Papers

Luminescence and photosynthesis of marine phytoplankton – a brief presentation of new results*

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Abstract

This volume contains a set of eight papers presenting the results of the latest research into the interaction of light with marine phytoplankton by teams from the Marine Physics Department at the IO PAS in Sopot, and the Department of Environmental Physics at the Pedagogical University of Słupsk. These results

were presented at the 'Second Workshop on Luminescence and Photosynthesis of Marine Phytoplankton' (Sopot–Paraszyno, 11–15 October 1999) sponsored by the Polish State Committee for Scientific Research. This introductory article discusses the most important assumptions and objectives of the research, and outlines the latest results. These are subsequently discussed in detail in the following papers: (1) Majchrowski & Ostrowska, *Influence of photo- and chromatic acclimation on pigment composition in the sea*, (2) Woźniak *et al.*, *Model of the 'in vivo' spectral absorption of algal pigments. Part 1. Mathematical apparatus*, (3) Majchrowski *et al.*, *Model of the 'in vivo' spectral absorption of algal pigments. Part 2. Practical applications of the model*, (4) Ostrowska *et al.*, *Variability of the specific fluorescence of chlorophyll in the ocean. Part 1. Theory of classical 'in situ' chlorophyll fluorometry*, (5) Ostrowska *et al.*, *Variability of the specific fluorescence of chlorophyll in the ocean. Part 2. Fluorometric method of chlorophyll a determination*, (6) Ficek *et al.*, *Influence of non-photosynthetic pigments on the measured quantum yield of photosynthesis*, (7) Ficek *et al.*, *Variability of the portion of functional PS2 reaction centres in the light of a fluorometric study*.

For the reader's convenience, we append a list of the symbols denoting the physical quantities used in the texts. The nomenclature and denotations are in line with the conventions employed in the subject literature.

1. Introduction

Light-induced processes in marine phytoplankton, that is to say the absorption of energy, luminescence, as well as photosynthesis and its response to environmental factors in the sea have been the subject of on-going experimental and theoretical investigations in our Sopot research group together with colleagues from Russia and Germany[1]. Earlier results of these investigations were published in a number of papers, the most important of which are those by Hapter *et al.* (1983), Woźniak *et al.* (1983, 1989, 1992a and b, 1994, 1995a and b, 1997, 1999), Koblentz-Mishke *et al.* (1985), Koblentz-Mishke (1987), Woźniak (1987, 1988, 1990), Ostrowska (1990), Woźniak & Ostrowska (1990a and b), Woźniak & Pelevin (1991), Smekot--Wensierski *et al.* (1992), Dera (1995), Kaurov *et al.* (1996), Pogosyan *et al.* (1997), Majchrowski & Ostrowska (1999). The present volume contains the main achievements presented at the 'Second Workshop on Luminescence and Photosynthesis of Marine Phytoplankton' by the Sopot group, after some modifications. They are described in this and the following seven papers by Majchrowski & Ostrowska (2000), Ficek *et al.* (2000a and b), Majchrowski *et al.* (2000), Ostrowska *et al.* (2000a and b), and Woźniak *et al.* (2000).

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[1]This was co-operation of the Sopot group with teams from the P. P. Shirshov Institute of Oceanology of the Russian Academy of Sciences in Moscow, Department of Biophysics of the Lomonosov University in Moscow, the GKSS Research Centre in Geesthacht, and the Max-Planck Institute for Meteorology in Hamburg.

The field of study presented and discussed in this set of papers is of great importance for a number of theoretical and practical reasons:

(1) Photosynthetic primary production in the World Ocean is one of the principal processes in the Earth's Biosphere (Steemann Nielsen 1975). The first link in the trophic chain of marine organisms, it is responsible for supplying the ecosystem with energy (see Lieth & Whittaker 1975, Kowda 1976, Vinogradov & Shushkina 1987, Kirk 1994).

(2) During photosynthesis free oxygen is released, so marine phytoplankton are one of the main regulators of the oxygen and carbon dioxide budgets in nature (Glantz 1988, Kellogg 1988). It also influences the greenhouse effect in the Earth's atmosphere (Trenberth 1992, Kożuchowski & Przybylak 1995).

(3) Luminescence methods, especially fluorometry, are the most effective and accurate methods of the *in situ* investigation of photosynthesis (Falkowski & Kiefer 1985, Falkowski *et al.* 1986, Kolber & Falkowski 1993, Matorin *et al.* 1996).

The main problems of present-day marine biophysics involve acquiring an accurate knowledge of the specificity of photosynthesis and luminescence, the prior process of light absorption, and deriving 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 the Sopot research group have had several detailed theoretical and practical objectives. As regards theory, they were:

(1) To determine the natural variability range of the principal 'photo-physiological characteristics' of marine phytoplankton, that is, the specific light absorption, specific fluorescence, the quantum yield of photosynthesis, and others, recorded under different environmental conditions in the World Ocean.

(2) To find statistical regularities and derive empirically verified mathematical relationships between the photophysiological characteristics and the main biotic and abiotic factors in the marine environment.

(3) To find relationships between the various luminescence and photosynthesis characteristics of marine phytoplankton.

The practical aims focused on the application of the above mathematical relationships in order to:

(1) Obtain a set of luminescence methods for determining the characteristics of phytoplankton photosynthesis.

(2) Derive mathematical models and algorithms to enable the characteristics of photosynthesis in the sea to be diagnosed and predicted on the basis of contact or remote (also satellite) optical sensing.

