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The current bio-optical study of marine phytoplankton*

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The paper presents the latest results obtained by the Sopot group (the teams of scientists from the Institute of Oceanology, Polish Academy of Sciences in Sopot, and Environmental Physics Department, Pomeranian Pedagogical University in Słupsk) in the bio-optical modelling of the principal light-stimulated processes occurring in marine algae, such as photo- and chromatic -acclimation, light absorption, fluorescence and photosynthesis of marine phytoplankton. The development of the models presented here has not been completed yet. Nevertheless, we have used them as a foundation on which it is possible to construct two practical algorithms for calculating various photosynthetic characteristics at different depths in the sea. The first one allows vertical distribution of the concentration of chlorophyll and other pigments, and primary production to be determined from three input data: chlorophyll *a* concentration, irradiance and temperature at the sea surface that can be measured remotely. The second one allows us to estimate these characteristic from *in situ* measurements of some fluorimeric properties of algae.

1. Introduction

The principal problems of present-day marine biophysics involve first, the acquisition of adequate knowledge of the specificity of photosynthesis and luminescence of marine phytoplankton, including the prior process of light absorption, and second, the derivation of appropriate mathematical models of these processes. The solutions to these problems are of immense theoretical and practical importance, as these models can be used as a basis for both remote (satellite) and contact fluorescence methods of monitoring biological productivity in the ocean.

The investigations in this field carried out so far by our research group have had several particular theoretical and practical objectives:

– Determining the natural variability ranges of the basic "photo-physiological characteristics" of marine phytoplankton, including the composition and concentration

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* Preliminary version of this paper was presented by Woźniak and Dera as an invited paper at the International Conference *Current Problems in Optics of Natural Waters*, St. Petersburg 2001 [1].

of pigment, the specific absorption of light, the specific fluorescence, and the quantum yield of photosynthesis, recorded under different environmental conditions in the ocean.

– Finding statistical regularities and deriving empirically verified mathematical relationships between the photo-physiological characteristics of the phytoplankton and the main biotic and abiotic factors in the marine environment.

– Finding relationships between the various luminescence and photosynthetic characteristics of marine phytoplankton.

– Obtaining luminescence methods for determining the characteristics of phytoplankton photosynthesis.

– Deriving mathematical models and algorithms enabling the characteristics of photosynthesis in the sea to be diagnosed and predicted by means of contact or remote optical sensing.

In order to achieve these aims, relevant empirical data sets from various regions of the World Ocean were collected and applied by our group. These data were supplemented with similar data sets gleaned from various papers and Internet pages. Altogether, over 4000 *in situ* points with relevant empirical data sets from about 600 stations were analysed. In most cases the data sets refer to primary production, pigment concentrations, spectral irradiance, water temperature, nutrients, and phytoplankton absorbance and fluorescence properties. The results of these investigations have been published in a number of papers, *e.g.*, those on empirical data collection can be found in [2]–[14], and those on the complex study and modelling in [1], [15]–[39].

2. Accessory pigment concentrations

The first problem to be analysed was the photo- and chromatic acclimation of the photosynthetic apparatus of phytoplankton [21], [22], [24]. These acclimation processes involve, among other things, the production of various accessory pigments (photosynthetic and photoprotecting) by the plant in quantities depending on the light conditions in the seawater. The following conclusions can be drawn from these analyses:

– Radiation in the short-wave spectral range (blue-green) is the factor controlling the concentration of photoprotecting carotenoids (PPC)[†]. These pigments include diadinoxanthin, alloxanthin, zeaxanthin, diatoxanthin, lutein, antheraxanthin, β-carotene, violaxanthin, neoxanthin and dinoxanthin. A mathematical relationship describing the concentration of photoprotecting carotenoids (relative to chlorophyll *a*) as a function of the "potentially destructive radiation" ($PDR^*(z)$) averaged in a layer Δz was derived. The $PDR^*(z)$ is defined as the radiation energy from the spectral range $\lambda < 480$ nm absorbed per unit mass of chlorophyll *a* (see explanations concerning Tab. 1).

[†]For the reader's convenience we append a list of symbols denoting physical quantities used in the text. The nomenclature and denotations are in the line with conventions employed in the related literature.

– The relative concentrations of accessory photosynthetic pigments (PSP), like chlorophylls *b*, chlorophylls *c* and photosynthetic carotenoids, *e.g*., fucoxanthin, 19'but-fucoxanthin, 19'hex-fucoxanthin, peridinin, prasinoxanthin and α-carotene, are little dependent on the absolute level of irradiance $E(\lambda)$, but they do show a strong dependence on the relative irradiance spectral distribution: $f(\lambda) = E(\lambda)/\mathrm{PAR}$ (where PAR is the irradiance of photosynthetically available radiation in spectral range 400–700 nm). The relevant statistical approximations describing the relations between the relative concentrations of a given PSP and the functions of spectral fitting averaged in a layer Δz have been found. The functions of spectral fitting $F_j(z)$ are defined below.

Examples of statistical relationships between the concentrations of these pigments (relative to chlorophyll *a*) and the functions introduced above are presented in

Table 1. Model formulae for determining pigment concentrations (after [24])

Pigment	Formulae	Equation
Photoprotecting carotenoids (PPC)	$C_{PPC}/C_a = 0.1758\langle \mathrm{PDR}^*\rangle_{\Delta z = 60\ \mathrm{m}} + 0.1760$	(1)
Photosynthetic carotenoids (PSC)	$C_{PSC}/C_a = 1.348\langle F_{PSC}\rangle_{\Delta z = 60\ \mathrm{m}} - 0.093$	(2)
Chlorophyll *b*	$C_b/C_a = 54.068\langle F_b\rangle^{5.157}_{\Delta z = 60\ \mathrm{m}} + 0.091$	(3)
Chlorophyll *c*	$C_c/C_a = \langle F_c\rangle_{\Delta z = 60\ \mathrm{m}} 0.0424\langle F_a\rangle^{-1.197}_{\Delta z = 60\ \mathrm{m}}$	(4)

where:

– chromatic acclimation factor $F_j(z)$ (so-called functions of spectral fitting, of PSC for the *j*-th pigment group chlorophyll *b* and chlorophyll *c*, respectively)

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

– photoacclimation factor $\mathrm{PDR}^*(z)$ (known as the potentially destructive radiation)

$$\mathrm{PDR}^*(z) = \int_{400\ \mathrm{nm}}^{480\ \mathrm{nm}} a^*_a(\lambda) \langle E_0(\lambda, z)\rangle_{day} \mathrm{d}\lambda\ ;$$

– $f(\lambda, z) = E(\lambda, z)/\mathrm{PAR}(z)$ denotes relative spectral distribution of irradiance in the PAR spectral range at depth z;

– $a^*_j(\lambda)$ denotes spectral specific absorption coefficient for the *j*-th group of "unpackaged" pigments. The numerical values of $a^*_j(\lambda)$ can be determined using the sub-algorithm given in [35];

– $a^*_{j,\max}(\lambda)$ – specific absorption coefficient at the maximum absorption spectral range of the *j*-th "unpackaged" pigment;

– $\langle E_0(\lambda, z)\rangle_{\mathrm{day}} \approx \langle 1.2 E_d(\lambda, z)\rangle_{\mathrm{day}}$ denotes daily mean spectral scalar irradiance at depth z;

– $E_d(\lambda, z)$ is spectral downward irradiance at depth z;

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

$z_1 = z - 30$ m if $z \geq 30$ m, and $z_1 = 0$ if $z < 30$ m, $z_2 = z + 30$ m. The mean values of $\langle F_j\rangle_{\Delta z}$ and $\langle \mathrm{PDR}^*\rangle_{\Delta z}$ in water layer Δz were taken in order to include the influence of water mixing.

