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Bio-optical relationships for estimating primary production in the Ocean*

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Abstract

Numerous empirical data from 9 large Polish-Russian research expeditions and other smaller expeditions to various regions of the World Ocean in 1978-1991 were used to compile this first approximate model of statistical relationships, chiefly between the concentration of chlorophyll *a* and the solar irradiance just below the sea surface on the one hand, and the vertical distribution of chlorophyll *a*, phytoplankton absorption spectra, downward irradiance attenuation spectra, the quantum yield of photosynthesis, as well as other mean diurnal characteristics of primary production in waters of different trophicity on the other. These model relationships served to work out an algorithm for computing the vertical distributions of light energy and primary production characteristics in particular types of sea water from data on chlorophyll *a* concentration and irradiance at the sea surface.

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Verification of these model formulas with the aid of empirical data from a variety of sources has shown that they provide good results – the mean statistical errors with respect to *in situ* measurements range from *ca* 10% to 80%, depending on the characteristic in question.

In order to improve the accuracy of this algorithm, a much larger number of statistical data will be needed, and closer attention will have to be paid to the effect of nutrients and other environmental factors on the characteristics being assessed. This algorithm could be especially useful in the remote sensing of primary production in the ocean.

1. Introduction

The assimilation of carbon and flow of energy through marine ecosystems has become one of the prime targets of oceanological research. This has resulted from the need to understand a) the mechanisms underlying the environmental changes taking place all over the planet and b) the methods by which their efficient global control would be feasible. A key process in the carbon and energy cycles in the World Ocean is primary production, and its study is an integral part of the Joint Global Ocean Flux Study (JGOFS, 1990). In most cases only the carbon flux is examined within the framework of this Project. The need for accurate assessments of primary production in the oceans has prompted many workers to seek and elaborate models and algorithms enabling it to be estimated by optical remote sensing methods.

The aim of this paper, too, is to perfect models and algorithms for assessing primary production in the sea. In order to gather sufficient empirical data, 9 large joint Polish–Russian research expeditions (Vinogradov, 1980; Koblentz-Mishke *et al.*, 1985; Vinogradov and Ozmidov, 1986; Koblentz-Mishke, 1987; *Oceanologia*, 28, 1990) and several separate ones (Vinogradov, 1971; Moroshkin, 1973; Semina, 1981, 1985; *Oceanologia*, 15, 1984; Ponomareva and Pasternak, 1985) were undertaken in various parts of the Indian Ocean, Atlantic, Pacific, Black Sea and Baltic from 1978 to 1991. During these expeditions we were able to make simultaneous measurements of the following parameters:

- *sea surface irradiance* $E_d(\lambda, t, 0)$ and its diurnal energy totals;
- *in situ primary production* $P(z)$;
- nutrient concentration in the water including *inorganic nitrogen* $\sum N_{inorg}(z)$;
- *chlorophyll a + phaeophytin concentration* $C_a(z)$ in the examined waters;
- *optical properties of the sea* $OPS(z)$, including *diffuse attenuation coefficient of downward irradiance spectra* $K_d(z, \lambda)$ and *phytoplankton absorption coefficient spectra in vivo* $a_{pi}(\lambda)$;

- other properties of the marine environment.

Some data from the literature were also used to improve and/or verify the models (Renk, 1973, 1990; Trzosińska, 1990; Nakonieczny *et al.*, 1991).

We then sought correlations between these quantities and worked out suitable statistical models of the processes involved. The preliminary results and the methodology of these investigations have already been published, mainly by Woźniak (Koblentz-Mishke *et al.*, 1985; Woźniak, 1987, 1988, 1990; Koblentz-Mishke and Woźniak, 1989; Woźniak and Ostrowska, 1990a,b; Woźniak and Pelevin, 1991; Pelevin *et al.*, 1991). Here we present a synthesis of these studies which, to a certain extent, generalizes the set of models for assessing states and forecasting primary production in oceans.

There now exist two different ways of estimating P in the sea. One, originally put forward by Ryther and Yentsch (1957), is well known and has been developed by other authors (see *e.g.* Patten, 1968; Platt and Gallegos, 1980; Platt, 1984). It is based on a model of the dependence of the assimilation number $AN = P/C_a$ on the *underwater irradiance* E_{PAR} (PAR denotes the *Photosynthetically Available Radiation* in the 400–700 nm range (Morel, 1978)). The other, proposed by Koblentz-Mishke (Koblentz-Mishke *et al.*, 1985) is based on a model of the dependence of the *photosynthetic efficiency (quantum yield)* $\Phi = \frac{P}{\eta_{PUR}}$ on the irradiance E_{PAR} . E_{PAR} and the spectral irradiance $E_d(\lambda)$ are input parameters of the method. They allow η_{PUR} , the *daily dose of Photosynthetically Usable Radiation* to be calculated (see formulas (19),(20)). Note that E_{PAR} is an input parameter of both methods.

So, in the former case, the chlorophyll concentration and E_{PAR} are needed to calculate P , whereas in the latter, the plankton absorption coefficient spectrum $a_{pl}(\lambda)$ and $E_d(\lambda)$ are required.

We prefer the second method, as $a_{pl}(\lambda)$ is a more accurate and direct characteristic of the photosynthetic apparatus, and correlates more closely with P than C_a . So far, however, this method has been little used because of the lack of sufficient data sets on $a_{pl}(\lambda)$. To circumvent this obstacle, we have for the time being applied a positive statistical model allowing us to estimate $a_{pl}(\lambda)$ using numerous data on C_a .

The latest verified version of our algorithm for assessing primary production P from the *surface chlorophyll a concentration* $C_a(0)$ and surface irradiance $E_d(\lambda, t, 0)$ is briefly described in this paper. One could call it a 'spectral algorithm' because of the terms $a_{pl}(\lambda)$ and $E_d(\lambda)$ in the expression for photosynthetic efficiency. It contains a set of models and statistical formulas based on the empirical material mentioned earlier and on

literature data. These models include the relationships between the bio-optical parameters listed earlier and the surface chlorophyll *a* + phaeophytin concentration $C_a(0)$, which in this paper acts as the index of productivity (trophicity) of World Ocean waters. Four main trophicity types are distinguished by the following values of $C_a(0)$ expressed in $[\text{mg m}^{-3}]$: oligotrophic (O), $C_a(0) \leq 0.2$, mesotrophic (M), $0.2 < C_a(0) \leq 0.5$, intermediate (I), $0.5 < C_a(0) \leq 1$ and eutrophic (E), $C_a(0) > 1.0$ (more detailed subdivisions are given in Table 1).

Table 1. Trophicity types, chlorophyll concentrations and the pigment indices of acetone extracts of phytoplankton from waters of different trophicity (authors' own investigations)

Trophicity type	C_a range mg m^{-3}	Number of data	Pigment index P_i	
			logarithmic mean	standard range of P_i variation
O-1	0.02 - 0.05	54	11.5	9.51 - 13.9
O-2	0.05 - 0.10	233	8.3	6.43 - 10.7
O-3	0.10 - 0.20	298	5.0	3.97 - 6.30
M	0.20 - 0.50	303	3.9	2.93 - 5.20
I	0.50 - 1.00	360	3.5	2.61 - 4.70
E-1	1.00 - 2.00	520	3.0	2.25 - 4.00
E-2	2.00 - 5.00	410	2.7	2.08 - 3.50
E-3	5.00 - 10.0	398	2.4	1.99 - 2.90
E-4	10.0 - 20.0	220	2.3	1.96 - 2.70

where

O - oligotrophic waters divided into 3 sub-types,

M - mesotrophic waters,

I - intermediate waters,

E - eutrophic waters divided into 4 sub-types,

all characterized by chlorophyll concentration C_a ranges.

2. An algorithm for estimating primary production and related characteristics

2.1. A block diagram of the algorithm

Figure 1 shows this algorithm. It contains separate input parameters for computations (blocks 2 and 3, plus block 1 which can be brought into use as an auxiliary), model formulas approximating the relationships between chlorophyll concentration, the optical properties of phytoplankton

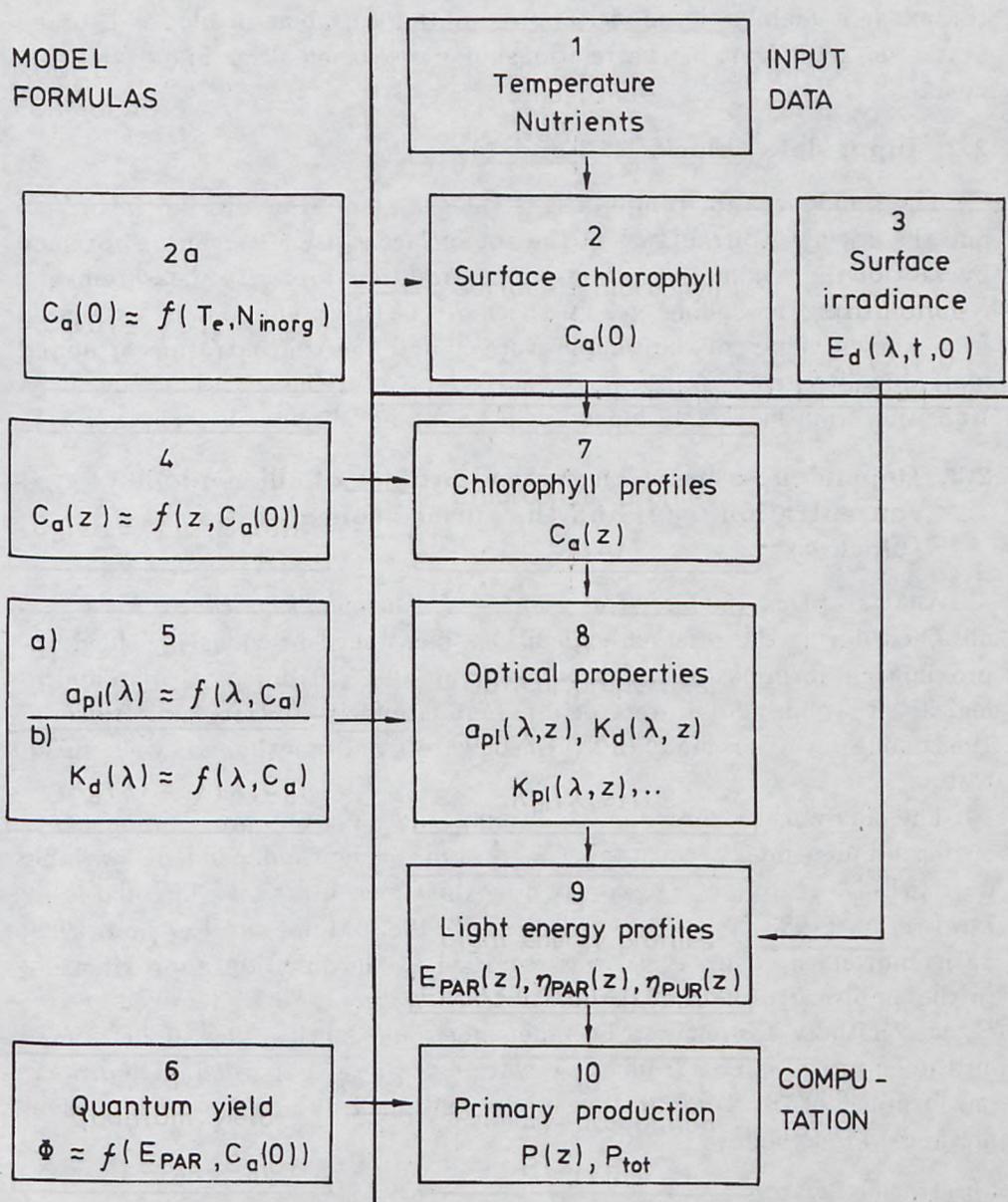


Fig. 1. Block diagram of the algorithm for estimating primary production and related characteristics in the sea