In order to achieve these aims, corresponding empirical data sets from different regions of the World Ocean, collected by the present authors and their co-workers, were applied. These data were supplemented by similar data published and available on the Internet. At present, some of the above aims have been accomplished, others not yet. The current state of these investigations and their results are outlined in this paper, while the details are given in the other seven papers of this volume.

To make these papers easier to read we have added an appendix giving the meanings of the symbols and abbreviations used in the texts. The notational convention used in earlier papers on this subject has been taken into account (see Morel & Prieur 1977, Dera 1992, Kolber & Falkowski 1993, Kirk 1994, Bricaud *et al.* 1995, 1998 and others).

2. A brief description of the investigations and their results

2.1. Pigments and the light absorption capacities of phytoplankton

The first problem analysed by our research group was the photo- and chromatic acclimation of the photosynthetic apparatus of phytoplankton. These acclimation processes involve, among other things, the production by the plant of various accessory pigments (photosynthetic and photoprotecting) in quantities depending on the light conditions in the seawater (see Steemann Nielsen 1975, Zvalinsky 1986). This has caused the absorption properties of algae to diversify in different seas and at different depths. This question is elucidated in detail by Majchrowski & Ostrowska (2000, this volume). The particular aim of this paper was to find a statistical relationship between the concentration of the principal accessory pigment groups of natural marine phytoplankton communities and the absolute levels and spectral distribution of underwater irradiation. To do this, empirical data from about 600 stations in different areas of oceans and seas were analysed. This material came from the authors' own investigations, publications, and bio-optical databases on the Internet. It consists of vertical profiles of different pigment concentrations (determined by chromatographic methods), and vertical and spectral distributions of underwater irradiance

(determined directly by optical measurements in the sea or indirectly using bio-optical models). In all, some 4000 points on the plot of pigment concentration versus underwater light field characteristics from different depths were analysed.

The following conclusions can be drawn from these analyses:

(1) 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. The mathematical relationship (see eqs. (3) and (4) in Majchrowski & Ostrowska 2000, this volume, p. 167) 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. $PDR^*(z)$ is assumed to be the radiation energy from the spectral range $\lambda < 480$ nm absorbed per unit mass of chlorophyll a.

(2) 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, α-carotene, are less dependent on the absolute level of irradiance $E_0(\lambda)$, but they do display a strong dependence on the relative irradiance spectral distribution: $f(\lambda) = E_0(\lambda)/PAR_0$. The relevant statistical approximations describing the relations between the relative concentrations of a given PSP and the 'functions of spectral fitting' F_j averaged in a layer Δz were found (see eqs. (1) and (5)–(7) in Majchrowski & Ostrowska 2000, this volume, pp. 161, 169).

These relationships were used to model phytoplankton light absorption coefficients and are discussed in two further papers presenting a model of phytoplankton light absorption capacities (Majchrowski $et\ al.$ 2000, Woźniak $et\ al.$ 2000, this volume).

Previous models of the $in\ vivo$ phytoplankton spectral specific absorption coefficient $a_{pl}^*(\lambda)$ (Woźniak & Ostrowska 1990b, Bricaud $et\ al.$ 1995, 1998) have usually considered its dependence on the chlorophyll a concentration in the sea but not its variation due to acclimation processes. As a result of these processes, however, the spectra of $a_{pl}^*(\lambda)$ vary widely according to geographical zone and depth in the sea (Koblentz-Mishke $et\ al.$ 1995, Babin $et\ al.$ 1996, Morel $et\ al.$ 1996, Allali $et\ al.$ 1997). The main aim of the first of the two papers on the light absorption capacity of phytoplankton mentioned earlier was to introduce the elementary acclimation effects, that is, photo- and chromatic acclimation, and also the pigment package effect to light absorption models (Morel & Bricaud 1981). This was done through

a synthesis of the following statistical generalisations and mathematical models, which were derived earlier:

(1) Relationships between different pigment concentrations and irradiance conditions in the sea, described above (Majchrowski & Ostrowska 2000, this volume).

(2) A model of light absorption by phytoplankton which allows the absorption coefficients to be determined from a knowledge of the concentrations of the main photosynthetic and photoprotecting phytoplankton pigment groups (see Woźniak *et al.* 1999).

(3) Bio-optical models of irradiance transmittance in Case 1 Oceanic Waters (Woźniak *et al.* 1992a, b) and Case 2 Baltic Waters (Woźniak *et al.* 1995a, b).

The synthesis leads to an improved model that enables the total *in vivo* phytoplankton light absorption coefficient and its components derived from photosynthetic and photoprotecting pigments to be estimated from the optical conditions at the sea surface (incoming PAR irradiance) and the index of the sea's trophicity. The precision of this and former models (Woźniak & Ostrowska 1990b, Bricaud *et al.* 1995) is analysed by Majchrowski *et al.* (2000) in this volume. Empirical verification of these models has shown that our algorithm permits the phytoplankton absorption properties to be estimated with a significantly greater accuracy than with the earlier models. For example, the statistical error σ_+ of estimating the mean absorption coefficient is about 36% for our model (Woźniak *et al.* 2000, this volume), 43% for the model by Bricaud *et al.* (1995), and almost 60% for the Woźniak & Ostrowska (1990b) model (see Table 1 in Majchrowski *et al.* 2000, this volume, p. 194).

