Algorithm for estimating primary production in the sea from satellite sensing*

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Abstract

The article presents an algorithm for determining primary production in the sea from multispectral, optical data obtained by satellite sensing. Unlike algorithms proposed by other authors, a number of less precise correlations between 'extremely distant' physical and biological parameters have been replaced by relationships based on marine plant physiology. In particular, the algorithm applies a semi-empirical mathematical model of light absorption by the photosynthetic apparatus specific to various natural phytocoenoses. The algorithm also combines the statistically generalized correlations between the efficiency of phytoplankton photosynthesis and optical depth.

1. Introduction

The determination of primary production in the seas and oceans is one of the most important tasks of modern oceanology (ISY Project, 1992).

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This task has developed from the observed increase in carbon dioxide concentration in the atmosphere in recent years and the subsequent greenhouse effect, resulting in an increase in the Earth's temperature (Glantz, 1988; Kellogg, 1988; Woźniak, 1990). It is well recognized that a considerable role in the observed climatological changes and in the condition of the terrestial biosphere is played by the overall production of the World Ocean, one of the very important links in the natural carbon circulation. Any solution to the problem of determining the global primary production of the World Ocean seems impossible without satellite observations.

The results of successful research on primary production carried out by American and Canadian teams (Balch *et al.*, 1989; Campbell and O'Reilly, 1988; Platt, 1986; Platt and Sathyendranath, 1988; Platt *et al.*, 1988; Sathyendranath *et al.*, 1989) have been well publicized. The authors analyzed the data from the archives of the CZCS scanner installed on the American satellite 'Nimbus'. However, the analytical problems are far from being finally solved. This is because of the many simplifications assumed in these analyses. For example, chlorophyll and other optically active components of seawater are most frequently determined from experimental data on the upward irradiance intensity in two spectral regions, *i.e.* by applying the ratio $I = \rho(\lambda_1/\ \rho(\lambda_2)$, where $\rho(\lambda)$ – spectral coefficient of irradiance reflection from the sea surface, λ – wavelength. Further, to determine the integral primary production $P_{\Sigma z}$ (*i.e.* the production in the vertical water column from the surface to the limit of the euphotic zone) the authors applied empirical relationships like $P_{\Sigma z} = A \cdot I^B$. The mean values of the empirical parameters A and B are very scattered. The parameters have been determined from limited experimental material and used in calculations of primary production in different regions of the World Ocean in various seasons. The authors also point out the many difficulties encountered in calibrating the CZCS equipment. In fact, the CZCS has not been operating for a long time now and the actual dates of installation and service of its analogues are rather vague.

For these reasons the present article aims to present a new, revised algorithm for determining primary production in the sea from satellite information. Compared with the earlier algorithms it differs in the following aspects:

- We suggest the application of multispectral information on irradiance emerging from the sea, similar to data obtained from the MKS–M scanner equipped with detectors covering 16 spectral channels from the visible and infrared range; the one in service at present is on the Soviet space station 'MIR'.

- We have attempted to avoid inaccurate correlations between the extremely distant physical properties and biological features; instead we have introduced relations based to a greater extent on marine plant physiology.

Compiling this algorithm also seems relevant because another scanner, MOZ, is to be sent into space, with a similar number of spectral channels to that of the MKS–M scanner. Thus the algorithm may serve to determine the primary production of vast regions of the World Ocean.

2. Major stages of the algorithm

A simplified block diagram of the algorithm for determining primary production in the sea from satellite information is shown in Figure 1. The diagram illustrates the successive stages of calculations (see the numbered blocks) taking into account various physical parameters and biological factors, which are input data or results of calculations at particular stages.

A satellite records the upward spectral radiation $L_{\uparrow}(\lambda)$, formed in the ocean-atmosphere optical system. The first stage of the algorithm introduces a so-called *atmospheric correction* (see block 1 in Fig. 1). This correction is carried out by modelling the natural fields of radiation in the atmosphere, with the application of the algorithms presented by Gordon (1978) and Sturm (1981). In the case of the MKS–M or MOZ scanners the correction methods have been presented by Malkevitch and Badayev (1988), and Zimmermann *et al.* (1985), and will not be discused here. The methods allow the determination of upward spectral radiation just over the sea surface and the components of this radiation $L^{w}_{\uparrow,s}(\lambda)$ emerging from the sea. The spectra of the natural downward irradiance of the sea surface $E_{\downarrow,s}(\lambda)$ are also determined. The parameters $L_{\uparrow,s}(\lambda)$ and $E_{\downarrow,s}(\lambda)$ are used to determine the basic parameters for subsequent calculations of the $\rho_w(\lambda)$ component of the coefficient of radiation reflection from the sea surface, resulting from radiation emerging from the water. The $\rho_w(\lambda)$ values are determined for each pixel of the satellite picture from the equation

$$\rho_w(\lambda) = \frac{\pi \cdot L^{w}_{\uparrow,s}(\lambda)}{E_{\downarrow,s}(\lambda)}, \tag{1}$$

The values of $\rho_w(\lambda)$ form the input data for the second important stage of the algorithm (see block 2 in Fig. 1), consisting of the solution of the 'inverse problem of hydrooptics'. This stage aims at determining either the optical coefficients or concentrations of the particular optically active components of seawater, including the approximate content of chlorophyll Ba^*.