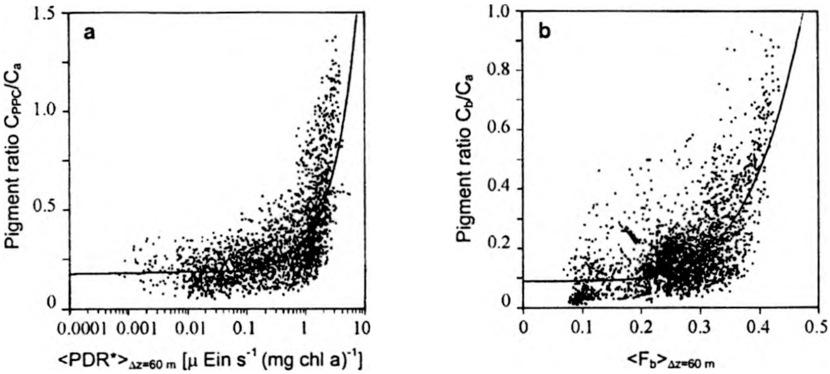

Fig. 1. Statistical dependences of: **a** – the ratio of photoprotecting carotenoids concentrations C_{PPC} to total chlorophyll a concentration C_a on the potentially destructive radiation $\langle \mathrm{PDR}^* \rangle_{\Delta z\,=\,60\text{ m}}$; **b** – the ratio of chlorophyll b concentration C_b to total chlorophyll a concentration C_a on the mean chromatic adaptation factor for chlorophyll b $\langle F_b \rangle_{\Delta z\,=\,60\text{ m}}$ ([22]).

Fig. 1. The relevant mathematical formulae of these relationships are given in Table 1.

These model formulae enable us to estimate vertical profiles of the relative concentration of accessory pigments in various trophic types of sea (in this paper, the surface chlorophyll a concentration $C_a(0)$ is taken to be the sea trophicity index). The results of such an estimation are given in Fig. 2.

3. Package effect factor

The package effect of pigments in living plant cells lowers the specific absorption coefficient of these pigments a^*_{pl} compared to the specific absorption coefficients a^*_{sol} of the same cellular matter ideally dispersed in solution. The effect is determined by a dimensionless factor $Q^* = a^*_{\mathrm{pl}}/a^*_{\mathrm{sol}}$, which is a function of the wavelength formulated as follows [40], [41]:

$$\begin{cases} Q^*(\lambda) = \frac{3}{2}\rho'(\lambda)\left\{1 + 2\frac{\exp(-\rho'(\lambda))}{\rho'(\lambda)} + \frac{2}{\rho'(\lambda)^2}[\exp(-\rho(\lambda)) - 1]\right\} \\ \rho'(\lambda) = a^*_{\mathrm{sol}}(\lambda)C_I d \end{cases} \tag{5}$$

where C_I – the intercellular chlorophyll a concentration, d – cell diameter.

In addition, the spectrum $Q^*(\lambda)$ depends on the water trophicity and depth in the sea, because the products $C_I d$ are subject to variation under different marine conditions (see the explanation in [42]). However, the relations of $C_I d$ with depth z or optical depth τ in the sea were found to be statistically similar to those of the

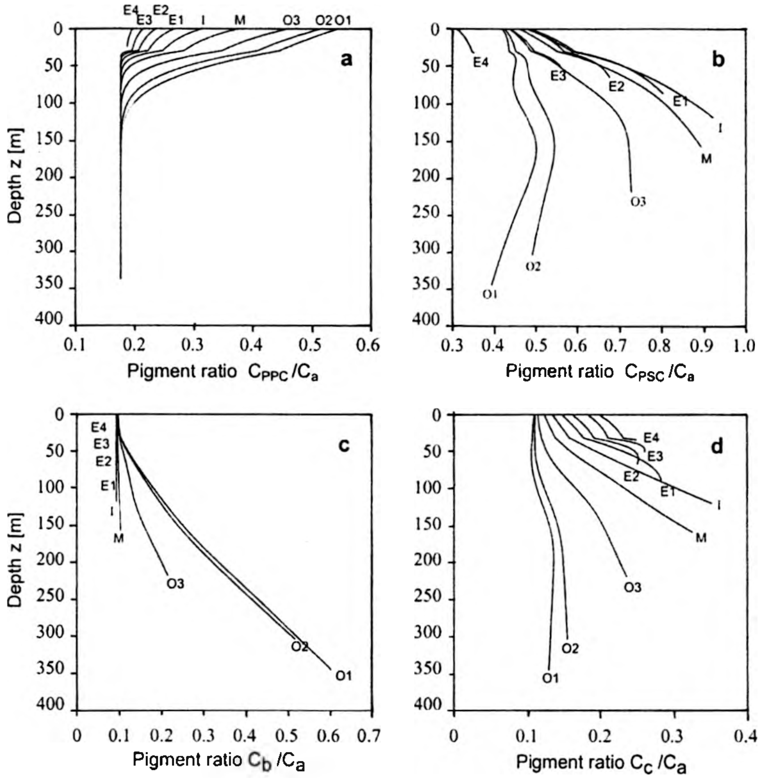

Fig. 2. Modelled profiles of pigment concentrations: **a** – relative concentrations of photoprotecting carotenoids for $PAR_0(0)$ = 520 μEin s^{-1} m^{-2} (see Eq. (1) in Tab. 1); **b** – relative concentrations of photosynthetic carotenoids (Eq. (2) in Tab. 1); **c** – relative concentrations of chlorophyll *b* (Eq. (3) in Tab. 1); **d** – relative concentrations of chlorophyll *c* (Eq. (4) in Tab. 1). Surface chlorophyll *a* concentrations $C_a(0)$ were assumed to represent the water trophic type index (according [29]) 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}, I – $C_a(0)$ = 0.7 mg tot.chl*a* m^{-3}, E1 – $C_a(0)$ = 1.5 mg tot.chl*a* m^{-3}, E2 – $C_a(0)$ = 3.5 mg tot.chl*a* m^{-3}, E3 – $C_a(0)$ = 7 mg tot.chl*a* m^{-3}, E4 – $C_a(0)$ = 15 mg tot.chl*a* m^{-3}, (E5 – $C_a(0)$ = 35 mg tot.chl*a* m^{-3}, E6 – $C_a(0)$ = 70 mg tot.chl*a* m^{-3} [22]).

chlorophyll concentrations $C_a(z)$ or $C_a(\tau)$ [29], [30] with the surface chlorophyll $C_a(0)$ (see Fig. 3**a**, **b**). Taking advantage of this similarity, the following formula was established

$$C_l d = 24.65 A (c C_a)^{0.75015} \tag{6}$$

where constant A = 1 mg tot.chl*a* m^{-2} and constant c = 1 m^3 (mg tot.chl*a*)$^{-1}$.