and sea water, underwater irradiance and photosynthetic efficiency (blocks 4, 5 and 6), as well as any characteristics of photosynthesis and the environment that can be calculated (blocks 7, 8, 9 and 10).

The discussion in this paper will centre around those aspects of the diagram which are innovative or contain new, more precise formulations than those to be found in the literature and our earlier publications. In this context it is mainly the model approximating formulas in blocks 4, 5 and 6 and the first draft of the relationship between blocks 2 and 1 that are meant.

2.2. Input data (blocks 2, 3 and 1)

The input data for computations (blocks 2 and 3 in Fig. 1), *i.e.* $C_a(0)$ and the downward irradiance at the sea surface $E_d(\lambda, t, 0)$, can be obtained by any of the available methods, *i.e.* traditional *in situ* measurements, remote sensing, modelling *etc.* Furthermore, $C_a(0)$ can be roughly estimated from known values of the temperature T and the concentration of bound inorganic nitrogen $\sum N_{inorg}$ in the surface layer of the sea. This suggested transition from block 1 to block 2 will be further discussed in chapter 4.

2.3. Dependences between vertical profiles of chlorophyll concentration $C_a(z)$ and the surface concentration $C_a(0)$ (block 4)

Analysis of *ca* 1500 vertical profiles of chlorophyll concentration $C_a(z)$ obtained during the research expeditions mentioned previously yielded approximating formulas of $C_a(z)$ as a function of $C_a(0)$ for particular hydrological situations and waters of different trophicity (Morel and Berthon, 1989): one set of profiles for stratified waters and another for well-mixed waters.

The analytical expression containing the sum of two components – a depth-independent constant C_{const} and a depth-dependent variable $C_m \exp\{-[(z - z_{max})\sigma_z]^2\}$ expressed by the Gauss function – postulated by Lewis *et al.* (1983) and others (Platt *et al.*, 1988; Morel and Berthon, 1989; Sathyendranath *et al.*, 1989) was regarded as the function approximating to the empirical profiles $C_a(z)$ in stratified waters. For well-mixed waters C_a was initially assumed to be independent of depth. The slight bumps on the empirical curves from these waters can be disregarded. The principal formulas of this computation model, obtained by non-linear regression methods, are as follows:

for stratified waters

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

where:

$$C_{const} = 10^{[-0.437 + 0.844 \log C_a(0) - 0.00888(\log C_a(0))^2]},$$

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

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

$$\sigma_z = 0.0408 + 0.217 \log C_a(0) + 0.00239(\log C_a(0))^2 + 0.00562(\log C_a(0))^3 + 0.00514(\log C_a(0))^4,$$

for other cases (well-mixed waters)

$$C_a(z) = C_a(0). \quad (2)$$

Formula (1) for stratified waters is based on experimental data (see Introduction) from 760 vertical profiles $C_a(z)$. Among them are 310 profiles of oligotrophic waters (O), 155 of mesotrophic waters (M), 102 of intermediate waters (I) and 193 of eutrophic waters (E). The relative errors in estimating $C_a(z)$ from formula (1) are defined as follows:

$$\varepsilon = \frac{C_{a,computed} - C_{a,measured}}{C_{a,measured}}. \quad (3)$$

The depth-dependent systematic error varies from -5.5% to $+7.5\%$, but the statistical error is 0% at the sea surface, $\pm 22.6\%$ at a depth equal to half the thickness of the euphotic zone $\frac{1}{2}z_e$, $\pm 33.7\%$ at the lower boundary of the euphotic zone ($1 z_e$) and $\pm 56.8\%$ at a depth of $1.5 z_e$.

The generalized dependences of the different features of $C_a(z)$ on $C_a(0)$ in the various trophic types of stratified and well-mixed waters are shown in Figure 2.

The left-hand side of Figure 2 shows the results of the empirical studies. Figure 2A contains examples of profiles, Figure 2B shows the average depth of the maximum $C_a(z)$, and Figure 2C its magnitude relative to $C_a(0)$. The relationship between these last two characteristics is much more distinct in stratified waters than in well-mixed waters. $C_a(z)$ maxima are situated deeper in stratified waters than in well-mixed ones.

The mathematical description of chlorophyll profiles by means of the Gauss formula in combination with the constant from formula (1) approximates to the shape of the $C_a(z)$ profiles for stratified waters (see Figs. 2D and 2F). In the other cases, straight lines are taken to be a first approximation (Fig. 2E);

Figure 2F shows the theoretical profiles in Figure 2D normalized with respect to $C_a(0)$; the absolute depth z is here replaced by the relative depth z/z_e , where z_e is the depth of the euphotic zone, *i.e.* the depth at which E_{PAR} falls as a result of attenuation to 1% of its surface value.

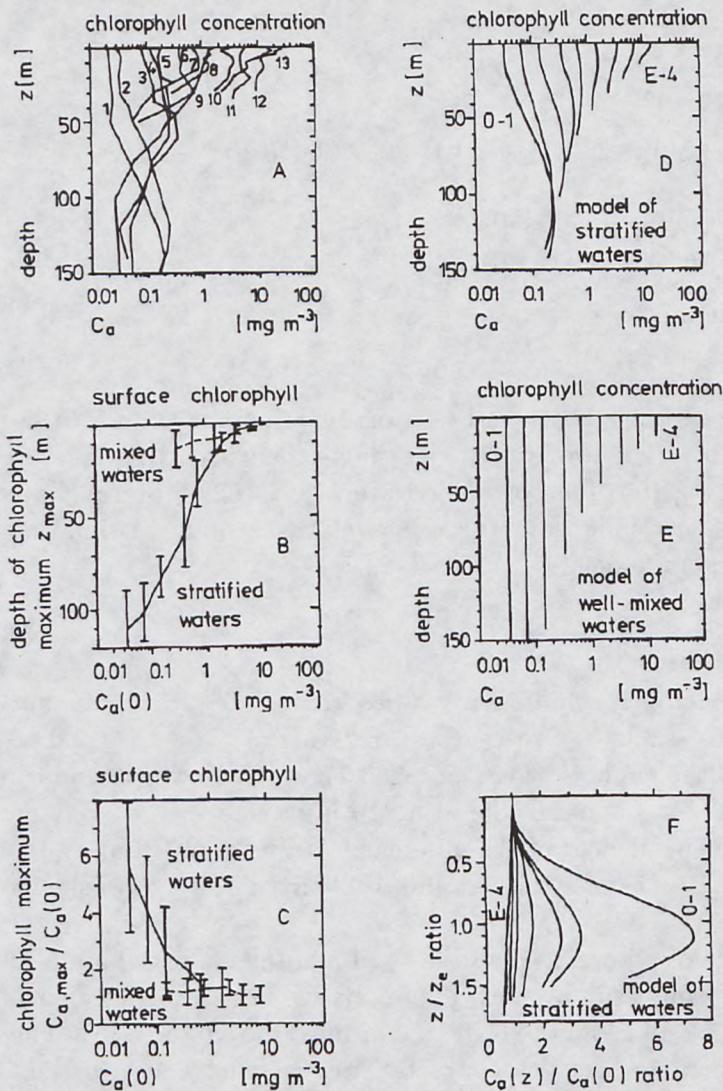


Fig. 2. Typical curves and parameters of vertical profiles of the chlorophyll concentration $C_a(z)$ (i.e. chlorophyll a + phaeophytin) in different seas as a function of the chlorophyll concentration $C_a(0)$ in the surface water layer. A — examples of empirical profiles: 1–3 Indian Ocean, 4–6 Atlantic, 7–9 Black Sea, 10–13 Baltic; B — averaged depths z of maximum chlorophyll concentration $C_a(z)$ together with standard deviations, C — averaged relative maxima $C_a(z_{max})/C_a(0)$ and standard deviations, D–F — model profiles in various trophic types of water determined from formulas 1 and 2. The curves from O-1 to E-4 in this Figure correspond to the average chlorophyll concentrations in the successive types of water given in Table 1

2.4. Relationship between phytoplankton light absorption $a_{pl}(\lambda)$ and chlorophyll concentration C_a (block 5a)

In its entirety, block 5 represents the formulas compiled in this paper approximating to the dependence of the absorptive properties of plankton (block 5a) and the attenuation coefficients of downward irradiance and its components (block 5b) on the chlorophyll concentration C_a . Both these sets of formulas can be used directly or indirectly in assessing primary production.

We shall first discuss block 5a, *i.e.* the model for estimating $a_{pl}(\lambda)$ spectra.