2.2. Phytoplankton luminescence and fluorescence methods of determining chlorophyll *a*

The model of phytoplankton light absorption capacities described above also has a practical utility in the analysis of the fluorescence properties of phytoplankton. The results of such analyses are described in the two papers by Ostrowska *et al.* (2000a and b) in this volume.

The first one analyses the range of variability of phytoplankton fluorescence properties in different trophic types of sea and at different depths. It also attempts to interpret the artificially induced phytoplankton fluorescence recorded *in vivo* with submersible fluorometers. To do this, the optical model of light absorption by phytoplankton mentioned above (Woźniak *et al.* 2000, this volume) was applied with the use of suitable empirical material collected by the authors in collaboration with a team from the

Department of Biophysics of the Lomonosov University in Moscow. The most important achievement of this work is a simple theoretical model of artificially excited phytoplankton fluorescence. This model takes into consideration the complex influence of three sets of factors (chlorophyll *a* concentration, various photophysiological characteristics of phytoplankton, and the optical characteristics of the fluorometer) on light absorption. It could be the basis of a *physically justifiable method* of determining the chlorophyll *a* concentration in seawater by means of *in situ* contact fluorometry.

The other paper on fluorometry (Ostrowska *et al.* 2000b, this volume) is of a more practical nature, formulating as it does two methods of determining chlorophyll *a* concentration in the sea by the measurement of artificially excited fluorescence with a submersible fluorometer. The first one, the not very precise method of *statistical correlation*, is based on the empirically established relationship between the intensity of fluorescence and chlorophyll *a* concentration. The second method, a *physical* one, is based on the theoretical model of phytoplankton fluorescence (Ostrowska *et al.* 2000a, this volume) in the relationships between the specific phytoplankton fluorescence intensity and the chlorophyll *a* concentration, the various photophysiological phytoplankton properties, and the optical characteristics of the instrument.

In order to assess these methods for practical utility they were tested empirically: the second (*physical*) one appears to be more accurate. With the *statistical correlation* method, the standard error factor of the chlorophyll *a* concentration is $x \approx 2.07$, with the *physical* method $x \approx 1.5$. This means that the statistical logarithmic error ranges from -52% to $+107\%$ for the former (*statistical*) and decreases to the -34% and $+51\%$ for the level latter (*physical*). Thus, modifying the methodology has served a useful purpose.

2.3. Photosynthesis quantum yield in the sea

The last problem to be discussed is the analysis of the photosynthetic quantum yield under various conditions at sea. The dependence of this quantum yield on a complex set of environmental factors is very complicated and difficult to describe, so in order to make this onerous task easier, we have made some simplifying assumptions. First of all, we assume that the expression describing the quantum yield can be written as the product of the theoretically maximum possible photosynthesis quantum yield and a number of dimensionless factors, which are functions of one or only a few environmental parameters. Such an expression, which is also compatible with the biophysical models of photosynthesis suggested by various authors (Falkowski & Kiefer 1985, Falkowski *et al.* 1986, Kolber & Falkowski 1993,

Rubin *et al.* 1994, Rubin 1995, Babin *et al.* 1996), has been formulated as follows:

$$
\left.
\begin{array}{rcl}
\Phi_1 & = & \Phi_2\, f_a \\
\Phi_2 & = & \Phi_{\max}\, f_\Delta\, f_c\, f_{E,t} \\
f_c & = & f_{c(N)}\, f_{c(\tau)}\, f_{c(PAR,\,inh)}
\end{array}
\right\},
\tag{1}
$$

where

Φ_1 – the observed quantum yield of phytoplankton photosynthesis, by which we mean the ratio of the number of assimilated carbon atoms to the number of quanta of light absorbed by all the phytoplankton pigments (photosynthetic and photoprotecting),

Φ_2 – the true quantum yield of phytoplankton photosynthesis, by which we mean the ratio of the number of assimilated carbon atoms to the number of quanta of light absorbed only by photosynthetic pigments of the phytoplankton,

$\Phi_{\max}$ – the maximum theoretical value of the photosynthetic quantum yield; a number of authors *e.g.* Grodziński (1972), Clayton (1980), have postulated that $\Phi_{\max} = 0.125$ atoms C quanta^{-1}, *i.e.* corresponding to a requirement of 8 quanta per molecule of assimilated CO_2,

f_a – a non-photosynthetic pigment absorption effect factor describing the decrease in the observed quantum yield in relation to the true quantum yield due to the presence in the plant of photoprotecting pigments that do not transfer absorbed energy to the PS2 reaction centres,

f_Δ – the inefficiency factor in energy transfer and charge recombination,

f_c – a portion of functional PS2 reaction centres,

$f_{c(N)}$ – 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 large depths,

$f_{c(PAR,\,inh)}$ – 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 (for example Morel 1991, Dera 1995 and papers cited there), also known as the light curve of photosynthetic efficiency at a given temperature.

