Invited paper

Modelling light and photosynthesis in the marine environment[*]

Bogdan Woźniak[1]
Jerzy Dera[1]
Dariusz Ficek[2]
Roman Majchrowski[2]
Mirosława Ostrowska[1]
Sławomir Kaczmarek[1]

[1] Institute of Oceanology,
Polish Academy of Sciences,
Powstańców Warszawy 55, PL–81–712 Sopot, Poland;
e-mail: wozniak@iopan.gda.pl

[2] Institute of Physics,
Pomeranian Pedagogical Academy in Słupsk,
Arciszewskiego 22 B, PL–76–200 Słupsk, Poland

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Abstract

The overriding and far-reaching aim of our work has been to achieve a good understanding of the processes of light interaction with phytoplankton in the sea and to develop an innovative physical model of photosynthesis in the marine environment, suitable for the remote sensing of marine primary production. Unlike previous models, the present one takes greater account of the complexity of the physiological processes in phytoplankton. We have focused in particular on photophysiological processes, which are governed directly or indirectly by light energy, or in which light, besides the nutrient content in and the temperature of seawater, is one of the principal limiting factors.

To achieve this aim we have carried out comprehensive statistical analyses of the natural variability of the main photophysiological properties of phytoplankton and their links with the principal abiotic factors in the sea. These analyses have made use of extensive empirical data gathered in a wide diversity of seas and oceans by Polish and Russian teams as well as by joint Polish-Russian expeditions. Data sets available on the Internet have also been applied. As a result, a set of more or less complex, semi-empirical models of light-stimulated processes occurring in marine phytoplankton cells has been developed. The trophic type of sea, photo-acclimation and the production of photoprotecting carotenoids, chromatic acclimation and the production of various forms of chlorophyll-antennas and photosynthetic carotenoids, cell adaptation by the package effect, light absorption, photosynthesis, photoinhibition, the fluorescence effect, and the activation of PS2 centres are all considered in the models. These take into account not only the influence of light, but also, indirectly, that of the vertical mixing of water; in the case of photosynthesis, the quantum yield has been also formulated as being dependent on the nutrient concentrations and the temperature of seawater. The bio-optical spectral models of irradiance transmittance in case 1 oceanic waters and case 2 Baltic waters, developed earlier, also are described in this paper.

The development of the models presented here is not yet complete and they all need continual improvement. Nevertheless, we have used them on a preliminary basis for calculating various photosynthetic characteristics at different depths in the sea, such as the concentration of chlorophyll and other pigments, and primary production. The practical algorithm we have constructed allows the vertical distribution of these characteristics to be determined from three input data: chlorophyll a concentration, irradiance, and temperature at the sea surface. Since all three data can be measured remotely, our algorithm can be applied as the 'marine part' of the remote sensing algorithms used for detecting marine photosynthesis.

1. Introduction

50 years have elapsed since the foundation of the Marine Station of the Polish Academy of Sciences (PAS) in Sopot in 1953, whose successor is today's Institute of Oceanology PAS (see Dera 2003). Among the first optical investigations carried out at the Marine Station in the 1950s were Secchi-disc measurements of water transparency and sea colour

measurements using the Forel scale. Towards the end of the fifties, a co-author of the present article, Jerzy Dera, began the construction there of a marine physics laboratory and initiated research in the field of marine optics (Dera 1963a, b), inspired by the subject literature of the day (e.g. Szuleykin 1959, Jerlov 1961a, b, 1964, Duntley 1962, 1963, and others). Gradually he organised in Sopot a team of specialists in marine optics, who undertook investigations into the optical properties of sea water (e.g. Dera et al. 1978), underwater irradiance (e.g. Dera & Olszewski 1967, 1978, Hapter et al. 1973, Olszewski 1973, 1983, 1984, Woźniak 1973, Woźniak & Montwiłł 1973, Czyszek et al. 1979, Dera & Stramski 1986, Kaczmarek & Dera 1998) and its interaction with marine phytoplankton. Studies of this kind are now routine in marine bio-optics (e.g. Dera 1967, 1995, Dera et al. 1975, Woźniak et al. 1980, 1989, Koblentz-Mishke et al. (eds.) 1985). During these investigations it was noticed that one of the key problems of bio-optics is the dependence of the absorption of light by phytoplankton on changing environmental conditions, which affect the pigment composition in cells. The study of this problem, already examined by numerous authors, e.g. Morel & Bricaud (1981), Bidigare et al. (1990), Bricaud et al. (1995, 1998), Babin et al. (1996a, b, c), was in the Sopot team successfully taken up by Woźniak & Ostrowska (1990a, b). Their results of studies of the absorption of light by phytoplankton pigments, together with studies of the properties of the light field in various seas, have been used in the modelling of bio-optical processes in the sea described below. This modelling has also made use of a plethora of empirical measurements from expeditions of Polish and Russian research vessels and literature data (see Tables 1 and 2). On the basis of this data, a new bio-optical classification of seas was developed, based on the concentration of chlorophyll a in the sea C_a (Woźniak & Pelevin 1991). In our work we refer to this parameter as the trophicity index or simply the trophicity of waters (see Table A2.1 in Annex 2). Further work involving data analysis and the ongoing enlargement of empirical data sets, led to numerous statistical links being established between the various factors governing marine photosynthesis (Woźniak et al. 1992a, b, 1997a, b, 2000, Majchrowski & Ostrowska 2000, Majchrowski et al. 2000, Ostrowska et al. 2000a, b). This also enabled the modelling, for example, of photo- and chromatic acclimation of phytoplankton cells, the pigment package effect and the photosynthetic yield (see Ficek et al. 2000a, b, Woźniak & Dera 2000, Woźniak et al. 2002a, b), and subsequently, the formulation of a comprehensive, state-of-the-art model of these processes, together with primary production in the sea as its final result. An essential aspect of this model is that the algorithm on which it is based can be adapted for use with remote-sensing techniques. This has been made possible by the small number of input parameters – sea surface chlorophyll, sea surface irradiance,

Table 1. Numbers of the stations from which the vertical profile data of the various quantities have been analysed for the given regions. The region location numbers are given on the map below this Table, p. 176

Region No. as given on the map	Measured quantities and number of stations				Number of references as given in Table 2
	$C_a(z)^{1)}$	$N(z)$, $temp(z)^{2)}$	$P(z)^{3)}$	OPS$(z)^{4)}$	
1	910	800	220	761	1,6
2	251	200	71	103	2
3	10	10	9		4
4	24	24	10		3
5	22	21	14		3
6	27	10	9	30	4
7	31	31	31	18	4
8	13	5	13		3
9	21	16	12		3
10	1	1			3
11	7	7			3
12	3	2	3		3
13	7	7	7		4
14	48	22	18	40	4
15	140	87	78		4
16	1	1	1	1	15
17	3				3
18	26	9	16		3
19	5		5		3
20	14	14	9		3
21	35	35	33	28	3, 7, 8, 9, 10
22	17	7	17		3
23	34	28	34		3
24	41	41			4
25	288	291	35		4
26	4	4			4
27	18	18	18	8	11, 12, 13, 14, 15, 16
28	35	26	26	18	5, 11, 12, 13, 14, 15, 16
29	32	32			5
30	35	8	31		3

Table 1. (*continued*)

Region No. as given on the map	Measured quantities and number of stations				Number of references as given in Table 2
	$C_a(z)$[1]	$N(z)$, $temp(z)$[2]	$P(z)$[3]	OPS(z)[4]	
31	42	24	19		3
32	21		16		3
33	53	25	25	25	3, 7, 8, 9, 10
34	13		12		3
35	89		78		3
36	50	49			4
37	198	204	13		4
38	58	55	36		4
39	10	6	6	10	5
40	11	1	2	4	5
41	78		60		5
42	19		19		5
43	119	4	42	9	3
44	15		15		3
45	36		14		3
46	7		7		3
47	37		35		3
48	4	4	4	2	4
49	14	14	14	6	4
50	70		69		5
51	4		2		5
52	145		71		3
53	14		14		3
54	57		57		3
55	22		18		3
56	12		8		3
57	5			10	4
58	8		4	10	4
59	3		1		5
60	12		9		5
61	19		17		5
62	57		51		3

Table 1. (*continued*)

Region No. as given on the map	Measured quantities and number of stations				Number of references as given in Table 2
	$C_a(z)^{1)}$	$N(z), temp(z)^{2)}$	$P(z)^{3)}$	OPS$(z)^{4)}$	
63	11		3		3
64	14		13		3
65	10		10		3
66	58	48	23	44	4
67	6				4
68	3				5
69	4		1		5
70	6		4		5
71	31		24		3
Total	3548	2191	1536	1127	

Comments:

[1] Vertical distributions of chlorophyll *a* and concentrations of other phytoplankton pigments (in some cases).

[2] Contents of different nutrients and temperatures in the euphotic layer.

[3] Vertical distributions of primary production.

[4] Vertical distributions of PAR irradiance and/or irradiance spectrum, and various optical properties of the sea water (OPS) and of the phytoplankton.
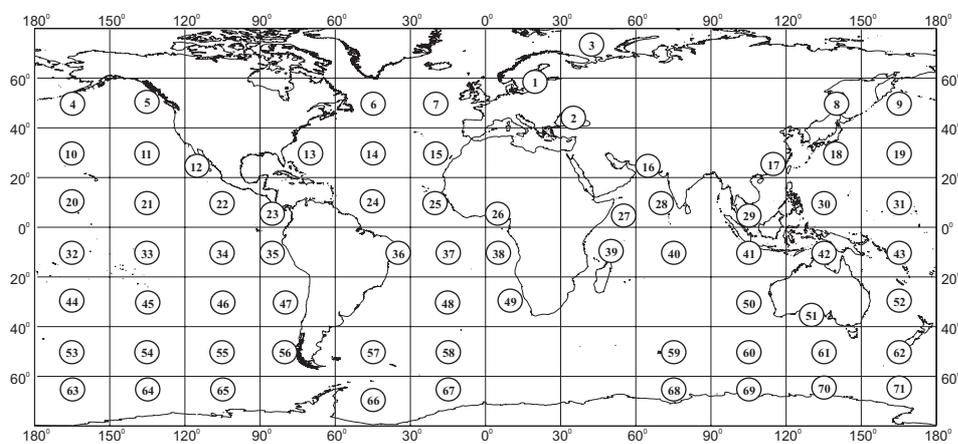
The region location numbers (1 to 71) apply to Table 1.

Table 2. The bio-optical database specification used in the analyses

Number	Experiment	Location	References
	1	6	7
1	Polish-Russian database	Baltic	Hapter et al. (1973), Dera et al. (1975), Gohs et al. (1978), Koblentz-Mishke et al. (eds.) (1985), Koblentz-Mishke (ed.) (1987), Dybern (ed.) (1989, 1991), *Oceanologia* 28 (1990), Olszewski (ed.) (1995), others
2		Black Sea	Koblentz-Mishke et al. (eds.) (1985) Vinogradov (ed.) (1980, 1985, 1991), Vinogradov & Ozmidov (eds.) (1986), others
3		Pacific	Vinogradov (ed.) (1971), Moroshkin (ed.) (1973), Monin & Shifrin (eds.) (1974), Ponomareva & Pasternak (1985), others
4		Atlantic	Moroshkin (ed.) (1973), Monin & Shifrin (eds.) (1974), *Oceanologia* 15 (1983), others
5		Indian Ocean	Semina (ed.) (1981, 1985), others
6	ULISSE	Baltic	Ooms (1996)
7	EqPac tt007	equatorial Pacific	Bidigare (1992a), Newton (1992a)
8	EqPac tt008	equatorial Pacific	Bidigare (1992b), Newton (1992b)
9	EqPac tt011	equatorial Pacific	Bidigare (1992c), Newton (1992c)
10	EqPac tt012	equatorial Pacific	Bidigare (1992d)
11	Arabian ttn-43	Arabian Sea	Goericke (1995a)
12	Arabian ttn-45	Arabian Sea	Bidigare (1995a), Trees (1995a)
13	Arabian ttn-49	Arabian Sea	Goericke (1995b)
14	Arabian ttn-50	Arabian Sea	Bidigare (1995b)
15	Arabian ttn-53	Arabian Sea	Bidigare (1995c), Trees (1995b)
16	Arabian ttn-54	Arabian Sea	Goericke (1995c), Marra (1995)

section B

MODEL FORMULAS

section A   INPUT DATA

1	2	3
Surface chlorophyll $C_a(0)$	Surface irradiance $PAR_0(0^+)$	Sea surface temperature *temp*

4
Statistical chlorophyll profile models
(*Woźniak et al. 1992a,b; 1995a*)
$C_a(z) = f(C_a(0))$

10
Chlorophyll depth profiles
$C_a(z)$

section C
CALCULATIONS

5
Bio-optical underwater irradiance transmittance models
(*Woźniak et al. 1992a,b; Kaczmarek & Woźniak 1995*)
$E_d(\lambda) = f(C_a, PAR_0(0^+))$

11
Optical properties and underwater irradiance fields
$... K_d(\lambda, z)...f_E(\lambda, z)...E_d(\lambda, z)...PAR(z)...$

6
Statistical model of photo- and chromatic acclimation
(*Majchrowski & Ostrowska 1999, 2000; Majchrowski 2001*)
$C_j = f(C_a, E_d(z, \lambda))$

12
Algal pigment depth profiles
$C_j(z)$

7
Model of spectral light absorption of algal pigments *in vivo*
(*Woźniak et al. 1999, 2000; Majchrowski 2001*)
$...Q^*(\lambda) = f(C_a)...$
$...a_{pl}(\lambda) = f(Q^*(\lambda), C_a, C_j)...$

13
Profiles of package functions and algal pigment light absorption capacity
$...Q^*(\lambda, z)...a_{pl}(\lambda, z), a_{pl,PSP}(\lambda, z)...$
— — — — — — — — — — — — — — — — — — —
Energy distributions
$PUR(z), PUR_{PSP}(z), \eta_{PUR}(z), \eta_{PUR,PSP}(z)$

8
Statistical relationships between chlorophyll *a*, temperature and inorganic nitrogen
(*Ficek 2001*)
$N_{inorg}(0) = f(C_a(0), temp)$
$N_{inorg}(z) = f(N_{inorg}(0))$

14
Inorganic nitrogen depth profiles
$N_{inorg}(z)$

9
Model of photosynthesis quantum yield
(*Woźniak & Dera 2000; Woźniak et al. 2002a; Ficek 2001*)
$\Phi = f(f_a, \tau, N_{inorg}, PAR, PUR_{PSP}, temp)$

15
Depth profiles of photosynthesis quantum yield
$\Phi(z)$

16
Depth profiles of primary production $P(z)$, total primary production P_{tot}

Fig. 1. Block diagram of the model of primary production in the sea

and temperature at the sea surface, all of which may be recorded by remote sensing. Of course, certain additional information about the basin in question is also required, the case classification of waters by Morel & Prieur (1977) and the dynamic and climatic type of basin (see Table 7 in Section 7, this paper, p. 210), to name but two examples. Such information can be gleaned from general descriptions of the ocean.

Parallel to these bio-optical studies, other aspects of marine optics have also been examined, as the growth of the Institute of Oceanology PAS in general and the hydro-optical laboratories in particular have permitted (see Dera 2003). A wide variety of papers in hydro-optics have been published – the following are examples of recent research in fields not directly connected with bio-optical modelling: Siegoczyński et al. (1994), Woźniak S. B. (1996, 1997), Witkowski et al. (1998), Kowalczuk (1999), Zapadka & Woźniak S. B. (2000), Piskozub et al. (2001), Zapadka et al. (2001), Kuśmierczyk-Michulec et al. (2002), Rozwadowska & Cahalan (2002), Darecki et al. (2003). The bio-optical modelling described here derived its inspiration from the results of very many earlier investigations, in particular those by André Morel and his team, whose papers we quote frequently in the course of the present article. The aim of our paper is to describe in as detailed a manner as possible all the component elements of the already-mentioned comprehensive model of primary production in the sea developed by our team at Sopot. Not only does it review earlier publications, it also presents numerous innovations for the very first time.

The results of the modelling and their interpretations are illustrated on the graphs. The block diagram in Fig. 1 presents an overview of the model. The detailed mathematical apparatus, for practical use, is given in Annex 1. Annex 2 provides a list of symbols and abbreviations.

2. General outline and block diagram of the primary production model

In order to achieve the aims of this study, marine photosynthesis and the factors governing this process were modelled mathematically.

A packet of various types of models was constructed. This includes:
- six detailed models providing for the determination of various optical and photosynthetic characteristics of the sea on the basis of environmental state parameters;
- a generalised bio-optical model enabling, among other things, the estimation of coefficients of light absorption by phytoplankton pigments, the quantum efficiency of photosynthesis, and the primary production of organic matter at given depths in the sea on the basis of remote esensing data of sea surface total chlorophyll a concentration $C_a(0)$, sea surface irradiance $PAR_0(0^+)$, and sea surface temperature $temp$.

This latter, generalised model is, as it were, a synthesis of the former six detailed models. Fig. 1 shows a block diagram of this model, which divides it into three sections: Section A – *input data*, essential for the calculations, Section B – the set of *model formulas* facilitating the *calculations*, Section C – the set of various computed biotic and abiotic properties of the environment, from the vertical distributions of chlorophyll $C_a(z)$ in the sea to the vertical distributions of the quantum efficiency of photosynthesis $\Phi(z)$, vertical distributions of primary production $P(z)$ and the total primary production in the water column P_{tot}.

Section A – the *input data* essential for the computations include:

– $C_a(0)$ (block 1) – surface concentration of the total chlorophyll a;

– $PAR_0(0^+)$ (block 2) – irradiance (scalar) by sunlight in the PAR spectral range (400–700 nm) just below the sea surface;

– $temp$ (block 3) – the temperature of the surface layer of the sea. For the sake of simplicity, we have assumed in this study a constant temperature throughout the photosynthetically active layer, just as in the mixed layer. This assumption may, of course, introduce some additional error to the primary production calculated for various depths in the sea. It can be demonstrated, however, that the error does not exceed 10%: it is negligible compared to the much larger error inherent in the empirical determination of primary production using the C^{14} technique.

As has been mentioned, these three principal input data of the model (blocks 1–3) can be determined by satellite remote sensing. Additional information on the type of basin (see Table 7 in Section 7) and deep mixed layer should be considered in order to select some of alternative equations of the model.

Section B – contains a complex set of *model formulas* taken from the partial models. In detail, they are:

– (block 4) statistical models of the vertical distributions of chlorophyll $C_a(z)$ in the sea, constructed for stratified seas (after Woźniak et al. 1992a, b) and Baltic waters with a mixed euphotic layer (after Woźniak et al. 1995a);

– (block 5) bio-optical underwater irradiance transmittance models for oceanic case 1 waters (after Woźniak et al. 1992a, b) and for Baltic case 2 waters (after Kaczmarek & Woźniak 1995);

– (block 6) a statistical model of photo- and chromatic acclimation containing model formulas defining the concentrations of individual photosynthetic and photoprotecting pigments (after Majchrowski & Ostrowska 1999, 2000, Majchrowski 2001);

– (block 7) a model of light absorption by phytoplankton *in vivo* (after Woźniak et al. 1999, 2000, Majchrowski et al. 2000, Majchrowski 2001), which takes account, among other things, of the pigment package effect in a cell, and photo- and chromatic adaptation effects;

– (block 8) statistically generalised interrelationships between the concentrations of inorganic nitrogen, chlorophyll *a* and the temperature in the sea, which, in particular, enable nitrogen concentrations at different depths in the sea to be determined from remote sensing data (after Ficek 2001);

– (block 9) a model of the quantum efficiency of marine photosynthesis, permitting this to be determined from the above-mentioned input data, including surface chlorophyll *a* as the trophicity index of the waters in question, and the previously calculated concentrations of nitrogen-containing nutrients (see e.g. Woźniak et al. 2002a).

Applying the input data (blocks 1–3) and using the *model formulas* (blocks 4–9), *calculations* are now carried out (Section C) of a series of biotic and abiotic properties of the marine ecosystem, from the vertical distributions of the chlorophyll concentration $C_a(z)$ (block 10) to the vertical distributions of the quantum yield of photosynthesis $\Phi(z)$ (block 15), and also of the primary production at various depths in the sea $P(z)$ and the total primary production in the water column P_{tot} (block 16).

The entire algorithm of this general model of photosynthesis, set out in tabular form suitable for numerical programming, is given in Annex 1. This algorithm merely presents the complete mathematical description of the problems analysed. The discussion and analysis of the individual component models will be found in the six following sections of this paper.