The chlorophyll concentration governs the coefficients of light absorption by phytoplankton $a_{pl}(\lambda)$, hence they vary across a range of three orders of magnitude (Fig. 3A). However, $a_{pl}(\lambda)$ is not directly proportional to C_a , especially in the short-wave region of the visible spectrum. This is illustrated by Figure 3B, which shows experimental spectra of the corresponding *coefficients of specific absorption* $a_{pl}^*(\lambda) = a_{pl}(\lambda)/C_a$ measured in natural waters with different chlorophyll *a* contents. They are largest in oligotrophic waters and decrease as C_a increases. This is due to the varying participation of accessory pigments in natural phytoplankton. This participation is greatest in phytoplankton from oligotrophic regions, and decreases as C_a increases (Fig. 3C). *Pigment indices* P_i (Margalef, 1960) were successfully used in a quantitative expression of this tendency; $P_i = a_{pl,ex}(433 \text{ nm})/a_{pl,ex}(661 \text{ nm})$, *i.e.* the ratio of light absorption or extinction of acetone extracts of pigments in the 433 nm band, in which most photosynthetic pigments absorb light, to absorption or extinction in the 661 nm band, in which practically only chlorophyll *a* absorbs light. There is a distinct correlation between the pigment index P_i and the chlorophyll concentration C_a (see Fig. 3D).

Thus, absorption spectra of acetone extracts of phytoplankton $a_{pl,ex}(\lambda)$ were compared with the chlorophyll concentration C_a in the above-mentioned 370 samples in which *in vivo* absorption spectra $a_{pl}(\lambda)$ were measured in absolute units by a direct *in vivo* method proposed by Yentsch (1960) and improved at the P. P. Shirshov Institute of Oceanology. The measurements were performed by means of a LOMO (USSR) SP-18 double-beam spectrophotometer with a light integrating sphere (Konovalov, 1985; Konovalov *et al.*, 1990).

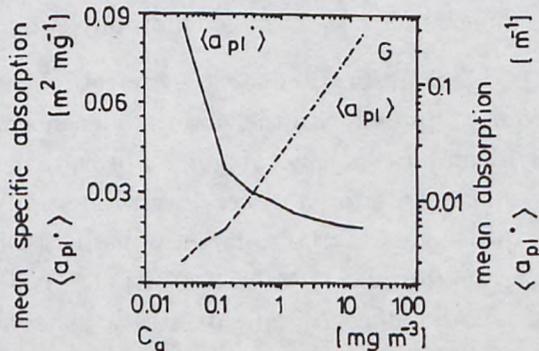
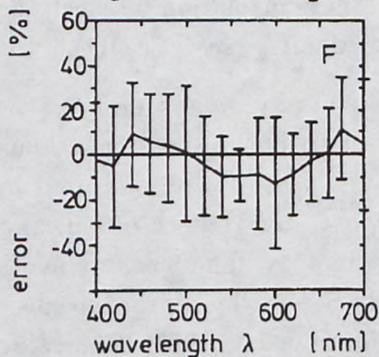
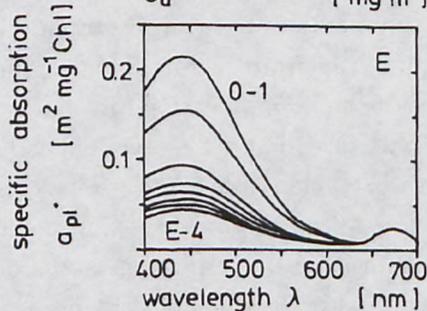
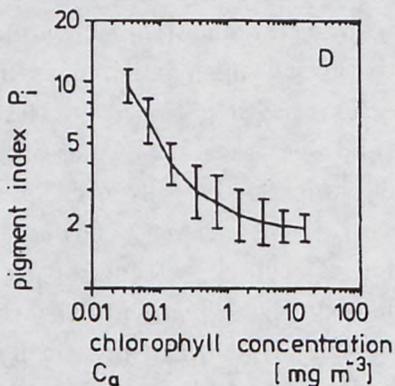
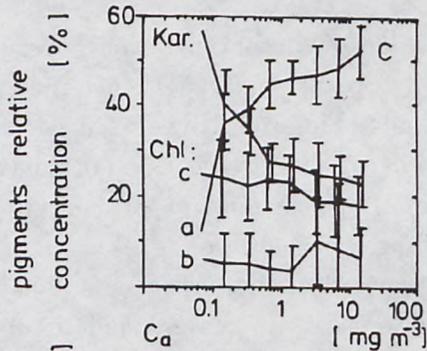
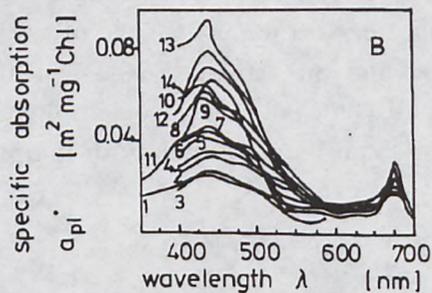
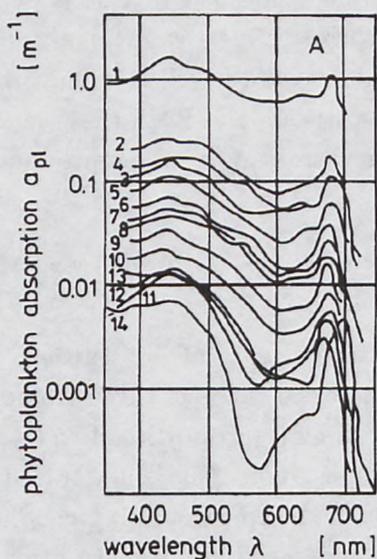


Fig. 3. Some optical and other physical characteristics of different trophic types of waters and natural phytoplankton populations. A, B — experimental spectra of light absorption coefficients by phytoplankton: volume $a_{pl}(\lambda)$ (A), specific $a_{pl}^*(\lambda)$ (B) observed in various waters with different chlorophyll concentration C_a [mg m^{-3}]. 1, 3 — different lakes in Japan (Kishino *et al.*, 1984), C_a : 56.0, 6.0; 2, 4–6 — Baltic Sea (Koblentz-Mishke *et al.*, 1985; Kononov, 1985), C_a : 6.0, 4.7, 2.6, 1.5; 7–10, 12, 13 — Black Sea (Koblentz-Mishke *et al.*, 1985; Kononov, 1985), C_a : 1.0, 0.9, 0.6, 0.33, 0.17, 0.14; 11, 14 — Pacific Ocean (Kishino *et al.*, 1986), C_a : 0.22, 0.10. C, D — statistical dependences of relative content contributions of the particular phytoplankton pigments in the summary pigment concentrations (C) and pigment index P_i (D) on the chlorophyll concentration C_a . Vertical segments represent standard deviations. E — theoretical spectra of specific light absorption coefficients by phytoplankton determined on the basis of equation (4) for various waters. The curves from O–1 to E–4 in this figure correspond to the average chlorophyll concentrations in the successive types of water given in Table 1. F — errors spectrum (see eq. (6)) of the light absorption coefficients determined from eq. (4): systematic (line), statistical (vertical segments); G — model dependences of absorption coefficients $\langle a_{pl}^* \rangle$ and $\langle a_{pl} \rangle$, averaged in the 400–700 nm range, on chlorophyll concentrations C_a .

The data were not divided into groups for stratified and mixed waters. The averaged measurements from regions of different trophicity are set out in Table 1. Using the same data one can determine spectra of phytoplankton $a_{pl}^*(\lambda)$ as functions of the pigment index P_i , on the basis of the preliminary model of the approximating formula (Woźniak, 1988; Woźniak and Ostrowska, 1990b):

$$\begin{aligned} a_{pl}^*(\lambda) = & (1.87 \times 10^{-2} P_i - 1.1 \times 10^{-2}) \exp[-1.2 \times 10^{-4} (\lambda - 441)^2] + \\ & + 6.45 \times 10^{-3} \exp[-3.5 \times 10^{-4} (\lambda - 608)^2] + \\ & + 2.33 \times 10^{-2} \exp[-1.4 \times 10^{-3} (\lambda - 675)^2], \end{aligned} \quad (4)$$

where P_i is the dimensionless pigment index and λ (nm) is the wavelength of light in the visible spectrum.

At the same time, one can insert the expression for the phytoplankton absorption coefficient spectra (Fig. 1 block 5a) into formula (4) on the basis of the definition of a_{pl}^* :

$$a_{pl}(\lambda) = C_a a_{pl}^*(\lambda). \quad (5)$$

Of the 370 pairs of *in vivo* absorption spectra $a_{pl}(\lambda)$ and acetone extracts of phytoplankton $a_{pl,ex}(\lambda)$ used in compiling formula (4), 94 were from oligotrophic waters (O), 36 from mesotrophic waters (M), 50 from intermediate waters (I) and 190 from eutrophic waters (E).

The wavelength-dependent relative error $\varepsilon(\lambda)$ of this estimation, given by formula (6), is depicted in Figure 3F.

$$\varepsilon(\lambda) = \frac{a_{pl,computed}(\lambda) - a_{pl,measured}(\lambda)}{a_{pl,measured}(\lambda)}. \quad (6)$$

Here, the systematic error varies within the range -14% to $+13\%$, while the statistical error lies in the range $\pm 30\%$. Any further choice of experimental data should tighten up this approximation and facilitate its use in the estimation of primary production, as the diagram in Figure 1 suggests.

Formulas (4) and (5) describe the absorption properties of phytoplankton as a function of two variables (P_i and C_a). But since a relationship between P_i and C_a has been found (Tab. 1 and Fig. 3D), these formulas allow the $a_{pl}(\lambda)$ and $a_{pl}^*(\lambda)$ spectra to be estimated from only the chlorophyll concentration. Figure 3E illustrates model spectra of this kind. The parameter of these curves is the chlorophyll concentration C_a , the index of the trophic type of waters with a given model spectral curve. Figure 3G illustrates the dependence of phytoplankton absorption coefficients $\langle a_{pl}^* \rangle$ and $\langle a_{pl} \rangle$, computed from formulas (4) and (5) and averaged in the 400–700 nm range, on the trophic water type, *e.g.* C_a .