With respect to these assumptions and using empirical data, we made a careful analysis of the natural variability of the quantum yield arising out of the variability of the chief environmental factors affecting photosynthesis. Some results of these investigations are presented in the two papers by Ficek *et al.* (2000a and b) in this volume. The first one aimed to determine the

influence of photoprotecting (non-photosynthetic) pigments on the observed quantum yield of marine photosynthesis. The energy absorbed by these pigments is not used in photosynthesis. Hence, the yield of this process (photosynthetic production regarded as the total energy absorbed by all phytoplankton pigments) is less than the true photosynthetic quantum yield (photosynthetic production regarded as energy absorbed only by photosynthetic pigments). To achieve this aim, the earlier model of marine phytoplankton absorption properties was invoked (see Woźniak *et al.* 2000, this volume). It was used to determine the components of total absorption introduced by photosynthetic and non-photosynthetic pigments in different trophic types of waters and at different depths in the sea. The so-called non-photosynthetic pigment factor f_a, which describes the ratio of the true and observed photosynthesis quantum yields, was estimated on the basis of this determination. The analysis shows that the value of f_a varies between 0.33 and 1 and depends on the trophic type of water and depth in the sea. The value of this factor is usually largest in eutrophic waters and becomes smaller in oligotrophic waters. The increase with depth in the sea is also characteristic, as can be seen in Ficek *et al.* (2000a), Fig. 1 in this volume, p. 235.

The second paper by Ficek *et al.* (2000b, this volume) is a preliminary statistical analysis of the relationships between the relative numbers of functional reaction centres PS2 (the so-called f_c factor) in the photosynthetic apparatus of marine phytoplankton and environmental factors. The analysis was based on measurements of f_c carried out by fluorometric methods (see Kolber & Falkowski 1993) in samples of seawater from different depths and of different trophic types. As a result of statistical generalisations, we established the analytical form of the relationship between f_c, the surface chlorophyll *a* concentration $C_a(0)$ (assumed to be the index of the sea's trophicity) and the optical depth τ (see eqs. (1) and (3) and Fig. 4 in Ficek *et al.* 2000b, this volume, pp. 245, 247, 249). This shows that f_c has a tendency to rise with rising trophicity. Moreover, the occurrence of an optimum depth in the sea with a maximum number of functional reaction centres for each type of trophicity is noticeable. Above and below this depth f_c decreases. We suggest the following explanation for these regularities: the decrease in the number of functioning centres PS2 near the surface is caused by the destructive influence of excess radiation, and in deeper layers by light deficiency.

The description of the photosynthesis quantum yield in these two papers by Ficek *et al.* (2000a and b) as presented at the Workshop is not complete according to eq. (1), because it does not take into consideration all the factors occurring in this equation. This description has since been

improved in Ficek's doctoral thesis (see Ficek 2000). On the basis of additional analyses of empirical data, the set of mathematical expressions describing the relationships between the other quantum yield factors and environmental parameters was established as follows:

- the dependence of the factor $f_{c(N)}$ on concentrations of selected nutrients:

$$f_{c(N)} = \frac{N_{\text{inorg.}}}{N_{\text{inorg.}} + 0.0585}, \tag{2}$$

  where $N_{\text{inorg.}}$ [μM] – concentration of inorganic nitrogen compounds (nitrate, nitrite, and ammonia) in the seawater,

- the dependence of the factor $f_{c(\tau)}$ on the optical depth τ in the sea:

$$f_{c(\tau)} = 1 - 0.0031\tau^2, \tag{3}$$

- the dependence of the factor $f_{c(PAR,\,inh)}$ on the irradiance $PAR(z)$ and the temperature t in the sea:

$$f_{c(PAR,\,inh)} = \exp\left(-0.00937\frac{PAR}{3.049 \times 10^{-5} \times 1.907^{\frac{t}{10}}}\right), \tag{4}$$

  where PAR is expressed in [Ein m^{-2} s^{-1}] and temperature t in [°C],

- the dependence of the factor $f_{E,\,t}$ on the Photosynthetically Usable Radiation by photosynthetic pigments PUR^*_{PSP} and temperature t:

$$f_{E,\,t} = \left[1 - \exp\left(-\frac{PUR^*_{PSP}}{8.545 \times 10^{-7} \times 1.874^{\frac{t}{10}}}\right)\right] \times$$
$$\times \frac{8.545 \times 10^{-7} \times 1.874^{\frac{t}{10}}}{PUR^*_{PSP}}, \tag{5}$$

  where PUR^*_{PSP} is expressed in [Ein (mg tot. chl a)$^{-1}$ s^{-1}].

The mean value of the inefficiency factor of energy transfer and charge recombination f_Δ for marine phytoplankton was established as:

$$f_\Delta = 0.600 \pm 0.112. \tag{6}$$

Taking eqs. (2)–(6) and the expressions for factor f_a (see eqs. (8)–(10) in Ficek *et al.* 2000a in this volume, pp. 234, 236) into consideration, and substituting them in eq. (1), we obtain a full description of the photosynthesis quantum yield. Thus, it is possible to determine the photosynthesis quantum yield at any depth in the sea from the trophic type index of water $C_a(0)$, water temperature t, nutrient concentrations N and optical conditions in the sea (optical depth τ, PAR and PUR^*_{PSP}).

3. Summary and conclusions

We carried out multilateral statistical analyses of the natural variability of the main photophysiological characteristics of phytoplankton and their links to the principal abiotic factors in the marine environment. These analyses were based on material from a large empirical database collected together with Russian co-workers and supplemented by Internet data, and led to the formulation of a set of semi-empirical models of the chief light-stimulated processes occurring in algae. These processes include photo-adaptation and the production of photoprotecting carotenoids, chromatic adaptation and the production of different types of chlorophyll antennas and photosynthetic carotenoids, the synthesis of organic matter, photoluminescence, activation of PS2 centres and others. These are preliminary models, without detailed descriptions of internal processes, and require further improvements. Nevertheless, they have introduced several unique elements, such as:

(1) The first mathematical description of the influence of irradiance conditions in the sea on the composition of phytoplankton pigments (see Majchrowski & Ostrowska 2000, this volume).

