
Papers

Model of the annual phytoplankton cycle in the marine ecosystem-assimilation of monthly satellite chlorophyll data for the North Atlantic and Baltic*

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Abstract

An annual-cycle model for the phytoplankton-zooplankton-nutrients ecosystem is presented for the North Atlantic and Baltic Sea. Satellite-derived surface chlorophyll data assimilation in the ecosystem model are discussed, and a number of methods of fitting model dynamics to the data are proposed. Statistical analysis of simulation results yields the main types of annual chlorophyll and primary production variability.

1. Introduction

The first mathematical models of plankton dynamics appeared during the 1950s. This newly developed ecological theory, based on principles of population regulation by competition and predator-prey interactions, was first proposed by Volterra, Kolmogorov, Lotka *etc.* In order to research the

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causes of global primary production, coastal sea oceanization and eutrophication, one can construct a simulation model of the annual cycle of matter within the marine ecosystem. Complicated ecosystem models utilizing a large number of variables, describing different plankton species and their lifecycles, attempt to provide a detailed description of marine ecosystems, but such models require a large number of unknown parameters, so their verification is complex (see Savchuk *et al.*, 1988; Fransz *et al.*, 1991, *etc.*). A simple model with a limited number of parameters gives sufficiently good results in ecosystem cycle simulation, both on global and synoptic scales (see Wroblewski, 1989; Gregg and Walsh, 1992 *etc.*) and in small-scale time and space features modelling (Druet and Zieliński, 1994).

Another approach to ecosystem description is a statistical model of ecosystem parameters. In recent decades oceanographers have had access to satellite ocean-colour data, such observations enabling surface chlorophyll concentration, and hence fields of surface phytoplankton concentration, to be estimated. Now we have developed tools for estimating the vertical structure of chlorophyll and primary production from surface observations (see Woźniak *et al.*, 1992). A monthly chlorophyll concentration field for the whole World Ocean was produced from CZCS scanner data (1978–1986) (Esaias *et al.*, 1986). This provided a database for the statistical analysis of the annual North Atlantic phytoplankton cycle (Platt *et al.*, 1991). CZCS data are analysed in a number of other papers (see *e.g.* Balch *et al.*, 1992).

Several papers propose a ‘hybrid’ approach in which satellite chlorophyll data are assimilated in a simple model of ecosystem dynamics (see Ishizaka, 1990; Semovski and Woźniak, 1994; Semovski *et al.*, 1994a,b, 1995). We find this approach more attractive because it combines principles of ecosystem population dynamics and hydrodynamic features with observations of some ecosystem factors.

In this paper we present a physical-bio-optical model of phytoplankton dynamics and methods of assimilating remote-sensing data. In its construction we have used the primary production, vertical chlorophyll structure and hydrooptical parameters model for the North Atlantic (Woźniak *et al.*, 1992) and the Baltic (Woźniak *et al.*, 1995a,b). The present model is, moreover, based on general principles of ocean upper layer dynamics, multispecies population dynamics, climatic data for surface irradiance and the mixed layer depth, and includes a stochastic term for small-scale vertical mixing processes.

Numerical methods of data assimilation in models, such as a Kalman filter, the ‘ajoint’ equation method and a direct least-squares-fit method are discussed.

The Empirical Orthogonal Functions analysis of the model results enables the main types of variability in the annual primary production and its regional distribution to be found.