2.5. Dependences of irradiance attenuation coefficients on chlorophyll concentration C_a (block 5b)

Like other authors (Baker and Smith, 1982; Smith and Baker, 1984; Smith *et al.*, 1989), we shall assume that $K_d(\lambda)$ is the sum of components responsible for the attenuation of irradiance by pure water $K_w(\lambda)$, phytoplankton $K_{pl}(\lambda)$ and other optically active admixtures. Some of them, like yellow substance and organic detritus (autochthonic substances), appear during the functioning of marine ecosystems and they are correlated with the chlorophyll concentration. Their partial attenuation coefficient is $K_\Delta(\lambda)$. Light attenuation by allochthonic admixtures (mineral suspensions, river-borne material *etc.*) are denoted by $\Delta K(\lambda)$. Thus

$$K_d(\lambda) = K_w(\lambda) + K_{pl}(\lambda) + K_\Delta(\lambda) + \Delta K(\lambda). \quad (7)$$

Following Morel and Prieur (1977) we distinguish two 'water cases'. 'Water case 1' (WC 1) is characterized by small concentrations of admixtures not directly correlated with C_a . Here we can assume $\Delta K(\lambda) \approx 0$. According to those workers, more than 98% of the waters in the World Ocean belong to this case as they are usually oligotrophic and stratified. The remainder, situated mostly in coastal zones of oceans and in enclosed seas, where $\Delta K(\lambda) > 0$, belong to 'Water case 2' (WC 2). The modification of this division of waters with respect to that in papers (Morel and Prieur, 1977; Morel, 1988) assumes finite and not zero values of $K_\Delta(\lambda)$ in WC 1.

Table 2. Values of the parameters in formulas (8), (9) and (10) for different wavelengths λ

λ	a_1	a_2	C_1	C_2	$k_{d,i}$	$k_{c,i}$	K_w
[μm]	[$\text{m}^3(\text{mg Chl})^{-1}$]	[$\text{m}^3(\text{mg Chl})^{-1}$]	[$\text{m}^2(\text{mg Chl})^{-1}$]	[m^{-1}]			
400	0.441	1.94	0.141	0.0531	0.0675	0.0251	0.0209
410	0.495	1.83	0.137	0.0720	0.0643	0.0273	0.0197
420	0.531	1.80	0.131	0.0730	0.0625	0.0284	0.0187
430	0.580	1.70	0.119	0.0730	0.0610	0.0309	0.0177
440	0.619	1.70	0.111	0.0733	0.0609	0.0317	0.0176
450	0.550	1.68	0.107	0.0690	0.0569	0.0308	0.0181
460	0.487	1.60	0.0950	0.0685	0.0536	0.0285	0.0189
470	0.500	1.59	0.0970	0.0660	0.0479	0.0265	0.0198
480	0.500	1.47	0.0780	0.0645	0.0462	0.0242	0.0205
490	0.509	1.53	0.0774	0.0610	0.0427	0.0221	0.0230
500	0.610	1.63	0.0672	0.0570	0.0389	0.0197	0.0276
510	0.594	1.85	0.0598	0.0480	0.0363	0.0182	0.0371
520	0.590	2.03	0.0610	0.0390	0.0319	0.0169	0.0473
530	0.693	2.02	0.0573	0.0337	0.0288	0.0144	0.0513
540	0.606	1.93	0.0506	0.0289	0.0285	0.0118	0.0567
550	0.514	1.91	0.0432	0.0217	0.0274	0.0106	0.0640
560	0.465	1.61	0.0425	0.0143	0.0248	0.0100	0.0720

Table 2. (continued)

λ [nm]	a_1 [m^3 (mg Chl) $^{-1}$]	a_2 [m^3 (mg Chl) $^{-1}$]	C_1 [m^2 (mg Chl) $^{-1}$]	C_2 [m^2 (mg Chl) $^{-1}$]	$k_{d,i}$ [m^2 (mg Chl) $^{-1}$]	$k_{c,i}$ [m^2 (mg Chl) $^{-1}$]	K_w [m^{-1}]
570	0.384	2.57	0.0288	0.0114	0.0240	0.00988	0.0810
580	0.399	3.49	0.0230	0.00820	0.0231	0.00987	0.107
590	0.365	3.60	0.0180	0.00619	0.0231	0.00970	0.143
600	0.333	3.90	0.0171	0.00478	0.0225	0.00944	0.212
610	0.304	3.95	0.0159	0.00337	0.0216	0.00918	0.236
620	0.316	4.03	0.0150	0.00173	0.0225	0.00936	0.264
630	0.421	4.10	0.0183	0.00135	0.0225	0.00944	0.295
640	0.420	5.08	0.0216	0.00058	0.0226	0.0105	0.325
650	0.346	5.40	0.0164	0.00045	0.0236	0.0133	0.343
660	0.348	—	0.0141	0	0.0260	0.0190	0.393
670	0.173	—	0.00939	0	0.0267	0.0230	0.437
675	0.173	—	0.00436	0	0.0270	0.0255	0.455
680	—	—	0	0	0.0258	0.0246	0.478
690	—	—	0	0	0.0190	0.0180	0.535
700	—	—	0	0	0.0125	0.0115	0.626

Table 2, together with formulas (8), (9), (10), obtained by nonlinear regression methods, represents the principal results of our approximation of the dependence of the three major optical functions in formula (7) on C_a .

The spectral downward irradiance attenuation coefficient

$$K_d(\lambda) = K_w(\lambda) + C_a \{C_1(\lambda) \exp[-a_1(\lambda)C_a] + k_{d,i}(\lambda)\} + \Delta K(\lambda), \quad (8)$$

its phytoplankton component

$$K_{pl}(\lambda) = C_a \{C_2(\lambda) \exp[-a_2(\lambda)C_a] + k_{c,i}(\lambda)\}, \quad (9)$$

and its component of the chlorophyll-correlated optically active admixtures

$$K_{\Delta}(\lambda) = K_d(\lambda) - [K_w(\lambda) + K_{pl}(\lambda)] = C_a \{C_1(\lambda) \exp[-a_1(\lambda)C_a] + C_2(\lambda) \exp[-a_2(\lambda)C_a] + k_{d,i}(\lambda) - k_{c,i}(\lambda)\}, \quad (10)$$

where $\Delta K(\lambda) = 0$ for WC 1 and $\Delta K(\lambda) > 0$ and variable for WC 2. For instance, our measurements in the central Baltic show that from May to July in 1980 and 1984, ΔK (from 250 data sets) averages $0.062 \pm 0.043 \text{ m}^{-1}$ and is practically nonselective with respect to wavelength.

The constants $C_1(\lambda)$, $C_2(\lambda)$, $k_{d,i}(\lambda)$, $k_{c,i}(\lambda)$, $a_1(\lambda)$, $a_2(\lambda)$ and $K_w(\lambda)$ are given in Table 2 for individual wavelengths λ . $K_w(\lambda)$ is the component of the coefficient $K_d(\lambda)$ due to attenuation by pure water only. Its magnitude was obtained from statistical analyses of 148 $K_d(\lambda)$ vs. C_a spectra from the Sargasso Sea for small C_a , i.e. $C_a < 0.06 \text{ mg} \cdot \text{m}^{-3}$, performed by extrapolating the curve of $K_d(\lambda) \approx f(C_a)$ to $K_d(\lambda) = f(C_a = 0) = K_w(\lambda)$ (23rd cruise of r/v 'Vityaz', 1991). To determine these parameters of the approximating formulas (8), (9), (10), 1229 empirical $K_d(\lambda)$ spectra were used together with data on chlorophyll concentration C_a (602 from oligotrophic waters (O), 290 from mesotrophic waters (M), 182 from intermediate waters (I) and 155 from eutrophic waters (E)). A total of 1041 $K_{pl}(\lambda)$ spectra vs. C_a were analysed including 230 O, 69 M, 52 I and 150 E. The relative errors of this estimation, defined as before (see formulas (3) and (6)) were: systematic depending on wavelength from -10 to +16%, statistical $\pm 48\%$, for $K_d(\lambda)$, and systematic from -10 to +18%, statistical $\pm 51\%$, for $K_{pl}(\lambda)$. $K_{pl}(\lambda)$ was measured indirectly, i.e. determined from the absorption $a_{pl}(\lambda)$ *in vivo* (380 samples) or the absorption $a_{pl,e}(\lambda)$ estimated using formulas (4) and (5), P_i from 661 samples, and the approximate equation $K_{pl}(\lambda) \approx 1.2a_{pl}(\lambda)$ (the value of 1.2 is approximately the reciprocal of the average cosine of the angular radiance distribution in the sea (Jerlov, 1976; Dera, 1992)).

Figure 4 illustrates the bio-optical classification of waters and their characteristics emerging from this model, as proposed earlier by Woźniak (Woźniak and Pelevin, 1991) and made more precise in the present paper. It shows sets of $K_d(\lambda)$ and its components $K_{pl}(\lambda)$ and $K_{\Delta}(\lambda)$ characteristic of the various trophic types of WC 1, whose index is $C_a(0)$. Figure 4D

compares the $K_d(\lambda)$ spectra, calculated for the corresponding C_a according to the above model, with those recorded in the Atlantic.