(2) The first nontrivial mathematical model of phytoplankton absorption properties that takes into consideration adaptation processes (photoacclimation, chromatic acclimation and the pigment package effect) (see Woźniak *et al.* 2000, this volume).

(3) Establishing relationships between specific phytoplankton fluorescence and surface chlorophyll *a* concentration (as the trophic index of the water) and optical depth in the sea (see Ostrowska *et al.* 2000a, this volume).

(4) Modification of the fluorometric method of determining chlorophyll *a* concentration in the sea (see Ostrowska *et al.* 2000b, this volume).

(5) A comprehensive relationship between the photosynthetic quantum yield of marine phytoplankton and a number of environmental factors (trophic type, light conditions, nutrient concentration, water temperature) (see Ficek *et al.* 2000a and b, this volume).

These mathematical descriptions may be useful in future constructions of ecological models and for improving the remote sensing of marine ecosystems.

Most of the investigations described in this set of papers are also analysed in detail in three doctoral dissertations: by Ficek (2000), Majchrowski (2000) and Ostrowska (2000).

References

Allali K., Bricaud A., Claustre H., 1997, *Spatial variations in the chlorophyll-specific absorption coefficients of phytoplankton and photosynthetically active pigments in the equatorial Pacific*, J. Geophys. Res., 102, 12413–12423.

Babin M., Morel A., Claustre H., Bricaud A., Kolber Z., Falkowski P. G., 1996, *Nitrogen- and irradiance-dependent variations of the maximum quantum yield of carbon fixation in eutrophic, mesotrophic and oligotrophic marine systems*, Deep-Sea Res., 43, 1241–1272.

Bricaud A., Babin M., Morel A., Claustre H., 1995, *Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: analysis and parameterisation*, J. Geophys. Res., 100, 13321–13332.

Bricaud A., Morel A., Babin M., Allali K., Claustre H., 1998, *Variations of light absorption by suspended particles with chlorophyll a concentration in oceanic (case 1) waters: analysis and implications for bio-optical models*, J. Geophys. Res., 103, 31033–31044.

Clayton R. K., 1980, *Photosynthesis: physical mechanisms and chemical patterns*, Cambridge Univ. Press, London–New York, 350 pp., (the authors used the Russian translation).

Dera J., 1992, *Marine physics*, Elsevier, Amsterdam–Oxford–New York–Tokyo, 516 pp.

Dera J., 1995, *Underwater irradiance as a factor affecting primary production*, Diss. and monogr., Inst. Oceanol. PAS, Sopot, 7, 110 pp.

Falkowski P. G., Kiefer D. A., 1985, *Chlorophyll a fluorescence in phytoplankton: relationship to photosynthesis and biomass*, J. Plankton Res., 7, 715–731.

Falkowski P. G., Wyman K., Ley A. C., Mauzerall D., 1986, *Relationship of steady-state photosynthesis to fluorescence in eukaryotic algae*, Biochim. Biophys. Acta, 829, 183–192.

Ficek D., 2000, *Modelling the quantum yield of photosynthesis in various marine systems*, Ph. D. thesis, Inst. Oceanol. PAN, Sopot, (in Polish).

Ficek D., Ostrowska M., Kuzio M., Pogosyan S. I., 2000b, *Variability of the portion of functional PS2 reaction centres in the light of a fluorometric study*, Oceanologia, 42 (2), 243–249.

Ficek D., Woźniak B., Majchrowski R., Ostrowska M., 2000a, *Influence of non-photosynthetic pigments on the measured quantum yield of photosynthesis*, Oceanologia, 42 (2), 231–242.

Glantz M. H. (ed.), 1988, *Societal responses to regional climate change. Forecasting by analogy*, West View Press, Boulder–London, 403 pp.

Grodziński D. M., 1972, *Plant biophysics*, Nauk. Dumka, Kiyev, 403 pp., (in Russian).

Hapter R., Woźniak B., Dobrowolski K., 1983, *Primary production in Ezcurra Inlet during the Antarctic summer of 1977/78*, Oceanologia, 15, 175–184.

Kaurov Yu. N., Pogosyan S. I., Mikaelyan A. S., Woźniak B., Hapter R., 1996, *Chlorophyll thermochemiluminescence as an indicator of the life activity of natural phytoplankton (evaluated in the course of the 23rd voyage of the research vessel 'Vityaz')*, Russian J. Plant Physiol., 43 (4), 552–559, (translated from Fiziol. Rast., 43 (4), 629–637).

Kellogg W. W., 1988, *Human impact on climate. The evolution of an awareness*, [in:] Glantz M. H. (ed.), (op. cit.), 9–33.

Kirk J. T. O., 1994, *Light and photosynthesis in aquatic ecosystems*, Cambridge Univ. Press, London–New York, 509 pp.

Koblentz-Mishke O. I. (ed.), 1987, *The ecosystems of the Baltic Sea in May–June 1984*, Izd. Inst. Okeanol. AN SSSR, Moskva, 439 pp., (in Russian).

Koblentz-Mishke O. I., Woźniak B., Kaczmarek S., Konovalov B. V., 1995, *The assimilation of light energy by marine phytoplankton. Part 1. The light absorption capacity of the Baltic and Black Sea phytoplankton (methods; relation to chlorophyll concentration)*, Oceanologia, 37 (2), 145–169.