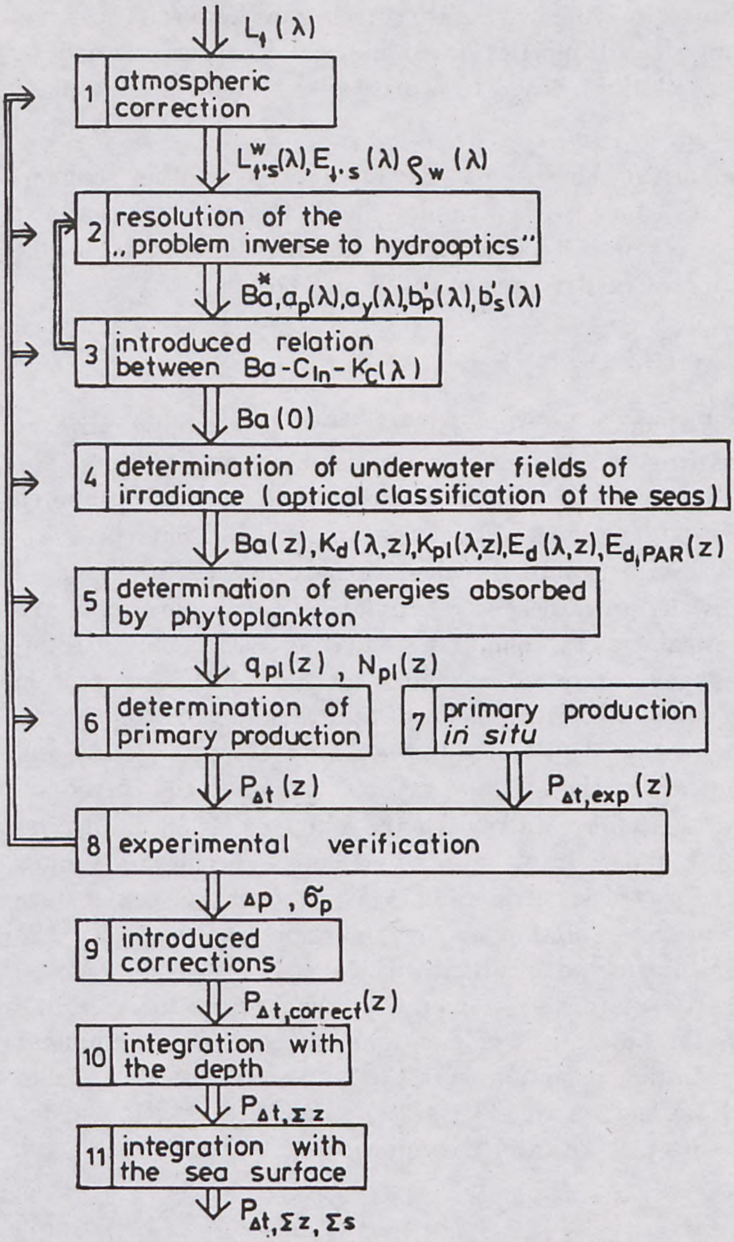

Fig. 1. Block diagram of the algorithm for assessing the primary production of the sea from satellite information (symbols explained in the text): 1 – atmospheric correction, 2 – solution of the 'inverse problem of hydrooptics', 3 – introduction of the relationship between $Ba - C_{In} - K_C(\lambda)$, 4 – determination of underwater fields of irradiance (optical classification of the seas), 5 – determination of energies absorbed by phytoplankton, 6 – determination of primary production, 7 – primary production measured *in situ*, 8 – experimental verification, 9 – introduction of corrections, 10 – integration over depth, 11 – integration over sea surface

This problem is solved by using the relationship, justified by various authors, combining the sea albedo with light absorption and light diffusion coefficients in seawater

$$\tilde{\rho}_w(\lambda) = C \cdot \frac{b'_w(\lambda) + b'_p(\lambda) + b'_s(\lambda)}{a_w(\lambda) + a_{pl}(\lambda) + a_p(\lambda) + a_y(\lambda) + b'_w(\lambda) + b'_p(\lambda) + b'_s(\lambda)}, \quad (2)$$

where

a_w, a_{pl}, a_p, a_y – respective light absorption coefficients of pure water, phytoplankton pigments, all suspensions except pigments and dissolved yellow substances,

b'_w, b'_p, b'_s – respective coefficients of light backscattering by water molecules, all suspensions and dissolved substances,

C – constant of a value close to 0.11 (Pelevin and Solomakha, 1989).