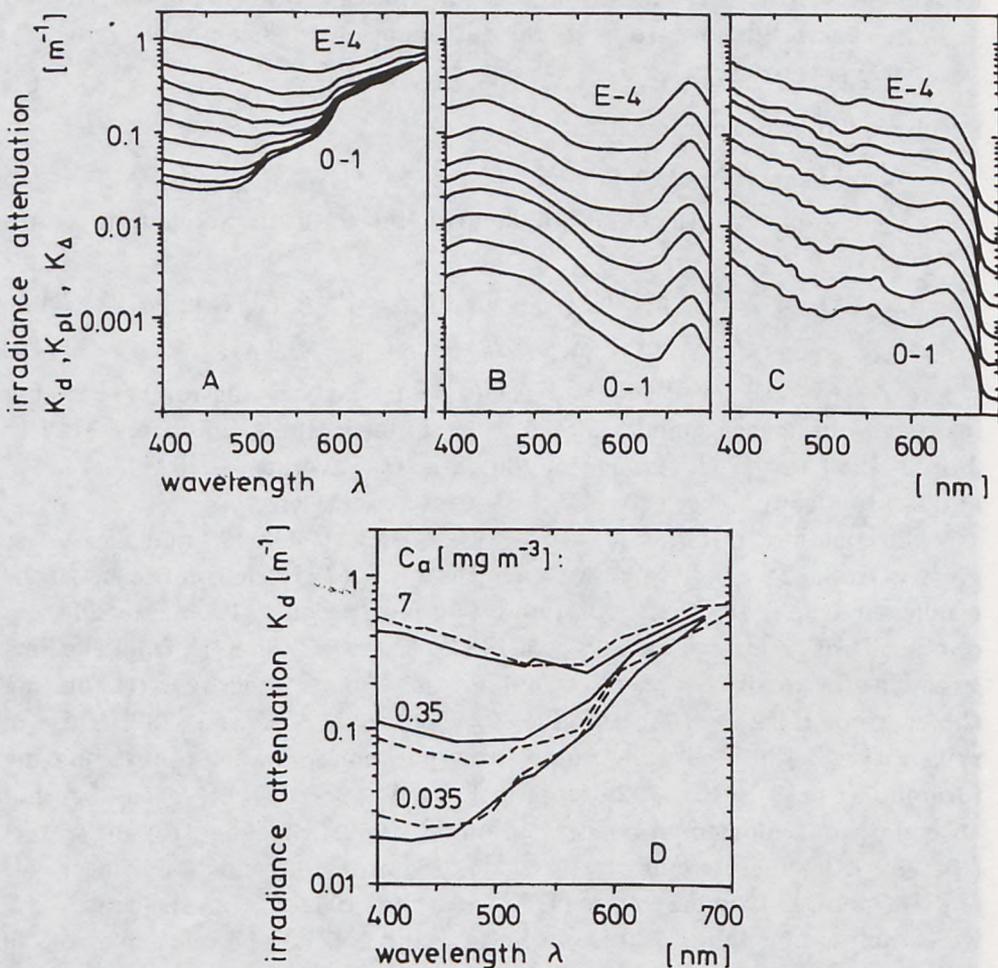


Fig. 4. The spectra of the downward irradiance attenuation coefficients in WC 1 according to Woźniak's bio-optical classification based on equations (8), (9), (10): A — total attenuation $K_d(\lambda)$, B — attenuation by phytoplankton $K_{pl}(\lambda)$, C — attenuation of other optically active substances K_{Δ} , D — comparison of spectra of downward irradiance attenuation coefficient ($K_d(\lambda)$) measured in various regions of the Atlantic (continuous lines) and calculated from this bio-optical classification (dashed lines) with different chlorophyll concentrations C_a [mg m^{-3}]

Similar bio-optical models (bio-optical classification of waters with the chlorophyll concentration being the bio-optical index of the water type) were put forward and used earlier by other authors (Smith and Baker, 1978, 1984; Baker and Smith, 1982; Morel, 1988). The above model with formulas (8), (9) and (10) seems to us to lead to a more accurate use of the formulas

discussed above, and can be applied directly in the algorithm to estimate marine primary production. Furthermore it has been based on large sets of empirical data other than those used to work out the earlier models.

2.6. Dependence of the quantum yield of photosynthesis Φ on underwater irradiance E_{PAR} in waters with different sea surface chlorophyll concentrations $C_a(0)$ (block 6)

The quantum yield of photosynthesis Φ , used in this paper as a measure of photosynthetic efficiency, is defined as the ratio of primary production expressed as the number of assimilated carbon atoms to the number of quanta absorbed by phytoplankton η_{PUR} [quanta m^{-3}]:

$$\Phi = \frac{A P}{12 \eta_{PUR}} \left[\frac{\text{atoms } C}{\text{quanta}} \right], \quad (11)$$

where

A - Avogadro number,

12 - mass number of carbon, and P is expressed in [$g \ m^{-3}$].

Thus, Φ was experimentally determined indirectly on the basis of *in situ* measurements of P , $E_d(\lambda)$ and $a_{pl}(\lambda)$. The last two quantities serve to determine η_{PUR} (see eq. (19)). The spectra of $a_{pl}(\lambda)$ can also be obtained by measuring P_i and using relationships (4) and (5).

The fact that the *in situ* photosynthetic efficiency increases with depth z in the sea owing to the attenuation of the irradiance $E_{PAR}(z)$ is a well known phenomenon (Bannister and Weidemann, 1984; Kishino *et al.* 1984; Kishino *et al.*, 1986). However, the relationships between $\Phi(z)$ and $E_{PAR}(z)$ observed in the oceans can be very different (Figs. 5A and 5B). Φ can differ by more than one order of magnitude for the same values of E_{PAR} . This differentiation diminishes considerably, however, if the results of studies from particular regions of the sea or seasons are analysed separately (see *e.g.* Fig. 5C). There is also an evident tendency for the photosynthetic efficiency to increase with productivity. Thus, by means of statistical methods, it has been possible to roughly formulate analytical expressions for the mean daily quantum yield Φ as a function of two variables - $E_{PAR}(z)$ and $C_a(0)$.

The hyperbolic functions (12), suggested by Kiefer and Mitchell (1983) among others, served as the approximating function. Experimentally determined profiles of $\Phi(z)$ and $E_{PAR}(z)$ (at 69 stations) were used for this purpose, including 25, 8, 5 and 31 for water types O, M, I and E respectively. 24 of these stations were mostly in the Atlantic and can be classified as case 1 waters, while at the other 45, mainly in the Baltic and Black Seas, both water cases were recorded. 791 empirical data sets were obtained from various depths at these stations. For the Baltic and Black Seas, Φ was determined from directly measured phytoplankton absorption spectra $a_{pl}(\lambda)$.

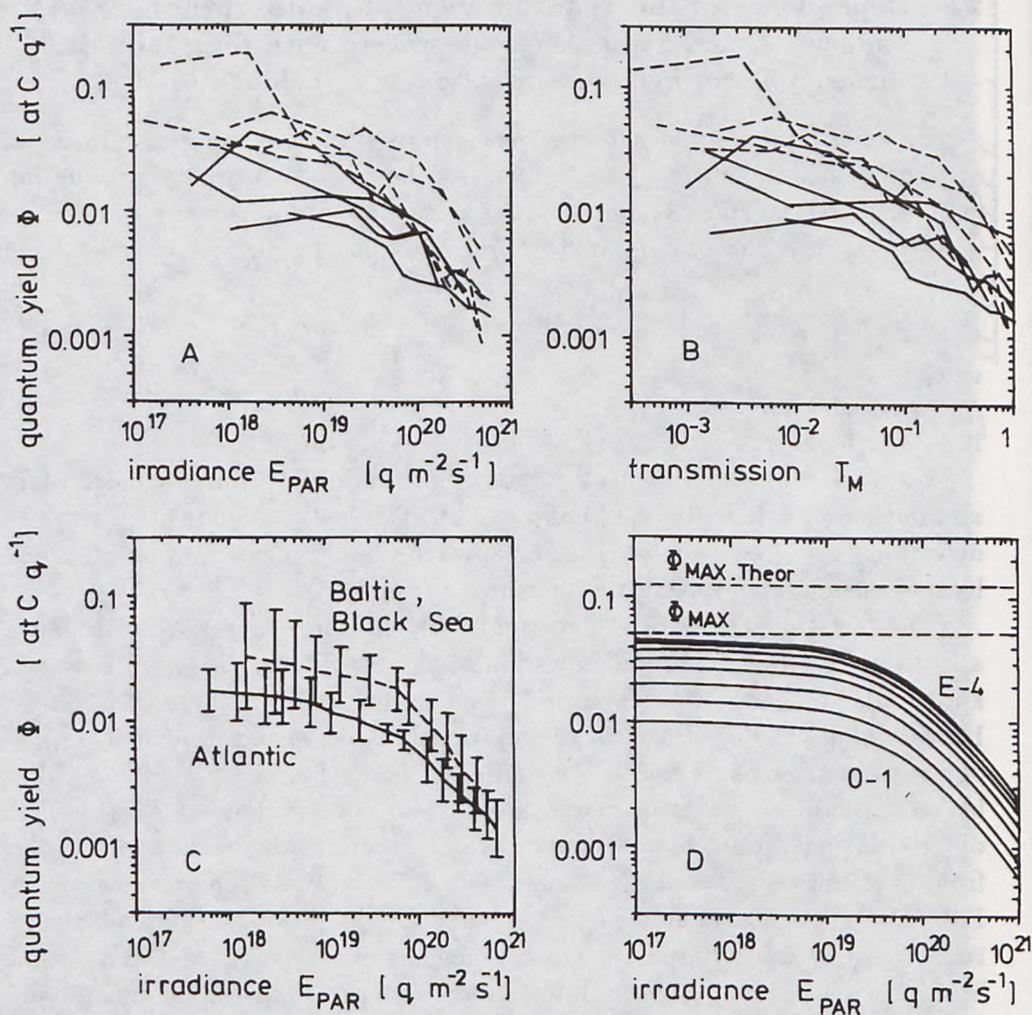


Fig. 5. The mean diurnal quantum yield of marine photosynthesis *vs.* underwater irradiance E_{PAR} and *vs.* relative underwater irradiance (transmission coefficient) $T_M = E_{PAR}(z)/E_{PAR}(0)$. A and B — typical empirical curves for meso- and eutrophic waters in the Baltic and Black Sea (dashed lines) and for oligotrophic waters in the Atlantic (continuous lines), C — averaged curves plus standard deviations: for meso- and eutrophic waters of the Baltic and Black Sea (dashed line), for oligotrophic waters of the Atlantic (continuous line), D — model curves for waters of different trophicity plotted using formulas (12) and (13). The curves from O-1 to E-4 in this figure correspond to the average chlorophyll concentrations in the successive types of water given in Table 1

The $a_{pl}(\lambda)$ spectra for the Atlantic were determined from measurements of acetone extracts using the model relationships (4) and (5).

The approximating formula (12) of the quantum yield $\Phi(z)$ [atoms C /quanta] was obtained by nonlinear regression as a function of $E_{PAR}(z)$ [quanta $m^{-2}s^{-1}$] and $C_a(0)$ [$mg\ m^{-3}$]. Two characteristic parameters of photosynthesis were used for this. One, Φ_{max} , was the *maximum quantum yield* Φ measured at weak irradiance and depends on the water's trophicity $C_a(0)$. The other was $E_{PAR,1/2}$, the logarithmic mean daily downward irradiance at which Φ decreases to 1/2 its maximum value $\Phi(E_{PAR,1/2}) = 1/2\Phi_{max}$. This latter parameter turned out to be practically independent of the sea's productivity and was statistically established as a constant (despite the large scatter). By contrast, the parameter Φ_{max} clearly rises with $C_a(0)$ and can be approximated by the hyperbolic function (13). Using nonlinear regression methods, we were able to obtain the following approximate formulas:

$$\Phi(z) = \Phi_{max} \frac{E_{PAR,1/2}}{E_{PAR,1/2} + E_{PAR}(z)}, \quad (12)$$

where

$$\Phi_{max} = \Phi_{MAX} \frac{C_a(0)^{0.66}}{0.44 + C_a(0)^{0.66}}. \quad (13)$$

The constant $E_{PAR,1/2} \approx 6.4 \times 10^{19}$ quanta $m^{-2}s^{-1}$, and in accordance with the standard deviation of $\log E_{PAR,1/2}$, the deviation of $E_{PAR,1/2}$ from the given mean value ranges from 3.7×10^{19} to 1.10×10^{20} quanta $m^{-2}s^{-1}$. The constant $\Phi_{MAX} = 0.051$ atoms C /quanta, with the standard deviation $0.026 < \Phi_{MAX} < 0.101$ atoms C /quanta is, according to this model, the largest boundary value of the quantum yield Φ in the sea, *i.e.* it is the asymptote of the maximum quantum yield found across in eutrophic waters in conditions of weak irradiance.