3. Statistical models of vertical chlorophyll distributions (block 4 in Fig. 1)

The concentrations of total chlorophyll *a* (C_a) measured in biologically active surface waters in various parts of the World Ocean vary over a scale of four orders of magnitude. According to Mordasova (1976), these concentrations range from c. 0.02 mg tot. chl *a* m^{-3} and less in the central areas of oceans to around 100 mg tot. chl *a* m^{-3} and more in bay waters of enclosed seas. Chlorophyll concentrations also vary with depth (see Fig. 2a). To analyse these variations in detail would exceed the scope of the present paper; this question has been explored elsewhere by a number of authors, e.g. Krey & Babenerd (1976), Mordasova (1976), Lewis et al. (1983),
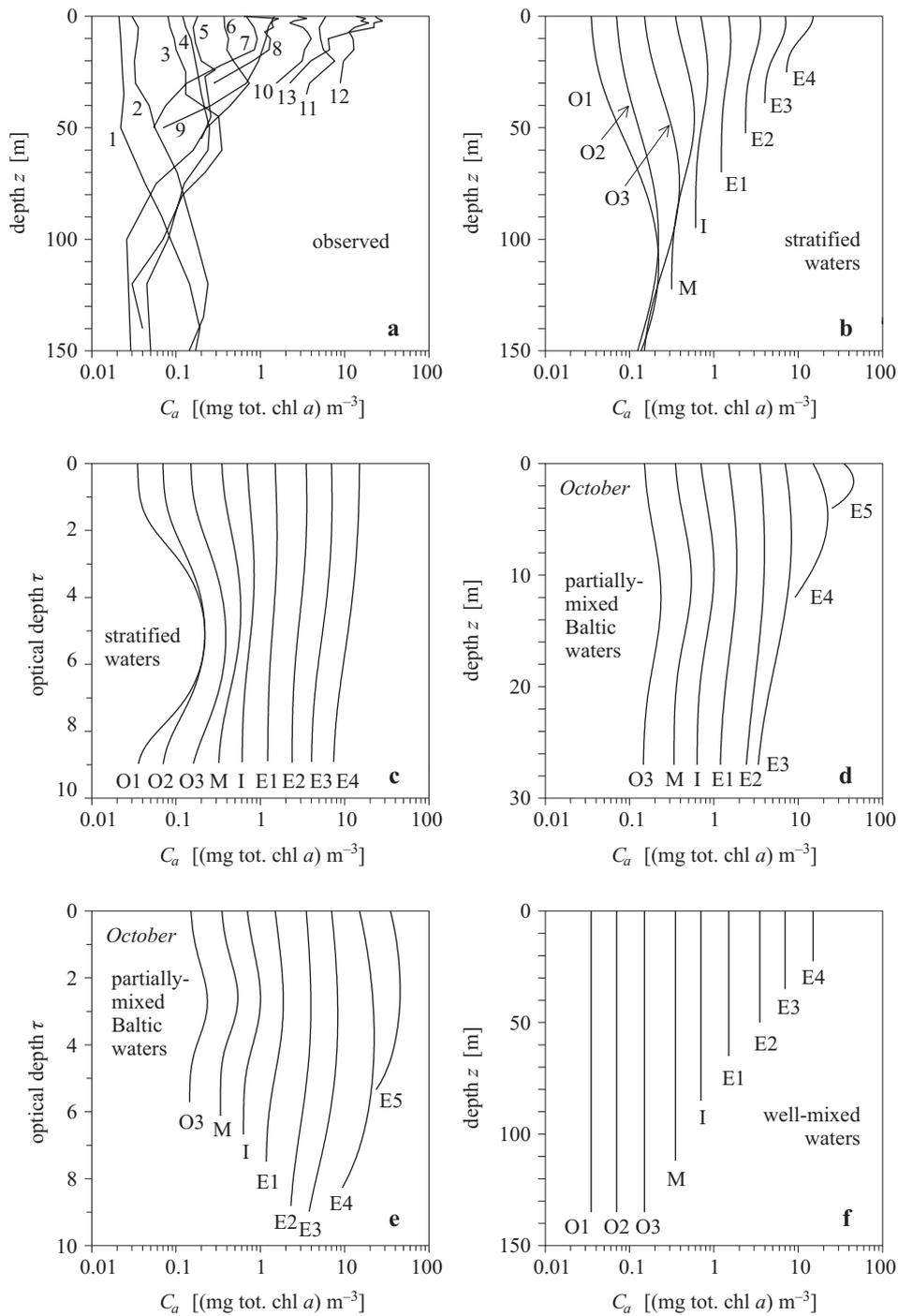
Fig. 2. Vertical distributions of the chlorophyll a concentrations C_a in various seas and oceans: (a) examples of empirical profiles from: (*continued* on page 183)

Karabashev (1987), Morel & Berthon (1989), Woźniak & Ostrowska (1990a). Here we shall focus on the analysis of one aspect of our model of photosynthesis, namely, the vertical chlorophyll a concentration profiles (see block 5 in Fig. 1). To this end we shall make use of the results of the relevant statistical analyses performed by Woźniak and his co-workers and discussed in, for example, Woźniak et al. (1992a, b, 1995a).

As Fig. 2a shows, the overall trend in most naturally-occurring vertical $C_a(z)$ profiles is that there is a single principal concentration peak. The meticulous analyses of the experimental material (c. 1500 $C_a(z)$ profiles from various regions of the World Ocean) presented earlier by Woźniak et al. (1992a, b, 1995a) show that this peak's 'distinctiveness', width and depth of occurrence in the sea depend on the trophicity of the sea basin in question $C_a(0)$, and on the degree of vertical stability of the water masses. This trend is most obvious in strongly stratified waters, but is much less distinct, and in some cases almost non-existent, in well-mixed waters. This situation inclined us to classify our experimental material into three groups with respect to stratified, partially-mixed and well-mixed waters. The stratified waters group comprises the vast, mostly oligo- and mesotrophic central regions of oceans, and to a large extent coincides with the optical case 1 waters, distinguished by Morel & Prieur (1977) on the basis of their optical properties. The other two groups – the partially-mixed and well-mixed waters – cover dynamically active ocean regions (divergence and convergence zones), as well as a number of shelf and enclosed seas. These groups coincide for the most part with the case 2 water category. It should be borne in mind, however, that neither the optical nor the dynamic division is entirely coincident. Thus, even though the waters in oceanic areas of convergence and divergence are mixed, most are classified as case 1 according to optical criteria. Conversely, in enclosed eutrophic seas such as the Baltic, there are periods – especially during the phytoplankton blooms – when the waters are strongly stratified, and yet from the optical standpoint they are usually regarded as case 2 waters.

In view of these regularities in measured $C_a(z)$ distributions, a number of authors have derived appropriate statistical formulas describing these distributions in different types of seas (e.g. Lewis et al. 1983, Platt et al. 1988, Morel & Berthon 1989, Sathyendranath et al. 1989).

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the Indian Ocean 1–3, the Atlantic Ocean 4–6, the Black Sea 7–9, the Baltic Sea 10–13; (b–f) model profiles of $C_a(z)$ in different types of sea: stratified waters (b, c), partially-mixed Baltic waters (d, e), well-mixed waters (f)

The trophicity types of basins and their symbols used on the graphs (O1–E5) are defined in Annex 2, Table A2.1

These formulas were developed with satellite remote sensing in mind: they express the total chlorophyll a concentrations at any depth in the sea $C_a(z)$ as a function of the surface concentration $C_a(0)$. A similar model formula, convenient for our recent modelling, has been worked out by Woźniak et al. (1992a, b, 1995a). It presents the following dependencies of the vertical distributions $C_a(z)$ on the surface concentration $C_a(0)$, expressed by the sum of a constant, i.e. depth-independent, component, and a depth-dependent component described by the Gaussian function

$$C_a(z) = C_a(0) \frac{C_{\text{const}} + C_m \exp\{-[(z - z_{\max})\sigma_z]^2\}}{C_{\text{const}} + C_m \exp\{-[(z_{\max})\sigma_z]^2\}}. \tag{1}$$

The several constants occurring in these expressions are functions of surface concentrations $C_a(0)$. The forms of these functions were derived from the relevant statistical analyses for the first two of the three distinct dynamic situations:

- for stratified waters (most oceanic regions)
  (after Woźniak et al. 1992a, b):

$$C_{\text{const}} = 10^{[-0.0437 + 0.8644 \log (C_a(0)) - 0.0888(\log (C_a(0)))^2]}, \tag{2}$$

$$\begin{aligned} C_m &= 0.269 + 0.245 \log (C_a(0)) + 1.51(\log (C_a(0)))^2 + \\ &\quad + 2.13(\log (C_a(0)))^3 + 0.81(\log (C_a(0)))^4, \end{aligned} \tag{3}$$

$$\begin{aligned} z_{\max} &= 17.9 - 44.6 \log (C_a(0)) + 38.1(\log (C_a(0)))^2 + \\ &\quad + 1.32(\log (C_a(0)))^3 - 10.7(\log (C_a(0)))^4, \end{aligned} \tag{4}$$

$$\begin{aligned} \sigma_z &= 0.0408 + 0.0217 \log (C_a(0)) + 0.00239(\log (C_a(0)))^2 + \\ &\quad + 0.00562(\log (C_a(0)))^3 + 0.00514(\log (C_a(0)))^4; \end{aligned} \tag{5}$$

- for partially mixed Baltic waters; the seasonally-dependent degree of mixing is taken into account, where the season is designated in the formulas by the day number of the year n_d (Woźniak et al. 1995a):

$$C_{\text{const}} = \left[0.77 - 0.13 \cos \left(2\pi \frac{n_d - 74}{365} \right) \right]^{C_a(0)}, \tag{6}$$

$$C_m = \frac{1}{2M} \left[(0.36)^{C_a(0)} + 1 \right] \left[M + 1 + (M - 1) \cos \left(2\pi \frac{n_d - 120}{365} \right) \right], \tag{7}$$

$$M = 2.25(0.765)^{C_a(0)} + 1, \tag{8}$$

$$\begin{aligned} z_{\max} &= 9.18 - 2.43 \log (C_a(0)) + 0.213(\log (C_a(0)))^2 + \\ &\quad - 1.18(\log (C_a(0)))^3, \end{aligned} \tag{9}$$

$$\begin{aligned} \sigma_z &= 0.118 - 0.113 \log (C_a(0)) - 0.0139(\log (C_a(0)))^2 + \\ &\quad + 0.112(\log (C_a(0)))^3. \end{aligned} \tag{10}$$

Figs. 2b, c and 2d, e show examples of modelled vertical distributions of chlorophyll a for stratified ocean waters and Baltic waters. The statistical errors of these models are depth-dependent. In the case of stratified ocean waters, this error is small in surface waters and increases with depth. For example, at the optical depth $\tau = 1$ it is c. 13%, for $\tau = 4.6$ (the depth of the euphotic layer) it is 33.7%, and for $\tau = 6.9$ it is 56.8%. In the case of Baltic waters, the statistical error is somewhat greater; the respective figures are c. 14.5% for an optical depth of $\tau = 1$, c. 49% for $\tau = 2.3$ and c. 68% for $\tau = 4.6$.

We have not yet succeeded in finding general analytical expressions for the $C_a(z)$ distributions in the group of well-mixed waters owing to their greater complexity. Since they are far less dependent on depth than stratified waters, we have assumed at the present stage of modelling that in well-mixed waters

$$C_a(z) = C_a(0) = \text{const}, \tag{11}$$

that is, that the distributions are homogeneous. In the future, this will, of course, need to be corrected.

4. Bio-optical underwater irradiance transmittance models (block 5 in Fig. 1)

The next element in our generalised model of marine photosynthesis is the model of irradiance transmission into the sea (see block 5 in Fig. 1). To simplify matters we have restricted the present analysis to downward irradiance since, as is well known, the upward irradiance is usually smaller than the downward irradiance by one or two orders of magnitude. For this reason it can safely be neglected in analyses of the optical conditions of marine photosynthesis.

It is well known that the natural irradiance conditions in the waters in different seas and oceanic regions vary a great deal. This variability is due to the diverse compositions of optically active admixtures – mainly dissolved organic substances and all kinds of suspended matter – in different types of waters. Their optical properties, among them the spectral coefficients of downward irradiance attenuation $K_d(\lambda)$, thus vary accordingly. As a consequence, there is variability in the spatial and spectral irradiance distributions (see Fig. 3). Nevertheless, there are many regularities permitting the classification of ocean and sea regions with similar optical properties. So for many years now, scientists have been developing ways of classifying the optical properties of natural marine basins, beginning with Jerlov (1976, 1978), (see e.g. Pelevin & Rutkovskaya 1978, Smith & Baker 1978, Baker & Smith 1982, Morel 1988, Woźniak & Pelevin 1991). Here we
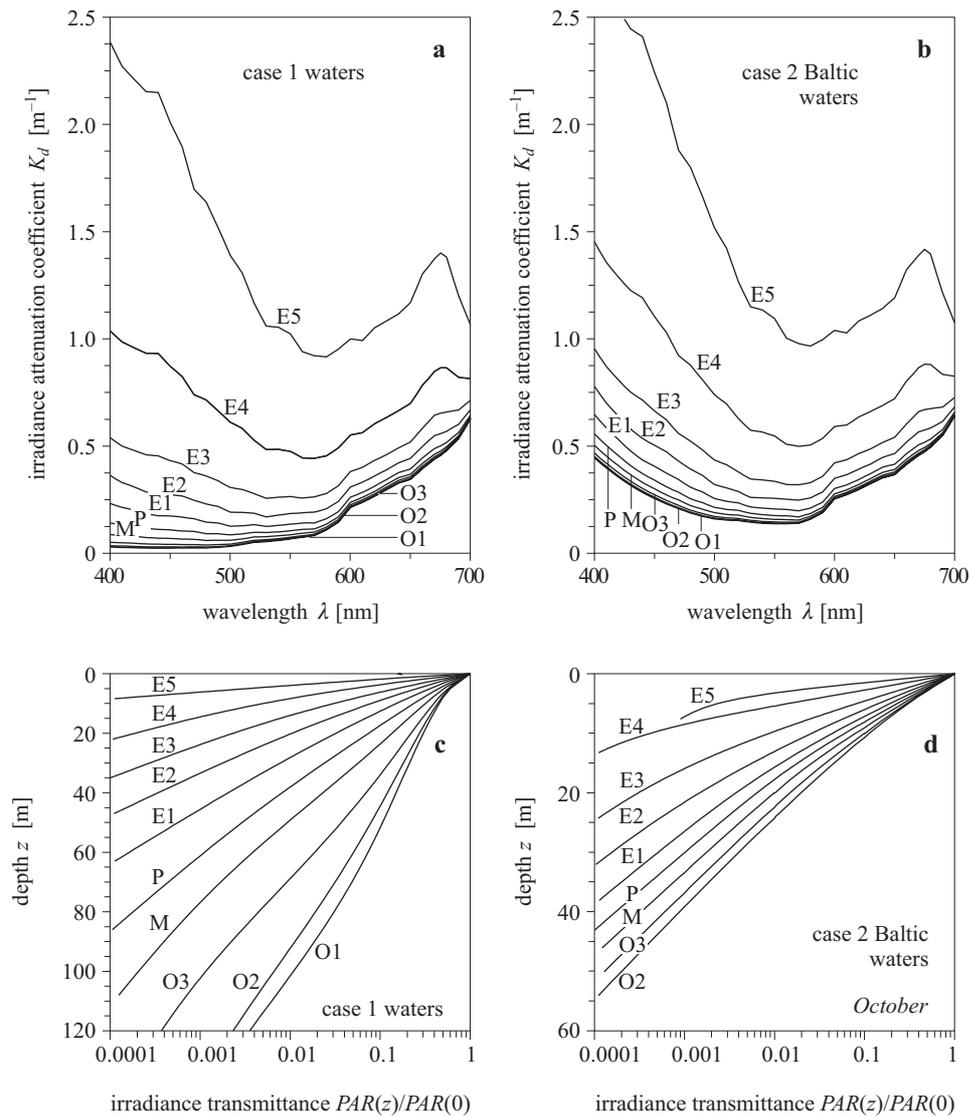
Fig. 3. Modelled spectra of the downward irradiance attenuation coefficient $K_d(\lambda)$ in different trophic types of basins (a and b) and vertical profiles of the irradiance transmittance $PAR(z)/PAR(0)$ in various trophic types of basin (c and d)

The trophicity types of basins and their symbols used on the graphs (O1–E5) are defined in Annex 2, Table A2.1

shall describe only the model of the optical properties of various types of sea that enables the most important spatial and spectral characteristics of the underwater irradiance to be defined using the bio-optical classification developed by Woźniak and his co-workers.

This classification, first put forward by Woźniak & Pelevin (1991), generalises the results of statistical analyses of the relations between the empirical spectra of the downward irradiance attenuation coefficient ($K_d(\lambda)$) and its components, and the chlorophyll a concentration in the water (C_a). It was later modified, and in its current form describes the relationships between the downward irradiance attenuation coefficients and the chlorophyll concentration C_a in various trophic types of sea and in the two water cases distinguished by Morel & Prieur (1977), i.e. oceanic case 1 waters and case 2 waters (e.g. the Baltic). In this classification it is assumed that the overall attenuation coefficient of the downward irradiance $K_d(\lambda)$ is the sum of the following terms (after Woźniak et al. 1992a, b, Kaczmarek & Woźniak 1995):

$$K_d(\lambda) = K_w(\lambda) + K_{pl}(\lambda) + K_\Delta(\lambda) + \Delta K(\lambda), \tag{12}$$

where the terms on the right hand side of this equation represent the components of the total downward irradiance attenuation coefficient derived from the various components of sea water:

$K_w(\lambda)$ – pure water;

$K_{pl}(\lambda)$ – phytoplankton;

$K_\Delta(\lambda)$ – optically active autogenic components of sea water (yellow substance, organic and inorganic detritus);

$\Delta K(\lambda)$ – allogenic components (e.g. various mineral and organic substances entering the sea from rivers and the atmosphere).

These coefficients are related to the chlorophyll concentration C_a by appropriate regression equations (which none the less have a definite physical sense – see Woźniak & Pelevin 1991):

$$K_d(\lambda) = K_w(\lambda) + C_a\{c_1(\lambda) \exp[-a_1(\lambda)C_a] + k_{d,\,i}(\lambda)\} + \Delta K(\lambda), \tag{13}$$

$$\Delta K(\lambda) = 0 \quad \text{for oceanic case 1 waters,} \tag{14}$$

$$\Delta K(\lambda) = b \exp[s(\lambda_0 - \lambda)] \quad \text{for Baltic case 2 waters,} \tag{15}$$

where

– the statistical values of the parameters $K_w(\lambda)$, $a_1(\lambda)$, c_1, $k_{d,\,i}(\lambda)$, presented in tabular form (for given wavelengths in the 400–750 nm interval with a step of $\Delta\lambda = 10$ nm) are given, e.g. in Woźniak et al. (1992a, b) – see Table A1.1 in Anex 1;

– the remaining parameters are (after Kaczmarek & Woźniak 1995):

$$b = \Delta K(\lambda_0) = 0.068 \; m^{-1}, \tag{16}$$

where $\lambda_0 = 550$ nm; $s = -0.014$ nm^{-1}.

These regression equations are based on the analysis of c. 1300 empirical data containing chlorophyll concentration measurements and spectral

attenuation coefficients of downward irradiance, and of around 1100 measurements of coefficients of light absorption by phytoplankton. The relative errors of the estimation of $K_d(\lambda)$ are: systematic, from –10 to +16%, depending on the wavelength, and statistical ±48%, and of $K_{pl}(\lambda)$ are: systematic, from –10 to +18%, and statistical ±51%.