The graphical representation of formula (6) is given in Fig. 3**c**. The formula is applied to determine $C_l d$ in the relevant equations of the phytoplankton absorption model presented later in this paper. The model showing the dependence of C_a on depth

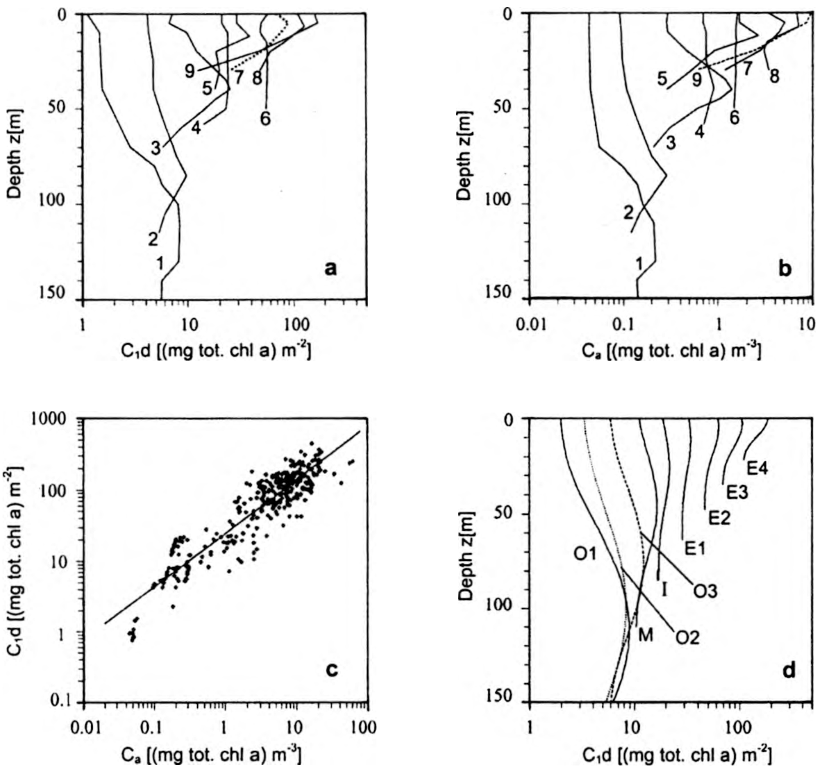

Fig. 3. Relations of the product $C_l d$ with the total chlorophyll *a* concentration C_a and depth in the sea. Examples of $C_l d$ vertical profiles: 1–3 Atlantic, 4–9 Baltic (**a**); examples of C_a concentration profiles for the same stations as in figure **a** (**b**); relationship between the product $C_l d$ and concentration C_a; observed (points) and approximated by Eq. (6) (line) (**c**); modelled vertical profiles of $C_l d$ in various trophic types of stratified case 1 waters (curves O1–E4 correspond to various water trophicities as in Fig. 2) (**d**). In figure **d** the $C_a[C_a(0), z]$ model was applied [29], [30], [35].

and surface chlorophyll concentration given in [30]–[32] can be applied together with formula (6) to determine the distribution of the products $C_l d$ in various types of seas (see the examples in Fig. 3**d**).

4. Specific absorption of light in phytoplankton

The specific light absorption coefficient of living phytoplankton can be expressed as follows:

$$a^*_{\mathrm{pl}}(\lambda) = C_a^{-1} Q^*(\lambda) \sum_j^n a_j^*(\lambda) C_j. \tag{7}$$

It is a function of many variables (explained in previous sections). In the previous model's formulae for the coefficient $a^*_{\mathrm{pl}}(\lambda)$, however, only its dependence on the chlorophyll concentration C_a in the sea was usually considered [42]–[44]. Those formulae did not take into consideration the changes in $a^*_{pl}(\lambda)$ due to the ability of phytoplankton to adapt to diverse underwater light conditions, as a result of which the coefficient takes different values in different regions and depths in the sea.

A further aim of our study was, therefore, to include the acclimation effects in the phytoplankton light absorption models, *i.e.*, to consider photoadaptation, chromatic adaptation and the pigment package effect. This was achieved by means of an appropriate compilation of statistical formulae and mathematical models elaborated earlier [17], [21]–[23], [35]–[37]. These included:

– relationships between various pigment concentrations and the underwater light properties in the sea, described in Sec. 2;

– the dependence of the pigment package effect on chlorophyll *a* concentration, described in Sec. 3;

– bio-optical models of light propagation in case 1 Oceanic Waters [29], [30] and case 2 Baltic Waters [32].

This compilation gave rise to a new model of light absorption by *in situ* living phytoplankton [35]–[37]. This model makes it possible to estimate the total light absorption coefficient of living phytoplankton and of its component photosynthetic and photoprotecting pigments. The required input data are only the PAR irradiance at the sea surface and the surface chlorophyll *a* concentration. An analysis testing the accuracy of the model and its comparison with previous models of this type [42], [44] is given in [23]. It demonstrates that the new algorithm leads to a much more accurate estimation of the phytoplankton absorption properties than the earlier model.

Examples of practical applications of the model are given in Figs. 4 and 5. Particularly important regularities of the vertical profiles of these absorption coefficients in various trophic types of waters are illustrated in Fig. 5, and these are:

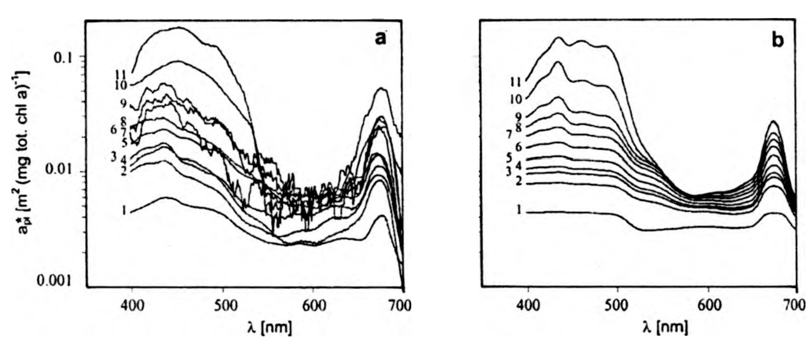

Fig. 4. Comparison of phytoplankton spectral specific absorption coefficients: **a** – measured *in situ*; **b** – determined with our model. The numbers allotted to the spectra indicate the following trophic types of seawater: 1 – $C_a(0)$ = 156 mg tot.chl*a* m^{-3}, 2 – $C_a(0)$ = 33.2 mg tot.chl*a* m^{-3}, 3 – $C_a(0)$ = 11.4 mg tot.chl*a* m^{-3}, 4 – $C_a(0)$ = 7.4 mg tot.chl*a* m^{-3}, 5 – $C_a(0)$ = 3.2 mg tot.chl*a* m^{-3}, 6 – $C_a(0)$ = 1.15 mg tot.chl*a* m^{-3}, 7 – $C_a(0)$ = 0.61 mg tot.chl*a* m^{-3}, 8 – $C_a(0)$ = 0.30 mg tot.chl*a* m^{-3}, 9 – $C_a(0)$ = 0.24 mg tot.chl*a* m^{-3}, 10 – $C_a(0)$ = 0.14 mg tot.chl*a* m^{-3}, 11 – $C_a(0)$ = 0.047 mg tot.chl*a* m^{-3} (after [23]).