2. Methods

We describe the large-scale features of the phytoplankton field by a system of equations covering mixing, sinking, growth as a function of light, temperature, nutrient availability, grazing, and death by ingestion. Our model is one without advection. The system of currents and its modification due to wind direction will be the next step in our investigations. We use a set of coupled partial differential equations as the governing equations of the ecosystem simulation analysis (see Fransz *et al.*, 1991; Gregg and Walsh, 1992).

$$\begin{aligned} \frac{\partial C_i}{\partial t} &= K_z \frac{\partial^2 C_i}{\partial z^2} + w_s \frac{\partial C_i}{\partial z} + \mu_i(T, C_1, C_2, C_3) - v_i(T, C_1, C_2, C_3) + \\ &- \gamma_i(C_i) + \xi, \end{aligned} \quad (1)$$

where the subscripts denote the concentration of the ecosystem components at time t and depth z , and where

C_1 – phytoplankton,

C_2 – zooplankton,

C_3 – nutrients (all in nitrogen units [mg N m^{-3}]),

K_z – kinematic eddy vertical diffusion coefficient [$\text{m}^2 \text{s}^{-1}$],

w_s – vector sinking rate [m d^{-1}],

μ_i – specific growth rate of system component concentration [d^{-1}],

v_i – specific ingestion rate of the system component by ‘herbivores’ [d^{-1}],

γ_i – mortality rate [d^{-1}],

T – temperature [$^{\circ}\text{C}$],

ξ – δ -correlated random process with a δ^2 dispersion describing short-correlated fluctuations in mixing, depending on mixed-layer depth variability (see Elsberry, 1978).

2.1. Physical model of mixing and sinking

The first term on the right-hand side in (1) is the diffusion term, which we assumed to be different for the upper mixed layer and below this layer. The depth of the mixed layer in this paper was calculated from climatic temperature data. The second term accounts for vertical sinking (not applicable to dissolved nutrients and zooplankton), and the remaining terms are biological process terms. To solve this set of equations one needs three separate numerical models to obtain the values of the variables: a physical mixing and sinking model; a bio-optical model to obtain the available surface solar

irradiance at different depths and the phytoplankton primary production; a biological process model to describe interactions between phytoplankton, zooplankton and nutrients as interaction between ‘prey’, ‘predator’ and ‘substrate’.

The vertical diffusion coefficient K_z plays a substantial role in every model of the sea. In Wroblewski and Richman (1987), a vertical eddy coefficient was computed specially for the plankton response model, equal to $1.88 \text{ m}^2 \text{ s}^{-1}$ for the wind-forcing weak vertical stratification upper layer and $0.22 \text{ m}^2 \text{ s}^{-1}$ for the cessation of the wind impulse. In Gaspar *et al.* (1990), similar values were used in studies of the vertical mixing intensity as applied to gas flux models. We will use different values of $K_{z,1}$, $K_{z,2}$ in the upper and lower layers.

Although laboratory sinking rates of diatoms range from only 1–10 m d^{-1} (Smayda, 1970), repeated daily field observations of the 1975 diatom spring bloom at the 80-m isobath in the Baltic Sea indicated apparent sinking rates of 30–50 m d^{-1} (Boungen *et al.*, 1981). Other field estimations vary from 3–4 m d^{-1} to 90–100 m d^{-1} (see Gregg and Walsh, 1992, where values of $w_s = 1\text{--}20 \text{ m d}^{-1}$ were used for plankton dynamics modelling) and similar values for the Baltic in Savchuk *et al.* (1988).

We used values of K_z and w_s in the above range for simulation. In subsection 4.2 we will also attempt to solve the problem of fitting these parameters to surface chlorophyll observations by the ‘ajoint’ method and by the method of direct target function minimization.

2.2. Biological model

Let us consider a population dynamics model of the ‘phytoplankton-zooplankton-nutrients’ system based on the general principles of population dynamics (see Kierstead and Slobodkin, 1953). For phytoplankton dynamics we have eq. (1) in the form

$$\frac{\partial C_1}{\partial t} = K_z \frac{\partial^2 C_1}{\partial z^2} + w_s \frac{\partial C_1}{\partial z} + P(C_1) - \text{Cons}(C_1, C_2) - \gamma_1(C_1) + \xi, \quad (1.1)$$

where the primary production term $P(C_1)$ is defined in Tab. 1 (see subsection 2.3), and the consumption term is