Beginning with these equations (12)–(16) for the bio-optical classification of waters (see Fig. 3) and applying the formal definitions and relationships between different optical functions (cf. e.g. Jerlov 1976, Dera 1992, Gordon 2002), we can determine the various characteristics of underwater irradiance fields required for modelling purposes (see block 11 in Fig. 1):

• the function of the relative spectral distribution of downward irradiance in the sea:

$$f_E(\lambda,\, z) = f_E(\lambda,\, 0) \exp\left[-\int\limits_0^z K_d(\lambda,\, z)dz\right];\tag{17}$$

• the spectral distributions of these irradiances:

$$E_d(\lambda,\, z) = PAR(0^+)f_E(\lambda,\, z);\tag{18}$$

• the transmittance of PAR energy into the sea:

$$T(z) = \int\limits_{400}^{700} f_E(\lambda,\, z)d\lambda;\tag{19}$$

• depth profiles of overall irradiances in the PAR range:

(downward vectors) $PAR(z) = PAR(0^+)\,T(z),$ (20)

(scalar) $PAR_0(z) \approx 1.2PAR(0^+)\,T(z),$ (20 a)

where $f_E(\lambda,\, 0) = E_d(\lambda,\, 0^+)/PAR(0^+)$ is a typical spectral function of the relative distribution of the downward irradiance at depth $z = 0$ with respect to PAR(0^+) entering the sea (given, e.g. in Woźniak & Hapter 1985, Dera 1995). In this paper, the following polynomial approximation has been applied to calculate the $f_E(\lambda,\, 0^+)$ dependency:

$$\begin{aligned}f_E(\lambda,\, 0^+) = {}&-1.3702 \times 10^{-12}\lambda^4 + 3.4125 \times 10^{-9}\lambda^3 - 3.1427 \times \\ &\times 10^{-6}\lambda^2 + 1.2647 \times 10^{-3}\lambda - 1.8381 \times 10^{-1},\end{aligned}\tag{21}$$

where λ is expressed in [nm].

Figs. 3 and 4e–h exemplify the results of various optical characteristics determined from the model for different trophic types of sea and the two optical cases of water. The optical characteristics predicted by the model are clearly a good approximation of the empirical data (see e.g. the empirical and modelled spectral distributions of irradiance doses illustrated in Fig. 4).
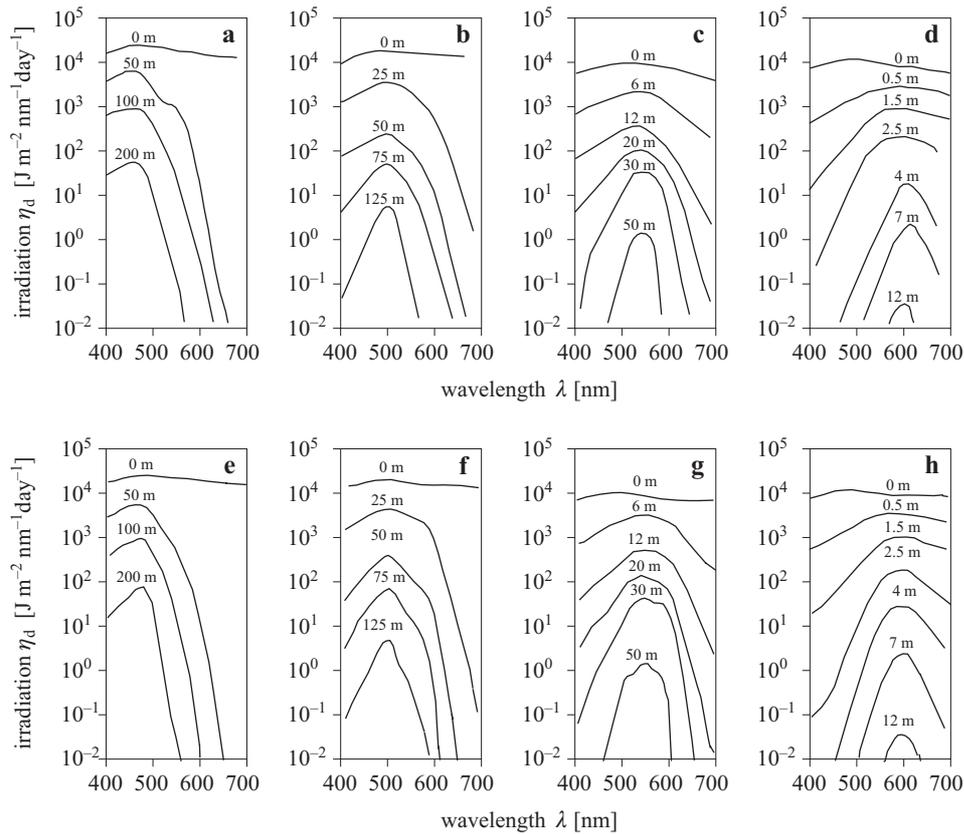
Fig. 4. Examples of spectral distributions of daily irradiance doses (irradiation) at different depths in the sea and for various surface concentrations of chlorophyll a, $C_a(0)$ [mg tot. chl a m^{-3}] of: (a, b, c, d) measured in various seas and oceans: Indian Ocean, $C_a(0) = 0.035$ mg tot. chl a m^{-3} (a), Arabian Sea, $C_a(0) = 0.32$ mg tot. chl a m^{-3} (b), Gulf of Burgas, $C_a(0) = 3.7$ mg tot. chl a m^{-3} (c), Puck Bay, $C_a(0) = 70$ mg tot. chl a m^{-3} (d); (e, f, g, h) modelled for different water types (the surface irradiances are assumed to be the same): O1 – $C_a(0) = 0.035$ mg tot. chl a m^{-3} (e), M – $C_a(0) = 0.35$ mg tot. chl a m^{-3} (f), E2 – $C_a(0) = 3.5$ mg tot. chl a m^{-3} (g), E6 – $C_a(0) = 70$ mg tot. chl a m^{-3} (h)

5. Statistical model of photo- and chromatic acclimation (block 6 in Fig. 1)

Besides chlorophyll a, the principal pigment involved in photosynthesis, phytoplankton contains a whole range of accessory pigments that affect its light absorption capacity to different extents (see Table 3). According to the parts these pigments play, they can be divided into two main groups (Steemann Nielsen 1975).

Table 3. Classification of plant pigments according to their function in the photosynthetic apparatus

	Pigments		
basic pigment	photosynthetic (PSP) 'antennas'	photoprotecting (PPP)	other functions

– chlorophyll *a* (bacteriochlorophyll *a*)	– chlorophylls *a*, *b*, *c* and others
	– phycobilins
	– PSC carotenoids including:
	  fucoxanthin,
	  19'but-fucoxanthin,
	  19'hex-fucoxanthin,
	  peridinin, prasinoxanthin,
	  α-carotene
		– PPC carotenoids including:
		  antheraxanthin,
		  diadinoxanthin,
		  alloxanthin, diatoxanthin,
		  dinoxanthin, lutein,
		  violaxanthin, neoxanthin,
		  zeaxanthin, β-carotene
			pheopigments

where
PSP – photosynthetic pigments,
PPP – photoprotecting pigments,
PSC – photosynthetic carotenoids,
PPC – photoprotecting carotenoids.

The first of these groups consists of the so-called *photosynthetic pigments* (PSP), which act as antennae absorbing light quanta. Among them, chlorophyll a is fundamental to the process of photosynthesis. The excitation energy of the accessory PSP migrates to the chlorophyll a at the PS1 and PS2 reaction centres (RC). The whole set of PSP contains all the chlorophylls (chlorophyll a, chlorophylls b, chlorophylls c, bacterial chlorophylls), as well as various photosynthetic carotenoids (PSC), such as fucoxanthin, 19′but-fucoxanthin, 19′hex-fucoxanthin, peridinin, prasino-xanthin, α-carotene (see e.g. Bidigare et al. 1990). The concentration of these pigments is related to the processes of chromatic acclimation. The other group of accessory pigments contains the so-called photoprotecting pigments (PPP) – their occurrence is governed by the process of photo-acclimation. It is the task of these pigments to protect the photosynthetic apparatus from high-energy light quanta (mainly in the spectral range $\lambda < 480$ nm), which could cause photo-oxidation of chlorophyll a molecules. The PPP include a wide variety of carotenoids, but principally (after Bidigare et al. 1990) diadinoxanthin, alloxanthin, zeaxanthin, diatoxanthin, lutein, antheraxanthin, β-carotene, violaxanthin, neoxanthin and dino-xanthin. The energy absorbed by these pigments is not utilised during photosynthesis.

Like the concentration of chlorophyll a, the concentrations of the accessory pigments of marine phytoplankton display considerable spatial and temporal variation, as shown in Fig. 5. The scale of differences is also similar, around four orders of magnitude. Additionally, the relative contents of these pigments, e.g. with respect to the chlorophyll a concentration, vary remarkably depending on the water trophicity and depth in the sea. This is illustrated in Fig. 5 where typical vertical distributions of the four main sets (sub-groups) of accessory pigments are presented (the photoprotecting carotenoids – PPC, chlorophylls b, chlorophylls c and photosynthetic carotenoids PSC). The differentiation in the relative concentrations of these accessory pigments evident from the figures suggests that it is without doubt related to the irradiance conditions of the plant cells and is due to the photo- and chromatic accommodation processes occurring in them.

The first of these processes, photo-adaptation, controls the content of accessory PPC. As can be seen from Fig. 5a, the relative concentrations of all these pigments decrease with depth. This is because at small depths, especially in oligotrophic waters, the absolute irradiance is large, and includes light from the blue region of the spectrum, i.e. from the spectral range capable of causing photo-oxidation of chlorophyll a. Under such conditions, the plant produces large quantities of protective pigments. At greater depths, however, the absolute quantities of radiant energy from
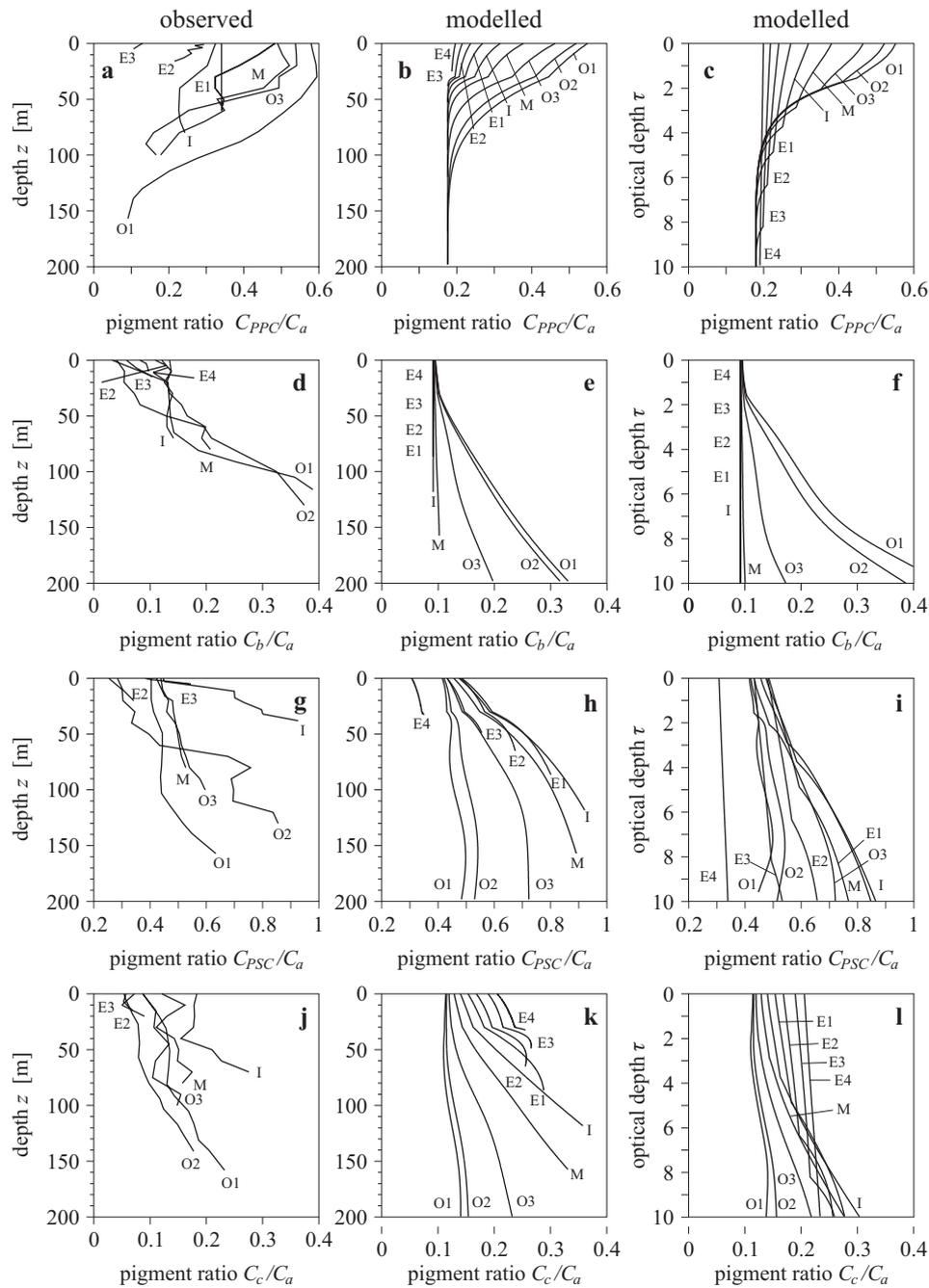
Fig. 5. Typical examples of depth profiles of the relative concentrations of accessory pigments: measured (a, d, g, j), modelled for real depth z [m] (b, e, h, k) and modelled for optical depth τ (c, f, i, l): photoprotecting carotenoids C_{PPC}/C_a (a, b, c), chlorophylls b, C_b/C_a (d, e, f), photosynthetic (*continued* on page 193)

the blue region are much smaller, so photo-protective pigments are not essential, and their relative concentrations decrease with depth.

In the case of chromatic adaptation, which controls the PSP content, the relationships are mostly inverse ones (Fig. 5d, g, j). The relative content of accessory antennas usually increases with depth, but this is not a universal property: in some cases, starting from certain depths, their content can fall. More complex still is the dependence of these relationships on the water trophicity, the index of which is the chlorophyll a concentration.

The problem of the adaptation of the photosynthetic apparatus in phytoplankton cells to the ambient underwater irradiance is a complex one and has been investigated by many authors (e.g. Steemann Nielsen 1975 and the papers cited therein, Zvalinsky 1986, Babin et al. 1996a, b, c). Among other things, relationships between the concentrations of individual accessory pigments in cells and the various optical characteristics of natural irradiance fields in the sea have been demonstrated. However, precise quantitative investigations of these relationships have not been carried out. It is only very recently that they were first subjected to quantitative analysis – in the papers by Woźniak et al. (1999), Majchrowski & Ostrowska (1999, 2000) and Majchrowski (2001).

These authors aimed to find statistical relationships between the concentrations of accessory pigments in natural populations of marine phytoplankton, and the absolute levels and spectral distributions of the underwater irradiance. To do this, they analysed empirical material from some 400 stations in different regions of the World Ocean. This data included vertical profiles of pigment concentrations and vertical spectral distributions of the downward irradiance. The analysis covered over 4500 points where the relations between the irradiance spectrum and the different pigment concentrations at various depths in the sea were measured. The most significant results will now follow in brief.

Chromatic acclimation

The statistical analyses of the measurement data yielded relations between the concentrations of individual accessory PSP, i.e. chlorophylls b, chlorophylls c and PSC, and the same characteristics of the irradiances. It appears that these concentrations are strongly dependent on the normalised

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carotenoids C_{PSC}/C_a (g, h, i), chlorophylls c, C_c/C_a (j, k, l). These profiles were determined for various trophic types of waters defined on the basis of the surface concentration of chlorophyll a

The concentrations, trophic types of waters and their symbols given on the graphs (O1–E4) are defined in Annex 2, Table A2.1

spectral distribution of the irradiance in the PAR spectral range $f(\lambda, z)$ $= E_d(\lambda, z)/PAR(z)$, but only slightly dependent on absolute irradiances $E_d(\lambda)$. The relevant statistical approximations describing the relationships between the relative concentrations of the individual PSP and the so-called spectral fitting functions F_i, averaged in the water layer $\Delta z = z_2 - z_1$ m in order to take account of mixing processes, are as follows:

$$C_{PSC} = (1.348 < F_{PSC} >_{\Delta z} - 0.093) \, C_a, \tag{22}$$

$$C_b = (54.07 < F_b >_{\Delta z}{}^{5.157} + 0.091) \, C_a, \tag{23}$$

$$C_c = (0.042 < F_a >_{\Delta z}{}^{-1.197} < F_c >_{\Delta z} \, C_a, \tag{24}$$

where

$$< F_j >_{\Delta z} = \frac{1}{z_2 - z_1} \int\limits_{z_1}^{z_2} F_j(z) dz, \tag{25}$$

$$z_1 = \begin{cases} 0 & \text{for} \quad z < 30\,\text{m} \\ z - 30\,\text{m} & \text{for} \quad z \geq 30\,\text{m} \end{cases}, \quad z_2 = z + 30\,\text{m}.$$

The spectral fitting functions F_j for the j-th pigment, otherwise known as *chromatic adaptation factors*, are taken to be

$$F_j = \frac{1}{a^*_{j,\,\text{max}}} \int\limits_{400\,\text{nm}}^{700\,\text{nm}} f(\lambda) \; a^*_j(\lambda) d\lambda, \tag{26}$$

where

$a^*_j(\lambda)$ – spectral specific coefficient of absorption for the j-th group of pigments (for chlorophyll a – $a^*_a(\lambda)$, for chlorophylls b – $a^*_b(\lambda)$, for chlorophylls c – $a^*_c(\lambda)$ and for PSC – $a^*_{PSC}(\lambda)$);

$a^*_{j,\,\text{max}}$ – specific absorptions of the j-th group of pigments at their spectral maxima;

$f(\lambda, z) = \frac{E_d(\lambda, z)}{PAR(z)}$ – normalised, spectral distribution function of irradiance in the sea.

Empirical validation of the above approximate formulas determining the relative concentrations of the individual PSP leads to the conclusion that its accuracy varies for different pigments. The best approximation was obtained for photosynthetic carotenoids; for chlorophylls c and b the formulas are somewhat less accurate. For instance, the standard error factor (determined in accordance with the explanation given in Table 5, this paper, p. 204) of the relative concentration of PSC (C_{PSC}/C_a) is c. 1.32. For the other photosynthetic pigments the standard error factor is slightly higher: c. 1.52 for (C_c/C_a) and c. 1.62 for (C_b/C_a).

Photo-acclimation

The analyses also showed that the occurrence of photoprotecting carotenoids (PPC) is controlled by radiation in the short-wave (blue) region of the PAR spectrum. The following mathematical form of the relationship describing the relative concentrations of PPC(z) (with respect to chlorophyll a) was established as a function of the so-called *Potentially Destructive Radiation* (PDR), averaged in the $\Delta z = z_2 - z_1$ layer in order to take account of mixing processes:

$$C_{PPC} = (0.1758 \times 10^6 < PDR^* >_{\Delta z} + 0.176)C_a, \tag{27}$$

where

$$< PDR^* >_{\Delta z} = \frac{1}{z_2 - z_1} \int\limits_{z_1}^{z_2} PDR^*(z)dz, \tag{28}$$

$$z_1 = \begin{cases} 0 & \text{for} \quad z < 30\,\text{m} \\ z - 30\,\text{m} & \text{for} \quad z \geq 30\,\text{m} \end{cases}, \quad z_2 = z + 30\,\text{m}.$$

By PDR^* we mean here the magnitude of the daily mean power of light from $\lambda < 480$ nm spectral range absorbed by unit mass of chlorophyll [Ein(mg tot. chl a)$^{-1}$ s^{-1}]. In actual fact this power should be taken from previous day of the study, when these data are not usually available. The similarity between the irradiance conditions during the measurement day and the day before is therefore assumed):

$$PDR^* = \int\limits_{\lambda=400\,\text{nm}}^{\lambda=480\,\text{nm}} a_a^*(\lambda) \; \langle E_0(\lambda) \rangle_{\text{day}} d\lambda, \tag{29}$$

where
$E_0(\lambda)$ – typical scalar irradiance in the medium;
$\langle E_0(\lambda) \rangle_{\text{day}}$ – mean daily scalar irradiance in the medium;
$a_a^*(\lambda)$ – specific coefficient of light absorption by chlorophyll a.

The accuracy of the estimate of photoprotecting pigments (PPC) from expression (27) is relatively good; empirical validation yields a standard error factor for the determination of (C_{PCC}/C_a) equal to 1.47.

On the basis of these dependencies (see eqs. (22)–(29)) one can define depth profiles of the changes in the principal pigment groups in various trophic types of seas, from oligotrophic to eutrophic. The results of these calculations are illustrated in Figs. 5b, c, e, f, h, i, k, l. Clearly, the modelled depth profiles showing the changes in concentrations of these pigments resemble the experimental profiles – see Figs. 5a, d, g, j.