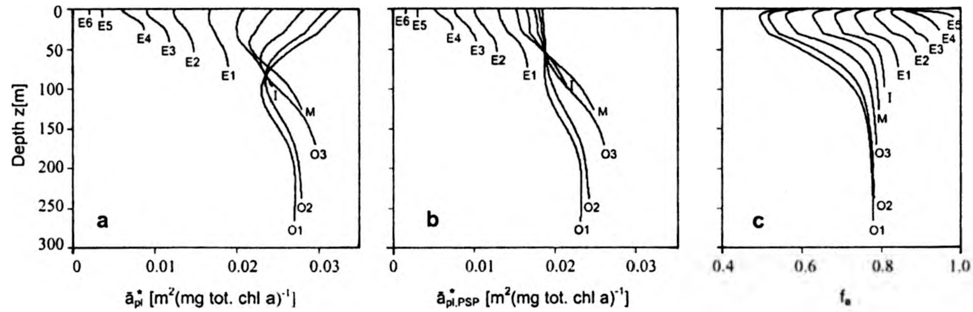

Fig. 5. Modelled depth profiles of mean: **a** – specific absorption coefficients for total phytoplankton pigments $\bar{a}^*_{\rm pl}$; **b** – photosynthetic pigments $\bar{a}^*_{\rm pl,\,PSP}$; **c** – non-photosynthetic pigment factor f_a. Curves O1–E4 correspond to various water trophicities as in Fig. 2, E5 – $C_a(0) = 35$ mg tot.chl*a* m^{-3}, E6 – $C_a(0) = 70$ mg tot.chl*a* m^{-3} ([19], [23]).

the calculated vertical profiles of the mean specific absorption coefficients of phytoplankton $\bar{a}^*_{\rm pl}$, for all pigments (Fig. 5**a**), and those of the photosynthetic pigment component $\bar{a}^*_{\rm pl,\,PSP}$ (Fig. 5**b**) and the non-photosynthetic pigment factor $f_a = \tilde{a}^*_{\rm pl,\,PSP}/\tilde{a}^*_{pl}$, that is, the ratio of the two mean specific absorption coefficients $\tilde{a}^*_{\rm pl,\,PSP}$ and $\tilde{a}^*_{\rm pl}$, averaged with the weight of the irradiance spectrum (Fig. 5**c**).

For photosynthetic pigments $\bar{a}^*_{\rm pl,\,PSP}$ (Fig. 5**b**), the mean specific absorption coefficient increases with depth. This increase seems to be caused by rising concentrations of accessory photosynthetic pigments (the reader is reminded that the coefficient is computed per unit mass of chlorophyll *a*). In the case of the total mean specific phytoplankton absorption coefficient (for all pigments) $\bar{a}^*_{\rm pl}$, there is a minimum at a certain depth in the vertical profile (Fig. 5**a**). This minimum moves towards the sea surface with increasing water trophicity. Above the minimum, the mean specific absorption coefficient $\bar{a}^*_{\rm pl}$ rises with the concentration of photo -protecting carotenoids. Below the minimum, the increase in the mean specific absorption coefficient $\bar{a}^*_{\rm pl}$ is due to a rise in the relative concentrations of accessory photosynthetic pigments. The earlier two models were unable to account for this effect; our new model enables us to do so.

5. Quantum yield of photosynthesis

The quantum yield of photosynthesis Φ in the sea is a complex function of a series of variable environmental factors, such as underwater irradiance, nutrient content, water temperature and water trophicity. Our study makes it possible to express this quantum yield as the product of the theoretical maximum quantum yield $\Phi_{\rm max} = 0.125$ atom C quanta^{-1} and six dimensionless factors ($f_a, f_\Delta, f_{c(N)}, f_{c(\tau)}, f_{c(\rm PAR,inh)}, f_{E,t}$) [19], [20], [38]. Being less than 1 in value, each of these factors is a measure of the decrease in quantum yield Φ compared to $\Phi_{\rm max}$, due to natural (internal) imperfections in the photosynthetic apparatus or to environmental (external) conditions unfavourable to plant growth. These factors are: f_a – a non-photosynthetic pigment absorption effect factor describing the decrease in the observed quantum yield in relation to Φ_{max} due to the presence of photo-protecting pigments in the plant which do not transfer absorbed energy to the PS2 reaction centres; f_Δ – the inefficiency factor in energy transfer and charge recombination; $f_{c(N)}$ – the factor describing the effect of nutrients on the portion of functional PS2 reaction centres; $f_{c(\tau)}$ – the factor describing the reduction in the portion of functional PS2 reaction centres at great depths; $f_{c(\mathrm{PAR,\,inh})}$ – the factor describing the reduction in the portion of functional PS2 reaction centres as a result of photoinhibition; $f_{E,t}$ – the classic dependence of photosynthesis on light and temperature (see, for example, [17], [45] and the papers cited therein), also known as the light curve of photosynthetic efficiency at a given temperature.

Each of these factors appears to be dependent on one or two environmental factors at most. The quantum yield of photosynthesis can therefore be expressed as follows [37]:

$$\begin{cases} \Phi = \Phi_{max} f_a f_\Delta f_{c(N)} f_{c(\tau)} f_{c(\mathrm{PAR,\,inh})} f_{E,t}, \\ \Phi_{max} = 0.125\ [\text{atom C (quanta)}^{-1}] \text{ or } [\text{mol C (Ein)}^{-1}]. \end{cases} \tag{8}$$

T a b l e 2. Photosynthesis quantum yield determining factors expressed through mathematical formulae describing their dependence on abiotic environmental factors, the sea trophicity index $C_a(0)$, and optical depth τ ([18]).

Mathematical description of dependences	Typical magnitude of variability in the World Ocean
$f_a = \tilde{a}^*_{\mathrm{pl,\,PSP}}/\tilde{a}^*_{\mathrm{pl}}$ where $\tilde{a}^*_{\mathrm{pl}} = f(C_a(0), \tau, \mathrm{PAR}(0))$, $\tilde{a}^*_{\mathrm{pl,\,PSP}} = f(C_a(0), \tau)$	0.33–1 (about 3 times)
$f_\Delta \approx 0.600 \pm 0.112$	nearly constant
$f_{c(\tau)} = 1 - 0.00310\tau^2$	0.72–1 (about 1.4 times)
$f_{c(N)} = \dfrac{N_{\mathrm{inorg}}}{N_{\mathrm{inorg}} + 0.0585}$	0.25–1 (about 4 times)
$f_{c(\mathrm{PAR,\,inh})} = \exp\left(-0.00937 \dfrac{\mathrm{PAR}}{3.049 \times 10^{-5} \times 1.907^{\mathrm{temp}/10}}\right)$	0.85–1 (less than 1.2 times)
$f_{E,t} = \left[1 - \exp\left(-\dfrac{\mathrm{PUR}^*_{\mathrm{PSP}}}{8.545 \times 10^{-7} \times 1.874^{\mathrm{temp}/10}}\right)\right]$	0.05–1 (about 20 times)
Φ – as the product, altogether	0.0002–0.075 (about 400 times)
Φ – as observed values	0.001–0.075 (about 100 times)

$C_a(0)$ – surface chlorophyll a concentration [mg tot.chl*a* m^{-3}], τ – optical depth in the sea (dimensionless), N_{inorg} [μM]– the sum of inorganic forms of nitrogen (N_{inorg} comprises nitrate, nitrite and ammonia,), PAR, inh – scalar irradiance in the PAR spectrum range [Ein m^{-2} s^{-1}], $\mathrm{PUR}^*_{\mathrm{PSP}}$ – radiation flux absorbed by photosynthetic pigments [Ein (mg tot.chl*a*)$^{-1}$ s^{-1}], temp – ambient water temperature [°C].