The relationship between the light absorption coefficient by phytoplankton pigments $a_{pl}(\lambda)$ and the chlorophyll concentration Ba^* is given by

$$a_{pl}(\lambda) = K_c(\lambda) \cdot Ba^*, \quad (3)$$

where

$K_c(\lambda)$ – specific absorption of phytoplankton pigments, *i.e.* absorption related to the unit of chlorophyll *a* concentration.

For the sake of simplicity it is assumed that the relative spectral functions of the absorption and diffusion coefficients, as well as the relationship between them in various basins, are known (Pelevin and Solomakha, 1989). The absolute values of the optical coefficients $a_w(\lambda)$ and $b'_w(\lambda)$ for water are also known. In the first iteration of this stage we assume an arbitrary spectrum $K_c(\lambda)$. Thus, the quantities $\rho_w(\lambda)$ become the functions of five variables: Ba^*, $a_p(\lambda_0)$, $a_y(\lambda_0)$, $b'_p(\lambda_0)$ and $b'_s(\lambda_0)$, where (λ_0) is an arbitrary wavelength. Determining these parameters, *i.e.* solving the 'inverse problem of hydrooptics', consists of selecting the parameters by minimizing the sum of squares S – that is, the differences between the reflection coefficients $\rho_w(\lambda_i)$ obtained from equation (1) and similar coefficients $\tilde{\rho}_w(\lambda_i)$ calculated from equation (2). The sum S is therefore

$$S = \Sigma_{i=1}^{M}[\rho_w(\lambda_i) - \tilde{\rho}_w(\lambda_i)]^2 \quad (4a)$$

where

M – number of the spectral channels in the scanner.

Pelevin and Solomakha (1989), and Badayev *et al.* (in preparation) have indicated that this minimization method gives good results for $M \geq 5$. The 'inverse problem of hydrooptics' can be solved by minimizing the S_1 modulus:

$$S_1 = | \rho_w(\lambda_j) - \tilde{\rho}_w(\lambda_j) |, \quad (4b)$$

i.e. the greatest difference between the $\bar{\rho}_w(\lambda_j)$ and $\rho_w(\lambda_j)$ coefficients determined for the j–th spectral channel, j belonging to the set $i = 0, 1, 2 \ldots, M$.

The chlorophyll a concentration Ba^* in the surface water layer, calculated from equation (4a) or (4b), is only estimated in the first cycle of block 2 of the algorithm (*i.e.* in the first iteration). This concentration is determined more precisely in block 3 of the algorithm (see Fig. 1), and then fed back to blocks 2, both blocks cooperating in the iteration cycle.

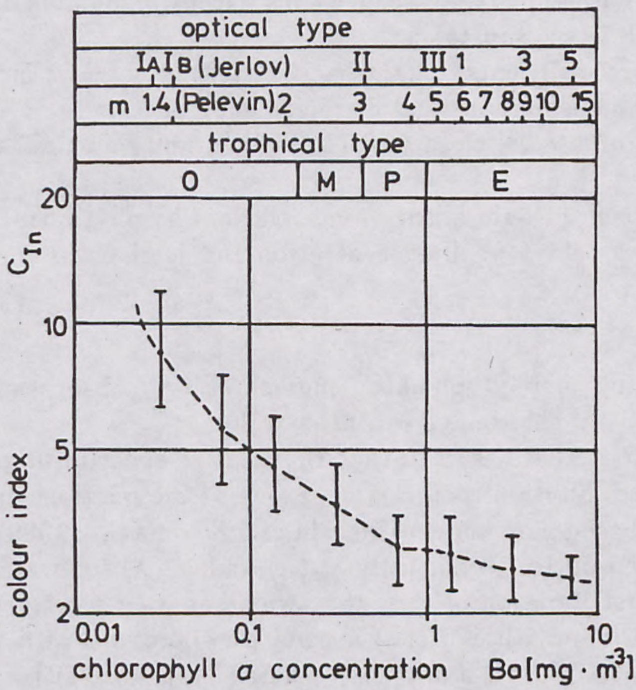

Fig. 2. Colour index of phytoplankton pigments C_{In} versus chlorophyll a concentration Ba averaged for the World Ocean. Vertical segments denote the standard deviation of C_{In} (based on the data from Tab. 1). O – oligotrophic sea ($Ba(O) < 0.2$ mg·m^{-3}, M – mesotrophic sea ($0.2 < Ba(O) < 0.5$ mg·m^{-3}) P – intermediate sea: meso-eutrophic ($0.5 < Ba(0) < 1.0$ mg·m^{-3}), E – eutrophic sea ($Ba(0) > 1.0$ mg·m^{-3})

Block 3 of the algorithm consists of the statistical relationships between the various physical and physiological characteristics of marine phytoplankton, developed by Woźniak and generalized for the World Ocean. In particular, these relationships concern

- $K_c(\lambda)$, *i.e.* the spectra of specific light absorption by phytoplankton,
- Ba, chlorophyll a concentration in seawater,

- C_{In}, colour index of phytoplankton pigments, *i.e.* the extinction ratio $Ex(\lambda)$ (or absorption) of acetone phytoplankton extracts in the 433 and 661 nm bands: $C_{In} = Ex(\lambda = 433 \text{ nm})/Ex(\lambda = 661 \text{ nm})$.