6. Model of spectral light absorption of algal pigments
   in vivo (block 7 in Fig. 1)

The process preceding and stimulating photosynthesis in plants is the absorption of light by plant pigments. That is why the spectra of light absorption by algae $a_{pl}(\lambda)$ are principally responsible for the photosynthetic properties of seas. As we know, the resultant light absorption capacity of algae depends on the contents of all the pigments – photosynthetic (PSP) and photoprotecting (PPP) – in their cells. So, assuming additive absorption, the overall coefficients of light absorption by algae a_{pl} are given by the sum

$$a_{pl}(\lambda) = a_{pl, PSP}(\lambda) + a_{pl, PPP}(\lambda), \tag{30}$$

where $a_{pl, PSP}$ are the coefficients of absorption by all photosynthetic pigments and $a_{pl, PPP}$ are the coefficients of absorption by all photoprotecting pigments. However, when analysing these coefficients for the purposes of modelling photosynthesis, we have to remember that under *in vivo* conditions, it is only PSP that transfer absorbed energy to chlorophyll a in the photosynthetic centres, where it can then be utilised for photosynthesis. Thus, solely the component $a_{pl, PSP}(\lambda)$ affects photosynthesis directly; light absorption by non-photosynthetic (photoprotecting) pigments $a_{pl, PPP}(\lambda)$ does not have a direct influence on the process.

The natural absorption properties of algae are strongly differentiated (see Fig. 6a). Detailed quantitative analyses of this differentiation with respect to various depths in the sea and different trophicities were carried out in some of our earlier papers, e.g. Woźniak & Ostrowska (1990a, b). Here, only the main points will be recapitulated, in so far as they are useful for modelling photosynthesis in algae.

The main factor differentiating the absorption properties of algae is the absolute concentration of chlorophyll a. The range of values of spectral coefficients $a_{pl}(\lambda)$ in waters of different trophicity and at different depths is thus generally similar to the spatial range of concentrations C_a and likewise covers four orders of magnitude. However, the inclusion of only the chlorophyll a concentration in the description of the coefficients a_{pl} will not suffice. The relevant evidence for this will be found in the differentiation of the spectral specific coefficients of absorption, i.e. $a_{pl}^* = a_{pl}/C_a$ (see Figs. 6b and 7a). This is due to the fact that in algae flourishing under a diversity of irradiance conditions, various quantities of different accessory pigments are produced during the processes of photo-adaptation and chromatic adaptation (see the previous section). Moreover, the effects of the overall absorption by pigments are also governed by the various ways in which they are packed in the
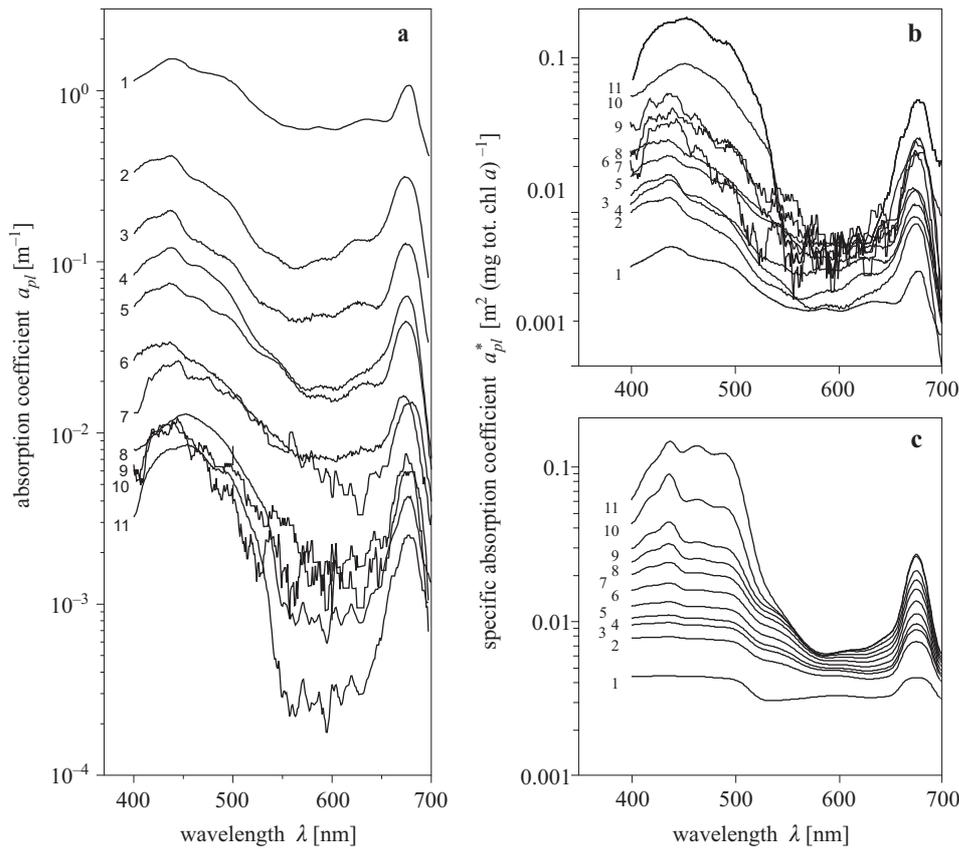
Fig. 6. Comparison of phytoplankton spectral absorption (a) and specific absorption (b, c) coefficients: measured *in situ* (a and b); determined with our model (c). The numbers allotted to the spectra indicate the following trophic types of seawater: $1 - C_a(0) = 156$ mg tot. chl a m^{-3}, $2 - C_a(0) = 33.2$ mg tot. chl a m^{-3}, $3 - C_a(0) = 11.4$ mg tot. ch 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 Majchrowski et al. 2000)

phytoplankton cells. These effects are described by the so-called package function $Q^*(\lambda)$, defined below by equation (30), and are discussed in detail in articles such as those by van de Hulst (1981) and Morel & Bricaud (1981).

The models of the absorption properties of algae constructed earlier (Woźniak & Ostrowska 1990b, Bricaud et al. 1995, 1998) are 'monocomponental' in nature, that is, the description of these properties takes only the concentration of chlorophyll a into consideration. They ignore the adaptive
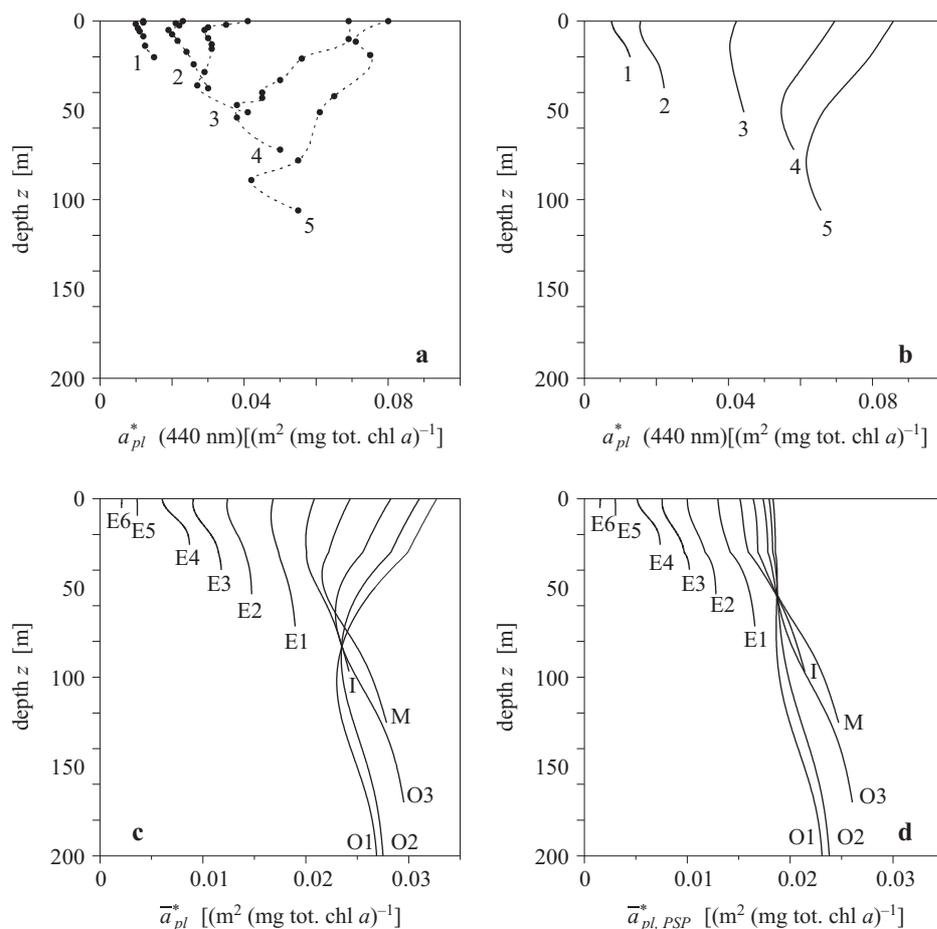
Fig. 7. Examples of observed (a) and modelled (b) depth profiles of specific absorption coefficients for $\lambda = 440$ nm in different trophic types of sea. Baltic Sea: $1 - C_a(0) \approx 16$ mg tot. chl a m^3, $2 - C_a(0) \approx 5.9$ mg tot. chl a m^3, $3 - C_a(0) \approx 1.1$ mg tot. chl a m^3; Black Sea: $4 - C_a(0) \approx 0.31$ mg tot. chl a m^3, $5 - C_a(0) \approx 0.13$ mg tot. chl a m^3 (data from cruises: r/v 'Siedlecki' (Baltic, 1981) and r/v 'Vityaz' (Black Sea, 1978) – see Koblentz–Mishke et al. (eds.) 1985).

Modelled depth profiles of mean specific absorption coefficients for total phytoplankton pigments $\bar{a}_{pl}$ (c) and for photosynthetic pigments $\bar{a}_{pl,PSP}$ (d) (after Majchrowski et al. 2000)

mechanisms mentioned above – photo- and chromatic accommodation, and the package effect. The magnitudes of $a_{pl}^*(\lambda)$ calculated with the aid of these models are thus considerably lacking in accuracy. Furthermore, they enable only the overall absorptions (by PSP and PPP) to be determined. They are therefore of limited usefulness in modelling photosynthesis, which is stimulated only by the light absorbed by PSP.

The first non-trivial model to take these nuances into account is the one developed by the present authors in recent years – it will be used in the later sections of this paper. Created in stages, it was based on Gaussian decompositions of a set of c. 1400 empirical spectra of $a_{pl}(\lambda)$, and on the relevant statistical analyses of the relations between the coefficients $a_{pl}(\lambda)$, the concentrations of the various pigments and the different characteristics of irradiance fields in the sea. The details of these procedures will be found, for example, in Woźniak et al. (1999, 2000), Woźniak (2000), Woźniak & Dera (2000), Majchrowski et al. (2000), and Majchrowski (2001). The model is a multi-component one, which means that it accounts for absorption by all the main groups of pigments. It enables not only the coefficients of overall absorption by all the algal pigments $a_{pl}(\lambda)$ and $a_{pl}^*(\lambda)$ to be determined: the component coefficients due to PSP and PPP $a_{pl,PSP}(\lambda)$, $a_{pl,PPP}(\lambda)$, $a_{pl,PSP}^*(\lambda)$ and $a_{pl,PPP}^*(\lambda)$ can also be found from the model. Analysis of the package function $Q^*(\lambda)$ is also possible.

The scope of the modelling process will now be outlined.

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 (unpackaged) a_{sol}^* of the same cellular matter, ideally dispersed in solution. The effect is determined by a dimensionless factor $Q^* = a_{pl}^*/a_{sol}^*$, which is a function of the wavelength formulated as follows (Morel & Bricaud 1981, van de Hulst 1981):

$$\left.\begin{array}{l} Q^*(\lambda) = (3/2)\{1 + 2[\exp(-\rho'(\lambda))/\rho'(\lambda)] + \\ \quad + [2/(\rho'(\lambda)^2)][\exp(-\rho(\lambda)) - 1]\} \\ p'(\lambda) = a_{sol}^*(\lambda)C_I\ d \end{array}\right\}, \qquad (31)$$

where C_I – the intracellular 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 conditions (see the explanation in Bricaud et al. 1995). 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 chlorophyll concentrations $C_a(z)$ or $C_a(\tau)$ with the surface chlorophyll $C_a(0)$ (see Figs. 8a and b). From this similarity, the following formula for $C_I\ d$ was established:

$$C_I\ d = 24.65\,C_a^{0.75015}, \qquad (32)$$

where $C_I\ d$ is given in [mg tot. chl a m^{-2}] and C_a in [mg tot. chl a m^{-3}].

The graphical representation of formula (32) is given in Fig. 8c. The formula is applied to determine $C_I\ d$ in the relevant equations of the phytoplankton absorption model presented later in this paper. The model

dependence of the chlorophyll concentration C_a on depth and surface chlorophyll concentration given in eqs. (1)–(5) can be applied together with formula (32) to determine the distribution of the products $C_I\, d$ in various types of seas (see the examples in Fig. 8d).
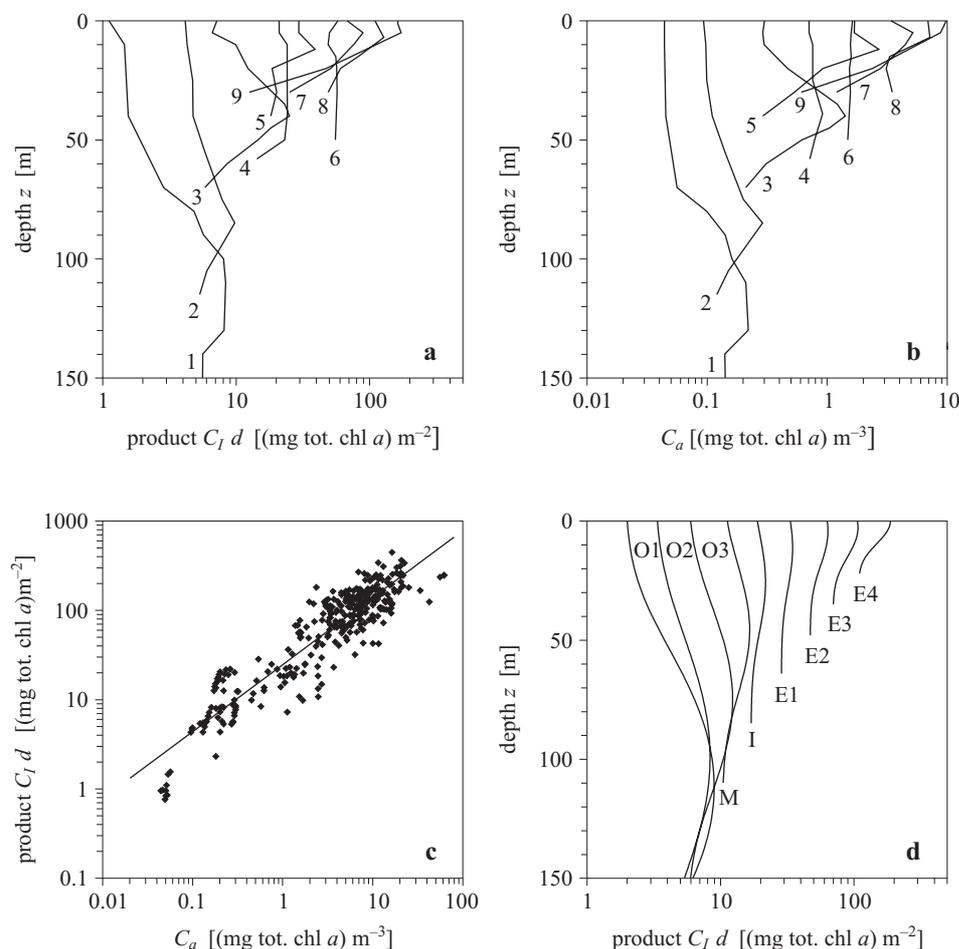
Fig. 8. Relations of the product $C_I\, d$ with the total chlorophyll a concentration C_a and depth in the sea (after Woźniak et al. 1999): 8a – empirical vertical profiles of the product $C_I\, d$: Atlantic – curves 1–3, Baltic – curves 4–9, 8b – examples of empirical total chlorophyll a concentration profiles $C_a(z)$ for the same stations as in 8a, 8c – relationship between the product $C_I\, d$ and the chlorophyll concentration C_a observed (points) and approximated by formula (32) (line), 8d – modelled vertical profiles of $C_I\, d$ in various trophic types of stratified case 1 waters (curves O1–E4 correspond to various water trophicities as defined in Annex 2, Table A2.1). In Fig. 8d the $C_a[C_a(0),\, z]$ model from Woźniak et al. (1992a, b) was applied

As this figure shows, the typical values of $C_I d$ vary over a range of almost three orders of magnitude and increase as the trophic index $C_a(0)$ does so. They are also depth-dependent: the nature of these changes is similar to that displayed by the vertical variability in chlorophyll concentration in seas of different trophicity (see e.g. Figs. 8d and 8b).

Absorption coefficient

The specific light absorption coefficient of living phytoplankton $a_{pl}^*(\lambda)$ can be expressed as follows:

$$a_{pl}^*(\lambda) = C_a^{-1} Q^*(\lambda) \sum_{j}^{n} a_j^*(\lambda) C_j, \tag{33}$$

(where a_j^* and C_j are the spectral specific absorption coefficients for the j-th group of 'unpackaged' pigments and their concentrations respectively). The similar components for PSP $a_{pl, PSP}^*(\lambda)$ and PPP $a_{pl, PPP}^*(\lambda)$ are

$$\begin{aligned} a_{pl, PSP}^*(\lambda) &= C_a^{-1} Q^*(\lambda)[a_a^*(\lambda)C_a + a_b^*(\lambda)C_b + a_c^*(\lambda)C_c + \\ &\quad + a_{PSC}^*(\lambda)C_{PSC}], \end{aligned} \tag{34}$$

and

$$a_{pl, PPP}^*(\lambda) = C_a^{-1} Q^*(\lambda)[a_{PPP}^*(\lambda)C_{PPP}]. \tag{35}$$

Owing to measurement difficulties, we have not taken phycobilin pigments into consideration in our model of the coefficients of absorption of light by phytoplankton. Nevertheless, as these pigments occur but rarely in marine algae (see e.g. Parsons et al. 1977, Woźniak & Ostrowska 1990a, Majchrowski 2001), their effect on the resultant absorption of light by natural plant communities can be neglected.

These expressions are functions of numerous variables (all except the coefficients $a_j^*(\lambda)$ explained in the previous sections). Gaussian analysis of the empirical material yielded formulas describing the specific spectral coefficients of absorption $a_j^*(\lambda)$ of the various groups of pigments: $a_a^*(\lambda)$ for chlorophyll a; $a_b^*(\lambda)$ for chlorophylls b; $a_c^*(\lambda)$ for chlorophylls c; $a_{PSC}^*(\lambda)$ for photosynthetic carotenoids (PSC); $a_{PPP}^*(\lambda)$ for photoprotecting pigments (PPP). They refer to the absorption of light by pigments in the unpackaged state and are expressed as the sum of Gaussian bands:

$$a_j^*(\lambda) = \sum_{i} a_{\max, i}^* \; e^{-\frac{1}{2}\left(\frac{\lambda - \lambda_{\max, i}}{\sigma_i}\right)^2}, \tag{36}$$

where
$\lambda_{\max, i}$ [nm] – the centre of the spectral peak of the band [nm];
σ_i [nm] – band dispersion;

$a^*_{\max, i}\,[\mathrm{m^2\,(mg\ pigment)^{-1}}]$ – specific absorption coefficient at the spectral peak of the band;

i – number of the band on the Gaussian curve for the main groups of phytoplankton pigments (i.e. chlorophylls a, chlorophylls b, chlorophylls c, PSC and PPC). The magnitudes $\lambda_{\max, i}$, σ_i and $a^*_{\max, i}$ are given in Table 4. The complete spectra of these coefficients are given in Fig. 9.
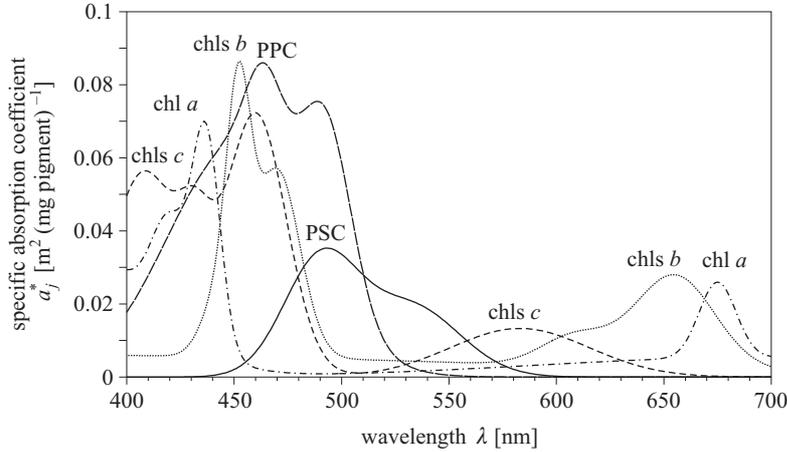
Fig. 9. 'Unpackaged' specific absorption spectra modelled for the major pigment groups

The coefficient of light absorption by all phytoplankton pigments $a_{pl}(\lambda)$, by PSP $a_{pl,PSP}(\lambda)$ and PPP $a_{pl,PPP}(\lambda)$ are determined from the specific absorption coefficient in accordance with the relationships:

$$a_{pl}(\lambda) = a^*_{pl}(\lambda)\,C_a, \tag{37}$$

$$a_{pl,PSP}(\lambda) = a^*_{pl,PSP}(\lambda)\,C_a, \tag{38}$$

$$a_{pl,PPP}(\lambda) = a^*_{pl,PPP}(\lambda)\,C_a. \tag{39}$$

Estimating errors and practical applications

The spectra of the coefficients of light absorption $a^*_{pl}(\lambda)$ by algae determined from the model are fairly good approximations of the corresponding empirical spectra. This is evident from the comparisons of the modelled and empirical spectra given in Figs. 6b and 6c. The accuracy of the model has been verified empirically: the magnitudes of mean coefficients $\overline{a_{pl}}$ (in the spectral range 400–700 nm) determined from known pigment compositions (C_j) with the aid of the model equations were compared with similar mean coefficients determined from empirical spectra $a_{pl}(\lambda)$. The relatively small errors shown up by this verification are given in Table 5.

