Influence of photo- and chromatic acclimation on pigment composition in the sea*

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Abstract

The aim of this work was to find statistical relationships between the concentrations of accessory pigments in natural populations of marine phytoplankton and the absolute levels and spectral distributions of underwater irradiance. To this end, empirical data sets from some 600 stations in different parts of the seas and oceans were analysed. These data were obtained from the authors' own research and from the Internet's bio-optical data base. They included the vertical distributions of the concentrations of various pigments (identified chromatographically) and the vertical and spectral distributions of the underwater irradiance measured *in situ* or determined indirectly from bio-optical models. The analysis covered a total of some 4000 points illustrating the dependence of pigment concentration on underwater irradiance characteristics, corresponding to different depths in the sea.

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The analysis showed that the factor governing the occurrence of photoprotecting carotenoids (PPC) is short-wave radiation $\lambda < 480$ nm. A mathematical relationship was established between the relative PPC concentration (relative with respect to the chlorophyll *a* concentration) and the magnitude of the absorbed radiative energy per unit mass of chlorophyll *a* from the spectral interval $\lambda < 480$ nm, averaged in the water layers $\Delta z = 60$ m (or less near the surface) to account for vertical mixing. This absorbed short-wave radiation ($\lambda < 480$ nm) was given the name of Potentially Destructive Radiation (PDR*(z)).

Analysis of the relationships between the concentrations of particular photosynthetic pigments (PSP), *i.e.* chlorophyll *b*, chlorophyll *c*, photosynthetic carotenoids (PSC), and the underwater irradiance characteristics indicated that these concentrations were only slightly dependent on the absolute level of irradiance $E_0(\lambda)$, but that they depended strongly on the relative spectral distribution of this irradiance $f(\lambda) = E_0(\lambda)/PAR_0$. The relevant approximate statistical relationships between the relative concentrations of particular PSP and the function of spectral fitting F_j, averaged in the layer Δz, were derived.

Certain statistical relationships between the pigment composition of the phtyoplankton and the irradiance field characteristics are due to the photo- and chromatic acclimation of natural populations of marine phytoplankton. These relationships can be applied in models of the coefficients of light absorption by phytoplankton.

1. Introduction

The adaptation and acclimation of marine phytoplankton is a complicated problem. It was discovered long ago that one of the main mechanisms of acclimation is a modification of the pigment composition in the photosynthetic apparatus (Steemann Nielsen 1975 and the papers cited there). It is also well known that relationships exist between the concentrations of accessory pigments and the different optical characteristics of natural light fields in a plant's growth environment (see our earlier papers: Woźniak *et al.* 1997, Majchrowski & Ostrowska 1999). However, these relationships have not yet been examined in detail.

The aim of this paper is to determine a set of statistical relationships between the concentrations of the various accessory pigments in natural marine phytoplankton and the absolute levels and spectral distributions of underwater light fields. To do this, we carried out a statistical analysis of our own empirical data and that available on the Internet.

2. Presentation of the physical problem

The photosynthetic apparatus of a plant contains not only chlorophyll *a* but also a lot of accessory pigments. We can divide all these pigments into two main types which perform different functions in plant cells (Bidigare *et al.* 1990). One of these types includes the Photosynthetic Pigments (PSP), which absorb light as if they were antennas: their excitation energy is used in photosynthesis with a certain efficiency. The accessory photosynthetic pigments absorb radiation energy over and above that absorbed by chlorophyll *a* and transfer it to chlorophyll *a*. Only chlorophyll *a* supplies energy directly to the photosynthetic process at the reaction centres. These accessory photosynthetic pigments are chlorophylls *b*, chlorophylls *c* and the photosynthetic carotenoids (PSC), such as fucoxanthin, 19′but-fucoxanthin, 19′hex-fucoxanthin, peridinin, prasinoxanthin and α-carotene. The concentration of these pigments is controlled by chromatic acclimation processes (Steemann Nielsen 1975, Zvalinsky 1986).

The second type of accessory pigments, known as Photoprotecting Pigments (PPP), protect the photosynthetic apparatus from very-high-energy photons, which are capable of destroying reaction centres and oxidising chlorophyll *a* molecules. Neither the energy absorbed by these pigments, nor that generated through their quenching of the chlorophyll *a* triplet state, is used for photosynthesis. PPP consist mainly of carotenoids: diadinoxanthin, alloxanthin, zeaxanthin, diatoxanthin, lutein, antheraxanthin, β-carotene, violaxanthin, neoxanthin and dinoxanthin, and their existence in the plant cells depends on the photoacclimation of the cells (Steemann Nielsen 1975, Zvalinsky 1986).

Figure 1 shows examples of vertical changes in PPP concentrations in relation to chlorophyll *a* for different types of seas: the decrease in PPP concentrations with depth for all trophic types of water is evident. High intensities of potentially harmful short-wave radiation in shallow waters elevate concentrations of photoprotecting carotenoids (PPC) in surface layer phytoplankton. In deep waters the absolute level of short-wave radiation is lower, hence there is no need for large quantities of PPP in cells. Their relative concentrations therefore decrease with depth.

Figure 2 shows examples of vertical profiles of relative PSC concentrations: these increase with depth. This depth-dependent behaviour of the phytoplankton pigment composition is due to the characteristic influence of optical factors on accessory pigment production.

The three sets of spectra in Fig. 3 help to show up the links between pigment concentrations and the spectral characteristics of underwater light fields. The specific absorption spectra (specific to unit mass of a particular pigment) of the main groups of pigments, *i.e.* chlorophylls *a*, chlorophylls *b*, chlorophylls *c*, PSC and PPC in the visible spectrum, are shown in Fig. 3a. Figs. 3b and 3c depict model spectra of the relative irradiance in oligotrophic ($C_a(0) = 0.035$ mg tot. chl a m^{-3}) and eutrophic ($C_a(0) = 35$ mg tot. chl a m^{-3}) seas at different depths. In both cases the optical depths are the same: 0.5, 1.15, 2.3, 4.6, 9.2. As one can see, in deep oligotrophic waters, the light is mainly from the blue-green spectral range.