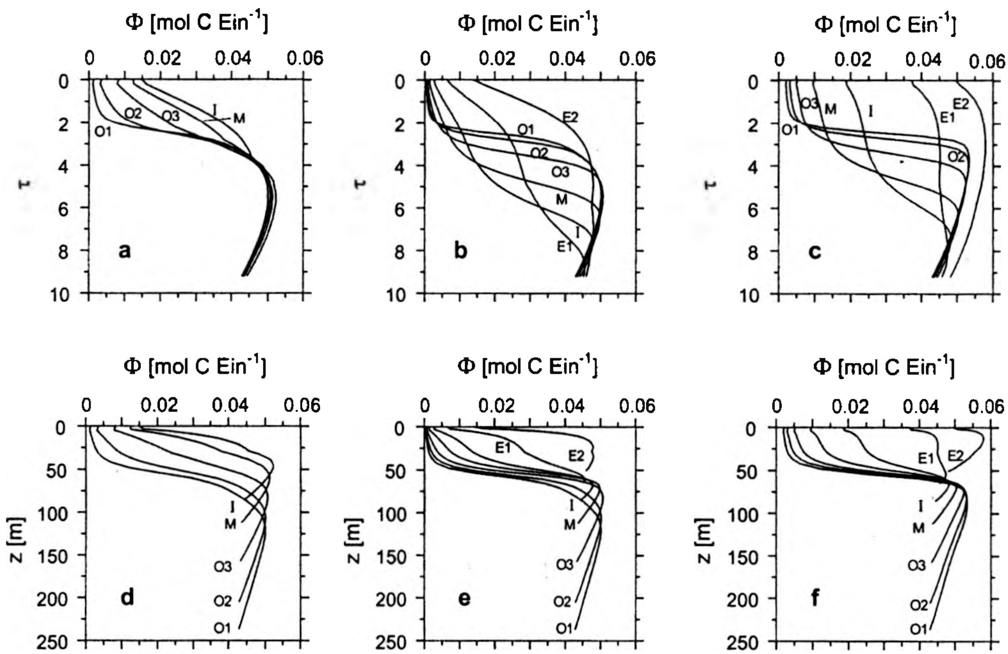

Fig. 6. Examples of model vertical profiles of photosynthesis quantum yield Φ for optical depth τ (figures **a**, **b**, **c**) and for real depth z (figure **d**, **e**, **f**), determined for different trophic types of the sea in different seasons and geographical regions of oceans: **a**, **d** – trophical zone, summer; **b**, **e** – temperate zone, winter; **c**, **f** – polar zone, winter. Curves O1–E2 correspond to various water trophicities as in Fig. 2 (after [18]).

Definitions of the individual factors are given in Tab. 2, together with their range of variability in the World Ocean, estimated from the model.

As can be seen from Tab. 2, the quantum yield Φ typically varies under different marine conditions by about 100 times, *i.e.*, two orders of magnitude. This is less than the product of the typical variability of all the factors, which can reach a figure of 400. This means that the activities of some of these factors cancel each other out. Light and temperature conditions have the greatest impact on the natural variability (range about ±20 times). Of somewhat less significance is the nutrient content, which may affect the quantum yield by a factor of 4[†]. Finally, threefold variations may occur as a result of variability in non-photosynthetic pigments f_a. The other factors affect the variability in quantum yield Φ to a much lesser extent. The vertical profiles of Φ determined from the model for different types of sea, different geographical zones and different seasons are shown in Fig. 6.

[†]This does not apply to absolute values of the primary production, which depends not only on quantum yield Φ, but also on the chlorophyll concentration C_a, which is the factor determining the magnitude of PUR. Consequently, the variability in primary production due to various concentrations of nutrients, and measured at different depths and seas, may be as much as two orders of magnitude.

6. Fluorescence capacity

The above model of light absorption by phytoplankton is also of great practical significance, *e.g.*, for explaining the phytoplankton fluorescence properties determined by means of submersible fluorometers. Initially, we applied it to the theoretical estimation of the range of variability of the specific fluorescence $F_0'^* = F_0'/C_a$ in various water types and depths. Here, F_0' means the *in vivo* fluorescence yield induced by a weak probe flash in the dark, measured in the ambient light-adapted state (according to the convention proposed by KOLBER and FALKOWSKI [46]). This fluorescence depends, among other factors, on the absorption properties and package state of pigments in the phytoplankton cells [25]

$$F_0'^* \text{ [arb. u.]} = \langle a^*_{\mathrm{pl,\,PSP}} \rangle_{I(\lambda)} \langle Q^* \rangle_{f_{\mathrm{fl}}(\lambda)} \tag{9}$$

where: $\langle a^*_{\mathrm{pl,\,PSP}} \rangle_{I(\lambda)}$ – mean specific absorption coefficient of photosynthetic pigments averaged with the weight of the exciting light spectrum; $\langle Q^* \rangle_{f_{\mathrm{fl}}(\lambda)}$ – mean value of the package effect function averaged with the weight of the spectrum of the fluorescent light emitted.

Vertical profiles of the specific fluorescence $F_0'^*(\tau)$ and $F_0'^*(z)$ in different trophic types of sea, determined from the model of phytoplankton light absorption, are given in Fig. 7. As one can see in this figure, the specific fluorescence generally falls with increasing water trophicity. The specific fluorescence also tends to increase with depth, especially in waters of low trophicity. Such behaviour is similar to that of the depth profiles of the mean absorption coefficients of phytoplankton photosynthetic pigments (see Fig. 5). However, the range of variability of the specific fluorescence recorded under natural conditions (about 50 times) is greater than that of the specific absorption

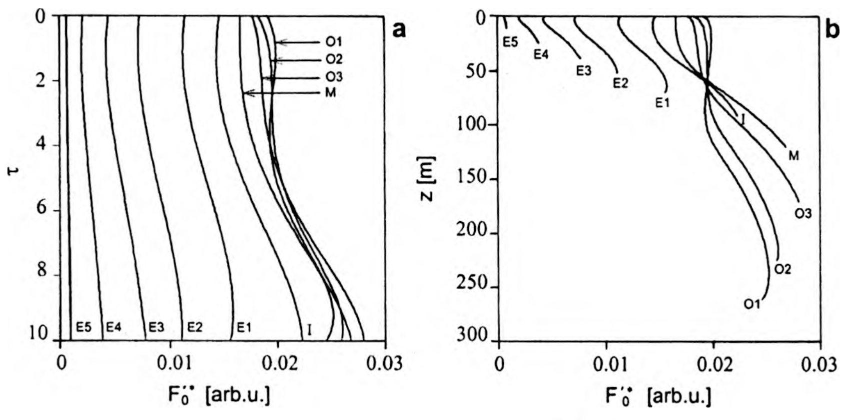

Fig. 7. Model vertical profiles of specific fluorescence $F_0'^*$ for **a** – optical depth τ and **b** – for real depth z, determined for different trophic types of sea. Curves O1–E5 correspond to various water trophicities as in Fig. 2 (after [25]).

coefficient (< 20 times). As Eq. (9) clearly indicates, this is because the specific fluorescence depends not only on the specific absorption but also on the mean package effect function. This latter factor decreases with increasing chlorophyll *a* concentration and varies by about one order of magnitude in different types of seas.