Figure 5D depicts these model curves of the dependence $\Phi(E_{PAR})$ for waters of different trophicity $C_a(0)$ drawn in accordance with formulas (12) and (13). This shows that the lowest quantum yields of photosynthesis, characteristic of the surface in superoligotrophic waters (O-1) (see Table 1 in section 2.4) where the irradiance is high, are of the order of 5×10^{-4} atoms C /quanta. The maximum value in such waters at low irradiance is of the order of $\Phi_{max}[C_a(0) < 0.05\ mg\ m^{-3}] \approx 0.01$ atoms C /quanta.

In eutrophic waters (E-4), the maximum quantum yields Φ_{max} approach the value $\Phi_{MAX} \approx 0.05$ atoms C /quanta. Empirical data from great depths in some extreme cases approach the theoretical absolute maximum quantum yield $\Phi_{MAX,theor} \approx 0.125$ atoms C /quanta quoted in the literature (see Govindjee, 1975).

Notice the distinct difference between the quantum yield Φ_{MAX} in the sea (see Figs. 5C and 5D) and $\Phi_{MAX,Theor}$. This difference may, of course, be due to the photosynthetic conditions obtaining in the sea, but it could also be due to the systematic underestimation of measurements of the *in situ* primary production P by the method using ^{14}C labelling and/or the systematic overestimation of the determinations of the phytoplankton absorption spectra $a_{pl}(\lambda)$.

2.7. Basic equations and principles of computations of the environmental characteristics of primary production in the sea (blocks 7–10)

The computation of the algorithm is based on well-known hydro-optical and biophysical formulas (Jerlov, 1976; Kirk, 1983; Dera, 1992). They enable the characteristics of the marine environment given in blocks 7–10 (Fig. 1) to be successively determined from concrete input data (blocks 2 and 3) using the previously discussed model relationships (blocks 4–6).

A knowledge of only the surface concentration of chlorophyll $C_a(0)$ is sufficient to determine directly the vertical chlorophyll distribution in the sea $C_a(z)$ (block 7), and from that, the vertical distributions of the optical properties $OPS(z)$, the depth of the euphotic zone z_e and the total chlorophyll content in this zone $C_{a,tot}$. The $C_a(z)$ profile is obtained by using formula (1) (section 2.3) for stratified waters or by assuming $C_a(z) = C_a(0) = \text{const}$ (formula (2)) for well-mixed waters. Then, knowing $C_a(z)$, one can determine the vertical distributions both of the spectral coefficients of light absorption by phytoplankton $a_{pl}^*(\lambda, z)$ and $a_{pl}(\lambda, z)$ from formulas (4) and (5) (section 2.4) and of the spectral downward irradiance attenuation coefficient for WC 1, $K_d(\lambda, z)$, as well as its components due to attenuation by phytoplankton $K_{pl}(\lambda, z)$ and other optically active admixtures correlated with chlorophyll $K_{\Delta}(\lambda, z)$ using formulas (8), (9) and (10) (section 2.5). For WC 2, the distributions of $\Delta K(\lambda, z)$ typical of the region of the sea and season, *i.e.* the component of the irradiance attenuation coefficient for optical allochthonic admixtures not correlated with chlorophyll, also need to be known to determine $K_d(\lambda, z)$. Once $K_d(\lambda, z)$ is known, the *depth of the euphotic zone* z_e can be determined, *i.e.* that depth in the sea to which 1% of $E_{PAR}(0)$ penetrates, from the following implicit formula:

$$0.01 = \int_{400\text{nm}}^{700\text{nm}} f_E(\lambda, 0) \left\{ \exp \left[- \int_0^{z_e} K_d(\lambda, z) dz \right] \right\} d\lambda, \quad (14)$$

(where $f_E(\lambda, 0) = E_d(\lambda, 0)/E_{PAR}(0)$ is the practically constant relative function of the spectral distribution of the solar incident irradiance (Jerlov, 1976; Dera, 1992)) and the *total chlorophyll a content* $C_{a,tot}$ in the euphotic zone:

$$C_{a,tot} = \int_0^{z_e} C_a(z) dz. \quad (15)$$

The next part of the algorithm (see block 9 in Fig. 1) requires a knowledge not only of $C_a(0)$ but also of the absolute values of the incident solar irradiance and their transmittance across the sea surface. This last one is assumed to be 0.94 ± 0.04 on average. Knowing the time curves of $E_d(\lambda, t, 0)$ (block 3) and the $OPS(z)$ defined earlier (block 8), the vertical distributions of photometric quantities can be successively defined using the formulas for:

- the downward spectral irradiance E_d [quanta $m^{-2} s^{-1} nm^{-1}$]:

$$E_d(\lambda, t, z) = E_d(\lambda, t, 0) \left\{ \exp \left[- \int_0^z K_d(\lambda, z) dz \right] \right\}, \quad (16)$$

- the daily irradiance dose in the *PAR* spectral range η_{PAR} [quanta m^{-2}]:

$$\eta_{PAR}(z) = \int_{t_r}^{t_s} \int_{400 \text{ nm}}^{700 \text{ nm}} E_d(\lambda, t, z) d\lambda dt, \quad (17)$$

where t_r and t_s are the sunrise and sunset times respectively;

- the average downward irradiance in the *PAR* spectral range on a given day E_{PAR} [quanta $m^{-2} s^{-1}$]:

$$E_{PAR}(z) = \eta_{PAR}(z) / \Delta t, \quad (18)$$

where Δt is the period of daylight (from sunrise to sunset);

- the daily quantities of energy absorbed by phytoplankton η_{PUR} [quanta m^{-3}] which are determined from approximate formulas either from the known distribution of the phytoplankton absorption coefficient $a_{pl}(\lambda, z)$:

$$\eta_{PUR}(z) \approx 1.2 \int_{t_r}^{t_s} \int_{400 \text{ nm}}^{700 \text{ nm}} E_d(\lambda, t, z) a_{pl}(\lambda, z) d\lambda dt, \quad (19)$$

or from the known distribution of the coefficient of irradiance attenuation by phytoplankton $K_{pl}(\lambda, z)$:

$$\eta_{PUR}(z) \approx \int_{t_r}^{t_s} \int_{400 \text{ nm}}^{700 \text{ nm}} E_d(\lambda, t, z) K_{pl}(\lambda, z) d\lambda dt. \quad (20)$$

Equation (20) was used for the computations in this paper.

The final stage of computations is the determination of the *vertical distribution of primary production* in the sea $P(z)$ and the *total primary production* in the water column P_{tot} (block 10 in Fig. 1) on the basis of a known $\eta_{PUR}(z)$ profile. The first $P(z)$ profile is obtained using the formula

$$P(z) = \Phi(z) \eta_{PUR}(z) \left[\frac{\text{atoms } C}{\text{m}^3} \right], \quad (21)$$

where the average daily quantum yield at different depths in the sea $\Phi(z)$ is determined from model dependences $\Phi \approx F[C_a(0), E_{PAR}]$ (see eqs. (12) and (13)), assuming the previously determined magnitudes of irradiances $E_{PAR}(z)$ at these depths. On the other hand, the total primary production is determined by integrating over the depths of the profiles $P(z)$:

$$P_{tot} = \int_0^{z(P=0)} P(z) dz, \quad (22)$$

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} .

3. The results of model computations and the experimental verification of the algorithm to estimate primary production

The algorithm was used to determine marine environmental characteristics (see blocks 7–10) describing the influx and utilization of solar radiant energy in photosynthesis in water with different trophicities and incident solar irradiance conditions.

For reasons of space we shall present only selected final results of the estimation, illustrating the relations between total primary production and the above-mentioned conditions, (see Figs. 6 and 7). The computations were done independently for two types of waters differing diametrically in the composition of their optically active admixtures and hydrological conditions:

A – stratified, WC 1 (where $\Delta K \approx 0$),

B – well-mixed, WC 2 (where $\Delta K > 0$).

In the latter computations (B) the component of the irradiance attenuation coefficient due to optical admixtures of water not correlated with chlorophyll was taken be $\Delta K = 0.062 \text{ m}^{-1}$, a value typical of the open southern Baltic in spring and summer.

Figure 6 depicts the interdependences of the total diurnal primary production per energy dose entering the sea $\eta_{PAR}(0)$ and the surface chlorophyll $C_a(0)$ calculated for various average irradiances $E_{PAR}(0)$. The *photosynthetic index* ε_{tot} , a measure of these relative productions, is defined as

$$\varepsilon_{tot} = \frac{k_{E/P} P_{tot}}{(k_{q/E})^{-1} \eta_{PAR}(0)} \approx 1.10 \times 10^{23} \frac{P_{tot}}{\eta_{PAR}(0)}, \quad (23)$$

where the energy equivalent of the mass of assimilated carbon $k_{E/P} \cong 40 \text{ kJ/g } C$, the quantum equivalent of the incident solar energy in the *PAR* spectrum (in the 400–700 nm range), $k_{q/E} \cong 2.75 \times 10^{18} \text{ quanta/J}$