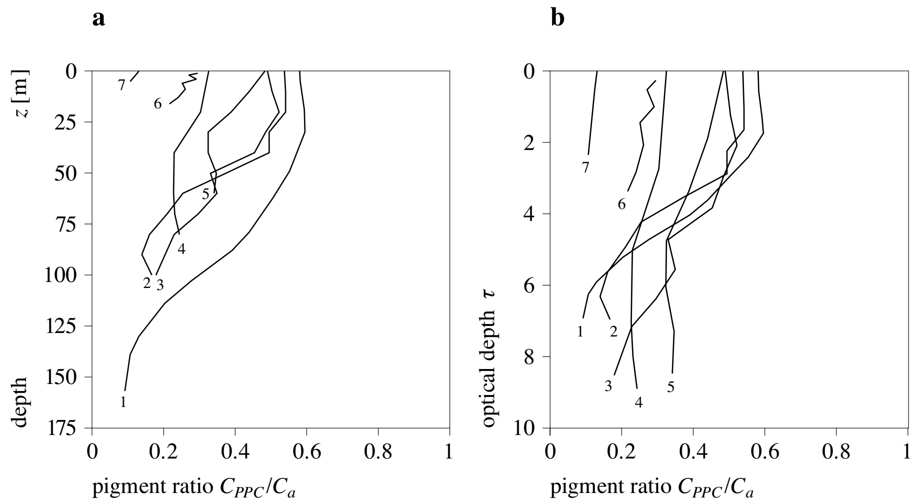
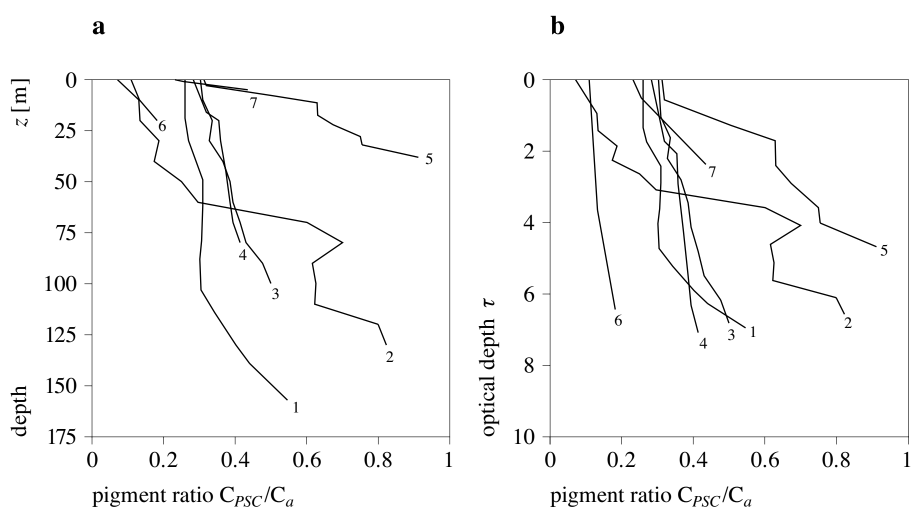


Fig. 1. Vertical profiles of typical examples of the ratio of photoprotecting carotenoids (C_{PPC}) to total chlorophyll a (C_a) for a real depth z (a); for an optical depth τ (b); recorded at the same stations with different surface total chlorophyll a concentrations $C_a(0)$: 1 – Polish-Russian database – Pacific ($C_a(0)$ = 0.05 mg tot. chl a m^{-3}); 2 – (Bidigare 1992a) – equatorial Pacific ($C_a(0)$ = 0.158 mg tot. chl a m^{-3}); 3 – (Goericke 1995b) – Arabian Sea ($C_a(0)$ = 0.341 mg tot. chl a m^{-3}); 4 – (Goericke 1995b) – Arabian Sea ($C_a(0)$ = 0.794 mg tot. chl a m^{-3}); 5 – (Goericke 1995b) – Arabian Sea ($C_a(0)$ = 1.38 mg tot. chl a m^{-3}); 6 – (Goericke 1995b) – Arabian Sea ($C_a(0)$ = 2.42 mg tot. chl a m^{-3}); 7 – (Olaizola 1996) – Baltic Sea ($C_a(0)$ = 7.09 mg tot. chl a m^{-3})



Under such conditions plants have to produce photosynthetic carotenoids, which act as additional 'antennas' absorbing energy. In eutrophic waters, blue-green light does not penetrate very deeply, so changes in pigment composition are less noticeable. Taking such regularities into consideration, we can try to find the optical parameters controlling the relative concentrations of different groups of pigments at different depths in the sea. A first attempt to determine these parameters can be found in Woźniak *et al.* 1997. In the present paper, we present an improved correlation between the relative photosynthetic pigment concentrations and the functions of spectral fitting, which we call chromatic adaptation factors:

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

where

$f(\lambda) = \frac{E_0(\lambda)}{PAR_0}$ – the relative spectral distribution of scalar irradiance in the sea,

$a^*_j(\lambda)$ – spectral specific absorption coefficient of the j-th pigment group,

$a^*_{j,\,\max}$ – values of the spectral specific absorption coefficient in the spectral maximum of the j-th group of pigments; the j-th group of pigments consists of a – chlorophyll a, b – chlorophyll b; c – chlorophyll c, PSC – photosynthetic carotenoids.

The function of spectral fitting F_j ranges from 0 to 1. It is equal to 0 when the pigment absorption spectrum does not overlap the underwater irradiance spectrum. If the *in situ* irradiance happens to have a narrow spectral wave band compatible with the absorption spectrum maximum of this j-th group of pigments, then F_j equals 1. This function depends on relative spectral distributions, not on absolute values of light energy.

Fig. 2. Vertical profiles of typical ratios of photosynthetic carotenoid concentrations (C_{PSC}) to total chlorophyll a (C_a) for a real depth z (a); for an optical depth τ (b); recorded at the same stations with different surface total chlorophyll a concentrations $C_a(0)$: 1 – Polish-Russian database – Pacific ($C_a(0) = 0.05$ mg tot. chl a m^{-3}); 2 – (Bidigare 1992a) – equatorial Pacific ($C_a(0) = 0.07$ mg tot. chl a m^{-3}); 3 – (Bidigare 1992c) – equatorial Pacific ($C_a(0) = 0.147$ mg tot. chl a m^{-3}); 4 – (Goericke 1995a) – Arabian Sea ($C_a(0) = 0.327$ mg tot. chl a m^{-3}); 5 – Polish-Russian database – Baltic Sea ($C_a(0) = 0.69$ mg tot. chl a m^{-3}); 6 – (Olaizola 1996) – Baltic Sea ($C_a(0) = 3.5$ mg tot. chl a m^{-3}); 7 – (Olaizola 1966) – Baltic Sea ($C_a(0) = 7.1$ mg tot. chl a m^{-3})