Table 1. Colour index of phytoplankton pigments in various natural phytocoenoses of different chlorophyll *a* concentration (Woźniak and Ostrowska, 1990a)

Phytocoenoses	Range of absolute chlorophyll *a* concentration Ba [$\mathrm{mg \cdot m^{-3}}$]	Colour index C_{In} [dimensionless]		Data
		Geometrical mean	Standard range of variability	
Oligotrophic	0.02–0.05	8.76	5.67–13.5	12
	0.05–0.10	5.60	3.70–8.46	150
	0.1–0.2	4.54	3.01–6.84	206
Mesotrophic	0.2–0.5	3.64	2.61–5.09	260
Intermediate: meso-eutrophic	0.5–1.0	2.86	2.11–3.89	270
Eutrophic	1–2	2.80	2.02–3.85	475
	2–5	2.65	1.97–3.57	460
	5–10	2.44	1.94–3.07	398
	10–20	2.30	1.87–2.82	220

These relationships are discussed in detail by Woźniak (1989), and Woźniak and Ostrowska (1990a,b). There is a significant correlation between the C_{In} index and chlorophyll *a* concentration Ba (see Fig. 2 and Tab. 1). Moreover, a relationship has been found between the $K_c(\lambda)$ spectrum and the C_{In} colour index expressed by the analytical equation (see also Fig. 3)

$$\begin{aligned} K_c(\lambda) &= (1.87 \cdot 10^{-2} \cdot C_{In} - 1.10 \cdot 10^{2}) \cdot \exp[-1.2 \cdot 10^{-4} \cdot \\ &\cdot (\lambda - 441)^2] + 6.45 \cdot 10^{-3} \cdot \exp[-3.3 \cdot 10^{-4} \cdot (\lambda - 608)^2] + \\ &+ 2.33 \cdot 10^{-2} \cdot \exp[-1.4 \cdot 10^{3} \cdot (\lambda - 675)^2], \end{aligned} \tag{5}$$

where
λ – light wavelength given in nm, and K_c in $[m^2 \cdot (\mathrm{mg \cdot chl}a)^{-1}]$.

Thus, the chlorophyll *a* concentration Ba^* estimated in the first iteration serves to obtain the C_{In} index (Tab. 1 or Fig. 2), and subsequently the $K_c(\lambda)$ spectrum (eq. 5). The modified $K_c(\lambda)$ spectrum is directed to the input of block 2 and the minimization of S or S_1 is repeated. In this way, by subsequent iterations, a sequence of calculated Ba_i^* concentrations is formed. The iteration is terminated by an appropriate convergence criterion. The final $Ba^*_{i=\max}{}'$ value, obtained at the output of the block, is considered the likely surface chlorophyll a concentration – $Ba(0)$, and this is the value applied in the following calculations.