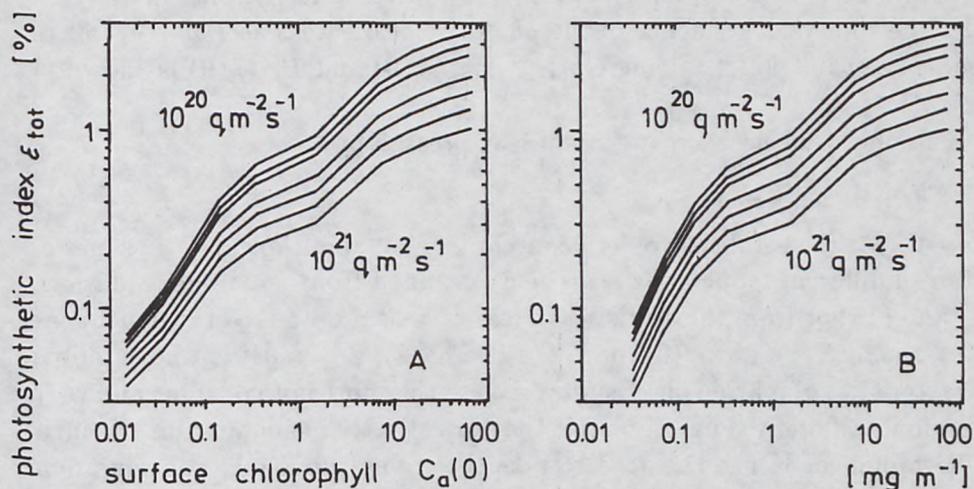


Fig. 6. Theoretical relationships between the photosynthetic index ϵ_{tot} (eq. 23) and the trophic index of the water (surface chlorophyll $C_a(0)$) determined from our model: A — for stratified WC 1, B — for well-mixed WC 2, assuming $\Delta K = 0.062 \text{ m}^{-1}$, i.e. the mean value for the open waters of the central Baltic in spring and summer. The curves plotted for various mean diurnal irradiances $E_{PAR}(0)$: 1×10^{20} , 2×10^{20} , 3×10^{20} , 5×10^{20} , 7×10^{20} , 8×10^{20} and 1×10^{21} [quanta $\text{m}^{-2} \text{ s}^{-1}$] (counting from the top)

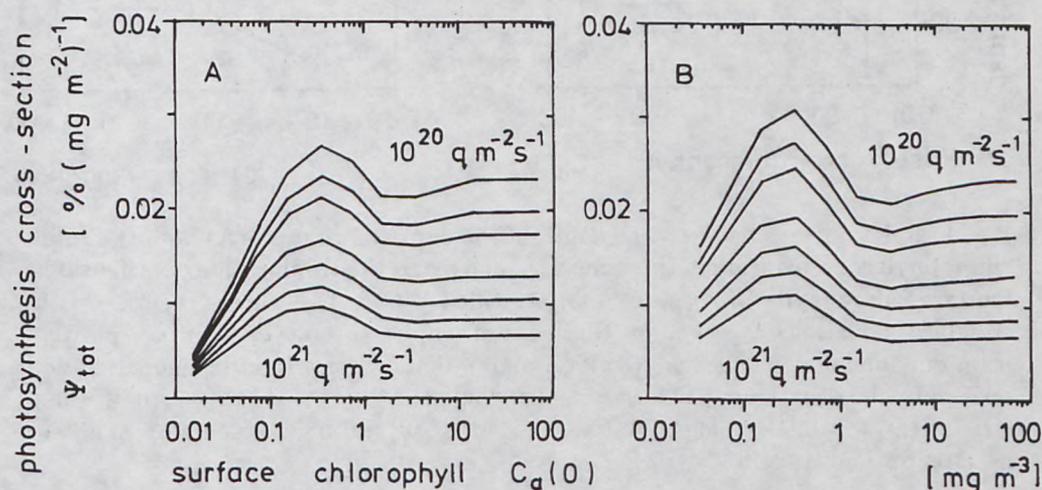


Fig. 7. Theoretical relationships between the photosynthesis cross-section per unit of areal chlorophyll Ψ_{tot} (eq. 24) and the trophic index of the water C_a . Explanations as in Figure 6

(Koblentz-Mishke *et al.*, 1985), and P_{tot} is expressed in $[g C m^{-2}]$. By contrast, the similar dependence of the *photosynthesis cross-section* per unit of *areal chlorophyll* Ψ_{tot} $[m^2 (mg Chl)^{-1}]$ on $C_a(0)$ and $E_{PAR}(0)$ is shown in Figure 7.

The photosynthesis cross-section is expressed by

$$\Psi_{tot} = \varepsilon_{tot}/C_{a,tot}, \quad (24)$$

where $C_{a,tot}$, the total chlorophyll content $[mg m^{-2}]$ in the euphotic zones of waters of different trophicities, can be determined from the model equations (14) and (15) or from the statistics of experimental data (see the dependences of z_e and $C_{a,tot}$ on $C_a(0)$ for WC 1 in Fig. 8). ε_{tot} and Ψ_{tot} , both global characteristics of marine photosynthesis, are therefore not constant and vary in value in different types of water; they are strictly dependent on the incident irradiance. Hence the need to take these conditions into consideration when modelling estimations of primary production in the sea.

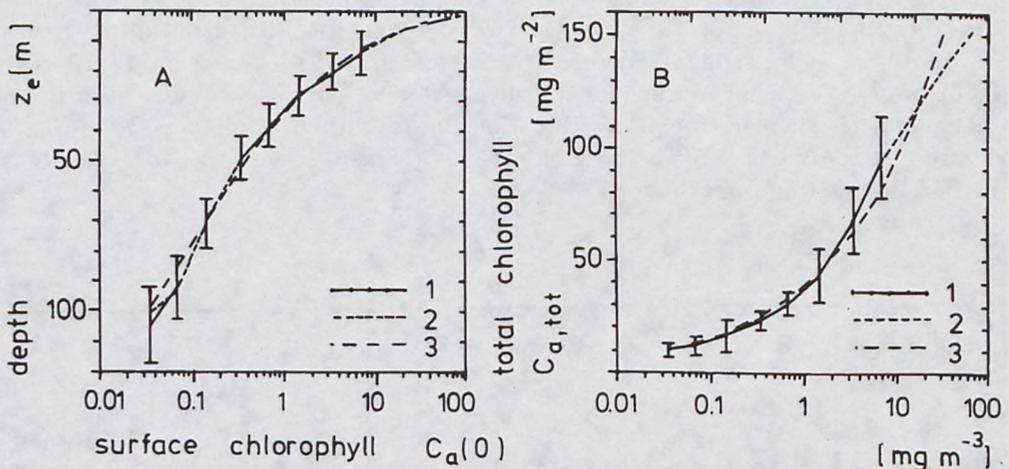


Fig. 8. Relationships between the depth of the euphotic zone z_e (A), and the total chlorophyll concentration in this zone $C_{a,tot}$ (B), and the trophic index of the water (surface chlorophyll $C_a(0)$) plotted for stratified WC 1. 1 — curves together with standard deviations averaged on the basis of empirical data, 2 — curves plotted from our model, 3 — an analytical approximation of these interdependences, described by the equations: (A) $\log z_e = -0.0899[\log C_a(0)]^2 - 0.444 \log C_a(0) + 1.54$; (B) $\log C_{a,tot} = 0.00192[\log C_a(0)]^2 + 0.394 \log C_a(0) + 1.58$ obtained by a nonlinear regression method

In addition, a preliminary experimental verification of the algorithm has been carried out for stratified WC 1, and well-mixed WC 2 on the basis of known $C_a(0)$ and conditions of incident solar irradiance represented by diurnal energy doses $\eta_{PAR}(0)$ and the corresponding mean diurnal irradiance

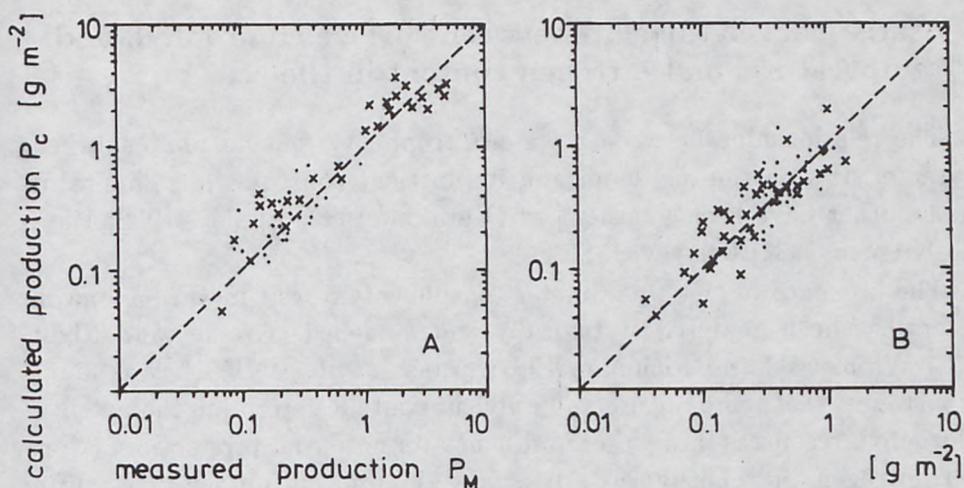


Fig. 9. Comparison of total primary production in the water column under unit area of sea surface estimated using our model P_C and measured *in situ* P_M . A — in stratified WC 1, from the Indian Ocean and Atlantic (authors' investigation) (dots), and empirical data from the Atlantic (Morel, 1978) (crosses); B — in well-mixed WC 2, from authors' (dots) and Renk's, 1973, 1990 (crosses) empirical data from the central Baltic

$E_{PAR}(0)$. To this end, the total production P_C computed using the model was compared with that measured directly in the sea P_M (see Figs. 9A and 9B). 54 points of dependence on the P_C vs. P_M plot were used for stratified WC 1 (26 from our own measurements made during the 16th and 23rd cruises of r/v 'Vityaz' in various regions of the Indian and Atlantic Oceans, and 28 obtained by modifying experimental data measured in various parts of the Atlantic during the WG-15 and CINECA-5 expeditions — see Tables 1a and 1b in Morel (1978)). 95 such points for the open waters of the southern Baltic were used as an example of well-mixed case 2 waters (47 from our own measurements and 48 from Renk (1973, 1990)). In both cases the data referred to seas with trophicities ranging from 0.02 to *ca* 18 mg m⁻³ for WC 1 and from 0.6 to 25 mg m⁻³ for WC 2. The estimated errors $(P_C - P_M)/P_M$ in this assessment are:

systematic +16%, statistical $\pm 40\%$ for stratified WC 1,

systematic +5%, statistical $\pm 42\%$ for well-mixed WC 2.

In view of the possible experimental errors in determining primary production, these errors can be regarded as small, an indication of the correctness and practicability of the algorithm.

4. Statistical relationship between surface chlorophyll and temperature, and nitrogen content in the sea

The relationships between a water's trophicity and its photosynthetic characteristics on the one hand and its nutrient content and temperature on the other have been investigated (Kethum, 1939; Eppley, 1972; Kiefer and Kremer, 1981; Belayev, 1987).