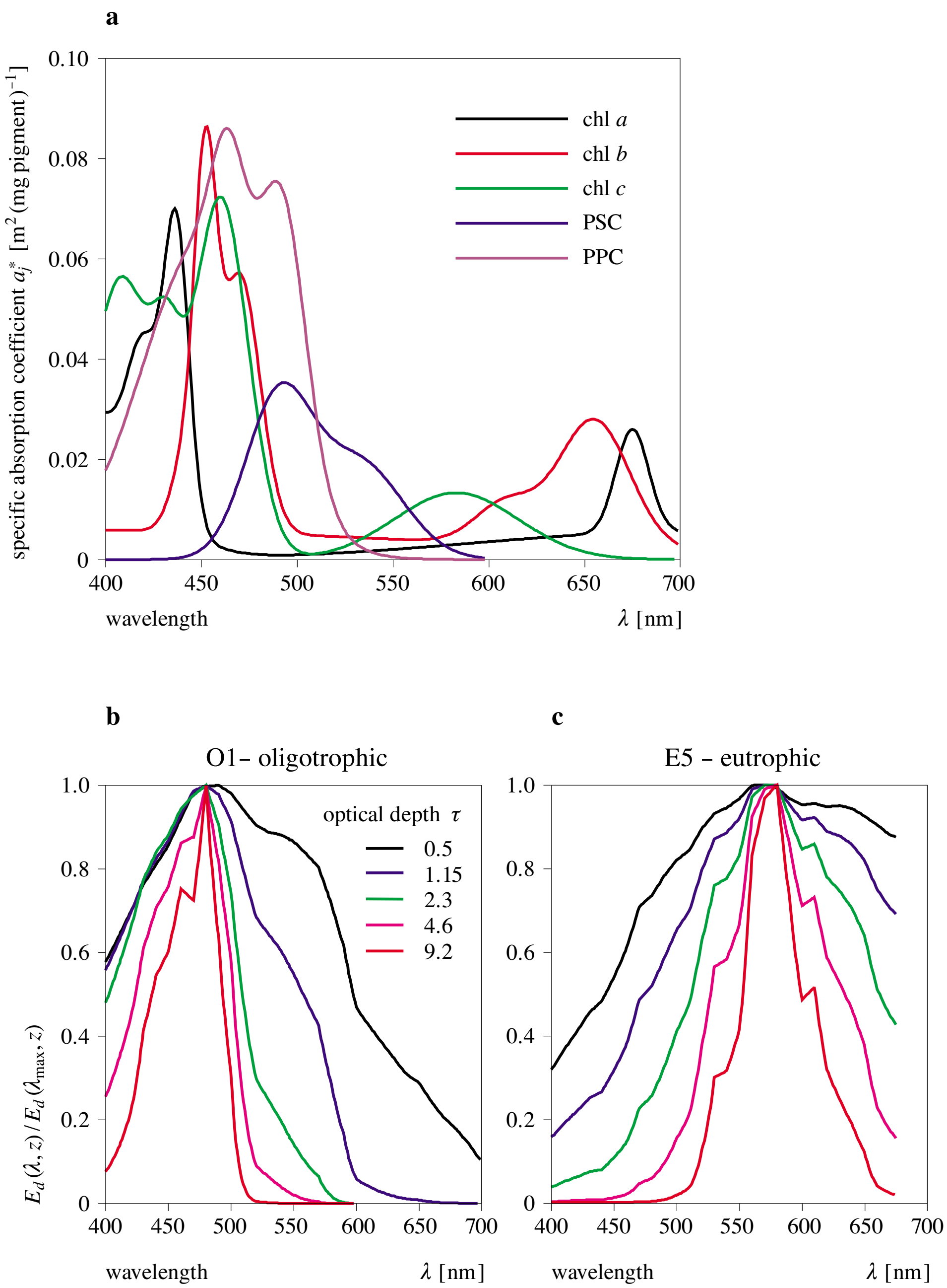


Fig. 3. Specific absorption spectra for the major 'unpackaged' pigment groups (after Woźniak *et al.* 1999) (a); downwelling irradiance spectra of Woźniak's water mass classification (Woźniak *et al.* 1992) for oligotrophic waters O1 – $C_a(0) = 0.035$ mg tot. chl a m^{-3} (b) and for eutrophic waters E5 – $C_a(0) = 35$ mg tot. chl a m^{-3} (c) at the same optical depths

Woźniak *et al.* (1997) determined another factor correlating with the relative PPC concentration. This factor depends on the absolute quantity of light energy from the short-wave band of the spectrum ($\lambda < 480$ nm; in practice 400–480 nm is applied in calculations). The best correlation was established for the factor known as Potentially Destructive Radiation (PDR):

$$PDR^* = \int_{400\,\mathrm{nm}}^{480\,\mathrm{nm}} a_a^*(\lambda)\ \langle E_0(\lambda)\rangle_{\mathrm{day}}\, d\lambda, \tag{2}$$

where

PDR^* – PDR energy absorbed per unit mass of chlorophyll,
$a_a^*(\lambda)$ – chlorophyll a specific spectral absorption coefficient,
$\langle E_0(\lambda)\rangle_{\mathrm{day}}$ – daily mean spectral scalar irradiance.

The PDR^* is equal to the energy from the blue-green spectral range absorbed by unit mass of chlorophyll a, and is potentially capable of photo-oxidising it. It turns out that the correlation is best if PDR^* at a given depth is replaced by the mean PDR^* at 60 m. In this way, vertical mixing of water is included in the calculation.

Woźniak *et al.* (1997) also give the respective statistical relationships between the relative concentrations of the main groups of pigments and the functions of spectral fitting F_j and/or PDR^*. These relationships were obtained from a sparse experimental data set (only about 200 empirical points for each event). In our opinion, the use of these relationships to calculate the concentrations of particular groups of pigments in different conditions is fraught with significant error. In the present work an enlarged database was used, and the modified relationships thereby obtained were more accurate.

3. Empirical data

To achieve our objective, empirical data from 608 sites in various regions of the World Oceans were analysed. We collected data from our own investigations and the Internet bio-optical database – the U. S. JGOFS Data System (see Table 1).

Our database included the following sets of empirical data:

(1) Phytoplankton pigment concentrations (different types of chlorophylls and carotenoids) determined by different methods, mainly by HPLC (High Performance Liquid Chromatography) or, in the nineteen-sixties and early seventies, by TLC (Thin Layer Chromatography).

(2) Spectral distributions of downward irradiance at various depths in the sea.