Table 4. Model characteristics of the specific absorption components of Gaussian bands (see eq. (36)) after Woźniak et al. (1999)

chlorophylls a (A-1 – A-6) and chlorophylls b (B-1 – B-6)

Characteristic	Gaussian band number											
	A-1	A-2	A-3	A-4	A-5	A-6	B-1	B-2	B-3	B-4	B-5	B-6
$\lambda_{\max, i}$	381	420	437	630	675	700	380	442	452	470	609	655
σ_i	33.8	8.25	6.50	89.8	8.55	101	194	7.45	5.6	10.5	16.0	18.5
$a^*_{\max, i}$	0.0333	0.0268	0.058	0.0005	0.0204	0.005	0.0059	0.0145	0.0631	0.0514	0.0083	0.0257

chlorophylls c (C-1 – C-4), photosynthetic (PSC-1, PSC-2) and photoprotecting (PPC-1 – PPC-3) carotenoids

Characteristic	Gaussian band number								
	C-1	C-2	C-3	C-4	PSC-1	PSC-2	PPC-1	PPC-2	PPC-3
$\lambda_{\max, i}$	408	432	460	583	490	532	451	464	493
σ_i	16.1	7.93	14.2	32.2	17.1	22.8	32.0	8.60	12.0
$a^*_{\max, i}$	0.0561	0.0234	0.0072	0.0133	0.0313	0.0194	0.0632	0.0253	0.0464

where
$\lambda_{\max, i}$ – centre of band [nm],
σ_i – dispersion of band [nm],
$a^*_{\max, i}$ – specific absorption coefficient at the maximum [m^2 (mg pigment)$^{-1}$].

Table 5. Errors of the estimation of the absorption coefficient $\bar{a}_{pl}$, determined using the described model

Arithmetic statistics		Logarithmic statistics			
systematic	statistical	systematic	standard error factor	statistical	
$\langle \varepsilon \rangle$ [%]	σ_ε [%]	$\langle \varepsilon \rangle_g$ [%]	x	σ_- [%]	σ_+ [%]
7.42	± 33.3	2.49	1.36	-26.5	36.0

where

$\varepsilon = (\bar{a}_{pl,C} - \bar{a}_{pl,M})/\bar{a}_{pl,M}$ – errors,

$(\bar{a}_{pl,M}$ and $\bar{a}_{pl,c})$ – measured and determined using the described model, values of absorption coefficient $\bar{a}_{pl}$,

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

σ_ε – standard deviation of errors (statistical error),

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

$\langle \log(\bar{a}_{pl,C}/\bar{a}_{pl,M})\rangle$ – mean of $\log(\bar{a}_{pl,C}/\bar{a}_{pl,M})$,

$\sigma_{\log}$ – standard deviation of $\log(\bar{a}_{pl,C}/\bar{a}_{pl,C})$,

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

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

$\sigma_+ = x - 1$.

These errors are also much smaller than the corresponding ones in our previous estimates for two earlier models: by Woźniak & Ostrowska (1990b), and by Bricaud et al. (1995). For example, the statistical error σ_+ for our present model is c. 36%, whereas for the model by Bricaud et al. it was 43%, and for the one by Woźniak & Ostrowska c. 59%. Clearly, the present model gives the best approximation of empirical data.

Examples of the model's practical applications are given in Fig. 7. This illustrates vertical profiles of these absorption coefficients in waters of various trophicities: the calculated vertical profiles of the total mean specific absorption coefficients of phytoplankton for all pigments (Fig. 7c) $\bar{a}_{pl}^*$, and those of the photosynthetic pigment component $\bar{a}_{pl,PSP}^*$ (Fig. 7d). For photosynthetic pigments $\bar{a}_{pl,PSP}^*$ (Fig. 7d), 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) $\bar{a}_{pl}^*$, there is a minimum at a certain depth in the vertical profile (Fig. 7c). This minimum moves towards the sea surface with increasing water trophicity. Above the minimum, the mean specific

absorption coefficient $\bar{a}_{pl}^*$ rises as the concentration of photoprotecting carotenoids does so. Below the minimum, the increase in the mean specific absorption coefficient $\bar{a}_{pl}^*$ is due to a rise in the relative concentrations of accessory photosynthetic pigments. The earlier two models were unable to explain this effect; our new model now enables this to be done.

7. Statistical relationships between chlorophyll a, temperature and inorganic nitrogen (block 8 in Fig. 1)

In our detailed model of photosynthetic yield (block 9 in Fig. 1), to be discussed in the next section, one of the abiotic environmental factors governing this yield is the concentration of nitrogenous nutrients in the water $N_{\mathrm{inorg}}(z)$. Without a knowledge of these concentrations at various depths in the sea, this model of quantum yield cannot be used as a component of the full model of primary production. Thus, we have to be able to estimate $N_{\mathrm{inorg}}(z)$ from remotely-sensed parameters like the surface total chlorophyll concentration $C_a(0)$ and surface temperature $temp$. Since the statistical relationships between $N_{\mathrm{inorg}}(z)$, and $C_a(0)$ and $temp$ have not yet been described mathematically, the authors had to attempt such a preliminary description (block 8 in Fig. 1), although this was not the final aim of this work, merely a means of achieving it.

To find these relationships, the empirical material was subjected to the requisite statistical analyses. Here, the assumption is that there are unequivocal relationships between the set of two marine abiotic factors – the nutrient content N_{inorg} and the temperature in the sea $temp$ – and the algal content of the water, the measure of which is the chlorophyll concentration (Kethum 1939, Eppley 1972, Kiefer & Kremer 1981, Belayev 1987). They result, among other things, from the character of the principal natural elemental cycles, whereby photosynthesis is one of the main processes controlling the intensity of these cycles (Parsons et al. 1977, Kremer & Nixon 1978, Gershanovich & Muromtsev 1982). The existence of these relationships has also been endorsed by appropriate empirical data (Koblentz-Mishke & Vedernikov 1977). They were subjected to a preliminary analysis in our earlier papers (Woźniak 1990, Woźniak et al. 1992a, b); the latest mathematical description of them is given in Ficek's dissertation (2001). With this formulation we can roughly estimate the surface concentration of nitrogen $N_{\mathrm{inorg}}(0)$ from known surface values of $C_a(0)$ and $temp$. After that, the vertical distribution of the inorganic nitrogen concentration $N_{\mathrm{inorg}}(z)$ can be determined from known values of $N_{\mathrm{inorg}}(0)$. There now follows a brief description of the consecutive stages of the analysis from which this description was developed.

The statistical dependencies of the sea's trophicity on the nitrogen content and temperature in the sea

The first stage of the analysis required an examination of the statistical relationships between the surface concentration of chlorophyll $C_a(0)$ and the mean concentration of nitrogen in the roughly 10-m-thick surface layer $N_{\mathrm{inorg}}(0)$, and between $C_a(0)$ and the surface temperature of the sea $temp$. Empirical examples of these relations are given in Fig. 10. In Fig. 10a, where 1344 empirical points of $C_a(0)$ versus $N_{\mathrm{inorg}}(0)$ have been plotted, it is quite hard to see any correlation. However, when these points are split into subgroups corresponding to narrower temperature intervals, a relationship between $C_a(0)$ and $N_{\mathrm{inorg}}(0)$ becomes apparent. With one exception, the concentrations $C_a(0)$ generally increase as the nitrogen content $N_{\mathrm{inorg}}(0)$ does so. This growth is roughly hyperbolic (cf. Fig. 10b) and to a first approximation can be described by an equation of the Michaelis-Menten type (Ketchum 1939). However, besides the areas where the empirical relations $C_a(0) = f(N_{\mathrm{inorg}}(0))$ are approximately described by the Michaelis-Menten equation, there are others which do not obey this rule. This occurs, for example, when temperatures lie between 0 and 10°C (cf. curve 1 in Fig. 10b). In these cases, above a certain optimum concentration
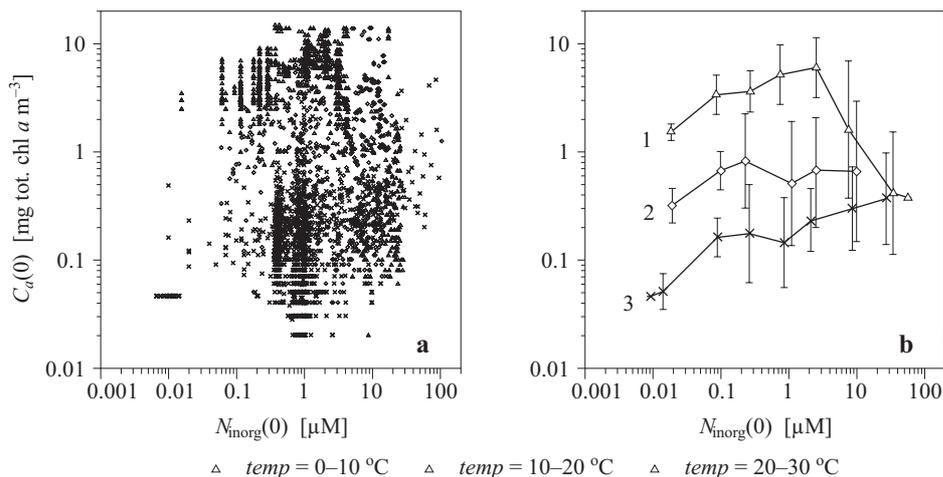
Fig. 10. Relationships between the surface concentration of chlorophyll $C_a(0)$ and the mean concentration of nitrogen in the roughly 10-m-thick surface layer $N_{\mathrm{inorg}}(0)$:
(a) plots of 1344 empirical points marked by ▲ for 0°–10°C, ♦ for 10°–20°C, × for a 20°–30°C temperature interval;
(b) average for three temperature intervals: 0°–10°C – curve 1, 10°–20°C – curve 2, 20°–30°C – curve 3

of nitrogen ($N_{\mathrm{inorg}}(0) \gtrsim 1\ \mu$M), the value of $C_a(0)$ drops as $N_{\mathrm{inorg}}(0)$ increases. This observation is difficult to explain. It could be due to the intrinsic differences in the phytoplankton species occurring under a diversity of natural conditions. There may be differences in the rates at which various forms of inorganic nitrogen are assimilated (see e.g. Grant 1967, Eppley et al. 1969), or the limitation of photosynthesis, under certain conditions, by nutrients other than nitrogen, such as phosphorus (Renk 1973). Apart from the limitations imposed by the available nutrients, the magnitudes characterising photosynthesis in nature are strongly correlated with the temperature of the water. Indications of this are evident from the different positions of the $C_a(0) = f(N_{\mathrm{inorg}}(0))$ plots in Fig. 10b for different temperature intervals.

The regularities inherent in these relations are also evident from Fig. 11. This shows a diagram of the relationships between the surface chlorophyll a concentration, $C_a(0)$ [mg tot. chl a m^{-3}], approximated by the isolines $C_a(0) = $ const, and the two variables – the inorganic nitrogen concentration $N_{\mathrm{inorg}}(0)$ [μM] and temperature $temp$ [$°$C]. The effect of temperature on this chlorophyll concentration is positive only over a narrow concentration range and at low temperatures. Furthermore, the increase in $C_a(0)$ with $temp$ is in practice detectable only in seas with average nitrogen concentrations. For instance, where $N_{\mathrm{inorg}}(0) \approx 1.0\ \mu$M, this increase is measurable in the interval from 0 to 6$°$C. On the other hand, at temperatures in excess of
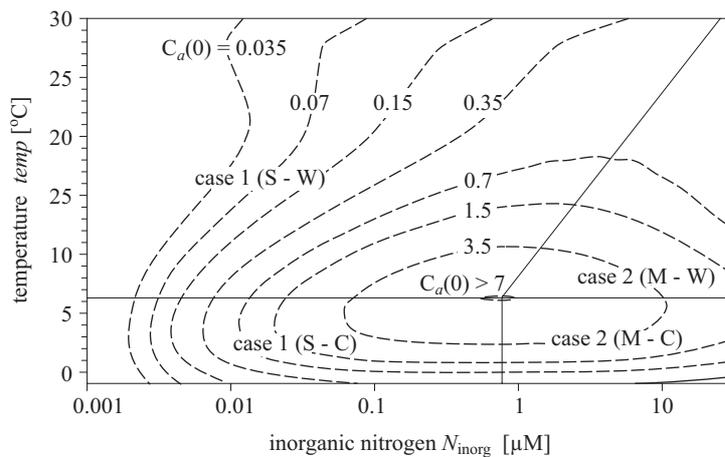
Fig. 11. A diagram showing the statistical relationships between the surface concentration of chlorophyll a, $C_a(0)$ [mg tot. chl a m^{-3}], approximated by the isolines $C_a(0) = $ const, and the two variables: the inorganic nitrogen concentration $N_{\mathrm{inorg}}(0)$ [μM] and temperature $temp$ [$°$C]. A data set from over 1300 stations in various oceanic regions was applied to the analysis

6°C, and also in seas with values of $N_{\text{inorg}}(0)$ differing from these means at temperatures well below 6°C, the chlorophyll concentration falls with increasing *temp*. The rate of this decrease depends on the nitrogen content $N_{\text{inorg}}(0)$: it is highest for $N_{\text{inorg}}(0) \approx 1$ μM and diminishes as nitrogen rises or falls from this value of 1 μM. It turns out that $C_a(0)$ resources in seas with very high nitrogen concentrations are the least temperature-sensitive.

Thus, for given concentrations of nitrogen $N_{\text{inorg}}(0)$, it is the 'cool' seas that have the largest phytoplankton resources (the highest concentrations of chlorophyll $C_a(0)$); in 'warm' seas $C_a(0)$ concentrations are lower. To recapitulate: the statistical function $C_a(0) = f(N_{\text{inorg}}(0), temp)$ reaches a maximum, probably the absolute one, in a certain interval of the variables $N_{\text{inorg}}(0)$ and *temp*. The highest $C_a(0)$ concentrations are recorded mostly in waters where the inorganic nitrogen concentration lies between 0.07 and 10 μM (av. c. 0.8 μM) and the temperature range is 2–11°C (av. c. 6°C). These are eutrophic and supereutrophic seas with chlorophyll concentrations of 3.5 mg tot. chl a m^{-3} at the very least; these values can be very much higher.

The surface $C_a(0) = f(N_{\text{inorg}}(0), temp)$ shown in Fig. 11 is described by a polynomial function of two variables (eq. (40)) with constant parameters. The equation describing this function, obtained by the non-linear regression of two variables, takes the form:

$$\log C_a(0) = \sum_{m=0}^{4} \left[\sum_{n=0}^{4} A_{m,n} (\log N_{\text{inorg}}(0))^n \right] temp^m, \tag{40}$$

where the values of the coefficients $A_{m,n}$ are given in Table 6.

Table 6. Constant coefficients $A_{m,n}$ of the polynomial given by eg. (40)

n\m	0	1	2	3	4
0	−0.01662	0.3502	−0.04418	0.001785	-2.430×10^{-5}
1	−0.04148	−0.01815	0.001975	3.991×10^{-5}	-2.259×10^{-6}
2	−0.05814	−0.02717	−0.001333	0.0001978	-4.019×10^{-6}
3	0.005918	0.004394	-3.613×10^{-5}	-2.484×10^{-5}	6.079×10^{-7}
4	−0.02117	−0.0004761	0.0007483	-5.039×10^{-5}	8.540×10^{-7}

A division of basins into 'optical-dynamic-climatic' types; an algorithm for determining the concentration of nitrogen $N_{\text{inorg}}(0)$ for remote sensing purposes

Satellite observations can provide information on the surface temperature *temp* and the surface concentration of chlorophyll $C_a(0)$. However, for an analysis of the quantum yield of photosynthesis this does not suffice: we need additional information about the inorganic nitrogen

concentration, particularly that at the surface $N_{\text{inorg}}(0)$. We therefore have to find the appropriate function $N_{\text{inorg}}(0) = f(C_a(0), temp)$. In the previous subsection we found some relations between these three variables $(C_a(0), temp, N_{\text{inorg}}(0))$ in the form of the function $C_a(0) = f(N_{\text{inorg}}(0), temp)$, that is, for various configurations of dependent and independent variables. Formally, the problem can be solved by an appropriate transposition of these variables. The first step in this approach would be to divide the area depicted in Fig. 11 into the four we have suggested, 'optical-dynamic-climatic' types i.e. case 1 (S–C), case 1 (S–W), case 2 (M–C) and case 2 (M–W). These correspond to the four natural areas covering various oceanic and coastal waters with respect to their dynamic state – stratified, i.e. poorly mixed, waters (S) and well-mixed waters (M) in different climatic zones, i.e. warm (W) with $temp > 6°\text{C}$ and cold (C) with $temp \leq 6°\text{C}$. In all cases the optical division of the waters in these basins into case 1 and case 2 waters according to Morel & Prieur's (1977) classification must also be taken into account.

The specifications and features of the suggested four 'optical-dynamic-climatic' types are given in Table 7.

Type named case 1(S–C) (i.e. mostly case 1 waters, stratified and cold) and type case 1 (S–W) (i.e. mostly case 1 waters, stratified and warm) cover areas with small and medium surface concentrations of nitrogen, in other words, the majority of the waters in the World Ocean. Mostly case 1 waters (less commonly case 2), they include basins of low or medium trophicity (O1 – E3, according to the notation given in Annex 2, Table A2.1). On the other hand, types case 2 (M–C) (i.e. mostly – but not always case 2 waters, mixed and cold) and case 2 (M–W) (i.e. mostly case 2 waters, mixed and warm) include waters with a high surface concentration of nitrogen. They are mainly coastal waters and enclosed seas with case 2 waters, and also regions where upwelling and convergence occur. As a rule, the trophicity of these basins (M – E3 and higher) are also higher than in basins of types 1 (S–C) and 1 (S–W).

Eq. (40), which enables a calculation of $C_a(0)$ in the area depicted in Fig. 11, was used to find the relationship (41) describing the nitrogen concentration. For basins of types 1 (S–C) and 1 (S–W) the $N_{\text{inorg}}(0)$ concentration was approximated with the polynomial 41 using the constant coefficients given in Table 8. But for basins of types 2 (M–C) and 2 (M–W), eq. (41) was used, but with the coefficients defined in Table 9.

$$\log N_{\text{inorg}}(0) = \sum_{m=0}^{4} \left[\sum_{n=0}^{4} A_{m,n} (\log C_a(0))^n \right] temp^m, \qquad (41)$$

where the values of the coefficients $A_{m,n}$ are given in Tables 8 and 9.

