE vol. 3222, 516—528.

Woźniak, B., Hapter, R., Maj, B., 1983. The inflow of solar energy and the irradiance of the euphotic zone in the region of Ezcurra Inlet during the Antarctic summer of 1977/78. Oceanologia 15, 141—174.

Woźniak, B., Krężel, A., Darecki, M., Woźniak, S.B., Majchrowski, R., Ostrowska, M., Kozłowski, Ł., Ficek, D., Olszewski, J., Dera, J., 2008. Algorithm for the remote sensing of the Baltic ecosystem (DESAMBEM). Part 1: Mathematical apparatus. Oceanologia 50 (4), 451—508.

Woźniak, B., Krężel, A., Dera, J., 2004. Development of a satellite method for Baltic ecosystem monitoring (DESAMBEM) — an ongoing project in Poland. Oceanologia 46 (3), 445—455.

Woźniak, B., Montwiłł, K., 1973. Methods and techniques of optical measurements in the sea. Stud. i Mater. Oceanol. 7, 71—108, (in Polish).

Woźniak, B., Pelevin, V.N., 1991. Optical classifications of the seas in relation to phytoplankton characteristics. Oceanologia 31, 25—55.

Woźniak, S.B., Meler, J., Lednicka, B., Zdun, A., Stoń-Egiert, J., 2013. Inherent optical properties of suspended particulate matter in the southern Baltic Sea. Oceanologia 53 (3), 691—729, http://dx.doi.org/10.5697/oc.53-3.691.

Wright, S.W., Jeffrey, S.W., Mantoura, R.F.C., Llewellyn, C.A., Bjørnland, T., Repeta, D., Welschmeyer, N., 1991. Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. Mar. Ecol.-Prog. Ser. 77, 183—196.

Wright, S.W., Shearer, J.D., 1984. Rapid extraction and high-performance liquid chromatography of chlorophylls and carotenoids from marine phytoplankton. J. Chromatogr. 294, 281—295.

Wulff, A., Wängberg, S.-A., 2004. Spatial and vertical distribution of phytoplankton pigments in the eastern Atlantic sector of the Southern Ocean. Deep-Sea Res. Pt. II, 51, 2701—2713, http://dx.doi.org/10.1016/j.dsr2.2001.01.002.

Zhang, D., Lavender, S., Muller, J.P., Walton, D., Karlson, B., Kronsell, J., 2017. Determination of phytoplankton abundances (Chlorophyll-*a*) in The optically complex inland water — The Baltic Sea. Remote Sci. Tot. Environ. 601—602, 1060—1074, http://dx.doi.org/10.1016/j.scitotenv.2017.05.245.

Zheng, G., DiGiacomo, P.M., 2017. Remote sensing of environment remote sensing of chlorophyll-a in coastal waters based on the light absorption coefficient of phytoplankton,. Remote Sens. Environ. 201, 331—341, http://dx.doi.org/10.1016/j.rse.2017.09.008.