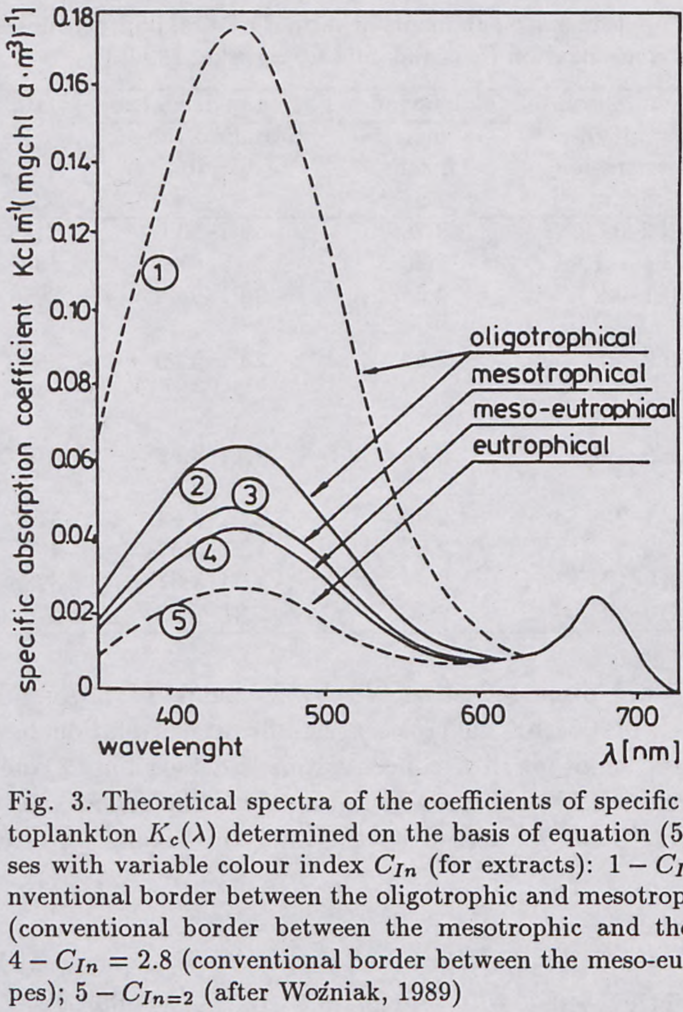

Fig. 3. Theoretical spectra of the coefficients of specific light absorption by phytoplankton $K_c(\lambda)$ determined on the basis of equation (5) for various phytocoenoses with variable colour index C_{In} (for extracts): $1 - C_{In} = 10$; $2 - C_{In} = 4$ (conventional border between the oligotrophic and mesotrophic types); $3 - C_{In} = 3.1$ (conventional border between the mesotrophic and the meso-eutrophic types); $4 - C_{In} = 2.8$ (conventional border between the meso-eutrophic and eutrophic types); $5 - C_{In=2}$ (after Woźniak, 1989)

The next task of the algorithm – see block 4 in Figure 1 – is to determine the underwater irradiance fields, in particular, the spectral and vertical distribution of downward irradiance in the sea – $E_d(\lambda, z)$, where z denotes depth, and vertical profiles of the upward irradiance integral in the PAR[1] range – $E_{d,\mathrm{PAR}}(z)$. This task is performed using the Woźniak, or Pelevin

[1]PAR – Photosynthetic Available Radiation. In oceanology PAR refers to the 400 nm to 700 nm range.

and Rutkovskaya optical classification (Woźniak and Pelevin, 1991). Should the Woźniak classification be applied, the input parameter, *i.e.* the optical index of the basin, is the surface concentration of chlorophyll a – $Ba(0)$, determined in the preceding step in block 3. In the case of the Pelevin and Rutkovskaya classification, the coefficient of vertical attenuation of the downward irradiance $K_d(\lambda = 500$ nm, $z = 0)$ measured just over the sea surface for the light wavelength $\lambda = 500$ nm can be applied as the input parameter. This coefficient is easily transformed into the Pelevin optical index m: $m = 100 \cdot K_d(\lambda = 500 \text{ nm})/2,3$. The value of $K_d(\lambda = 500$ nm, $z = 0)$ can also be determined from the absorption and diffusion coefficients obtained in blocks 2 and 3 of the algorithm, by means of the approximate relationship (concerning the surface layer)

$$K_d \cong \frac{1}{\mu} \cdot [a_w + a_{pl} + a_p + a_y + b_w^{'} + b_p^{'} + b_s^{'}], \tag{6}$$

where

μ – mean cosine of the distribution of the light beam penetrating the sea surface.

Woźniak and Pelevin (1991) have pointed out that Woźniak's classification makes it possible to determine the vertical profile of chlorophyll a concentration $Ba(z)$, the related changes of spectral distributions of the total light attenuation coefficients $K_d(\lambda, z)$, and the contribution of phytoplankton pigments in the total attenuation $K_{pl}(\lambda, z)$. This procedure yields relatively accurate underwater fields of irradiance, and enables the determination of the elements of the balance of light absorbed in the sea, in which the changes in the concentration of optically active components in seawater with depth are taken into account. Thus, the underwater fields of downward spectral irradiance are determined from the relationship

$$E_d(\lambda, z) = T_w \cdot E_{\downarrow,s}(\lambda) \cdot \exp[-\int_0^z K_d(\lambda, z) \cdot d\,z], \tag{7}$$

where the coefficient of irradiance transmission through the sea surface is assumed to be $T_w = 0.94$, with an error usually not exceeding $\pm 3 - 4\%$.

The integral downward irradiance in the PAR range is determined by integrating $E_d(\lambda, z)$ over the wavelength range from 400 to 700 nm

$$E_{d,\text{PAR}}(z) = \int_{400 \text{ nm}}^{700 \text{ nm}} E_d(\lambda, z) \cdot d\lambda. \tag{8}$$