Table 1. The empirical database specification

Experiment	Stations		Sets of measurements		Location	References, or name of person measuring pigment concentrations	Optical measurements	
	of PSP analyses	of PPC analyses	of PSP analyses	of PPC analyses			at the surface	at different depths
Polish-Russian database	126	46	333	219	Baltic Sea, Black Sea, Pacific	Koblentz-Mishke & Semenova (1975), Semenova (1975), Kornushenko *et al.* (1980)	+	+
ULISSE	91	30	268	82	Baltic Sea	Olaizola (1996)	+	+
eqPac tt007	39	39	428	428	equatorial Pacific	Bidigare (1992a)	39 sites Newton (1992a)	–
eqPac tt008	33	33	234	234	equatorial Pacific	Bidigare (1992b)	2 sites Newton (1992b)	– –
eqPac tt011	44	44	482	482	equatorial Pacific	Bidigare (1992c)	38 sites Newton (1992c)	– –
eqPac tt012	34	34	215	215	equatorial Pacific	Bidigare (1992d)	–	–
Arabian ttn-43	77	77	530	530	Arabian Sea	Goericke (1995a)	–	–
Arabian ttn-45	29	29	255	255	Arabian Sea	Bidigare (1995a)	–	–
Arabian ttn-49	72	72	505	505	Arabian Sea	Goericke (1995b)	–	–
Arabian ttn-50	29	–	210	–	Arabian Sea	Bidigare (1995b)	–	–
Arabian ttn-53	34	–	389	–	Arabian Sea	Bidigare (1995c)	–	–
total	608	404	3849	2950				

Direct measurements of the downward spectral irradiance distribution were made only during the collection of data denoted in Table 1 as the Polish-Russian database and the ULISSE[1] experiment (at 217 of the stations in question). In the other cases, unfortunately, only the total, not the spectral, irradiance at the sea surface was measured, and/or optical measurements in the sea were carried out sporadically. Thus, if surface-measured optical data were unavailable, we assumed the surface spectral $PAR(0)$ irradiance typical of the relevant geographical zone (Timofeyev 1983). From this, the underwater light field distributions in the various trophic types of seas were estimated according to the algorithm given in Woźniak *et al.* (1992). This algorithm is based on a bio-optical model of the relationship between the spectral downward irradiance attenuation coefficient and the chlorophyll a concentration in the sea. The errors inherent in such estimations with reference to underwater irradiation attenuation coefficients are of the order of 10%; the estimations are thus deemed sufficiently accurate (see Woźniak *et al.* 1992). The relevant data is specified in Table 1.

The following quantities were determined from the input data for statistical analyses:

(1) The relative concentrations of PPC, PSC, chl b, chl c, defined as the rates C_{PPC}/C_a, C_{PSC}/C_a, C_b/C_a and C_c/C_a respectively, where C_a denotes the sum of chl a and divinyl chl a at given depths in the sea.

(2) Typical PDR^* values for these depths determined from eq. (2) using the spectra of the specific light absorption coefficient of chlorophyll a according to Woźniak *et al.* (1999).

(3) The different functions of spectral fitting (F_a, F_b, F_c, F_{PSC}) typical of these depths, determined from eq. (1) using the spectra of the light absorption coefficients of different pigments according to Woźniak *et al.* (1999).

About 3000 points of C_{PPC}/C_a, *versus* PDR^* relations, and about 4000 points of C_j/C_a, *versus* F_j relations at different depths in the sea were examined altogether.

4. Results and discussion

The analyses confirm that the short-wave (blue-green) part of the PAR range is the factor controlling the occurrence of photoprotecting carotenoids (PPC). A mathematical relationship is given describing the

[1]Underwater Light Seatruth Satellite Experiment, in co-operation with the Commission of the European Union Joint Research Centre, Ispra, Italy and the Institute of Oceanology PAS (Ooms, 1996).