The model of specific fluorescence was utilised in a recently formulated physical method of measuring chlorophyll *a* concentration in the sea [25]–[28].

The next step in our study was to analyse the so-called maximum F'_m and variable F'_v ($F'_v = F'_m - F'_0$), the phytoplankton *in vivo* fluorescence yield, according to the notation proposed by KOLBER and FALKOWSKI [46]. It turned out that these fluorescences are closely related to the observed quantum yield of photosynthesis, in accordance with the formula after [28].

$$\Phi(z) = \frac{\mathrm{KPUR}^*_{\mathrm{PSP},0} Q_{10}^{\mathrm{temp}(z)/10^{\circ}\mathrm{C}}}{\mathrm{PUR}^*_{\mathrm{PSP}}(z)} \left[1 - \exp\left(-\frac{\mathrm{PUR}^*_{\mathrm{PSP}}(z)}{\mathrm{KPUR}^*_{\mathrm{PSP},0} Q_{10}^{\mathrm{temp}(z)/10^{\circ}\mathrm{C}}}\right)\right] \Phi_{\max} \frac{F'_v(z)}{F'_m(z)} \tag{10}$$

where: $\mathrm{PUR}^*_{\mathrm{PSP}}(z) = X(z)\langle a^*_{\mathrm{pl,\,PSP}}(z)\rangle_{I(\lambda)} \mathrm{PAR}_0(z)$, $\Phi_{\max} = 0.125$ [molC Ein^{-1}], $\mathrm{KPUR}^*_{\mathrm{PSP},0} = 8.39\times10^{-7}$ [Ein s^{-1} (mg tot. chl*a*)$^{-1}$], $Q_{10} = 1.9$, and $X(z)$ – parameter resulting from the phytoplankton light absorption model.

Formula (10) is applied in our new fluorometric method of determining primary production in the sea, described briefly in the next section.

7. Useful models of primary production

The model description of the photo-physiological properties of algae was applied, among other things, to derive three useful models of primary production $P(z)$ in the sea. They are briefly specified in Tab. 3.

The basic model [18] is based on a model description of the relationship between the photo-physiological properties of phytoplankton cells and environmental factors. It enables primary production to be estimated from the chlorophyll *a* concentration $C_a(z)$, irradiance PAR(z), nutrients $N_{\mathrm{inorg}}(z)$, and water temperature temp(z) data in the study area.

The second model, the remote sensing model [18], is a simplified version of the basic one, where the direct dependence of the quantum yield of photosynthesis on the

T a b l e 3. Models of primary production with empirically verified statistical errors given (where $P(z)$ [mgC m^{-3}] and P_{tot} [mgC m^{-2}] – primary production at different depths in the sea and the total production in the euphotic zone, respectively).

	Input data	Statistical errors σ [%]	
		For $P(z)$	For P_{tot}
Basic model	$C_a(z)$, PAR(z), $N_{\mathrm{inorg}}(z)$, temp(z)	± 42.5	± 24.0
Remote sensing model	$C_a(0)$, PAR(0), temp(0)	± 137	± 45.0
Fluorometric model	PAR(z), $F'_0(z)$, $F'_m(z)$, temp(z)	± 49.8	± 23.8

nutrient concentration in the water is not taken into consideration. Because of this simplification, the model makes it possible to estimate the primary production from only three variables – $C_a(0)$, PAR(0), temp(0) – which are available by satellite remote sensing.

The third model is based on a simplified dependence of the primary production on the fluorescence $F_0'(z)$ and $F_m'(z)$, together with the irradiance PAR(z) and temperature temp(z) simultaneously measured *in situ* [28]. It is the basis of the fluorometric method of determining primary production by means of the "PumpProbe" submersible fluorometers.

As can be seen from Tab. 3, the statistical errors of estimating primary production with these models are relatively small; the models may therefore have practical utility.

7. Conclusions

Empirical research and a theoretical analysis of the relationships between the main photo-physiological characteristics of marine algae (specific absorption coefficients, specific fluorescence, quantum yield of photosynthesis) and underwater irradiance, along with other environmental factors in the sea, were carried out. As a result, modified bio-optical models of phytoplankton photo- and chromatic-acclimation, light absorption, luminescence and photosynthesis with respect to various environmental factors in the sea were derived. The models enable us to determine the physiological parameters of phytoplankton for various trophic types of sea and various depths in the sea. The difference between the new and previous models is that the former is physical; this means that they are based on mathematical formulae of profound physical significance. As they are based on both remote sensing and direct (fluorescence) methods of determining biological productivity, these models may be useful for the ecological monitoring of oceans.

Appendix

List of symbols and abbreviations denoting the physical quantities used in this paper.

Symbol	Denotes	Units
a_a^*	specific light absorption coefficient of chlorophyll *a* in solvent	m^2 (mg tot.chl*a*)$^{-1}$
a_j^*	specific absorption coefficient of the *j*-th pigment group	m^2 (mg pigment)$^{-1}$
$a_{j,\max}^*$	specific light absorption coefficient at the maximum absorption spectral range of the *j*-th "unpackaged" pigment	m^2 (mg pigment)$^{-1}$
a_{pl}^*	specific light absorption coefficient of phytoplankton	m^2 (mg tot.chl*a*)$^{-1}$
$a_{pl,\,PSP}^*$	specific light absorption coefficient of photosynthetic pigments	m^2 (mg tot.chl*a*)$^{-1}$
a_{sol}^*	specific light absorption coefficient of some cellular mater dispersed in solution	m^2 (mg tot.chl*a*)$^{-1}$