This equation can serve to determine the vertical profile of the relative PAR irradiance, *i.e.* the $T_M(z)$ coefficients of transmission expressed as the ratios

$$T_M(z) = \frac{E_{d,\text{PAR}}(z)}{E_{d,\text{PAR}}(z = 0)} \tag{9}$$

The next stage of the programme (block 5 in Fig. 1), using the parameters calculated in the previous stages, leads to the determination of the PAR radiation energy absorbed by phytoplankton at various depths in unit volume and in a given time. The energy is expressed in absolute energy units $q_{pl}(z)$, or in respective numbers of quanta $N_{pl}(z)$, and the calculations are conducted according to the generally accepted hydrooptical relationships

$$q_{pl}(z) = \int_{400\ nm}^{700\ nm} K_d(\lambda, z) \cdot E_d(\lambda, z) \cdot \left[1 - R_d(\lambda, z) + \frac{1}{K_d(\lambda, z)} \cdot \frac{dR_d(\lambda, z)}{dz}\right] \cdot U_{pl}(\lambda, z) \cdot d\lambda, \tag{10}$$

or

$$N_{pl}(z) = \frac{1}{h \cdot c} \cdot \int_{400\ \mathrm{nm}}^{700\ \mathrm{nm}} \lambda \cdot K_d(\lambda, z) \cdot E_d(\lambda, z) \cdot \left[1 - R_d(\lambda, z) + \frac{1}{K_d(\lambda, z)} \cdot \frac{dR_d(\lambda, z)}{dz}\right] \cdot U_{pl}(\lambda, z) \cdot d\lambda, \tag{11}$$

where

h – Planck's constant,

c – velocity of light in a vacuum,

$R_d(\lambda, z)$ – reflection function of the downward irradiance. In marine practice R_d is usually very small ($R_d \ll 1$) and can therefore be neglected.

The last quantity with integrals $U_{pl}(\lambda, z)$, denotes the spectral distribution of the relative contribution of the light absorbed by phytoplankton pigments in the total absorption of light by seawater $a_{pl}(\lambda, z)$

$$U_{pl}(\lambda, z) = \frac{a_{pl}(\lambda, z)}{a(\lambda, z)}. \tag{12}$$

The spectrum of $U_{pl}(\lambda, z)$ at depth z can be determined in various ways. For instance, assuming for the purposes of simplification that the total absorption coefficient $a(\lambda, z)$ changes with depth only as a result of changes in the phytoplankton pigment absorption constituent $a_{pl}(\lambda, z)$, and neglecting the vertical variability of the specific absorptions of pigments, $K_c(\lambda, z) = K_c(\lambda, z = 0)$, we have

$$a_{pl}(\lambda, z) = K_c(\lambda, z = 0) \cdot Ba(z); \tag{13}$$

the relative contributions $U_{pl}(\lambda, z)$ can be estimated from the relative vertical profile of chlorophyll $l_{Ba}(z) = Ba(z \text{ or } T_M)/Ba(z = 0)$, in accordance with the equation

$$U_{pl}(\lambda, z) = \frac{l_{Ba}(z) \cdot a_{pl}(\lambda, z = 0)}{a_w(\lambda) + l_{Ba}(z) \cdot a_{pl}(\lambda, z = 0) + a_p(\lambda, z = 0) + a_z(\lambda, z = 0)}. \tag{14}$$

However, in reality, the concentrations of optically active components (and thus the constituents of absorption), the composition of photosynthetic pigments, and the ensuing specific absorption $K_c(\lambda, z)$, vary in vertical profiles (Woźniak and Ostrowska, 1990a,b). These facts have to be included in the algorithm to improve the accuracy of calculations. They can be introduced either by adopting the known local profiles (typical of the region or season) or by introducing certain general rules, *e.g.* from the vertical profiles of the $K_d(\lambda, z)$ and $K_{pl}(\lambda, z)$ coefficients determined from the Woźniak classification extended to the basins. In the latter case the $U_{pl}(\lambda, z)$ contributions are calculated as follows:

$$U_{pl}(\lambda, z) = \frac{K_{pl}(\lambda, z)}{K_d(\lambda, z)}. \tag{15}$$

The following stage of the algorithm, probably the most original one, consists of determining the vertical profiles of phytoplankton primary production $P(z)$ (block 6 in Fig. 1). We suggest accomplishing this by using the previously calculated energies absorbed by phytoplankton pigments $q_{pl}(z)$ or $N_{pl}(z)$, taking into account the rules determining Q_{III}, and Q_{IV}, the respective energy and quantum efficiencies of marine phytoplankton photosynthesis under natural conditions in the sea. The energy effectiveness of photosynthesis is defined as the degree of conversion of the energy absorbed by the pigments of the photosynthetic apparatus to the energy of the biomass produced, *i.e.* the ratio

$$Q_{III} = \frac{k_e \cdot P}{q_{pl}}, \tag{16}$$

where

P – primary production expressed as the amount of assimilated carbon,

k_e – energetic equivalent of the assimilated carbon, $k \approx 9.6\ \mathrm{cal \cdot mg^{-1}}$ 'C' (Koblentz-Mishke *et al.*, 1985).

Similarly, the quantum efficiency of photosynthesis is expressed as the number of carbon atoms assimilated following the absorption of one quantum of radiant energy, *i.e.* the ratio

$$Q_{IV} = \frac{\frac{P}{Ac} \cdot L_m}{N_{pl}}, \tag{17}$$

where

A_c – the mass of one mole of carbon, $A_c \approx 12$ g,

L_m – the Loschmidt number, *i.e.* the number of atoms or molecules in one mole of the substance.