$$\text{Cons}(C_1, C_2) = R_m \wedge C_1 C_2 [1 - \exp(-\wedge C_1)].$$

Note that in accordance with the principles of the model (Woźniak *et al.*, 1992), and unlike the usual approach to primary-production term parametrization in population models, we do not have any term in the phytoplankton equations responsible for the dependence of primary production on nutrient limitation (usually in the form of the Mihaelis-Menten formula). In the calculation we also used in eq. (1.1) the usual expression for the phytoplankton production term in the form $\omega(C_3)P(C_1)$, $\omega(C_3) = C_3/(K_s + C_3)$,

where k_s – the nutrient uptake half-saturation constant [mgN m^{-3}] and $k_s = 0.2$ (after Wroblewski, 1989). Note that these different expressions for the production term in (1.1) do not lead to a significant difference between the computation results. The use of a nutrient limitation term leads to a similar but smoother solution.

– For zooplankton dynamics eq. (1) takes another form

$$\frac{\partial C_2}{\partial t} = K_z \frac{\partial^2 C_2}{\partial z^2} + (1 - \beta)\text{Cons}(C_1, C_2) - \gamma_2 C_2 + \xi, \quad (1.2)$$

– and the corresponding nutrient dynamics equation takes the form

$$\frac{\partial C_3}{\partial t} = K_z \frac{\partial^2 C_3}{\partial z^2} + \beta\text{Cons}(C_1, C_2) + \gamma_1 C_1 + \gamma_2 C_2 - P(C_1) + \xi. \quad (1.3)$$

Here, the model parameters and variables are γ_1, γ_2 – phytoplankton and zooplankton mortality rate [d^{-1}]; R_m – maximum herbivore ingestion rate [d^{-1}]; β – unassimilated fraction of herbivore grazing ration, dimensionless; Λ – Ivlev herbivore grazing constant [$\text{m}^3 \text{mgN}^{-1}$]. Typical values of basic constants were taken from Wroblewski, 1989): $\beta = 0.3$, $\Lambda = 0.5$, $\gamma_1 = 0.1$, $\gamma_2 = 0.04$.

For the values of specific Baltic zooplankton-phytoplankton interaction parameters we used the observations of Arndt (1989), Styczyńska-Jurewicz and Łotocka (1989), and Kivikl *et al.* (1993). Zooplankton grazing is a complex process depending on the diurnal migrations of copepod grazers and the variability of grazing stress during the year. Existing models used different assumptions of the grazing rate – from the constant R_m (Wroblewski, 1989) to its variability during the spring-bloom period (Gregg and Walsh, 1992) in the range 0.1–1. This range of variability is in agreement with observed values for the Baltic. Values of R_m in this range will be used in the model. In subsection 4.2 we will attempt to solve the problem of fitting parameters to the surface chlorophyll observations by using two numerical methods.

2.3. Variability of the relationship between carbon, chlorophyll and nutrients in phytoplankton cells

It is well-known that the carbon-to-chlorophyll C/C_a and nutrients-to-chlorophyll C_1/C_a relationships in living phytoplankton cells are important environmental characteristics which vary in accordance with the annual cycle and in different regions. Some Baltic observations can be found in Gershanovitch (1984). It is also well-known that population dynamics models are sensitive to variations in this parameter value – see the discussion in Wroblewski (1989) and the numerical sensitivity analysis in Franz *et al.* (1991). In models, some constant values of the C/C_a and C_1/C_a ratios are usually used. In the present model, however, we treat these parameters

as variable and dependent on chlorophyll concentrations, according to Woźniak's unpublished observations and literature analysis. The reason for this is the fact that chlorophyll concentration in living phytoplankton cells can be used as an index of the trophic type of sea waters. This type determines the species of phytoplankton and the C/C_a ratio. The C/C_1 ratio can be taken to be 5.0 for atoms (see Eppley, 1981). Field estimation from the literature yields the dependence between chlorophyll concentration and carbon (by weight) in phytoplankton cells (Tab. 1).