Table 7. The suggested division of marine basins into 'optical-dynamic-climatic' types

A – general characteristics

	Stratified	Mixed
cold ($\leq 6°C$)	case 1 (S–C)	case 2 (M–C)
warm ($> 6°C$)	case 1 (S–W)	case 2 (M–W)

B – selected characteristics and relations with other classifications

The 'optical–dynamic-climatic' type of basin	Optical types of water	Trophic types of basin [**]	Occurrence	Direction [*] of change of $C_a(0)$
1 (S–C) (*stratified-cold*)	case 1	O1, O2, O3, M, I, E1, E2, E3	Mainly central areas of oceans in the polar zone far from convergence zones	$N_{inorg} \uparrow$; $temp \uparrow$
1 (S–W) (*stratified-warm*)	case 1	O1, O2, O3, M, I, E1, E2, E3	Mainly the central areas of oceans	$N_{inorg} \uparrow$; $temp \downarrow$
2 (M–C) (*mixed-cold*)	case 2 and case 1	M, I, E1, E2, E3	Mainly well-mixed oceanic waters e.g. in convergence zones and shelf seas in the polar zone	$N_{inorg} \downarrow$; $temp \uparrow$
2 (M–W) (*mixed-warm*)	case 2	I, E1, E2, E3	Mainly warm shelf seas and enclosed seas	$N_{inorg} \downarrow$; $temp \downarrow$

Explanations:

[*] $N_{inorg} \uparrow$ or $temp \uparrow$ denotes an increase in the total chlorophyll concentration $C_a(0)$ with a rise in the given magnitude, and $N_{inorg} \downarrow$ or $temp \downarrow$ denotes a fall in $C_a(0)$ with a rise in the given magnitude.

[**] The symbols of basin trophicity types are defined in Annex 2, Table A2.1.

These equations permit the calculation of $N_{inorg}(0)$ from known values of $C_a(0)$ and *temp*, that is, data indirectly obtainable via satellite. A certain ambiguity does occur when one has to decide which polynomial to apply, and which set of coefficients – from Table 8 or Table 9. The determining criterion could be the fact that waters of types 2 (M–C) and 2 (M–W) occur mainly in enclosed seas, or in oceanic areas of upwelling or convergence; the distribution of these areas in the World Ocean is known. The errors in estimating N_{inorg} are discussed at the end of this section.

Table 8. Coefficients $A_{m,n}$ of the polynomial given by eg. (41) for basin types 1 (S–C) and 1 (S–W)

n\m	0	1	2	3	4
0	−0.4439	−0.7505	0.09589	−0.003615	4.436×10^{-5}
1	2.484	−0.4689	0.04222	−0.0004128	-1.859×10^{-5}
2	1.770	−0.2990	0.03181	−0.0006141	-1.060×10^{-5}
3	0.7978	−0.1743	0.02489	−0.00101434	9.150×10^{-6}
4	0.1175	−0.03246	0.005077	−0.0002381	2.964×10^{-6}

Table 9. Coefficients $A_{m,n}$ of the polynomial given by eg. (41) for basin types 2 (M–C) and 2 (M–W)

n\m	0	1	2	3	4
0	0.1266	0.8041	−0.1047	0.004451	-6.005×10^{-5}
1	−2.552	0.1986	0.001471	−0.002248	7.821×10^{-5}
2	−0.9345	1.466	−0.2002	0.008399	-8.009×10^{-5}
3	−4.484	0.1747	−0.04111	0.003619	-4.557×10^{-5}
4	−0.3184	0.1735	0.01230	−0.004568	0.0001418

The statistical description of depth profiles of the inorganic nitrogen concentrations $N_{\mathrm{inorg}}(z)$ in the sea

In the next step of the statistical analyses attention was focused on finding an analytical description of the vertical distributions of the inorganic nitrogen concentration $N_{\mathrm{inorg}}(z)$ in terms of the surface concentration $N_{\mathrm{inorg}}(0)$. The analysis was limited to a thin surface layer of the sea, i.e. to depths no greater than twice the thickness of the euphotic layer.

The general trend in most empirical vertical profiles of $N_{\mathrm{inorg}}(z)$ shows that the nitrogen concentration in the surface layer remains nearly invariable in most cases and is roughly equal to the surface concentration $N_{\mathrm{inorg}}(0)$. A considerable increase in N_{inorg}, as compared to the surface concentration, is detectable only at great depths in oligotrophic waters (see Fig. 12); These deep zones are separated from the surface layer by a layer in which abrupt changes in nitrogen concentration occur. In the case of waters with a small surface nitrogen concentration, this layer is very distinct; it can be located quite precisely and can be referred to as the *nitrocline*. This *nitrocline* usually occurs at the depths where the thermocline and pycnocline are recorded. Conversely, in waters with high surface concentrations of nitrogen (mostly eutrophic waters), this layer is rather indistinct, if it exists at all. Statistical analyses have shown that the *nitrocline* gradient is very steep and is present at the greatest depths in waters with a very low surface
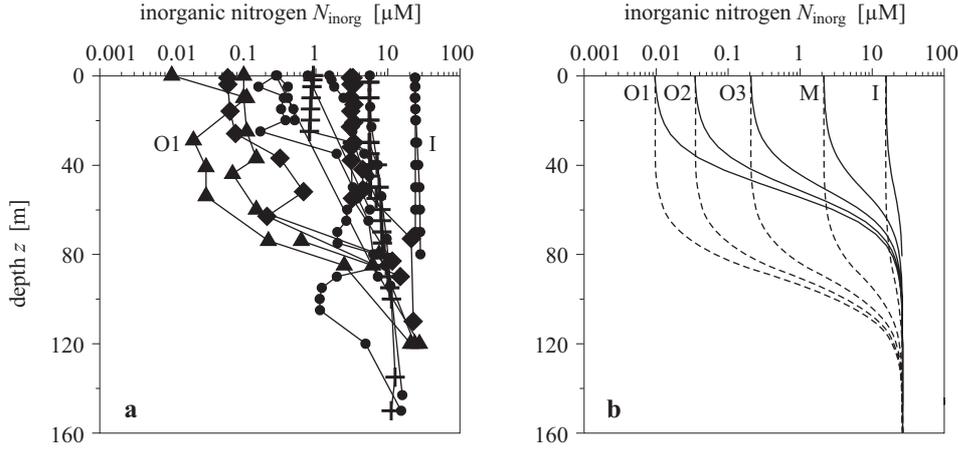
Fig. 12. Vertical profiles of inorganic nitrogen concentrations in various seas: (a) empirical profiles; (b) modelled profiles: continuous lines – assuming a 40-m-deep mixed layer, dashed lines – assuming a 90-m-deep mixed layer

The symbols of basin trophicity on the graph (O1–O3, M, I) are defined in Annex 2, Table A2.1

concentration of nitrogen $N_{\mathrm{inorg}}(0)$. By contrast, in waters with a higher concentration of nitrogen, the *nitrocline* has a progressively gentler gradient, and its depth of occurrence is gradually reduced, so that in waters with a very high nitrogen concentration it lies just beneath the surface.

Our model description takes account of these regularities in the vertical $N_{\mathrm{inorg}}(z)$ profiles. The empirical $N_{\mathrm{inorg}}(z)$ profiles applied were restricted to depths no greater than double the thickness of the euphotic layer z_e. The thickness of the layer z_e was calculated from the formula (Woźniak et al. 1992b) as follows:

$$\log z_e = -0.0899 \left(\log \left(C_a(0)\right)\right)^2 - 0.444 \log \left(C_a(0)\right) + 1.54. \tag{42}$$

Using non-linear regression, the various $N_{\mathrm{inorg}}(z)$ profiles were approximated by means of triparameter functions to the hyperbolic tangent (tgh):

$$\log N_{\mathrm{inorg}}(z) = \log N_{\mathrm{inorg}}(0) + b \, \mathrm{tgh}\!\left(\frac{z - z_{Nc}}{a}\right) - b \, \mathrm{tgh}\!\left(\frac{-z_{Nc}}{a}\right), \tag{43}$$

where z_{Nc} – depth corresponding to the centre of the *nitrocline*,

$$a = 18.8 \text{ m} \quad \text{and} \quad b = \frac{N_{\mathrm{inorg}}^{\max} - \log N_{\mathrm{inorg}}(0)}{1 - \mathrm{tgh}\!\left(-\frac{z_{Nc}}{a}\right)}, \tag{44\,a}$$

$$N_{\mathrm{inorg}}^{\max} \approx 26.3 \ \mu M. \tag{44\,b}$$

Additionally, an equation was found to enable parameter z_{Nc} to be replaced by a magnitude that can be more readily determined, i.e. by the mixing depth z_m. This relation is given by eq. (45).

$$z_{Nc} = 2.39 \ z_m{}^{0.83}. \tag{45}$$

Example model $N_{\mathrm{inorg}}(z)$ profiles found with the aid of equations (43)–(44) are given in Fig. 12b. As we can see, they indicate the same trends and empirical distributions.

Estimating the errors of the statistical relationships

During the empirical validation of the statistical relationships presented here between the surface chlorophyll concentration $C_a(0)$, surface and depth profiles of the inorganic nitrogen concentration ($N_{\mathrm{inorg}}(0)$ and $N_{\mathrm{inorg}}(z)$) and the surface temperature of the sea, the respective errors in the estimates were assessed. The error of the estimate of $C_a(0) = f(\log N_{\mathrm{inorg}}(0), temp)$ was assessed by comparing the values of $C_a(0)$ obtained with the aid of a polynomial from measured values. For example, the standard deviation of the ratio $x = C_a(0)_C / C_a(0)_M$ (where $C_a(0)_C$ and $C_a(0)_M$ are estimated from eq. (40) and measured respectively) lies in the interval $0.43 \leq x \leq 2.33$. The error is thus considerable. However, bearing in mind the fact that natural concentrations of chlorophyll vary over four orders of magnitude, this error is tolerable at the present stage of the modelling. Moreover, the polynomial given by formula (40) can be implemented to obtain a rough idea of the trophic type of the basin (the index of which is given by values of $C_a(0)$) on the basis of known nitrogen concentrations and temperatures. However, such estimates are not necessary in our model. Here we use the transformation of the function $C_a(0) = f(N_{\mathrm{inorg}}(0), temp)$ (see eq. (40)) to the form $N_{\mathrm{inorg}}(0) = f(C_a(0), temp)$ (see eq. (41)), which enables the inorganic nitrogen concentration in the surface layer to be determined from known values of the surface chlorophyll concentration and the temperature of the water.

The errors of the estimation of $N_{\mathrm{inorg}}(0)$ were also examined. The independent variables in the first stage were $temp$ and $N_{\mathrm{inorg}}(0)$, and $C_a(0)$ was calculated using eq. (40). Then, $N_{\mathrm{inorg}}(0)$ was obtained from $C_a(0)$ and $temp$ data using eq. (41). The errors of this circumstantial verification are given in Table 10. The statistical error σ_+ of this estimation is c. 60%, a relatively low figure. Eq. (41) can therefore be used initially in the further modelling of the quantum yield of photosynthesis.

Finally, the errors of the approximation of the vertical profiles of $N_{\mathrm{inorg}}(z)$ were assessed on the basis of known surface concentrations $N_{\mathrm{inorg}}(0)$ and also mixed-layer depths. To this end, the nitrogen concentrations obtained from measurements were compared with those yielded by

the model (see eqs. (43), (44) and (45)). The values of these errors are
set out in Table 11. They are quite substantial. Nevertheless, seeing that
natural values of N_{inorg} concentrations are subject to a very wide scatter,
the results of this approximation can be regarded as satisfactory, and the
model described by equations (43)–(45) is an adequate reflection of the
measured statistical values. Even though at the present stage our model
is far from perfect, we have decided to apply it in our further calculations,
since modelling the concentration of nitrogen was not the principal aim of
this work. In the future, this model will, of course, have to be improved.

Table 10. Errors of the estimation of the $N_{\mathrm{inorg}}(0) = f(\log C_a(0), temp)$ model

Arithmetic statistics		Logarithmic statistics			
systematic	statistical	systematic	standard error factor	statistical	
$\langle \varepsilon \rangle$ [%]	σ_ε [%]	$\langle \varepsilon \rangle_{\mathrm{g}}$ [%]	x	σ_- [%]	σ_+ [%]
15.7	± 83.5	1.72	1.607	-37.8	60.7

where errors of the estimations of $N_{\mathrm{inorg}}(0) = f(\log C_a(0))$ were determined in the
same way as the absorption estimation errors (see Table 5).

Table 11. Errors of the estimation of the $N_{\mathrm{inorg}}(z)$ model

Arithmetic statistics		Logarithmic statistics			
systematic	statistical	systematic	standard error factor	statistical	
$\langle \varepsilon \rangle$ [%]	σ_ε [%]	$\langle \varepsilon \rangle_{\mathrm{g}}$ [%]	x	σ_- [%]	σ_+ [%]
42.2		28.9	2.534	-60.5	153

where errors of the estimations of $N_{\mathrm{inorg}}(z)$ were determined like absorption
estimation errors (see Table 5).

8. Model of the quantum yield of photosynthesis (block 9 in Fig. 1)

The model of quantum yield of phytoplankton photosynthesis Φ is
described in detail in volume 44 of *Oceanologia* (Woźniak et al. 2002a).
Therefore, in this paper, its basic premises are merely reiterated.

The definition of the quantum yield of photosynthesis, averaged over
a time interval, can be formulated as follows:

$$\Phi = \frac{\mathrm{P}}{12\eta_{PUR}} \left[\frac{\mathrm{atoms\,C}}{\mathrm{quanta}} \right] \text{ or } \left[\frac{\mathrm{mol\,C}}{\mathrm{Ein}} \right], \tag{46}$$

where 12 is the mass number of carbon, P is the primary production expressed in [gC m^{-3}] and η_{PUR} is the radiation dose of the PAR spectrum range absorbed by phytoplankton in a certain time interval [Ein m^{-3}]. A time interval of 24 hours is usually applied in our model.

With respect to instantaneous values, this expression takes the form:

$$\Phi = \frac{P^B}{PUR^*} = \frac{P^B}{PAR_0 \; \tilde{a}_{pl}^*},$$

(47)

where

P^B [mol C (mg tot. chl a)$^{-1}$ s^{-1}] – rate of photosynthesis, also known as the assimilation number, i.e. the production in unit time referred to unit mass of chlorophyll a;

PUR^* [Ein (mg tot. chl a)$^{-1}$ s^{-1}] – the number of quanta absorbed by phytoplankton pigments in unit time referred to unit mass of chlorophyll a;

$\tilde{a}_{pl}^*$ [m^2 (mg tot. chl a)$^{-1}$] – mean specific absorption coefficient for phytoplankton weighted by the irradiance spectrum, i.e.

$$\tilde{a}_{pl}^* \approx (PAR_0)^{-1} \, 1.2 \int_{400\,\text{nm}}^{700\,\text{nm}} E_d(\lambda) a_{pl}^*(\lambda) d\lambda = (PAR)^{-1} \int_{400\,\text{nm}}^{700\,\text{nm}} E_d(\lambda) a_{pl}^*(\lambda) d\lambda. \quad (48)$$

Though the least well understood aspect of photosynthesis, the quantum yield as defined here is its most salient characteristic, and must be included in any mathematical model of the process (Banister 1979, Kiefer & Mitchell 1983, Smith et al. 1989, Platt et al. 1992). That is why it has been the subject of empirical study by numerous authors (e.g. Eppley & Sharp 1975, Ley & Mauzerall 1982, Koblentz-Mishke et al. 1985, Cleveland et al. 1989; see also Babin et al. 1996a and the papers cited therein) or modelled theoretically and statistically (Kolber & Falkowski 1992, 1993, Geider et al. 1993, Woźniak et al. 1997a, b). These investigations have shown that the quantum yield of photosynthesis depends on a number of environmental factors. Owing to the vast differences in the values of these factors in the ocean, quantum yields Φ measured in different seas and at different depths vary over a range of about two orders of magnitude. No one has yet provided a quantitative definition of the relationships between the quantum yield Φ and the set of environmental parameters such as the underwater irradiance, nutrient content, water temperature and water trophicity that is broad enough to approximate this range of Φ values. Partial solutions to the problem were offered by two simplified mathematical models developed by the teams from Villefranche-sur-Mer (Morel 1991, Antoine & Morel 1996, Antoine et al. 1996, Morel et al. 1996) and Sopot (Woźniak et al. 1992a, b, 1995a, Dera 1995). However, the accuracy of these models is low, because

of the numerous simplifications made and the non-recognition of the direct influence of nutrients on the photosynthetic yield. We have tried to remove these deficiencies from our earlier models.

Numerous researchers have found inorganic nitrogen to be the nutrient limiting photosynthesis in most areas of the World Ocean (e.g. Buogis 1976, Koblentz-Mishke & Vedernikov 1977, Belayev 1987, Wróblewski 1989, Babin et al. 1996a, Morel et al. 1996). So we took the nitrogen concentration N_{inorg} into account in the modelling.

The quantum yield Φ in our model is expressed as a product of the theoretical maximum quantum yield $\Phi_{\text{MAX}} = 0.125 \text{ atom C quanta}^{-1}$ and six dimensionless factors f_i, which appear, to a good approximation, to be dependent on one or two environmental factors and the optical depth at most (Ficek et al. 2000a, b, Woźniak & Dera 2000, 2001). Each of these factors, less than 1 in value, are a measure of the decrease in Φ compared to Φ_{MAX} due to natural (internal) imperfections in the photosynthetic apparatus or to external conditions unfavourable to plant growth (see Woźniak et al. 2002a, b). Such an expression is compatible with the biophysical models of photosynthesis suggested by others (Falkowski & Kiefer 1985, Falkowki et al. 1986, Kolber & Falkowski 1993, Rubin et al. 1994, Rubin 1995, Babin et al. 1996a, Ostrowska 2001).

The quantum yield of photosynthesis can therefore be expressed as follows:

$$\left.\begin{array}{l} \Phi = \Phi_{\text{MAX}} \; f_a \; f_\Delta \; f_{c(N)} \; f_{c(\tau)} \; f_{c(PAR,\text{inh})} \; f_{E,temp} \\ \Phi_{\text{MAX}} = 0.125 \, [\text{atoms C } (\text{quanta})^{-1}] \; \text{ or } \; [\text{mol C } (\text{Ein})^{-1}] \end{array}\right\}, \quad (49)$$

where the six dimensionless factors are:

f_a — a non-photosynthetic pigment absorption effect factor describing the decrease in the observed quantum yield in relation to Φ_{MAX} – this is due to the presence in the plant of photo-protecting pigments that do not transfer absorbed energy to the PS2 reaction centres;

f_Δ — the inefficiency factor in energy transfer and charge recombination;

$f_{c(N)}$ — 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;

$f_{c(PAR,\text{inh})}$ — the factor describing the reduction in the portion of functional PS2 reaction centres as a result of photoinhibition;

$f_{E,temp}$ — the classic dependence of photosynthesis on light and temperature (for example, Morel 1991, Dera 1995, Ficek 2001

and the papers cited there), also known as the light curve of photosynthetic efficiency at a given temperature.

Mathematical formulas describing the factors and their dependence on abiotic environmental parameters, the sea trophicity index $C_a(0)$, and optical depth τ, are given in Annex 1, eqs. (A1.37)–(A1.42). They are described in the paper by Woźniak et al. (2002a), where magnitudes of their variability and vertical profiles in ocean and coastal waters of various trophicity are also discussed and illustrated in detail.