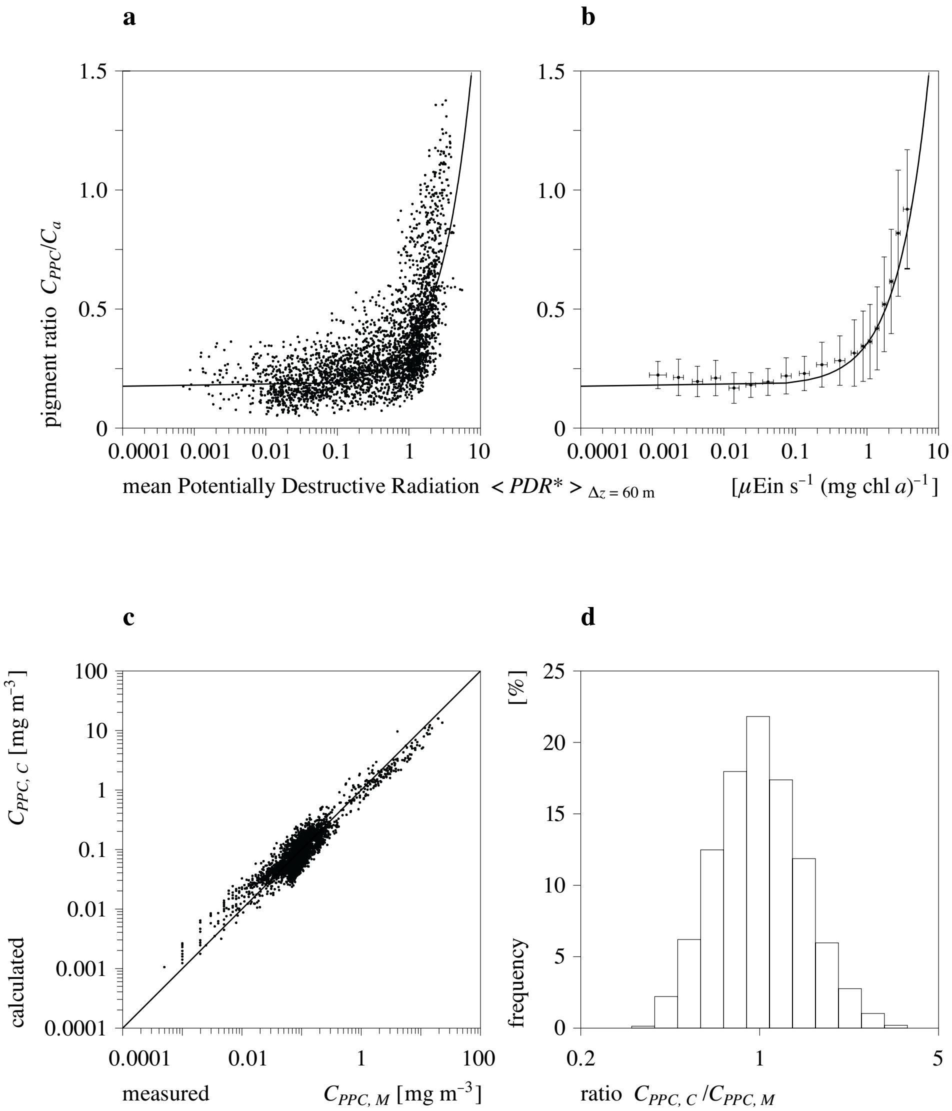


Fig. 4. Results of a statistical analysis of regularities in the occurrence of photoprotecting carotenoids (PPC): statistical dependence of the ratio of photoprotecting carotenoid concentrations C_{PPC} to total chlorophyll a C_a on the mean Potentially Destructive Radiation $< PDR^* >_{\Delta z = 60\,\mathrm{m}}$ (dots – measurements, solid line – calculated from eq. (3)) (a); mean values and standard deviations of the ratio of photoprotecting carotenoid concentrations C_{PPC} to total chlorophyll a C_a as a function of the mean Potentially Destructive Radiation $< PDR^* >_{\Delta z = 60\,\mathrm{m}}$ (points with error bars – mean values, solid line – calculated from eq. (3)) (b); comparison between calculated $C_{PPC,C}$ and measured $C_{PPC,\,M}$ photoprotecting carotenoid concentrations at various stations and depths in the sea (c); frequency distribution of the ratio $C_{PPC,\,C}/C_{PPC,\,M}$ (d)

relative concentrations of $C_{PPC}(z)/C_a(0)$ as a function of the Potentially Destructive Radiation (the energy of spectral range $400 < \lambda < 480$ nm absorbed per unit mass of chlorophyll a – $PDR^*(z)$), averaged in the $\Delta z = 60$ m layer (or less near the surface – see explanation to eq. (4)) to account for vertical mixing (published earlier in Majchrowski & Ostrowska 1999):

$$C_{PPC} = (0.1758 < PDR^* >_{\Delta z = 60\,\mathrm{m}} + 0.1760)\, C_a, \tag{3}$$

where

$$< PDR^* >_{\Delta z} = \frac{1}{z_2 - z_1} \int_{z_1}^{z_2} PDR(z)^* dz, \tag{4}$$

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

Figures 4a and b shows the functional form of eq. (3) with the experimental points.

To estimate errors, measured PPC concentrations ($C_{PPC,M}$) were compared with the PPC concentrations ($C_{PPC,C}$) calculated from eq. (3) using known C_a and PDR^* data. The results are presented in Figs. 4c and 4d. Table 2 gives the calculated errors of the estimation. As can be seen, the statistical error σ_+ is 47%, so the accuracy of the model may be assumed satisfactory.

Table 2. Relative errors in estimating photoprotecting carotenoid concentrations from the model formula (3) at various depths in the seas

	Arithmetic statistics		Logarithmic statistics			
	systematic	statistical	systematic	standard error factor	statistical	
	$\langle \varepsilon \rangle$ [%]	σ_ε [%]	$\langle \varepsilon \rangle_g$ [%]	x	σ_- [%]	σ_+ [%]
C_{PPC}	7.80	± 45.0	–0.220	1.47	–32.0	46.9

where

$\varepsilon = (C_{PPC,C} - C_{PPC,M})/C_{PPC,M}$ – errors,

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

σ_ε – standard deviation of errors (statistical error),

$\langle \varepsilon \rangle_g = 10^{[\langle \log (C_{PPC,C}/C_{PPC,M}) \rangle]} - 1$ – logarithmic mean of errors,

$\langle \log (C_{PPC,C}/C_{PPC,M}) \rangle$ – mean of $\log (C_{PPC,C}/C_{PPC,M})$,

$\sigma_{\log}$ – standard deviation of $\log (C_{PPC,C}/C_{PPC,M})$,

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

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

$\sigma_+ = x - 1$.