Koblentz-Mishke O. I., Woźniak B., Ochakovskiy Yu. E. (eds.), 1985, *Utilisation of solar energy in the photosynthesis of the Baltic and Black Sea phytoplankton*, Izd. Inst. Okeanol. AN SSSR, Moskva, 336 pp., (in Russian).

Kolber Z., Falkowski P. G., 1993, *Use of active fluorescence to estimate phytoplankton photosynthesis 'in situ'*, Limnol. Oceanogr., 38 (8), 1646–1665.

Kowda W. A., 1976, *Biosphere and man*, [in:] *Biosphere and its resources*, PWN, Warszawa, 9–58, (in Polish).

Kożuchowski K., Przybylak R., 1995, *The greenhouse effect*, Wiedza Powszechna, Warszawa, 220 pp., (in Polish).

Lieth H., Whittaker R. H., 1975, *Primary productivity of the biosphere*, Springer Verlag, Berlin–Heidelberg–New York, 339 pp.

Majchrowski R., 2000, *Influence of irradiance on the light absorption characteristics of marine phytoplankton*, Ph. D. thesis, Inst. Oceanol. PAN, Sopot, (in Polish).

Majchrowski R., Ostrowska M., 2000, *Influence of photo- and chromatic acclimation on pigment composition in the sea*, Oceanologia, 42 (2), 157–175.

Majchrowski R., Ostrowska M., 1999, *Modified relationships between the occurrence of photoprotecting carotenoids of phytoplankton and Potentially Destructive Radiation in the sea*, Oceanologia, 41 (4), 589–599.

Majchrowski R., Woźniak B., Dera J., Ficek D., Kaczmarek S., Ostrowska M., Koblentz-Mishke O. I., 2000, *Model of the 'in vivo' spectral absorption of algal pigments. Part 2. Practical applications of the model*, Oceanologia, 42 (2), 191–202.

Matorin D. N., Venediktov P. S., Konev Yu. N., Kazemirko Yu. V., Rubin A. B., 1996, *Application of a double-flash, impulse, submersible fluorimeter in the determination of photosynthetic activity of natural phytoplankton*, Transactions Russian Acad. Sci. – Earth Sci. Sec., 350 (7), 1159–1161.

Morel A., 1991, *Light and marine photosynthesis: a spectral model with geochemical and climatological implications*, Prog. Oceanogr., 26, 263–306.

Morel A., Antoine D., Babin M., Dandonneau Y., 1996, *Measured and modeled primary production in the northeast Atlantic (Eumeli JGOFS program): the impact of natural variations in photosynthetic parameters on model predictive skill*, Deep-Sea Res., 43, 1273–1304.

Morel A., Bricaud A., 1981, *Theoretical results concerning light absorption in a discrete medium and application to specific absorption of phytoplankton*, Deep-Sea Res., 28, 1375–1393.

Morel A., Prieur L., 1977, *Analysis of variations in ocean color*, Limnol. Oceanogr., 22 (4), 709–722.

Ostrowska M., 1990, *Fluorescence 'in situ' method for the determination of chlorophyll a concentration in sea*, Oceanologia, 29, 175–202.

Ostrowska M., 2000, *Using the fluorometric method for marine photosynthesis investigations in the Baltic*, Ph. D. thesis, Inst. Oceanol. PAN, Sopot, (in Polish).

Ostrowska M., Majchrowski R., Matorin D. N., Woźniak B., 2000a, *Variability of the specific fluorescence of chlorophyll in the ocean. Part 1. Theory of classical 'in situ' chlorophyll fluorometry*, Oceanologia 42 (2), 203–219.

Ostrowska M., Matorin D. N., Ficek D., 2000b, *Variability of the specific fluorescence of chlorophyll in the ocean. Part 2. Fluorometric method of chlorophyll a determination*, Oceanologia, 42 (2), 221–229.

Pogosyan S. I., Sivchenko M. A., Maximov V. M., Ostrowska M., 1997, *Physiological heterogenity of an algal population: classification of 'Scenedesmus quadricauda' cenobia by the features of their photosynthetic apparatus*, Oceanologia, 39 (2), 163–175.

Rubin A. B., 1995, *Principles of organisation and regulation of primary processes of photosynthesis*, OHTI PHC RAN, Moskva, 33, 38 pp., (in Russian).

Rubin A. B., Kononenko A. A., Shaitan K. V., Paschenko V. Z., Riznichenko G. Yu., 1994, *Electron transport in photosynthesis*, Biophysics, 39 (2), 173–195.

Smekot-Wensierski W., Woźniak B., Grassl H., Doerffer R., 1992, *Die Absorptionseigenschaften des marinen Phytoplanktons*, GKSS 92/E/105, GKSS–Forschungszentrum Geesthacht GMBH, Geesthacht, 104 pp.

Steemann Nielsen E., 1975, *Marine photosynthesis with special emphasis on the ecological aspect*, Elsevier, Amsterdam–New York–Tokyo, 141 pp.

Trenberth K. E. (ed.), 1992, *Climate system modelling*, Cambridge Univ. Press, London–New York, 788 pp.

Vinogradov M. E., Shushkina E. A., 1987, *Functioning of pelagic plankton communities in the ocean*, Nauka, Moskva, 240 pp., (in Russian).

Woźniak B., 1988, *Halfempirical mathematical modelling of phytoplankton absorption properties of the World Ocean*, Proc. 16th Conf. Baltic Oceanogr., Inst. Mar. Res., Kiel, 1160–1169.