Measured Φ_M and modelled Φ_C quantum yields are compared in Fig. 13; the calculated errors of the estimation of Φ_C are given in Table 12.
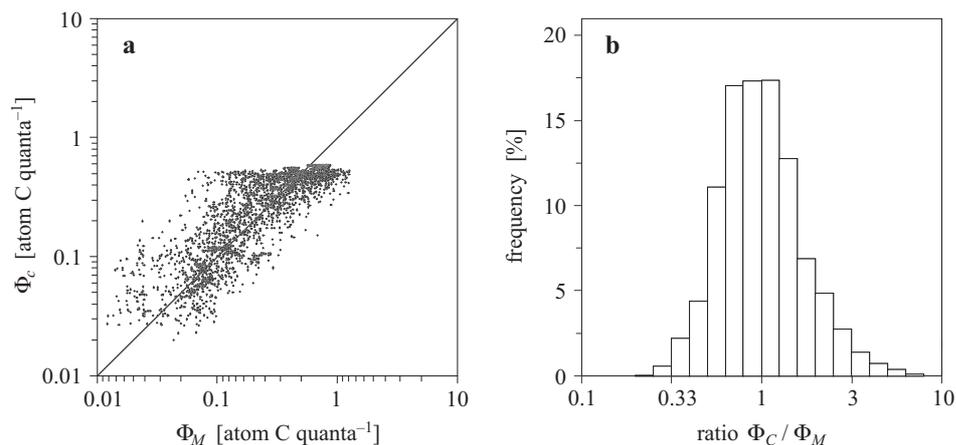
Fig. 13. Comparison of the measured Φ_M and the modelled Φ_C quantum yields of photosynthesis (a) and the histogram of the ratio Φ_C/Φ_M (b) at different stations and at various depths in the sea, determined according to the model of the quantum yield of photosynthesis described briefly in this paper and in full detail in Woźniak et al. (2002a)

Table 12. Errors of the estimation of the quantum yield of photosynthesis Φ determined using the model described by Woźniak et al. (2002a)

Arithmetic statistics		Logarithmic statistics			
systematic	statistical	systematic	standard error factor	statistical	
$\langle \varepsilon \rangle$ [%]	σ_ε [%]	$\langle \varepsilon \rangle_g$ [%]	x	σ_- [%]	σ_+ [%]
6.0	± 42.5	-1.4	1.53	-34.6	53.1

where errors of the estimations of Φ were determined in the same way as the absorption estimation errors (see Table 5).

9. Final remarks and conclusions

The prime objective of our long-term investigations, the development of a state-of-the-art mathematical model of primary production in the sea, has been achieved to a good approximation. Although it still needs refinement, our model does take into consideration many more factors affecting the inflow and utilisation of sunlight during the processes of marine photosynthesis than models presented earlier in the literature (see e.g. Morel 1991, Woźniak et al. 1992a, b, 1995a, b, Dera 1995, Antoine & Morel 1996, Antoine et al. 1996, Morel et al. 1996). It is thus far more comprehensive and more 'physical' than earlier primary production models of a similarly statistical nature. This is due to the fact that, although the parameters of our model were determined by statistical analyses of empirical material, the forms of the mathematical equations were established on the basis of thoroughly justified physical premises that take account of the biological nature of these processes.

Taken into consideration for the first time in a model of marine photosynthesis, the key formulas in this model consist of two sets of relationships between the photophysiological characteristics of phytoplankton and environmental factors in the sea. The first set consists of formulas describing photo- and chromatic acclimation, that is, the direct effect of irradiance conditions on the pigment composition of the phytoplankton and their indirect effect on its light absorption capacities. The second comprises formulas describing the influence on the photosynthetic quantum yield of a whole range of environmental factors like the irradiance conditions, nutrient concentrations, water temperature and trophicity.

The model described in this article and the full algorithm of its complex components is ready for a number of applications, and its accuracy, noted in the description of the various components, is satisfactory, given the current stage of development.

Two possible applications are particularly interesting and important.

One is the use of the model's relationships to determine a variety of photosynthetic characteristics at different depths in the sea on the basis of known irradiance conditions, temperature, nutrient content and basin trophicity. It is possible, for example, to analyse the differentiation in the photophysiological properties of algae and primary production in the different seasons in the Earth's marine systems on the basis of known, typical configurations of environmental conditions in different regions of the World Ocean.

Another could be its implementation in the remote monitoring of marine ecosystems, e.g. by satellite. The data of three remotely-sensed quantities – surface irradiance $PAR(0^+)$, surface total chlorophyll a concentration

$C_a(0)$ and temperature at the sea surface $temp$ – will suffice to estimate statistical values of all the following quantities: where

- vertical profiles of total chlorophyll a concentration $C_a(z)$;
- vertical profiles of irradiance attenuation and underwater irradiance fields $E_d(\lambda, z)$, $PAR(z)$;
- concentration depth profiles of other, accesory phytoplankton pigments $C_j(z)$;
- light absorption coefficients of pigments $a_{pl}(\lambda)$, $a_{pl,PSP}(\lambda)$, $a_{pl,PPP}(\lambda)$;
- vertical distributions of energy absorbed by pigments $PUR(z)$, $PUR_{PSP}(z)$;
- a rough estimate of inorganic nitrogen depth profiles $N_{\text{inorg}}(z)$;
- depth profiles of the photosynthesis quantum yield $\Phi(z)$;
- depth profiles of primary production $P(z)$, the total primary production in water column P_{tot}, and also the quantity of oxygen released photosynthetically.

We are studying both of these possible applications, and we shall publish the results in a subsequent article.

The bio-optical modelling by our Sopot Group is still being developed and will continue. Recently, our attention has been focused on the case 2 waters of the Baltic, which are being studied within the framework of an extensive (Polish) national project (PBZ–KBN 056/P04/2001: *Development of a satellite method of monitoring the Baltic ecosystem*, the implementation of which began in 2002.

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Annex 1

Mathematical apparatus of the general model of marine photosynthesis for remote sensing purposes

The mathematical apparatus of the general model of marine primary production with all its component bio-optical relationships are given here as a kind of algorithm. It follows the consecutive blocks of the diagram presented in Fig. 1 of this paper. The algorithm has been developed for practical use in the remote sensing of bio-optical properties of the sea.

Section A

Input parameters of the model are the surface chlorophyll concentration $C_a(0)$ [mg tot. chl a m^{-3}] (**Block 1**), the surface downward irradiance $PAR(0^+)$ [Ein m^{-2} s^{-1}] or scalar irradiance $PAR_0(0^+)$ [Ein m^{-2} s^{-1}] (**Block 2**) and the sea surface temperature $temp$ [°C] (**Block 3**).

Section B

The model formulas are:

Block 4: relationships between the vertical profiles of the chlorophyll a concentration $C_a(z)$ and its surface concentration $C_a(0)$:

$$C_a(z) = C_a(0)\frac{C_{\mathrm{const}} + C_m \exp\{-[(z - z_{\max})\sigma_z]^2\}}{C_{\mathrm{const}} + C_m \exp\{-[(z_{\max})\sigma_z]^2\}}, \tag{A1.1}$$

where

- for stratified oceanic waters (Woźniak et al. 1992a, b):

$$C_{\mathrm{const}} = 10^{[-0.0437 + 0.8644 \log (C_a(0)) - 0.0888(\log (C_a(0)))^2]},$$

$$C_m = 0.269 + 0.245 \log (C_a(0)) + 1.51(\log (C_a(0)))^2 + \\ + 2.13(\log (C_a(0)))^3 + 0.81(\log (C_a(0)))^4,$$

$$z_{\max} = 17.9 - 44.6 \log (C_a(0)) + 38.1(\log (C_a(0)))^2 + \\ + 1.32(\log (C_a(0)))^3 - 10.7(\log (C_a(0)))^4,$$

$$\sigma_z = 0.0408 + 0.0217 \log (C_a(0)) + 0.00239(\log (C_a(0)))^2 + \\ + 0.00562 (\log (C_a(0)))^3 + 0.00514(\log (C_a(0)))^4;$$

- for Baltic waters – preliminary (Woźniak et al. 1995a):

$$C_{\mathrm{const}} = \left[0.77 - 0.13 \cos \left(2\pi \frac{n_d - 74}{365}\right)\right]^{C_a(0)},$$

$$C_m = \frac{1}{2M}\left[(0.36)^{C_a(0)} + 1\right]\left[M + 1 + (M - 1)\cos \left(2\pi \frac{n_d - 120}{365}\right)\right],$$

$M = 2.25(0.765)^{C_a(0)} + 1,$

$z_{\max} = 9.18 - 2.43 \log(C_a(0)) + 0.213(\log(C_a(0)))^2 - 1.18(\log(C_a(0)))^3,$

$\sigma_z = 0.118 - 0.113 \log(C_a(0)) - 0.0139(\log(C_a(0)))^2 + 0.112(\log(C_a(0)))^3,$

n_d – the day number of the year.

Block 5: bio-optical relationships for estimating the following optical quantities (according to Woźniak et al. 1992a, b, 1995a, b, Kaczmarek & Woźniak 1995):

• optical depth in the sea:

$$\tau(z) = -\ln T(z); \tag{A1.2}$$

• downward irradiance relative spectral distribution functions:

$$f_E(\lambda, z) = f_E(\lambda, 0) \exp\left[-\int_0^z K_d(\lambda, z) dz\right]; \tag{A1.3}$$

• transmittance of irradiance PAR through the water column:

$$T(z) = \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} f_E(\lambda, z) d\lambda; \tag{A1.4}$$

• downward spectral irradiance:

$$E_d(\lambda, z) = PAR(0^+) f_E(\lambda, z); \tag{A1.5}$$

• overall irradiances in the PAR range:

(downward vectors) $\qquad PAR(z) = PAR(0^+)T(z),$ $\qquad$ (A1.6a)

(scalar) $\qquad PAR_0(z) \approx 1.2 PAR(0^+)T(z),$ $\qquad$ (A1.6b)

where

$K_d(\lambda, z)$ $\qquad$ – downward spectral irradiance diffuse attenuation coefficient,

$f_E(\lambda, 0) \equiv f(\lambda, 0)$ – normalised typical spectral distribution of irradiance PAR entering the sea (see Woźniak & Hapter 1985, Dera 1995).

$$\int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} f_E(\lambda, 0) d\lambda = 1.$$

This function $f_E(\lambda, 0)$ is described by the approximate polynomial expression:

$$f_E(\lambda, 0) = -1.3702 \times 10^{-9} \lambda^4 + 3.4125 \times 10^{-6} \lambda^3 - 3.1427 \times 10^{-3} \lambda^2 + 1.2647\lambda - 1.8381 \times 10^2, \tag{A1.7}$$

where λ is expressed in [nm].

The coefficient $K_d(\lambda, z)$ is related to the chlorophyll concentration $C_a(z)$:

$$K_d(\lambda, z) = K_w(\lambda) + C_a(z)\{c_1(\lambda) \exp\left[-a_1(\lambda)C_a(z)\right] + k_{d,i}(\lambda)\} + \Delta K(\lambda), \tag{A1.8}$$

where

$$\Delta K(\lambda) = \begin{cases} 0 & \text{for oceanic case 1 waters,} \\ 0.068 \exp[-0.014\ (\lambda - 550)] & \text{for Baltic case 2 waters.} \end{cases}$$

The constants $c_1(\lambda)$, $a_1(\lambda)$, $k_{d,i}(\lambda)$ and the attenuation of pure water $K_w(\lambda)$ are given in Table A1.1.

Block 6: Relationships between pigment concentrations and acclimation factors (according to Majchrowski & Ostrowska 1999, 2000):

• for photosynthetic pigments at depth z:

$$\frac{C_{PSC}}{C_a} = 1.348 < F_{PSC} >_{\Delta z} - 0.093, \tag{A1.9}$$

$$\frac{C_b}{C_a} = 54.07 < F_b >_{\Delta z}^{5.157} + 0.091, \tag{A1.10}$$

$$\frac{C_c}{C_a} = 0.042 < F_a >_{\Delta z}^{-1.197} < F_c >_{\Delta z}; \tag{A1.11}$$

• for photoprotecting carotenoids at depth z:

$$\frac{C_{PPC}}{C_a} = 0.1758 \times 10^6 < PDR^* >_{\Delta z} + 0.176, \tag{A1.12}$$

where

C_b, C_c, C_{PSC}, C_{PPC} [mg pigment m^{-3}] – respective concentrations of chlorophylls b, chlorophylls c, photosynthetic carotenoids PSC and photoprotecting carotenoids PPC;

$< F_a >_{\Delta z}$, $< F_b >_{\Delta z}$, $< F_c >_{\Delta z}$, $< F_{PSC} >_{\Delta z}$, $< PDR^* >_{\Delta z}$ – mean values of *chromatic acclimation factors* and the *photo-adaptation factor* in a water layer $\Delta z = z_2 - z_1$:

$$< F_j >_{\Delta z} = \frac{1}{z_2 - z_1} \int_{z_1}^{z_2} F_j(z)\, dz, \tag{A1.13a}$$

$$< PDR^* >_{\Delta z} = \frac{1}{z_2 - z_1} \int_{z_1}^{z_2} PDR^*(z)\, dz, \tag{A1.14a}$$

where

j – pigment group index (a, b, c or PSC),
$z_1 = z - 30$ m if $z \geq 30$ m and $z_1 = 0$ if $z < 30$ m, $z_2 = z + 30$ m.

The mean values in water layer Δz have been taken in order to include the influence of water mixing.

The acclimation factors were defined as functions of specific absorption coefficients of various pigment groups of the phytoplankton and selected properties of the underwater light field (according to Woźniak et al. 1999):

- chromatic acclimation factor for the j-th group of pigments (so-called Fitting Functions):

$$F_j(z) = \frac{1}{a_{j,\,\max}^*} \int\limits_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} f(\lambda, z) a_j^*(\lambda) d\lambda; \qquad (A1.13b)$$

- photo-acclimation factor (known as the Potentially Destructive Radiation):

$$PDR^*(z) = \int\limits_{400\,\mathrm{nm}}^{480\,\mathrm{nm}} a_a^*(\lambda) \ \langle E_0(\lambda, z)\rangle_{\mathrm{day}} d\lambda, \qquad (A1.14b)$$

where

$f(\lambda, z) = f_E(\lambda, z)/T(z) = E_d(\lambda, z)/PAR(z)$ – normalised spectral distribution of irradiance in the PAR spectral range at depth z:

$a_j^*(\lambda)$ – spectral specific absorption coefficient for the j-th group of 'unpackaged' pigments (i.e. in solvent), determined by equation (A1.16) (see below, block 7).

Block 7: Model relationships between different optical capacities of marine phytoplankton and pigment concentrations (according to Woźniak et al. 1999):

- relationship between the product $C_I\,d$ and the chlorophyll concentration C_a at depth z:

$$C_I\,d = 24.65\,C_a^{0.75015}, \qquad (A1.15)$$

where

C_I [mg tot. chl a m^{-3}] – intracellular chlorophyll a concentration,

d [m] – cell diameter, (C_a value given in [mg tot. chl a m^{-3}]);

- relationships between the specific absorption coefficient of 'unpackaged' pigments (i.e. in solvent) and chlorophyll a concentration:

   (**i**) for the j-th pigment group:

$$a_j^*(\lambda) = \sum_i a_{\max,\,i}^* \ e^{-\frac{1}{2}\left(\frac{\lambda - \lambda_{\max,\,i}}{\sigma_i}\right)^2}, \qquad (A1.16)$$

where

$\lambda_{\max,\,i}$ [nm] – the centre of the spectral peak of the band [nm],

σ_i[nm] – dispersion of the band,

$a^*_{\max, i}$ [m^2 (mg pigment)$^{-1}$] – specific absorption coefficient in the spectral peak of band,

i – Gaussian band numbers of major groups of phytoplankton pigments (e.g. chlorophylls a, chlorophylls b, chlorophylls c, photosynthetic carotenoids PSC and photoprotecting carotenoids PPC). The values of $\lambda_{max, i}$, σ_i and $a^*_{\max, i}$ are given in Table 4 in this paper.

(**ii**) for photosynthetic pigments PSP (in solvent – index S):

$$a^*_{PSP}(\lambda) = \tfrac{1}{C_a} \left[C_a\, a^*_a(\lambda) + C_b\, a^*_b(\lambda) + C_c\, a^*_c(\lambda) + C_{PSC}\, a^*_{PSC}(\lambda) \right],$$
$$\text{(A1.17)}$$

(**iii**) for photoprotecting pigments PPP (in solvent – index S):

$$a^*_{PPP}(\lambda) = \tfrac{1}{C_a} \left[C_{PPC}\, a^*_{PPC}(\lambda) \right], \qquad\qquad\qquad \text{(A1.18)}$$

(**iv**) for all the phytoplankton pigments (in solvent – index S):

$$a^*_{pl, S}(\lambda) = a^*_{PSP}(\lambda) + a^*_{PPP}(\lambda); \qquad\qquad\qquad \text{(A1.19)}$$

• the relationship between the package effect spectral function $Q^*(\lambda)$, the product $C_I\, d$ and the 'unpackaged' absorption coefficient $a^*_{pl, S}$:

$$Q^*(\lambda) = \tfrac{3}{2\rho'(\lambda)} \left[1 + \frac{2e^{-\rho'(\lambda)}}{\rho'(\lambda)} + 2\frac{e^{-\rho'(\lambda)}-1}{\rho'^2(\lambda)} \right], \qquad\qquad \text{(A1.20)}$$

where

$\rho' = a^*_{pl, S}\, C_I\, d$ (the so-called optical parameter of cell size);

• the relationships between *in vivo* absorption coefficients, 'unpackaged' absorption coefficients and the package effect function:

(**i**) total for all phytoplankton pigments:

$$\left.\begin{aligned} a_{pl}(\lambda) &= C_a\, a^*_{pl}(\lambda) \\ a^*_{pl}(\lambda) &= Q^*(\lambda) a^*_{pl, S}(\lambda) \end{aligned}\right\}, \qquad\qquad\qquad \text{(A1.21)}$$

(**ii**) for photosynthetic pigments PSP:

$$\left.\begin{aligned} a_{pl, PSP}(\lambda) &= C_a\, a^*_{pl, PSP}(\lambda) \\ a^*_{pl, PSP}(\lambda) &= Q^*(\lambda) a^*_{PSP}(\lambda) \end{aligned}\right\}, \qquad\qquad\qquad \text{(A1.22)}$$

(**iii**) for photoprotecting pigments:

$$\left.\begin{aligned} a_{pl, PPP}(\lambda) &= C_a\, a^*_{pl, PPP}(\lambda) \\ a^*_{pl, PPP}(\lambda) &= Q^*(\lambda) a^*_{PPP}(\lambda) \end{aligned}\right\}; \qquad\qquad\qquad \text{(A1.23)}$$

- these coefficients constitute the basins for determining the number of quanta of light absorbed by:

(**i**) all phytoplankton pigments:

$$PUR(z, t) = \int\limits_{400\,\text{nm}}^{700\,\text{nm}} E_0(\lambda, z, t)a_{pl}(\lambda, t)d\lambda, \tag{A1.24}$$

(**ii**) all phytoplankton pigments per unit mass of chlotophyll a:

$$PUR^*(z, t) = \int\limits_{400\,\text{nm}}^{700\,\text{nm}} E_0(\lambda, z, t)a_{pl}^*(\lambda, t)d\lambda = \tilde{a}_{pl}^*(z, t)PAR_0(z, t), \tag{A1.25}$$

(**iii**) photosynthetic phytoplankton pigments:

$$PUR_{PSP}(z, t) = \int\limits_{400\,\text{nm}}^{700\,\text{nm}} E_0(\lambda, z, t)a_{pl,\,PSP}(\lambda, t)d\lambda, \tag{A1.26}$$

(**iv**) photosynthetic phytoplankton pigments per unit mass of chlorophyll a:

$$PUR_{PSP}^*(z, t) = \int\limits_{400\,\text{nm}}^{700\,\text{nm}} E_0(\lambda, z, t)a_{pl,\,PSP}^*(\lambda, t)d\lambda =$$
$$= \tilde{a}_{pl,\,PSP}^*(z, t)PAR_0(z, t), \tag{A1.27}$$

(**v**) daily quanta doses absorbed by phytoplankton:

$$\eta_{PUR}(z) = \int\limits_{t_{\text{rise}}}^{t_{\text{set}}} PUR(z, t)dt, \tag{A1.28}$$

$$\eta_{PUR,\,PSP}(z) = \int\limits_{t_{\text{rise}}}^{t_{\text{set}}} PUR_{PSP}(z, t)dt, \tag{A1.29}$$

where
$E_0(\lambda, z, t)$ – spectral scalar irradiance ($E_0 \approx 1.2E_d$),
$\tilde{a}_{pl}^*$ – mean specific absorption coefficient of phytoplankton, weighted by the irradiance spectrum,
$\tilde{a}_{pl,\,PSP}^*$ – mean specific absorption coefficient of photosynthetic pigments weighted by the irradiance spectrum,
t_{rise} – time of sunrise; t_{set} – time of sunset.