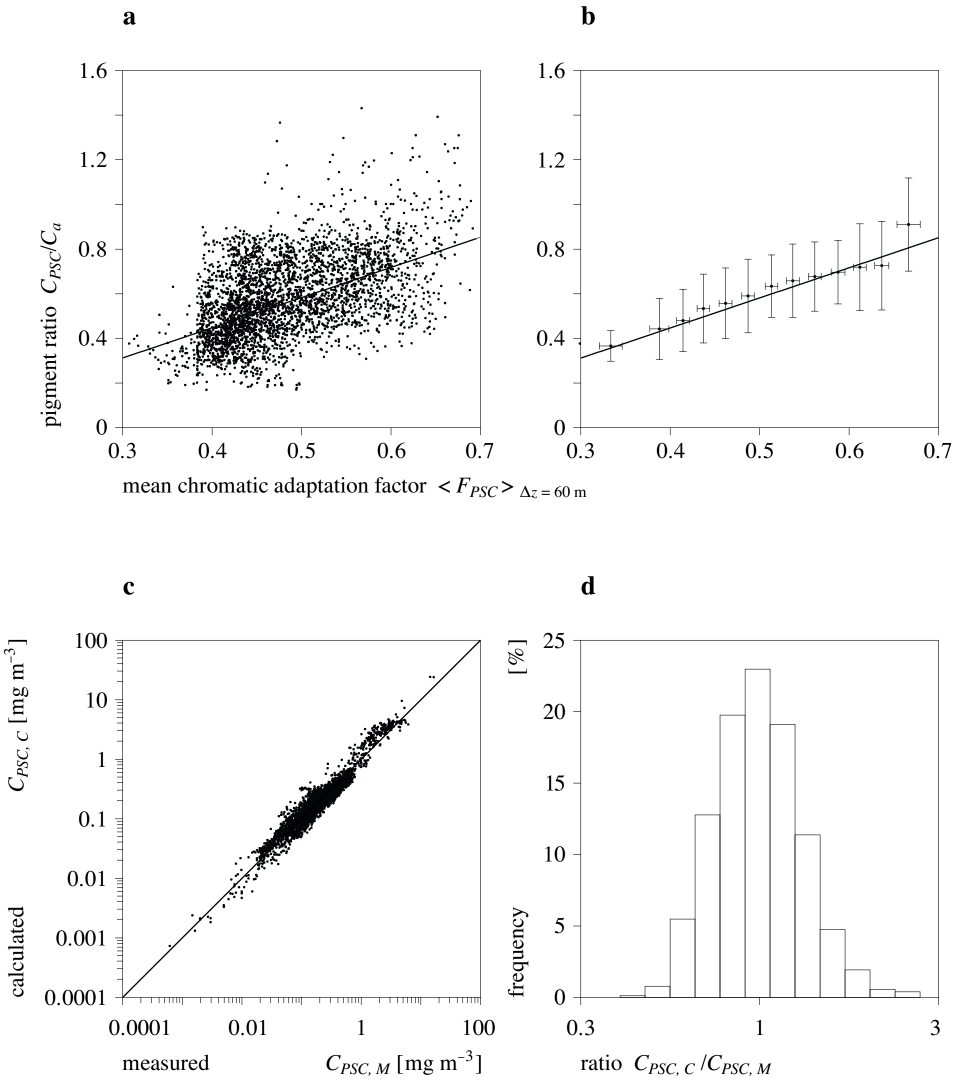


Fig. 5. Results of a statistical analysis of regularities in the occurrence of photosynthetic carotenoids (PSC): statistical dependence of the ratio of photosynthetic carotenoid concentrations C_{PSC} to total chlorophyll *a* C_a on the mean chromatic adaptation factor for photosynthetic carotenoids $< F_{PSC} >_{\Delta z=60\,\mathrm{m}}$ (dots – measurements, solid line – approximated by eq. (5)) (a); mean values and standard deviations of the ratio of photosynthetic carotenoid concentrations C_{PSC} to total chlorophyll *a* C_a as a function of the mean chromatic adaptation factor for photosynthetic carotenoids $< F_{PSC} >_{\Delta z=60\ \mathrm{m}}$ (points with error bars – mean values, solid line – approximated by eq. (5)) (b); comparison of calculated $C_{PSC,\,C}$ (eq. (5)) and measured $C_{PSC,\,M}$ photosynthetic carotenoid concentrations at various stations and depths in the sea (c); frequency distribution of the ratio $C_{PSC,\,C}/C_{PSC,\,M}$ (d)

Analysis of the relationships between particular accessory photosynthetic pigments (PSP) (*i.e.* chls b, chls c, photosynthetic carotenoids (PSC)) and underwater irradiance characteristics shows that they depend only slightly on the absolute irradiance level $E_0(\lambda)$, but strongly on the relative spectral distribution $f(\lambda) = E_0(\lambda)/PAR_0$. The corresponding statistical approximations of the relationships between the relative concentrations of particular PSP and the function of spectral fitting eq. (1) averaged in the $\Delta z = 60$ m layer were found.

The following relationships describing the relative concentrations of particular photosynthetic pigments are proposed:

$$C_{PSC} = (1.348 \; < F_{PSC} >_{\Delta z = 60\,\mathrm{m}} - 0.093)\, C_a, \tag{5}$$

$$C_b = (54.07 \; < F_b >^{5.157}_{\Delta z = 60\,\mathrm{m}} + 0.0907)\, C_a, \tag{6}$$

$$C_c = (0.042 \; < F_a >^{-1.197}_{\Delta z = 60\,\mathrm{m}} < F_c >_{\Delta z = 60\,\mathrm{m}})\, C_a. \tag{7}$$

The relationship for the relative chlorophyll c concentration was the most difficult to determine. The problem was that the spectral properties of chlorophylls c are similar to those of chlorophylls a. We did manage to find the relationship after considering the two functions of spectral fitting: F_a for chlorophylls a and F_c for chlorophylls c.

Relationships (5), (6) and (7) with experimental points (or mean values of the experimental data range) as a background are illustrated in Figs. 5a, 5b, 6a, 6b, 7a and 7b. A verification of these formulae in the form of a comparison of measured and calculated individual pigment concentrations (Figs. 5c, 6c and 7c), as well as error histograms (Figs. 5d, 6d and 7d), and calculated errors (Table 3) are also given. The statistical errors (σ_+ *ca* 32% for PSC, 68% for chlorophylls b and 52% for chlorophylls c) seem to be at a satisfactory level at this stage of the investigation.

Table 3. The relative errors in estimating particular pigment concentrations from the model: for photosynthetic carotenoid concentrations C_{PSC} (eq. (5)), for chlorophyll b concentrations C_b (eq. (6)), and for chlorophyll c concentrations C_c (eq. (7))

	Arithmetic statistics		Logarithmic statistics			
	systematic $\langle\varepsilon\rangle$ [%]	statistical σ_ε [%]	systematic $\langle\varepsilon\rangle_g$ [%]	standard error factor x	statistical σ_- [%]	statistical σ_+ [%]
C_{PSC}	3.96	± 32.0	–0.220	1.32	–24.2	31.9
C_b	15.4	± 72.5	–0.0695	1.68	–40.4	67.9
C_C	9.46	± 51.5	–0.0008	1.52	–34.2	52.0

The errors are calculated in the same way as in Table 2.