Table 1. Dependence of chlorophyll concentration C_a on carbon (by weight) in phytoplankton cells (after Woźniak – unpublished results)

Chlorophyll concentration C_a [mg m ⁻³]	Carbon-to-chlorophyll ratio (by weight)
0.05 – 0.1	7.143
0.1 – 0.2	16.14
0.2 – 0.4	35.75
0.5 – 1.0	67.60
1.0 – 2.0	90.00
2.0 – 5.0	87.80
5.0 – 10.0	89.03
10.0 – 20.0	89.28
20.0 – 30.0	90.71

This interdependence can be approximated by the function

$$C/C_a \approx \frac{90C_a}{C_a + 0.477}.$$

2.4. Bio-optical model for the primary production term

The primary production P in eq. (1.1) is the process defining the carbon and energy cycles in the World Ocean. In a number of papers, different methods have been used to estimate primary production, both simple (review in Balch *et al.*, 1992) and more sophisticated (Morel, 1991; Platt *et al.*, 1991; Woźniak *et al.*, 1992).

Most bio-optical models were developed only for Waters Case 1 (WC1) in Morel's terminology (Morel and Prieur, 1977). The main attribute of WC1 is the fact that the chlorophyll a + pheophytin a determine the principal optical features. Another type of water, the so-called Waters Case 2, which comprises approximately 2% of the World Ocean, is the most productive. However, Baltic waters cannot be described by models suitable for WC1 either. We will use the primary production model by Woźniak *et al.* (1992) for the North Atlantic.

The first bio-optical model of primary production for Baltic waters was developed in Woźniak *et al.* (1995a). It is based on a database of optical observations and the quantum yield of primary production, the observations having been made in a number of Polish and Russian research cruise vessels.

3. Climatic data, initial conditions and assimilation data

An array of the calculated monthly available surface irradiance was produced for the North Atlantic in 5×5 -degree ‘squares’ at the Hydrometeorological Centre of Russia in accordance with the algorithm in Girdiuk *et al.* (1992). We use this data as a source of available surface irradiance in the model.

The mixed-layer depth was determined for the North Atlantic on the basis of the temperature-salinity 1×1 -degree array from Levitus (1982), and for the Baltic on the 1×0.5 -degree temperature array (Lenz, 1971). The mixed-layer depth was calculated in accordance with the criterion of the vertical gradient maximum. We use this criterion because the depth of the gradient maximum often corresponds to the depth of the chlorophyll maximum (‘liquid bottom’) (see *e.g.* Kiefer and Kremer, 1981). The same data array was the source of climatic surface temperatures for the primary production formulas in Tab. 2.

For initial North Atlantic nutrient concentrations we use the data from Glover (1988). The Baltic initial nutrient concentration field was determined from the data in Trzosińska (1990), Perrila (1988) and Wulff and Rahm (1988), and is the amount of nitrate brought into the mixed layer by deep convection in wintertime and riverine input.

The CZCS-derived monthly surface chlorophyll field (Esaias *et al.*, 1986) was produced by a numerical procedure developed for the Atlantic Ocean. The accuracy of this estimation for a number of ocean regions was studied in Balch *et al.* (1992). We cannot be sure that methods of chlorophyll content estimation which are correct for Atlantic waters will be suitable for the eutrophic, low-salinity waters of the Baltic. Using a chlorophyll soundings database from the Institute of Oceanology, Sopot, (see Woźniak *et al.*, 1995b), we have made a preliminary ‘secondary calibration’ of computed CZCS data for the Baltic. The calibration curve has the following form (according to Woźniak and Semovski – unpublished results):

$$\log_{10}(\hat{C}_a = 0.32 + 0.58 \log_{10}(C_{a,CZCS}) - 0.052 \sin[2\pi \times (n_m - 1)/6] + 0.185 \sin[2\pi \times (n_m - 1)/24],$$

where n_m is the number of the month. The two trigonometrical functions describe the impact of dissolved organic matter during the year: the first –

autogenic dissolved organics, the second – allogenic dissolved organics generated from sediments during spring and autumn storm events.