The efficiency of photosynthesis increases with depth owing to decreasing PAR irradiation (Bannister and Weidemann, 1984; Kishino *et al.*, 1984, 1986). Koblentz-Mishke and Woźniak presented the first general statistical

Table 2. Statistical relationship of the *in situ* phytoplankton photosynthesis versus optical depth, averaged for the mesotrophic and eutrophic basins of the World Ocean (Koblentz-Mishke *et al.*, in preparation)

Transmission in the sea T_M [%]	Energy efficiency Q_{III} [dimensionless]	Quantum yield Q_{IV} [atoms C/quantum]
100	$4.70 \cdot 10^{-3}$	$2.07 \cdot 10^{-3}$
	$2.12 \cdot 10^{-3} - 9.91 \cdot 10^{-3}$	$9.14 \cdot 10^{-4} - 4.71 \cdot 10^{-3}$
80	$7.06 \cdot 10^{-3}$	$3.48 \cdot 10^{-3}$
	$3.70 \cdot 10^{-3} - 13.5 \cdot 10^{-3}$	$1.81 \cdot 10^{-3} - 6.68 \cdot 10^{-3}$
60	$1.06 \cdot 10^{-2}$	$5.22 \cdot 10^{-3}$
	$5.97 \cdot 10^{-3} - 1.87 \cdot 10^{-2}$	$2.93 \cdot 10^{-3} - 9.31 \cdot 10^{-3}$
40	$1.63 \cdot 10^{-2}$	$7.24 \cdot 10^{-3}$
	$9.18 \cdot 10^{-3} - 2.88 \cdot 10^{-2}$	$4.02 \cdot 10^{-3} - 1.31 \cdot 10^{-2}$
20	$2.58 \cdot 10^{-2}$	$1.30 \cdot 10^{-2}$
	$1.68 \cdot 10^{-2} - 3.96 \cdot 10^{-2}$	$8.32 \cdot 10^{-3} - 2.03 \cdot 10^{-2}$
10	$3.63 \cdot 10^{-2}$	$1.88 \cdot 10^{-2}$
	$2.63 \cdot 10^{-2} - 5.01 \cdot 10^{-2}$	$1.21 \cdot 10^{-2} - 2.91 \cdot 10^{-2}$
5	$4.39 \cdot 10^{-2}$	$2.15 \cdot 10^{-2}$
	$2.68 \cdot 10^{-2} - 7.18 \cdot 10^{-2}$	$1.30 \cdot 10^{-2} - 3.56 \cdot 10^{-2}$
2	$5.24 \cdot 10^{-2}$	$2.56 \cdot 10^{-2}$
	$2.83 \cdot 10^{-2} - 9.68 \cdot 10^{-2}$	$1.39 \cdot 10^{-2} - 4.72 \cdot 10^{-2}$
1	$5.60 \cdot 10^{-2}$	$2.74 \cdot 10^{-2}$
	$2.58 \cdot 10^{-2} - 1.21 \cdot 10^{-1}$	$1.26 \cdot 10^{-2} - 5.98 \cdot 10^{-2}$

where

- the upper number denotes the geometrical mean of the respective efficiency type,
- the lower number denotes the minimum and maximum efficiency, according to the standard deviation of efficiency logarithm range,
- the optical depth expressed as transmission in the sea T_M, of the downward irradiance integral in the PAR range (400–700 nm) (see eq. (9)).

generalization in this field (Koblentz-Mishke *et al.*, in preparation). The statistical relationships between the mean daily efficiencies of photosynthesis Q_{III} and Q_{IV} and the optical depth in the sea characterized by the coefficient of transmission of the underwater PAR irradiation into the basin T_M (see eq. (9)) have been demonstrated and proved in this paper. The relationships, presented in Table 2 and Figure 4 apply well to the various mesotrophic and eutrophic basins[2] of the World Ocean. Primary production in a given time Δt is calculated using the statistical relationships and the

[2]The experimental material is insufficient to analyze these relationship for oligotrophic basins.