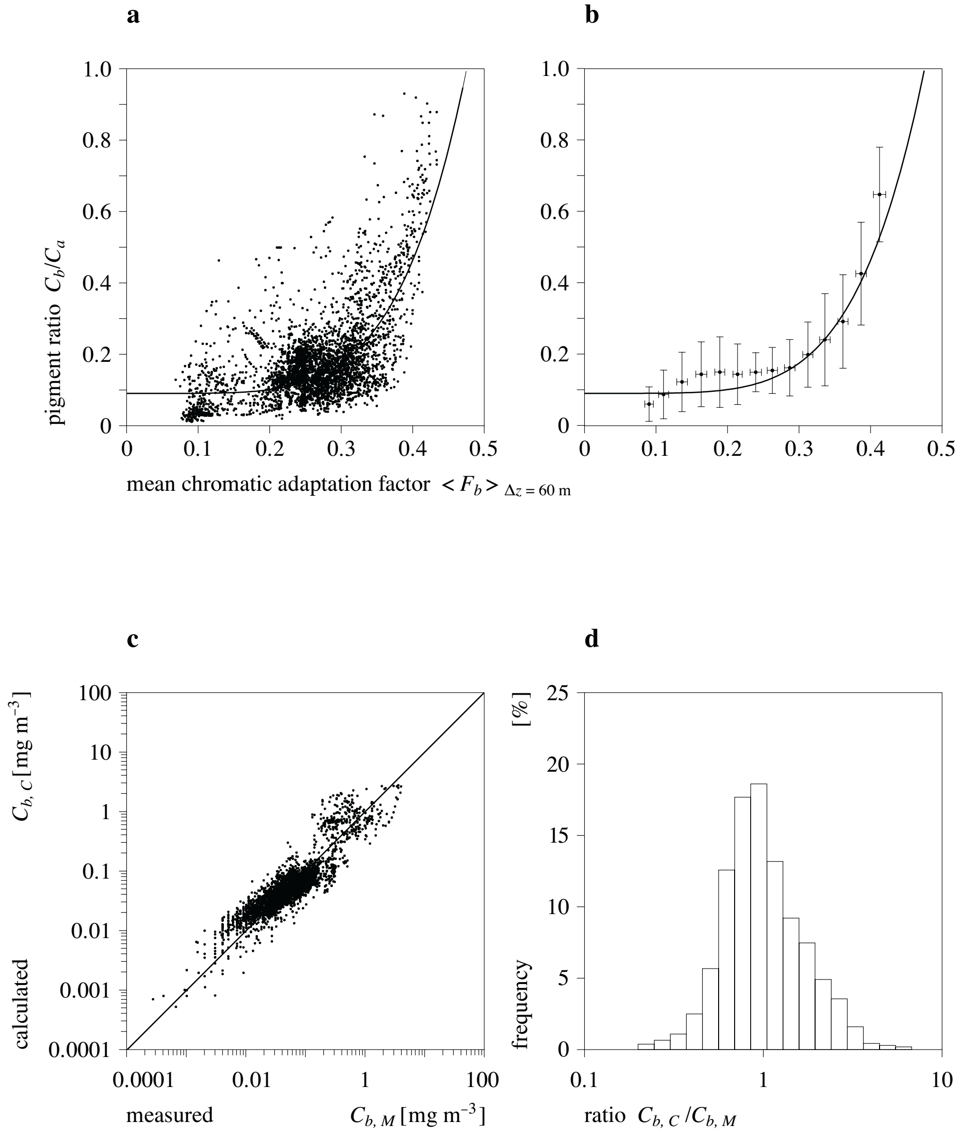


Fig. 6. Results of a statistical analysis of regularities in the occurrence of chlorophyll b: dependence of the ratio of chlorophyll b concentration C_b to total chlorophyll a concentration C_a on the mean chromatic adaptation factor for chlorophyll b, $< F_b >_{\Delta z = 60\ \mathrm{m}}$ (dots – measurements, solid line – calculated from eq. (6)) (a); mean values and standard deviations of the ratio of chlorophyll b concentration C_b to total chlorophyll a concentration C_a as a function the mean chromatic adaptation factor for chlorophyll b $< F_b >_{\Delta z = 60\ \mathrm{m}}$ (points with error bars – mean values, solid line – approximated by eq. (6)) (b); comparison of calculated $C_{b,\,C}$ (eq. (6)) and measured $C_{b,\,M}$ chlorophyll b concentrations at various stations and depths in the sea (c); frequency distribution of the ratio $C_{b,\,C}/C_{b,\,M}$ (d)

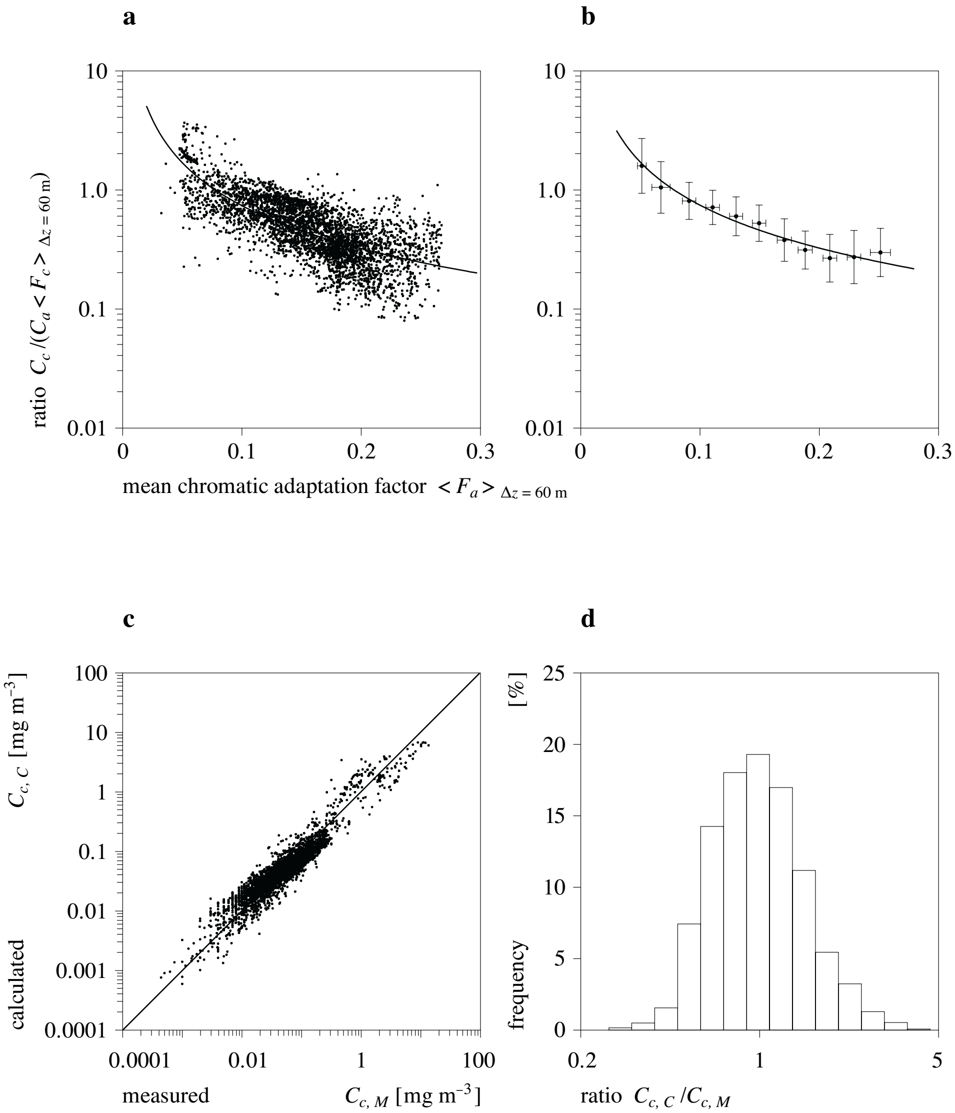


Fig. 7. Results of a statistical analysis of regularities in the occurrence of chlorophyll c: statistical dependence of the ratio of chlorophyll c concentration C_c to product of total chlorophyll a concentration C_a and mean F_c, on the mean chromatic adaptation factor for chlorophyll a, $< F_a >_{\Delta z=60\,\mathrm{m}}$ (dots – measurements, solid line – calculated from eq. (7)) (a); mean values and standard deviations of the ratio of chlorophyll c concentration C_c to product of total chlorophyll a concentration C_a and mean F_c as a function the mean chromatic adaptation factor for chlorophyll a $< F_a >_{\Delta z=60\,\mathrm{m}}$ (points with error bars – mean values, solid line – approximated by eq. (7)) (b); comparison of calculated $C_{c,\,C}$ (eq. (7)) and measured $C_{c,\,M}$ chlorophyll c concentrations at various stations and depths in the sea (c); frequency distribution of the ratio $C_{c,\,C}/C_{c,\,M}$ (d)