$\bar{a}^*_{\mathrm{pl}}$	mean specific light absorption coefficients of phytoplankton	m^2 (mg tot.chl*a*)$^{-1}$
$\bar{a}^*_{\mathrm{pl,\,PSP}}$	mean specific light absorption coefficients of photosynthetic pigments	m^2 (mg tot.chl*a*)$^{-1}$
$\tilde{a}^*_{\mathrm{pl}}$	mean specific absorption coefficient weighted by the irradiance spectrum	m^2 (mg tot.chl*a*)$^{-1}$
$\tilde{a}^*_{\mathrm{pl,\,PSP}}$	$\tilde{a}^*_{\mathrm{pl}}$ of photosynthetic pigments	m^2(mg tot.chl*a*)$^{-1}$
$\langle a^*_{\mathrm{pl,\,PSP}}\rangle_{I(\lambda)}$	mean specific absorption coefficient of photosynthetic pigments averaged with the weight of the exciting light spectrum	m^2(mg tot.chl*a*)$^{-1}$
C_a	sum of chlorophylls *a* + pheo, or total chlorophyll (chl*a* + divinyl chl*a*) concentrations	mg tot.chl*a* m^{-3}
$C_a(0)$, $C_a(z)$ or $C_a(\tau)$	sum of chlorophylls *a* + pheo, or total chlorophyll (chl*a* + divinyl chl*a*) concentrations in the surface water, at depth z or optical depth τ	mg tot.chl*a* m^{-3}
C_b,C_c,C_{PPC}, C_{PSC}	concentrations of chls *b*, chls *c*, photoprotecting carotenoids, photosynthetic carotenoids	mg pigment m^{-3}
C_I	intercellular chlorophylls *a* concentration	mg tot.chl*a* m^{-3}
C_j	concentration of the *j*-th group of "unpackaged" pigments	mg pigment m^{-3}
d	cell diameter	m
$E(\lambda)$	spectral irradiation	Ein $\mathrm{m}^{-2}\mathrm{s}^{-1}\mathrm{nm}^{-1}$
$E_0(\lambda)$	spectral scalar irradiance	Ein $\mathrm{m}^{-2}\mathrm{s}^{-1}\mathrm{nm}^{-1}$
$\langle E_0(\lambda, z)\rangle_{\mathrm{day}}$	daily mean spectral scalar irradiance at depth z	Ein $\mathrm{m}^{-2}\mathrm{s}^{-1}\mathrm{nm}^{-1}$
$E_d(\lambda, z)$	spectral downward irradiance at depth z	Ein $\mathrm{m}^{-2}\mathrm{s}^{-1}\mathrm{nm}^{-1}$
$f(\lambda)$	spectral distribution of natural irradiance	nm^{-1}
f_a	non-photosynthetic pigment factor	dimensionless
$f_{c(N)}$	factor describing the effect of nutrients on the portion of functional PS2 reaction centres	dimensionless
$f_{c(\tau)}$	factor describing the reduction in the portion of functional PS2 reaction centres	dimensionless
$f_{c(\mathrm{PAR,inh})}$	factor describing the reduction in portion of functional PS2 reaction centres as a result of photoinhibition	dimensionless
$f_{E,t}$	classical dependence of photosynthesis on light and temperature	dimensionless
$f_{\mathrm{fl}}(\lambda)$	relative spectral distribution of emitted light photoinduced by phytoplankton	nm^{-1}
f_Δ	inefficiency factor in energy transfer and charge recombination	dimensionless
F'_0, F'_m	*in vivo* phytoplankton fluorescence yield induced by a weak probe flash in the dark, and following a saturating flash, measured in a light-adapted state	conv.units
F'_v	so-called variable fluorescence ($F'_v = F'_m - F'_0$)	conv.units
F'^*_0	specific fluorescence (per unit of chlorophyll *a* mass)	conv.units

$\langle F_a \rangle_{\Delta z = 60\ m}$ $\langle F_b \rangle_{\Delta z = 60\ m}$ $\langle F_c \rangle_{\Delta z = 60\ m}$ $\langle F_{PSC} \rangle_{\Delta z = 60\ m}$	mean values of chromatic adaptation factors for chl*b*, for chl*c*, for photosynthetic caretonoids in 60 m-water layer	dimensionless
$I(\lambda)$	spectrum of light excitation, which depends on the light source used in the instrument	quanta $m^{-2} nm^{-1} s^{-1}$
$KPUR^{*}_{PSP,0}$	so-called photosynthesis saturation PUR_{PSP} energy for temp = 0°	Ein(mg tot.chl*a*)$^{-1}$ s^{-1}
N		
$N_{inorg.}$	concentration of inorganic nitrogen	µM
$P(z)$	primary production at depth z in the sea	mgC m^{-3}
P_{tot}	total production in the euphotic zone	mgC m^{-2}
PAR	photosynthetically available radiation in spectral range 400–700 nm	
PAR	irradiance of photosynthetically available radiation	Ein m^{-2} s^{-1}
PAR_0	scalar irradiance of photosynthetically available radiation	Ein m^{-2} s^{-1}
PDR^{*}	potentially destructive radiation (per unit of chlorophyll *a* mass)	µEin (mg chl*a*)$^{-1}$ s^{-1}
$\langle PDR^{*} \rangle_{\Delta z = 60\ m}$	mean PDR* value in a 60-m-deep water layer	µEin (mg chl*a*)$^{-1}$ s^{-1}
PUR^{*}	photosynthetically utilised radiation (per unit of chlorophyll *a* mass)	Ein (mg tot.chl*a*)$^{-1}$ s^{-1}
PUR^{*}_{PSP}	part of PUR^{*} due to photosynthetic pigments	Ein (mg tot.chl*a*)$^{-1}$ s^{-1}
PPP	non-photosynthetic (photoprotecting) pigments	
PSC	photosynthetic carotenoids	
PSP	photosynthetic pigments	
PS2	photosystem 2	
Q*	package effect function	dimensionless
$\langle Q^{*} \rangle_{f_{fl}(\lambda)}$	mean value of the package effect function averaged with the weight of the spectrum of the fluorescent light emitted	dimensionless
Q_{10}	factor describing the increase in saturation $KPUR^{*}_{PSP}$ energy caused by a temperature increase Δtemp = 10 °C.	dimensionless.
O	oligotrophic	
M	mesotrophic	
I or P	intermediate	
E	eutrophic	
temp	temperature in euphotic zone	°C
X	ratio of the mean specific absorption (averaged with the weight of the irradiance spectrum, averaged with the weight of exciting light spectrum)	dimensionless
z	real depth in the sea	m

z_1		m
z_2		m
Δz	water layer thickness	m
Φ	quantum yield of photosynthesis	molC Ein^{-1}
Φ_{max}	maximal theoretical quantum yield of photosynthesis = 0.125	molC Ein^{-1} or atoms C $quanta^{-1}$
Φ_{fl}	quantum yield of fluorescence	dimensionless
λ	wavelength of the light	nm
ρ'	optical parameter of cell	dimensionless
τ	optical depth in the sea	dimensionless

References

[1] WOŹNIAK B., DERA J., *Bio-optical modelling of the photo-physiological properties of marine algae*, [In] Proc. St. Petersburg Int. Conf. *Current Problems in Optics of Natural Waters*, 2001, pp. 39–49.

[2] BEKASOVA O.D., KONOVALOV B.V., KOSAKOWSKA A., KACZMAREK S., Oceanologia **28** (1990), 123.

[3] BOJANOWSKI R., Oceanologia **15** (1984), 21.

[4] HAPTER R., WOŹNIAK B., DOBROWOLSKI K., Oceanologia **15** (1984), 175.

[5] KOBLENTZ-MISHKE O.J., WOŹNIAK B., OCHAKOVSKIJ Y.E., [Eds.], *Utylization of Solar Energy in the Photosynthesis Process of the Baltic and Black Seas Phytoplankton* (in Russian), Academy of Sciences of the USSR, P.P. Shirshov Institute of Oceanology, Moscow 1985, p. 336.

[6] KOBLENTZ-MISHKE O.J., *The Ecosystems of the Baltic Sea in May–June 1984* (in Russian), Academy of Sciences of the USSR, P.P. Shirshov Institute of Oceanology, Moscow 1987, p. 439.