Woźniak B., 1987, *Semi-empirical mathematical model of photosynthesis process in marine phytoplankton and optical method of estimating the global primary production in the sea*, Bull. PAS, Earth Sci., 35, 71–89.

Woźniak B., 1990, *Statistical relations between photosynthesis and abiotic conditions of the marine environment; an initial prognosis of the World Ocean productivity ensuing from warming up of the Earth*, Oceanologia, 29, 147–174.

Woźniak B., Dera J., Ficek D., Majchrowski R., Kaczmarek S., Ostrowska M., Koblentz-Mishke O. I., 2000, *Model of the 'in vivo' spectral absorption of algal pigments. Part 1. Mathematical apparatus*, Oceanologia, 42 (2), 177–190.

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

Woźniak B., Dera J., Koblentz-Mishke O. I., 1992a, *Bio-optical relationships for estimating primary production in the Ocean*, Oceanologia, 33, 5–38.

Woźniak B., Dera J., Koblentz-Mishke O. I., 1992b, *Modelling the relationship between primary production, optical properties, and nutrients in the sea*, Ocean Optics 11, Proc. SPIE, 1750, 246–275.

Woźniak B., Dera J., Majchrowski R., Ficek D., Koblentz-Mishke O. I., Darecki M., 1997, *'IO PAS initial model' of marine primary production for remote sensing application*, Oceanologia, 39 (4), 377–395.

Woźniak B., Dera J., Semovski S., Hapter R., Ostrowska M., Kaczmarek S., 1995a, *Algorithm for estimating primary production in the Baltic by remote sensing*, Stud. i Mater. Oceanol., 68, 91–123.

Woźniak B., Hapter R., Dera J., 1989, *Light curves of marine plankton photosynthesis in the Baltic*, Oceanologia, 27, 61–78.

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., Ostrowska M., 1990a, *Composition and resources of photosynthetic pigments of the sea phytoplankton*, Oceanologia, 29, 91–115.

Woźniak B., Ostrowska M., 1990b, *Optical absorption properties of phytoplankton in various seas*, Oceanologia, 29, 117–146.

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

Woźniak B., Smekot-Wensierski W., Darecki M., 1995b, *Semi-empirical modelling of backscattering and light reflection coefficients in WC1 seas*, Stud. i Mater. Oceanol., 68, 61–90.

Woźniak B., Smekot-Wensierski W., Doerfer R., Grassl H., 1994, *On the relationship between spectral reflected irradiance at the sea surface and optical properties of marine phytoplankton*, Ocean Optics 12, Proc. SPIE, 2258, 976–993.

Zvalinsky V. I., 1986, *Principles of influence of light intensity and spectral composition on marine phytoplankton*, Ph. D. thesis (2nd degree), Akad. Nauk Beloruskoy SSR, Minsk, (in Russian).

Appendix

List of symbols and abbreviations denoting the physical quantities used in this and the other papers in this volume (Ficek *et al.* 2000a and b, Majchrowski & Ostrowska 2000, Majchrowski *et al.* 2000, Ostrowska *et al.* 2000a and b, Woźniak *et al.* 2000)

Symbol	Denotes	Units
a	light absorption coefficient of:	m^{-1}
a_{pl}	– phytoplankton	m^{-1}
$a_{pl,S}$	– phytoplankton pigments in solvent	m^{-1}
a_a, a_b, a_c	– chlorophylls a, b, c in solvent	m^{-1}
a_{PPC}	– photoprotecting carotenoids in solvent	m^{-1}
a_{PPP}	– photoprotecting pigments in solvent	m^{-1}
a_{PSC}	– photosynthetic carotenoids in solvent	m^{-1}
a_{PSP}	– photosynthetic pigments in solvent	m^{-1}
a^*	specific absorption coefficient of:	
a_{pl}^*	– phytoplankton	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
$\tilde{a}_{pl}^*$	mean specific absorption coefficient weighted by the irradiance spectrum	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
$\tilde{a}_{pl,PSP}^*$	$\tilde{a}_{pl}^*$ of photosynthetic pigments	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
$a_{pl,S}^*$	– phytoplankton pigments in solvent	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
a_a^*	– chlorophylls a in solvent	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
a_b^*	– chlorophylls b in solvent	$\text{m}^2\,(\text{mg chl}\,b)^{-1}$
a_c^*	– chlorophylls c in solvent	$\text{m}^2\,(\text{mg chl}\,c)^{-1}$
$a_{pl,PSP}^*$ or a_{PSP}^*	– photosynthetic pigments	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
a_{PSC}^*	– photosynthetic carotenoids in solvent	$\text{m}^2\,(\text{mg}\,PSC)^{-1}$
a_{PPC}^*	– photoprotecting carotenoids in solvent	$\text{m}^2\,(\text{mg}\,PPC)^{-1}$
$a_{PSP,S}^*$	– photosynthetic pigment in solvent	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
$a_{PPP,S}^*$	– photosynthetic pigment in solvent	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
$a_{pl,PPP}^*$ or a_{PPP}^*	– photoprotecting pigments	$\text{m}^2\,(\text{mg tot. chl}\,a)^{-1}$
$a_{\max,i}^*$	specific absorption coefficient of the i-th Gaussian band at the maximum	$\text{m}^2\,(\text{mg pigment})^{-1}$
a_j^*	specific absorption coefficient of the j-th pigment group	$\text{m}^2\,(\text{mg pigment})^{-1}$