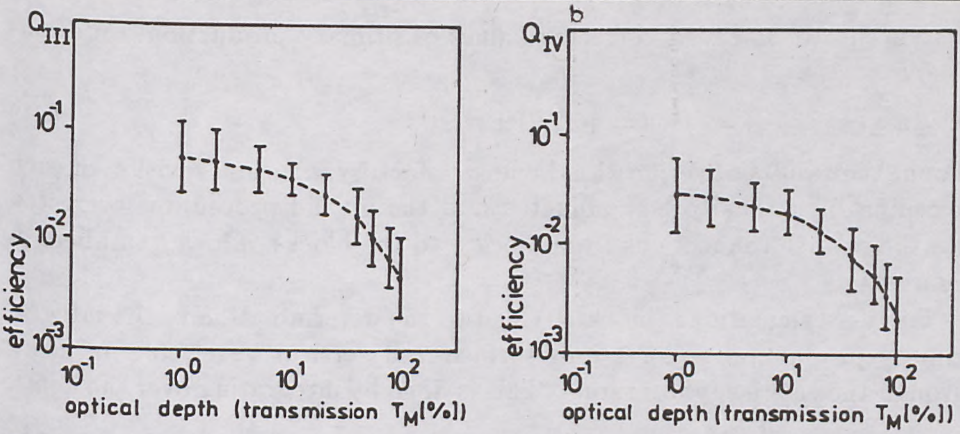

Fig. 4. Statistical relationships between the efficiency of phytoplankton photosynthesis *in situ* (a – energetic efficiency Q_{III}, b – quantum efficiency Q_{IV}) and the optical depth in the sea. The relationships have been averaged for the mesotrophic and eutrophic basins of the World Ocean (based on Tab. 2)

quantity of radiant energy absorbed $q_{pl}(z)$ or $N_{pl}(z)$ (after transformation of equations (16) and (17)) from the equations

$$P_{\Delta t}(z) = \frac{1}{k_e} \cdot Q_{III}(z) \cdot q_{pl}(z) \cdot t_E, \tag{18}$$

or

$$P_{\Delta t}(z) = \frac{A_c}{L_m} \cdot Q_{IV}(z) \cdot N_{pl}(z) \cdot t_E, \tag{19}$$

where $Q_{III}(T_M)$ and $Q_{IV}(T_M)$ are determined from the data listed in Table 2 or in Figure 4, while the transfer from the variable T_M to the variable z is accomplished by means of equation (9) using the vertical profiles of $E_{d,PAR}(z)$.

Equations (18) and (19) also contain the time multiplier t_E, determining the time Δt for which production is specified. The multiplier is equal to the ratio of the total radiant energy dose reaching the sea surface in time Δt – $\eta_{\downarrow,s,\Delta t}$, to the instantaneous irradiation of this surface $E_{\downarrow,s}$ at the moment of satellite information reception

$$t_E = \frac{\eta_{\downarrow,s,\Delta t}}{E_{\downarrow,s}}. \tag{20}$$

An important stage of the algorithm is the experimental verification of the indirect method of determining primary production from satellite information (block 8 in Fig. 1).

The verification is carried out by measuring primary production directly in the sea $P_{\Delta t,\mathrm{exp}}(z)$ (block 7) and comparing the results with the data calculated. The verification aims to determine the systematic errors ΔP and random errors σ_p of the method. By introducing these errors in block 9, more accurate, so-called corrected values of primary production are calculated

$$P_{\Delta t,\mathrm{correct}}(z) = [P_{\Delta t}(z) + \Delta P] \pm \sigma_p. \tag{21}$$

Should the results of verification be unsatisfactory, a formal revision of each preceding block has to be conducted and the invalid procedures corrected (see the reverse connections from block 8 to the blocks of lower numbers in Figure 1).

Further calculations (block 10) lead to the determination of the integral primary production under a unit surface in a vertical water column down through the entire euphotic zone. This is done by integrating over the depth

$$P_{\Delta t,\Sigma z} = \int_0^{z_{\max}} P_{\Delta t,\mathrm{correct}}(z) \cdot d\,z, \tag{22}$$

where

$z_{\max}$ – the limit of the euphotic zone, *i.e.* the depth reached by only about 1% of the PAR irradiation penetrating the sea surface.

Satellite data enable primary production in vast regions of the World Ocean (block 11 in Fig. 1) – $P_{\Delta t,\Sigma z,\Sigma s}$ – to be determined. For this purpose the production $P_{\Delta t,\Sigma z}$ is integrated over the surface Σs

$$P_{\Delta t,\Sigma z,\Sigma s} = \int_{\Sigma_s} P_{\Delta t,\Sigma_z} \cdot ds, \tag{23}$$

where

Σ_s – the analyzed sea surface,

ds – element of the surface.

3. Final remarks

The algorithm presented in this article serves to determine primary production ($P_{\Delta t,\mathrm{correct}}(z)$, $P_{\Delta t,\Sigma_z}, P_{\Delta t,\Sigma_z,\Sigma_s}$) in the sea from satellite information, without the need for specific *in situ* experiments. An exception is the verification block (No. 8 in Fig. 1), which can be run in the early stage of the algorithm.

The block structure of the algorithm makes it possible to exchange appropriate blocks with information from *in situ* experiments, or to modify the blocks with new experimental data. Possible examples are modification of the statistical relationship between the various physical and physiological properties of phytoplankton (*e.g.* in the set of parameters: $K_c(\lambda)$, Ba, C_{In} – see block 3 of the algorithm), or the modification of the relationships between photosynthetic efficiency and optical depth (block 6 of the algorithm).

The general features of the algorithm suggest that it is practicable. We plan to implement it within the next year.

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