Block 8: The statistical relationships between inorganic nitrogen concentration $N_{\text{inorg}}(z)$, surface chlorophyll a concentration $C_a(0)$, and surface temperature $temp$, are as follows (according to Ficek 2001):

$$\log N_{\text{inorg}}(z) = \log N_{\text{inorg}}(0) + b\,\text{tgh}\left(\tfrac{z-z_{Nc}}{a}\right) - b\,\text{tgh}\left(\tfrac{-z_{Nc}}{a}\right), \tag{A1.30}$$

where
(**i**) the surface inorganic nitrogen $N_{\text{inorg}}(0)$ is given by:

$$N_{\text{inorg}}(0) = 10^{\sum\limits_{m=0}^{4}\left[\sum\limits_{n=0}^{4} A_{m,n}(\log C_a(0))^n\right] temp^m}, \tag{A1.31}$$

the values of coefficients $A_{m,n}$ are given in Table 8 for types: case 1 (S–C) and case 1 (S–W) basins and in Table 9 for types: case 2 (M–C) and case 2 (M–W) basins (see division into 'optical-dynamic-climatic' types in Table 7);

(**ii**) the coefficients a and b, and concentration $N_{\text{inorg}}^{\max}$ are:

$$a = 18.8 \text{ m}, \qquad b = \frac{N_{\text{inorg}}^{\max} - \log N_{\text{inorg}}(0)}{1 - \text{tgh}\left(-\frac{z_{Nc}}{a}\right)}, \tag{A1.32}$$

$$N_{\text{inorg}}^{\max} \approx 26.3 \, \mu M, \tag{A1.33}$$

$z_{Nc} = 2.39 \, z_m^{0.83}$ – depth corresponding to the centre of the *nitrocline*,
$$\tag{A1.34}$$

$z_m \text{ [m]}$ – mixing depth.

Block 9: The model relationships between the quantum yield of photosynthesis and environmental parameters are as follows (according to Woźniak & Dera 2000, Ficek 2001, Woźniak et al. 2002a):

$$\left.\begin{array}{l} \Phi = \Phi_{\text{MAX}} f_a \, f_\Delta \, f_c \, f_{E,temp} \\[4pt] f_c = f_{c,(N)} f_{c,(\tau)} f_{c(PAR,\text{inh})} \end{array}\right\}, \tag{A1.35}$$

where

- $\Phi_{\text{MAX}} = 0.125 \text{ atom C quanta}^{-1}$ (theoretical maximum value of the quantum yield of photosynthesis); $\tag{A1.36}$

- the non-photosynthetic pigment factor:

$$f_a = \frac{\tilde{a}_{pl,PSP}^*}{\tilde{a}_{pl}^*} \quad \text{or} \quad f_a = PUR_{PSP}^*/PUR^*; \tag{A1.37}$$

- the inefficiency factor in energy transfer and charge recombination:

$$f_\Delta = 0.6; \tag{A1.38}$$

- the relative number of functional reaction centres:

the factor describing the influence of nutrient concentration on the number of functional centres:

$$f_{c(N)} = \frac{N_{\text{inorg}}}{N_{\text{inorg}} + 0.0585} \tag{A1.39}$$

(where: N_{inorg} – *inorganic nitrogen concentration given in*
$[\mu M] \equiv [\mu\text{mol dcm}^{-3}]$),
the factor describing the reduction in the portion of functional PS2 reaction centres at large depths:

$$f_{c,(\tau)} = 1 - 0.0031 \, \tau^2, \tag{A1.40}$$

the factor decribing the reduction in the portion of functional PS2 reaction centres as a result of photoinhibition:

$$f_{c(PAR,\,\text{inh})} = \exp\left(-0.00937\frac{PAR}{3.049 \times 10^{-5} \times 1.907^{temp/10}}\right); \qquad (A1.41)$$

- the classic dependence of photosynthesis on light and temperature (Dera 1995 and the papers cited there), also known as the light curve of photosynthetic efficiency at given temperature:

$$f_{E,temp} = \left[1 - \exp\left(-\frac{PUR^*_{PSP}}{8.545 \times 10^{-7} \times 1.874^{temp/10}}\right)\right] \times \frac{8.545 \times 10^{-7} \times 1.874^{temp/10}}{PUR^*_{PSP}}.$$
$$(A1.42)$$

Section C

The principles of the computations are:

Block 10: vertical profiles of chlorophyll $C_a(z)$ can be calculated from input data $C_a(0)$ using eq. (A1.1).

Block 11: vertical profiles of the optical depth $\tau(z)$, relative function of spectral distribution of downward irradiance $f_E(\lambda, z)$, irradiance PAR transmittance $T(z)$, downward spectral irradiance diffuse attenuation coefficient $K_d(\lambda, z)$ and vertical profiles of irradiances: $E_d(\lambda, z)$, $PAR(z)$ (or $PAR_0(z)$) can be calculated from their relationships with $C_a(z)$ and irradiance $PAR(0^+)$ input data using eqs. (A1.2)–(A1.8).

Block 12: vertical profiles of the relative concentration of particular phytoplankton pigments C_j/C_a can be determined from the optical properties of the sea and vertical profiles of chlorophyll a concentrations using eqs. (A1.9)–(A1.14).

Block 13: vertical profiles of the marine phytoplankton total spectral absorption coefficient and its components, and of the number of quanta and daily quanta doses absorbed by phytoplankton and the vertical distribution of the package effect spectral function $Q^*(\lambda, z)$ can be determined from basic unpackaged absorption coefficients, the package effect function and chlorophyll concentrations using eqs. (A1.15)–(A1.29).

Block 14: vertical profiles of inorganic nitrogen concentration $N_{\text{inorg}}(z)$ can be calculated from the surface chlorophyll a concentration $C_a(0)$ and sea surface temperature *temp* using eqs. (A1.30)–(A1.34).

Block 15: vertical profiles of the quantum yield of photosynthesis $\Phi(z)$ can be determined from the vertical PAR distribution (eq. (A1.6a)), the number of quanta absorbed by phytoplankton, PUR and PUR^*_{PSP} (eqs. (A1.25) and (A1.26)), vertical distribution of inorganic nitrogen (eqs. (A1.30)–(A1.34)) and temperature input data using eqs. (A1.35)–(A1.42).

Block 16: the vertical distribution of the daily primary production $P(z)$ [g C m^{-3}] can be determined from the quantum yield of photosynthesis $\Phi(z)$ (eqs. (A1.35)–(A1.42)) and daily dose of η_{PUR} [Ein m^{-3}] distribution (eq. (A1.29)) using formal relationships:

$$P(z) = 12 \times \Phi(z) \, \eta_{PUR}(z). \tag{A1.43}$$

The total daily primary production in the water column P_{tot} [g C m^{-2}] is determined by numerical integration over the depth of the profiles $P(z)$:

$$P_{\text{tot}} = \int_{0}^{z(P=0)} P(z) dz, \tag{A1.44}$$

where $z(P=0)$ is the depth at which primary production falls to a level so small that it does not affect the overall production P_{tot}.

Table A1.1. Values of parameters in the bio-optical classification of seas used in the model equation (A1.8) (after Woźniak et al. 1992a, b)

λ	a_1	c_1	$k_{d,i}$	K_w
[nm]	[m^3 (mg tot. chl a)$^{-1}$]	[m^2 (mg tot. chl a)$^{-1}$]		[m^{-1}]
400	0.441	0.141	0.0675	0.0209
410	0.495	0.137	0.0643	0.0197
420	0.531	0.131	0.0626	0.0187
430	0.580	0.119	0.0610	0.0177
440	0.619	0.111	0.0609	0.0176
450	0.550	0.107	0.0569	0.0181
460	0.487	0.0950	0.0536	0.0189
470	0.500	0.0970	0.0479	0.0198
480	0.500	0.0780	0.0462	0.0205
490	0.509	0.0774	0.0427	0.0230
500	0.610	0.0672	0.0389	0.0276
510	0.594	0.0598	0.0363	0.0371
520	0.590	0.0610	0.0319	0.0473
530	0.693	0.0573	0.0288	0.0513
540	0.606	0.0506	0.0285	0.0567
550	0.514	0.0432	0.0274	0.0640
560	0.465	0.0425	0.0248	0.0720
570	0.384	0.0288	0.0240	0.0810
580	0.399	0.0230	0.0231	0.107
590	0.365	0.0180	0.0231	0.143
600	0.333	0.0171	0.0225	0.212
610	0.304	0.0159	0.0216	0.236
620	0.316	0.0150	0.0225	0.264
630	0.421	0.0183	0.0225	0.295
640	0.420	0.0216	0.0226	0.325
650	0.346	0.0164	0.0236	0.343
660	0.348	0.0141	0.0260	0.393
670	0.173	0.00939	0.0267	0.437
675	0.173	0.00436	0.0270	0.455
680		0	0.0258	0.478
690		0	0.0190	0.535
700		0	0.0125	0.626
710		0	0.0045	1.000
720		0	0.0014	1.360
730		0	0.00041	1.810
740		0	7.1×10^{-5}	2.393
750		0	1.3×10^{-5}	2.990

Annex 2

List of symbols and abbreviations denoting the physical quantities used in this paper and the division of marine basins into biological types:

Symbol	Denotes	Units
a	light absorption coefficient of:	m^{-1}
a_{pl}	– phytoplankton	m^{-1}
$a_{pl,S}$	– phytoplankton pigments in solvent	m^{-1}
$a_{pl,PPP}$	– all photoprotecting pigments	m^{-1}
$a_{pl,PSP}$	– all photosynthetic pigments	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	$m^2 \, (mg \, tot. \, chl \, a)^{-1}$
$a_{pl,S}^*$	– phytoplankton pigments in solvent	$m^2 \, (mg \, tot. \, chl \, a)^{-1}$
a_a^*	– chlorophylls a in solvent	$m^2 \, (mg \, tot. \, chl \, a)^{-1}$
a_b^*	– chlorophylls b in solvent	$m^2 \, (mg \, chl \, b)^{-1}$
a_c^*	– chlorophylls c in solvent	$m^2 \, (mg \, chl \, c)^{-1}$
$a_{pl,PSP}^*$	– photosynthetic pigments	$m^2 \, (mg \, tot. \, chl \, a)^{-1}$
$a_{pl,PPP}^*$	– photoprotecting pigments	$m^2 \, (mg \, tot. \, chl \, a)^{-1}$
a_{PSC}^*	– photosynthetic carotenoids in solvent	$m^2 \, (mg \, PSC)^{-1}$
a_{PPC}^*	– photoprotecting carotenoids in solvent	$m^2 \, (mg \, PPC)^{-1}$
a_{PSP}^*	– photosynthetic pigments in solvent	$m^2 \, (mg \, tot. \, chl \, a)^{-1}$
a_{PPP}^*	– photoprotecting pigments in solvent	$m^2 \, (mg \, tot. \, chl \, a)^{-1}$
$a_{max,i}^*$	specific absorption coefficient for the i-th Gaussian band at the maximum	$m^2 \, (mg \, pigment)^{-1}$
a_j^*	specific absorption coefficient of the j-th pigment group	$m^2 \, (mg \, pigment)^{-1}$
$a_{j,max}^*$	specific absorption coefficient of the j-th pigment group at their spectral maxima	$m^2 \, (mg \, pigment)^{-1}$
a_{sol}^*	specific absorption coefficients (unpackaged) of the same cellular matter, ideally dispersed in solution	$m^2 \, (mg \, pigment)^{-1}$

Annex 2

List of symbols and abbreviations (*continued*)

Symbol	Denotes	Units
$\tilde{a}_{pl}^{*}$	mean specific absorption coefficient of phytoplankton weighted by the irradiance spectrum	$\mathrm{m}^2\,(\mathrm{mg\ tot.\ chl}\,a)^{-1}$
$\tilde{a}_{pl,\,PSP}^{*}$	mean specific absorption coefficient of photosynthetic pigments weighted by the irradiance spectrum	$\mathrm{m}^2\,(\mathrm{mg\ tot.\ chl}\,a)^{-1}$
$\bar{a}_{pl}$	mean absorption coefficients for total phytoplankton pigments	m^{-1}
$\bar{a}_{pl,\,PSP}$	mean absorption coefficients for photosynthetic pigments	m^{-1}
$\bar{a}_{pl}^{*}$	mean specific phytoplankton absorption coefficient for all pigments	$\mathrm{m}^2\,(\mathrm{mg\ tot.\ chl}\,a)^{-1}$
$\bar{a}_{pl,\,PSP}^{*}$	mean specific absorption coefficient for photosynthetic pigments	$\mathrm{m}^2\,(\mathrm{mg\ tot.\ chl}\,a)^{-1}$
C_a	sum of chlorophylls a + pheo, or total chlorophyll (chl a + divinyl chl a) concentrations	$\mathrm{mg\ tot.\ chl}\,a\ \mathrm{m}^{-3}$
$C_a(0)$ $C_a(z)$ 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	$\mathrm{mg\ tot.\ chl}\,a\ \mathrm{m}^{-3}$
$C_b,\ C_c,\ C_{PPC}$ $C_{PSC},\ C_{PPP}$	concentrations of chls b, chls c, photoprotecting carotenoids, photosynthetic carotenoids, photoprotecting pigments	$\mathrm{mg\ pigment\ m}^{-3}$
C_I	intracellular chlorophylls a concentration	$\mathrm{mg\ tot.\ chl}\,a\ \mathrm{m}^{-3}$
C_j	concentrations of the j-th group of 'unpackaged' pigments	$\mathrm{mg\ pigments\ m}^{-3}$
d	cell diameter	m
$E_0(\lambda)$	spectral scalar irradiance	$\mathrm{Ein\ m}^{-2}\ \mathrm{s}^{-1}\ \mathrm{nm}^{-1}$

Annex 2

List of symbols and abbreviations (*continued*)

Symbol	Denotes	Units
$E_d(\lambda)$	spectral downward irradiance	Ein m^{-2} s^{-1} nm^{-1}
$\langle E_0(\lambda)\rangle_{\text{day}}$	mean daily scalar irradiance in the medium	Ein m^{-2} s^{-1} nm^{-1}
$f(\lambda)$	normalised spectral distribution of downward irradiance	nm^{-1}
$f_E(\lambda)$	relative spectral distribution function of downward irradiance	nm^{-1}
f_a	non-photosynthetic pigment factor	dimensionless
f_c	portion of functional PS2 reaction centres	dimensionless
f_Δ	inefficiency factor 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	dimensionless
$f_{c(PAR,\text{inh})}$	the factor describing the reduction in the portion of functional PS2 reaction centres as a result of photoinhibition	dimensionless
$f_{E,temp}$	the classic dependence of photosynthesis on light and temperature	dimensionless
F_a, F_b, F_c, F_{PSC}	chromatic adaptation factors for chls a, chls b, for chls c, for photosynthetic caretonoids	dimensionless
F_j	the spectral fitting functions for the j-th pigment, otherwise known as *chromatic adaptation factors*	dimensionless
$< F_j >_{\Delta z}$	mean values of *chromatic acclimation factors* for the chls a in a water layer Δz	dimensionless
$< F_a >_{\Delta z}$	mean values of *chromatic acclimation factors* for the chls a in a water layer Δz	dimensionless

Annex 2

List of symbols and abbreviations (*continued*)

Symbol	Denotes	Units
$< F_b >_{\Delta z}$	mean values of *chromatic acclimation factors* for the chls b in a water layer Δz	dimensionless
$< F_c >_{\Delta z}$	mean values of *chromatic acclimation factors* for the chls c in a water layer Δz	dimensionless
$< F_{PSC} >_{\Delta z}$	mean values of *chromatic acclimation factors* for the photosynthetic caretonoids in a water layer Δz	dimensionless
i	Gaussian band numbers of major groups of phytoplankton pigments (e.g. chlorophylls a, chlorophylls b, chlorophylls c, photosynthetic carotenoids PSC and photoprotecting carotenoids PPC)	
j	pigment group index (e.g. chlorophylls a, chlorophylls b, chlorophylls c, photosynthetic carotenoids PSC and photoprotecting carotenoids PPC)	
$K_d(\lambda)$	downward irradiance attenuation coefficient	m^{-1}
$K_{pl}(\lambda)$	downward irradiance attenuation coefficient of phytoplankton	m^{-1}
K_w	the attenuation of pure water	m^{-1}
$K_\Delta(\lambda)$	downward irradiance attenuation coefficient of optically active autogenic components of sea water (yellow substance, organic and inorganic detritus)	m^{-1}
$\Delta K(\lambda)$	downward irradiance attenuation coefficient of allogenic components (e.g. various mineral and organic substances entering the sea from rivers and the atmosphere)	m^{-1}
n_d	the day number of the year	dimensionless
N_{inorg}	concentration of inorganic nitrogen	μM

Annex 2

List of symbols and abbreviations (*continued*)

Symbol	Denotes	Units
P_{tot}	total primary production in the water column	gC m^{-2}
$P(z)$	vertical distributions of primary production	gC m^{-3}
PAR	photosynthetically available radiation	
PAR	downward 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	Ein m^{-2} s^{-1}
PDR^*	potentially destructive radiation (per unit of chlorophyll a mass)	Ein (mg tot. chl a)$^{-1}$ s^{-1}
$< \mathrm{PDR}^* >_{\Delta z=30\,\mathrm{m}}$	mean PDR* value in a water layer Δz	Ein (mg tot. chl a)$^{-1}$ s^{-1}
PUR	photosynthetically used radiation	
PUR	number of quanta absorbed by pigments	Ein m^{-3} s^{-1}
PUR^*	number of quanta absorbed by pigments (per unit of chlorophyll a mass)	Ein (mg tot. chl a)$^{-1}$ s^{-1}
PUR_{PSP}	part of PUR due to photosynthetic pigments	Ein m^{-3} s^{-1}
PUR^*_{PSP}	part of PUR* due to photosynthetic pigments	Ein (mg tot. chl a)$^{-1}$ s^{-1}
PSP	photosynthetic pigments	
PPP	non-photosynthetic (photoprotecting) pigments	
PSC	photosynthetic carotenoids	
PPC	photoprotecting carotenoids	
PS1	photosystem 1	
PS2	photosystem 2	

Annex 2

List of symbols and abbreviations (*continued*)

Symbol	Denotes	Units
Trophic type symbols:		
O	oligotrophic	
M	mesotrophic	
I or P	intermediate	see Table A2.1 below
E	eutrophic	
Q^*	package effect function	dimensionless
RC	reaction centres	
$temp$	temperature in the euphotic zone	°C
t_{rise}	time of sunrise	
t_{set}	time of sunset	
$T(z)$	transmittance of irradiance PAR through the water column	dimensionless
z	real depth in the sea	m
z_e	depth of the euphotic zone (depth of 1% of the surface PAR irradiance)	m
z_{Nc}	depth corresponding to the middle of the nitrocline	m
z_m	mixing depth	m
Δz	thickness of water layers	m
Φ_{MAX}	maximum quantum yield of carbon fixation (of photosynthesis)	atoms C quanta^{-1} or mol C Ein^{-1}
Φ	quantum yield of carbon fixation (of photosynthesis)	atoms C quanta^{-1} or mol C Ein^{-1}
Φ_M	measured quantum yield of carbon fixation (of photosynthesis)	atoms C quanta^{-1} or mol C Ein^{-1}
ΦC	modelled quantum yield of carbon fixation	atoms C quanta^{-1} or mol C Ein^{-1}
η_d	irradiation	Jm^{-2} nm^{-1} (day^{-1})
η_{PUR}	the radiation dose of the PAR spectrum range absorbed by the phytoplankton in a certain time interval	Ein m^{-3}

Annex 2

List of symbols and abbreviations (*continued*)

Symbol	Denotes	Units
$\eta_{PUR,\,PSP}$	the radiation dose of the PAR spectrum range absorbed by the photosynthetic pigments in a certain time interval	Ein m^{-3}
λ	wavelength of the light	nm
$\lambda_{\mathrm{max},\,i}$	centre of the Gaussian band	nm
ρ'	optical parameter of a cell	dimensionless
σ_i	dispersion of band	nm
τ	optical depth in the sea	dimensionless
σ_i	dispersion of the Gaussian band	nm
(0)	a surface layer of the sea, remotely sensed and not defined closely	m
(0^+)	level just below the sea surface	m
(0^-)	level just above the sea water	m

Table A2.1. Division of marine basins into biological types

Trophic type of the basin waters	Basin trophicity symbol	Range of chlorophyll a concentration C_a [mg tot. chl a m^{-3}]	Mean concentration of chlorophyll a (trophicity index) C_a [mg tot. chl a m^{-3}]
oligotrophic	O1	0.02 ÷ 0.05	0.035
	O2	0.05 ÷ 0.10	0.075
	O3	0.10 ÷ 0.20	0.15
mesotrophic	M	0.2 ÷ 0.5	0.35
intermediate	I	0.5 ÷ 1.0	0.75
eutrophic	E1	1 ÷ 2	1.5
	E2	2 ÷ 5	3.5
	E3	5 ÷ 10	7.5
	E4	10 ÷ 20	15
	E5	> 20	–