[7] KONOVALOV B.V., BELYAYEVA G.A., BEKASOVA O.D., KOSAKOVSKA A., Oceanologia **28** (1990), 25.

[8] OLSZEWSKI J., Oceanologia **15** (1984), 111.

[9] OOMS M.C. [Ed.], *ULISSE – Underwater Light Seatruth Satellite Experiment. Data Catalogue*, Commission of the European Union, Joint Research Centre, Ispra, Italy, Polish Academy of Science, Institute Ocanology, Sopot, Poland, Special Publication 1.96.29, 1996, p. 506.

[10] VINOGRADOV M.E. [Ed.], *Functioning of Pelagic Communities in the Tropical Regions of the Ocean-Materials of the 44-th Cruise of r/v Vityaz* (in Russian), [Ed.] Nauka, Moscow 1971, p. 271.

[11] VINOGRADOV M.E., *Pelagic Ecosystems in the Black Sea* (in Russian), [Ed.] Nauka, Moscow 1980, p. 248.

[12] VINOGRADOV M.E., OZMIDOV R.V. [Eds.], *Investigations of Pelagic Ecosystems in the Black Sea* (in Russian), Academy of Sciences of the USSR, P.P. Shirshov Institute of Oceanology, Moscow 1986, p. 277.

[13] WOŹNIAK B., HAPTER R., MAJ B., Stud. Mater. Oceanol. **68** (1984), 91.

[14] ZVALINSKY V.I., BEKASOVA O.D., KACZMAREK S., KOSAKOWSKA A., Oceanologia **28** (1990), 39.

[15] ANTAL T.K., VENEDIKTOV P.S., MATORIN D.N., KONEV YU.N., WOZNIAK B., RUBIN A.B., Oceanologiya **41** (2001), 860 (in Russian).

[16] ANTAL T.K., VENEDIKTOV P.S., MATORIN D.N., OSTROWSKA M., WOŹNIAK B., RUBIN A.B., Oceanologia **43** (2001), 291.

[17] DERA J., *Underwater irradiance as a factor affecting primary production*, Disserations and Monographs, Institute of Oceanology, Polish Academy of Sciences, Sopot, No. 7, (1995) p. 110.

[18] FICEK D., *Modelling the quantum yield of photosynthesis in different marine basins* (in Polish), Disserations and Monographs, Institute of Oceanology, Polish Academy of Sciences, Sopot, No. 14, (2001), p. 224.

[19] FICEK D., MAJCHROWSKI R., OSTROWSKA M., WOŹNIAK B., Oceanologia **42** (2000), 231.

[20] FICEK D., OSTROWSKA M., KUZIO M., POGOSYAN S.I., Oceanologia **42** (2000), 243.

[21] MAJCHROWSKI R., OSTROWSKA M., Oceanologia **41** (1999), 589.
[22] MAJCHROWSKI R., OSTROWSKA M., Oceanologia **42** (2000), 157.
[23] MAJCHROWSKI R., WOŹNIAK B., DERA J., FICEK D., KACZMAREK S., OSTROWSKA M., KOBLENTZ-MISHKE O.I., Oceanologia **42** (2000), 191.
[24] MAJCHROWSKI R., Studia i Rozprawy, No. 1, Pomeranian Pedagogical University, Słupsk 2001, p. 131 (in Polish).
[25] OSTROWSKA M., MAJCHROWSKI R., MATORIN D.N., WOŹNIAK B., Oceanologia **42** (2000), 203.
[26] OSTROWSKA M., MATORIN D.N., FICEK D., Oceanologia **42** (2000), 221.
[27] OSTROWSKA M., WOŹNIAK B., DERA J., MAJCHROWSKI R., FICEK D., MATORIN D.N., KUZIO M., *Theory of classical "in situ" chlorophyll fluorometry; Fluorimetric method of chlorophyll a determination*, [In] CD-ROM – Ocean Optics XV, paper No. 1064, Office of Naval Research Ocean, Atmosphere, and Space S&T Department, 2000, p. 11.
[28] OSTROWSKA M., *Using the fluorometric method for marine photosynthesis investigations in the Baltic* (in Polish), Disserations and Monographs, Institute of Oceanology, Polish Academy of Sciences, Sopot, No. 15, (2001) p. 194.
[29] WOŹNIAK B., DERA J., KOBLENTZ-MISHKE O.I., Oceanologia **33** (1992), 5.
[30] WOŹNIAK B., DERA J., KOBLENTZ-MISHKE O.I., Proc. SPIE **1750** (1992), 246.
[31] WOŹNIAK B., SMEKOT-WENSIERSKI W., DOERFER R., GRASSL H., Proc. SPIE **2258** (1994), 976.
[32] WOŹNIAK B., DERA J., SEMOVSKI S., HAPTER R., OSTROWSKA M., KACZMAREK S., Stud. Mater. Oceanol. **68** (1995), 91.
[33] WOŹNIAK B., SMEKOT-WENSIERSKI W., DARECKI M., Stud. Mater. Oceanol. **68** (1995), 61.
[34] WOŹNIAK B., DERA J., MAJCHROWSKI R., FICEK D., KOBLENTZ-MISHKE O.J., DARECKI M., Oceanologia **39** (1997), 377.
[35] WOŹNIAK B., DERA J., MAJCHROWSKI R., FICEK D., KACZMAREK S., KOBLENTZ-MISHKE O.I., Oceanologia **41** (1999), 187.
[36] WOŹNIAK B., DERA J., FICEK D., MAJCHROWSKI R., KACZMAREK S., OSTROWSKA M., KOBLENTZ-MISHKE O.I., Oceanologia **42** (2000), 177.
[37] WOŹNIAK B., DERA J., FICEK D., MAJCHROWSKI R., KACZMAREK S., OSTROWSKA M., KOBLENTZ-MISHKE O. I., *Model of "in vivo" spectral absorption of algal pigments*, [In] CD-ROM – Ocean Optics XV, paper No. 1062, Office of Naval Research Ocean, Atmosphere, and Space S&T Department, p. 11.
[38] WOŹNIAK B., DERA J., Oceanologia **42** (2000), 137.
[39] WOŹNIAK B., *Algorithm of Gaussian analysis of marine phytoplankton absorption spectra set for using in biocolor programme*, [In] Słupskie Prace Matematyczno-Przyrodnicze, No. 13a, 2000, p. 329.
[40] HULST VAN DE H.C., *Light Scattering by Small Particles*, Dover Pub. Inc., New York 1981, p. 470.
[41] MOREL A., BRICAUD A., Deep-Sea Res. **28** (1981), 1375.
[42] BRICAUD A., BABIN M., MOREL A., CLAUSTRE H., J. Geophys. Res. **100** (1995), 13321.
[43] BRICAUD A., MOREL A., BABIN M., ALLALI K., CLAUSTRE H., J. Geophys. Res. **103** (1998), 31033.
[44] WOŹNIAK B., OSTROWSKA M., Oceanologia **29** (1990), 117.
[45] MOREL A., Prog. Oceanogr. **26** (1991), 263.
[46] KOLBER Z., FALKOWSKI P.G., Limnol. Oceanogr. **38** (1993), 1646.

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