Appendix

List of symbols and abbreviations (continued)

Symbol	Denotes	Units
C_a	sum of chlorophylls a + pheo, or total chlorophyll (chl a + divinyl chl a) concentrations	mg tot. chl a m^{-3}
$C_a(0)$	sum of chlorophylls a + pheo, or total chlorophyll (chl a + divinyl chl a) concentrations in the surface water	mg tot. chl a m^{-3}
$C_a(z)$ or $C_a(\tau)$	sum of chlorophylls a + pheo, or total chlorophyll (chl a + divinyl chl a) concentrations 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} mg pigment m^{-3} mg pigment m^{-3}
C_I	intercellular chlorophylls a concentraction	mg tot. chl a m^{-3}
d	cell diameter	m
$f(\lambda)$	spectral distribution of natural irradiance	nm^{-1}
f_a	non-photosynthetic pigment factor	dimensionless
f_c	portion of functional PS2 reaction centres	dimensionless
f_Δ	factor of inefficiency in energy transfer and charge recombination	dimensionless
$f_{c(N)}$	the factor describing the effect of nutrients on the portion of functional PS2 reaction centres	dimensionless
$f_{c(\tau)}$	the factor describing the reduction in the portion of functional PS2 reaction centres at large depths	dimensionless
$f_{c(PAR,\,inh)}$	the factor describing the reduction in the portion of functional PS2 reaction centres as a result of photoinhibition	dimensionless

Appendix

List of symbols and abbreviations (continued)

Symbol	Denotes	Units
$f_{E,t}$	the classic dependence of photosynthesis on light and temperature	dimensionless
$f_{fl}(\lambda)$	relative spectral distribution of fluorescence light by phytoplankton	nm^{-1}
F_0, F_m	*in vivo* phytoplankton fluorescence yield induced by a weak probe flash in the dark (initial), and following a saturating flash (maximal), measured in a dark-adapted state where non-photochemical quenching is at a minimum	arbitrary units
F'_0, F', F'_m	*in vivo* phytoplankton fluorescence yield induced by a weak probe flash in the dark, under ambient light, and following a saturating flash, all measured in a light-adapted state	arbitrary units
F_a, F_b, F_c, F_{PSC}	chromatic adaptation factors (the so-called functions of spectral fitting) for chl a, chl b, for chl c, for photosynthetic carotenoids	dimensionless
$E(\lambda)$ or $E_0(\lambda)$	spectral scalar irradiance	Ein m^{-2} s^{-1} nm^{-1}
$E_d(\lambda)$	spectral downward radiance	Ein m^{-2} s^{-1} nm^{-1}
HPLC	High Performance Liquid Chromatography	
I_c	total intensity of fluorescence excitation light	Ein m^{-2} s^{-1}
$I(\lambda)$	spectrum of light excitation, which depends on the light source used by the instrument	Ein m^{-2} nm^{-1} s^{-1}
K_{PAR}	PAR irradiance attenuation coefficient	m^{-1}

Appendix

List of symbols and abbreviations (continued)

Symbol	Denotes	Units
$KPAR$	photosynthesis saturation PAR irradiance	Ein m^{-2} s^{-1}
$KPUR^*$	photosynthesis saturation PUR energy	Ein (mg tot. chl a)$^{-1}$ s^{-1}
$KPUR^*_{PSP}$	photosynthesis saturation PUR$_{PSP}$ energy	Ein (mg tot. chl a)$^{-1}$ s^{-1}
$N_{\text{inorg.}}$	concentration of inorganic nitrogen	μM
P_i	pigment index of acetone extract of phytoplankton (ratio of principal maxima of light absorption: 430 and 663 nm)	dimensionless
PAR	photosynthetically available radiation	
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	
PDR^*	potentially destructive radiation (per unit of chlorophyll a mass)	μEin (mg chl a)$^{-1}$ s^{-1}
$< PDR^* >_{\Delta z=60\,\text{m}}$	mean PDR* value in a 60-m-deep water layer	μEin (mg chl a)$^{-1}$ s^{-1}
PUR	photosynthetically usable radiation	
PUR^*	photosynthetically usable 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}
PSP	photosynthetic pigments	

Appendix

List of symbols and abbreviations (continued)

Symbol	Denotes	Units
PPP	non-photosynthetic (photoprotecting) pigments	
PSC	photosynthetic carotenoids	
PPC	photoprotecting carotenoids	
PS2	photosystem 2	
Trophic type symbols:		
O	oligotrophic	
M	mesotrophic	
I or P	intermediate	
E	eutrophic	
Q^*	package effect function	dimensionless
t	temperature in euphotic zone	°C
z	depth in the sea	m
z_e	depth of euphotic zone (level of 1% of the surface PAR irradiance)	m
Δz	thickness of water layers	m
Φ_{fl}	quantum yield of fluorescence	dimensionless
$\Phi_{\max}$	maximum quantum yield of photosynthesis	atoms C quanta^{-1}
Φ_1	observed quantum yield of photosynthesis	atoms C quanta^{-1}
Φ_2	true quantum yield of photosynthesis	atoms C quanta^{-1}
β	pathlength amplification correction factor	dimensionless
λ	wavelength of the light	nm
$\lambda_{\max, i}$	centre of absorption Gaussian band	nm
ρ'	optical parameter of cell	dimensionless
τ	optical depth in the sea	dimensionless
σ_i	dispersion of absorption Gaussian band	nm