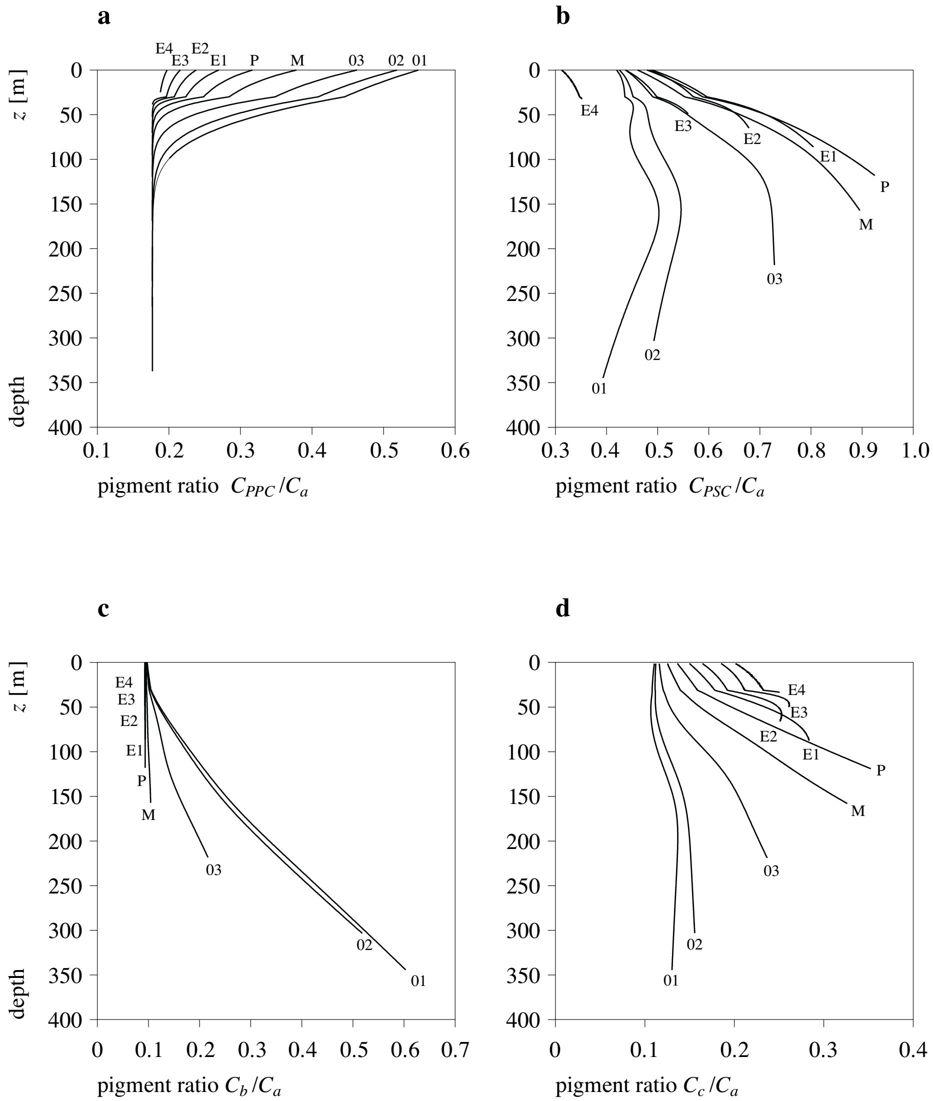


Fig. 8. Modelled profiles of pigment concentrations: relative concentrations of photoprotecting carotenoids for $PAR_0\,(0^+) = 520$ μEin s^{-1} m^{-2} (see eq. (3)) (a); relative concentrations of photosynthetic carotenoids (eq. (5)) (b); relative concentrations of chlorophyll b (eq. (6)) (c); relative concentrations of chlorophyll c (eq. (7)) (d); surface chlorophyll a concentrations $C_a(0)$ were assumed to represent the water trophic type index (according to Woźniak *et al.* 1992), where: O1 – $C_a(0) = 0.035$ mg tot. chl a m^{-3}; O2 – $C_a(0) = 0.07$ mg tot. chl a m^{-3}; O3 – $C_a(0) = 0.15$ mg tot. chl a m^{-3}; M – $C_a(0) = 0.35$ mg tot. chl a m^{-3}; P – $C_a(0) = 0.7$ mg tot. chl a m^{-3}; E1 – $C_a(0) = 1.5$ mg tot. chl a m^{-3}; E2 – $C_a(0) = 3.5$ mg tot. chl a m^{-3}; E3 – $C_a(0) = 7$ mg tot. chl a m^{-3}; E4 – $C_a(0) = 15$ mg tot. chl a m^{-3}

The relationships established (see eqs. (3), (5), (6) and (7)) enable the vertical profiles of the main pigment group concentrations to be estimated in different types of seas – from oligotrophic to eutrophic waters. Examples of such relationships are shown in Fig. 8: from this, the similarity of the calculated vertical profiles to the experimental ones given in Figs. 1 and 2 is evident.

5. Conclusion

According to our findings, the short-wave (blue-green) part of the PAR spectral range is the factor governing the occurrence of photoprotecting carotenoids (PPC) in phytoplankton cells. A mathematical relationship has been established to describe the relative concentrations of photoprotecting carotenoids PPC(z) (in relation to chlorophyll a) as a function of the Potentially Destructive Radiation $PDR^*(z)$, averaged in a water layer of around $\Delta z = 60$ m to account for vertical mixing.

The accessory PSP (chls b, chls c, photosynthetic carotenoids (PSC)) were found to be strongly dependent on the relative spectral distribution of irradiance $f(\lambda) = E_0(\lambda)/PAR_0$ but only slightly dependent on the level of irradiance. The corresponding statistical approximations of the relationships between the relative concentration of a particular photosynthetic pigment PSP and the function of spectral fitting F_j (averaged in an approximately 60 m water layer) were determined.

The statistical tendencies of the relationships between the phytoplankton pigment compositions and the light field characteristics discussed in this paper are due to the photo- and chromatic acclimation of natural marine phytoplankton populations. The relationships obtained have been applied in models of phytoplankton light absorption in various types of water and different depths in the sea (Woźniak *et al.* 2000 and Majchrowski *et al.* 2000, this volume).

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