The influence of these parameters on photosynthesis in various marine waters has been analysed statistically and modelled (Kremer and Nixon, 1978; Wróblewski and Richman, 1987; Frasz *et al.*, 1991). It was found, for instance, that temperature and nutrient content determine the extent of chlorophyll resources in a water and hence its potential production. Moreover, nitrogen and phosphorus are usually the limiting nutrients in marine photosynthesis (Parsons *et al.*, 1977; Gershanovich and Muromtsev, 1982). However, no coherent description yet exists of these relationships over the whole range of variability of temperature and nutrient concentration in the World Ocean. We attempted to produce such a description in our earlier work (Koblentz-Mishke and Vedernikov, 1977; Woźniak, 1990), where for various waters we analysed the maximum rate of primary production per unit mass of chlorophyll (P/C_a) and the surface chlorophyll $C_a(0)$, among other parameters, as functions of two variables: the mean euphotic zone temperature T_e and the mean inorganic nitrogen content $\sum N_{inorg}$ in the *ca* 10 m - thick surface layer. $\sum N_{inorg}$ was taken to be the total inorganic nitrogen content in nitrate NO_3^- , nitrite NO_2^- and ammonium NH_4^+ ions. As work on this problem has not yet been completed (see block 2a in Fig. 1), we shall merely present, by way of example, the modified statistical dependence $C_a(0) \approx f[\sum N_{inorg}, T_e]$ in the form of the plot in Figure 10, based on the analysis of some 1200 suitable data (including *ca* 800 from the Baltic). This figure gives the approximate position of the relevant $C_a(0) = \text{const}$ isolines on the T_e vs. $\sum N_{inorg}$ plot and enables the trophicity to be roughly assessed from a knowledge of the above abiotic conditions. Waters displaying moderate temperatures and intermediate nutrient contents clearly have the highest trophicity.

However, $C_a(0)$ assessments done in this way are rather inaccurate; 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 $C_a(0)$ estimated from the plot and measured *in situ* respectively) lies in the interval $0.38 \leq x \leq 2.6$.

This wide scatter is due chiefly to the fact that in our analysis we considered only inorganic nitrogen compounds. The chlorophyll concentration is probably closely correlated with the total nitrogen content, *i.e.* not only the nitrogen contained in inorganic nutrients, but also that in the organic

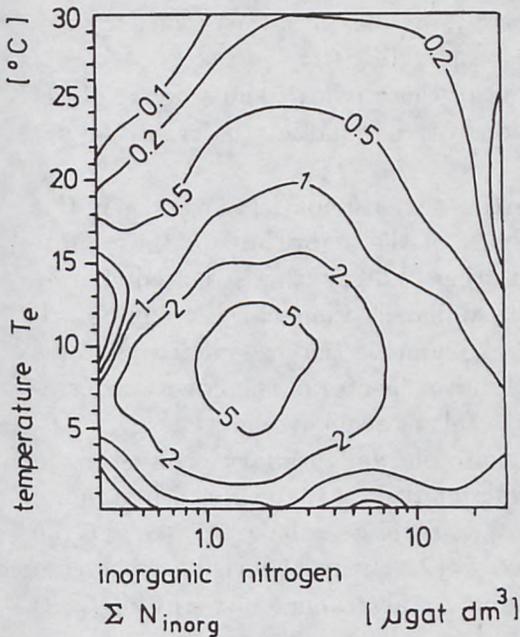


Fig. 10. The averaged relationship between surface chlorophyll (chl *a* + phaeo) in various regions of the World Ocean $C_a(0)$ and the average water temperatures in euphotic zones T_e and average sub-surface inorganic nitrogen concentrations (0–10 m) ΣN_{inorg} . The Figure shows approximate positions of isolines $C_a(0) = \text{const}$ for various $C_a(0)$ [mg m^{-3}] on T_e vs. ΣN_{inorg} plot

substances – organisms, dissolved organic matter and detritus. To characterize this and other dependences of photosynthesis on abiotic factors more accurately is the object of our studies.

5. Final remarks and conclusions

Our model of the relationship between primary production and the various physical and chemical factors of the marine environment is a preliminary one and requires further expansion and adjustment. In particular the modelling procedure needs to be developed, and the statistical model formulas linking the chlorophyll concentration (chl *a* + phaeo) C_a with the content of various nutrients and their forms of occurrence in the sea have to be established. The model formulas relating photosynthesis to irradiance, the optical properties of waters and their trophicity also need adjusting, which will require far more empirical data for statistical analyses than are at present available. This applies in particular to the most innovative relationships – between the spectral coefficients of light absorption by phyto-

plankton and chlorophyll concentration C_a , and between the quantum yield, and the underwater irradiance and chlorophyll $C_a(0)$.

The present preliminary description of these relationships does not yet provide sufficiently accurate estimations of the characteristics of the sea discussed in this paper.

Despite these limitations the approximate mathematical formulas in this version of the model can be used as part of the algorithm for the remote estimation of primary production and other photosynthesis-related characteristics of the sea. The following vertical distributions can thereby be calculated: the concentration of chlorophyll pigments (chl a + phaeo), spectra of light absorption by phytoplankton *in vivo*, spectra of the downward irradiance attenuation coefficient, diurnal totals of available light energy PAR , the PUR energy absorbed by phytoplankton, and primary production in the sea. To do so, however, the following input data (determined by remote sensing) must be known: surface chlorophyll (chl a + phaeo) $C_a(0)$, and the spectrum of diurnal surface irradiance $E_d(\lambda, t, 0)$ in the visible spectrum as a function of time or only the diurnal total irradiance energy $\eta_{PAR}(0)$ entering the sea.

As regards the assessment of primary production, our algorithm seems to us to be more accurate than those published earlier. This is chiefly because we have taken into account the relationships between the quantum yield of photosynthesis, and the trophic index of a water $C_a(0)$ and the irradiance E_{PAR} . So, integral photosynthetic characteristics in the water column, *i.e.* the photosynthetic index ε_{tot} (23) or the photosynthesis cross-section Ψ_{tot} (24), both closely related to the quantum yield, may play a key role in the estimation of primary production.

Knowing ε_{tot} or Ψ_{tot} for particular irradiance conditions at the sea surface $E_{PAR}(0)$ and particular surface chlorophyll $C_a(0)$ enables the total primary production to be determined from the solar radiant energy doses $\eta_{PAR}(0)$ entering the sea by means of the formulas (from a transformation of eqs. (23) and (24)):

for $\eta_{PAR}(0)$ expressed in [quanta m^{-2}]

$$P_{tot} = 9.09 \times 10^{-24} \varepsilon_{tot} \eta_{PAR}(0) \quad [g C m^{-2}]$$

for $\eta_{PAR}(0)$ expressed in [J m^{-2}]

$$P_{tot} = 2.5 \times 10^{-5} \varepsilon_{tot} \eta_{PAR}(0) \quad [g C m^{-2}]$$

or

$$P_{tot} = 2.5 \times 10^{-5} \eta_{PAR}(0) \Psi_{tot}(0) C_{a,tot} \quad [g C m^{-2}].$$

The range and causes of the variability of ε_{tot} or Ψ_{tot} in nature have been examined (Platt *et al.*, 1988; Sathyendranath *et al.*, 1989). The possibility of regarding Ψ_{tot} as a biogeochemical 'constant' in simple models has been considered (Platt, 1984). The 'constant' Ψ_{tot} defined by Morel (1978, 1988) on the basis of 30 measurements made during the WG-15 and CINECA-5 expeditions is $\Psi_{tot} = 7 \times 10^{-5} \text{ m}^2(\text{mg Chl})^{-1}$ within $\pm 50\%$ at $1\sigma^1$. Our model takes account of the diversity of Ψ_{tot} values in the World Ocean and also describes quantitatively the dependence of this parameter on the trophic index and conditions of incident solar irradiance (Fig. 7). It is therefore a step towards solving the problem.

Some doubts might be expressed concerning the quantitative accuracy of the formulas in some blocks of the algorithm (Fig. 1) because of uncertainties in determining the absolute coefficients of light absorption by phytoplankton $a_{pl}(\lambda)$. In comparison with the results of others (Haardt and Maske, 1981; Privoznik *et al.* 1978), the specific coefficients $a_{pl}^*(\lambda)$ used in our model are somewhat higher in value particularly for oligotrophic ecosystems. This could be due to systematic methodological errors in the measurements of $a_{pl}(\lambda)$ on which our model relationships have been based. Which of these absorption coefficients is correct we cannot state unequivocally at present. If, however, we assume that our coefficients $a_{pl}(\lambda)$ have been systematically overestimated, then clearly other characteristics determined from them must also be erroneous; *e.g.* the coefficients $K_{pl}(\lambda)$ and energies η_{PUR} are overestimated, but the quantum yields Φ are too low. On the other hand, if primary production P is estimated as the product $\Phi \times \eta_{PUR}$, these errors cancel themselves out, so that the computed values of $P(z)$ and P_{tot} are close to the actual values. Preliminary verification of our model shows that our estimates are quite accurate (section 3, Figs. 9A and 9B).

A further cause of underestimated quantum yields Φ , both measured experimentally and modelled, could be the fact, suggested by a number of authors (Koblentz-Mishke *et al.*, 1985; Vinogradov and Shushkina, 1987), that primary production determined by ^{14}C labelling is inaccurate. These errors - if they occur - are also transferred to the estimated primary production, which in this situation approaches not the real level of production but that perhaps underestimated by the radioisotope methods.

Our model is particularly suitable for modelling primary production and related characteristics in WC 1. If it is to be applied to WC 2 as

¹Morel's (1978) empirical data indicate that this figure was arrived at on the basis of primary productions measured under similar solar incident irradiance conditions at all stations. In 25 cases, the mean diurnal irradiance $E_{PAR}(0)$ was high, ranging from 5.5×10^{20} to 8×10^{20} quanta $\text{m}^{-2}\text{s}^{-1}$, whereas under natural conditions such irradiance ranges from *ca* 1×10^{20} or less to *ca* 1×10^{21} quanta $\text{m}^{-2}\text{s}^{-1}$.

well, further investigations are necessary for each region and season in order to determine the typical values of $\Delta K(\lambda)$, (the component of the spectral coefficients of irradiance attenuation – see formula (7) or (8)) with ‘local’ formulas referring to particular regions of the sea or seasons.

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