Table 2. Model of the North Atlantic and Baltic primary production (Woźniak *et al.*, 1992, 1995a)

Input parameters of the model are the chlorophyll concentration vertical profile $C_a(z)$ [mg m^{-2}], available solar irradiance at surface $E_d(\lambda, t, 0)$ [mE m^{-2}] and sea surface temperature T [$^{\circ}\text{C}$].

Model formulas are:

1. Dependences of the downwelling irradiance attenuation coefficient $K_d(\lambda)$ [m^{-1}] and its phytoplankton component $K_{pl}(\lambda)$ [m^{-1}] on chlorophyll concentration C_a are given by

$$K_d(\lambda) = K_w(\lambda) + C_a\{A_1(\lambda)\exp[-a_1(\lambda)C_a] + k_{d,i}(\lambda)\} + \Delta K(\lambda), \quad (2)$$

$$K_{pl}(\lambda) = C_a\{A_2(\lambda)\exp[-a_2(\lambda)C_a] + k_{c,j}(\lambda)\}. \quad (3)$$

For the North Atlantic $\Delta K(\lambda) = 0.0$, for the Baltic

$$\Delta K(\lambda) = 0.068\exp[-0.014(\lambda - 550)], \quad (4)$$

where λ – [nm].

For the values of constant $A_1(\lambda)$, $a_1(\lambda)$, $k_{d,i}(\lambda)$, $A_2(\lambda)$, $a_2(\lambda)$, $k_{c,i}(\lambda)$, and the attenuation of pure water $K_w(\lambda)$, see Woźniak *et al.* (1992).

2. Dependences of the photosynthetic quantum yield $\Phi(z)$ [quanta (atom C) $^{-1}$] on underwater irradiance $E_{PAR}(z)$ in PAR (photosynthetic active radiance 400–700 nm) range,

sea surface chlorophyll concentration $C_a(0)$ and euphotic zone temperature T_e are given by

$$\Phi(z) = \Phi_{\max} \frac{E_{PAR,1/2}}{E_{PAR,1/2} + E_{PAR}(z)}, \quad \Phi_{\max} = \Phi_{MAX}(T_e) \frac{C_a(0)^{0.66}}{0.44 + C_a(0)^{0.66}}. \quad (5)$$

For the North Atlantic $\Phi_{MAX}(T_e) = 0.51 = \text{const}$; for the Baltic

$$\Phi_{MAX}(T_e) = 0.0157(Q_{10})^{T_e/10},$$

where the constants are $E_{PAR,1/2} = 6.4 \cdot 10^{19}$ [quanta $\text{m}^{-1} \text{s}^{-1}$] and $Q_{10} = 1.77$ (let T_e be approximately equal to sea surface temperature T).

Principle of computation of some of the environmental characteristics of primary production in the sea:

1. Vertical profiles of spectral optical properties $K_d(\lambda, z)$ and $K_{pl}(\lambda, z)$ can be calculated on the basis of $C_a(z)$ using eqs. (2), (3) and (4).

2. Vertical profiles of the downward spectral irradiance

$E_d(\lambda, t, z)$ [quanta $\text{m}^{-2} \text{s}^{-1} \text{nm}^{-1}$], the daily irradiance dose in the PAR spectral range $\eta_{PAR}(z)$ [quanta m^{-2}], the average irradiance in the PAR range $E_{PAR}(z)$ [quanta $\text{m}^{-2} \text{s}^{-1}$] and the daily energy absorbed by phytoplankton $\eta_{PUR}(z)$ [quanta m^{-3}] can be calculated on the basis of $K_d(\lambda, z)$, $K_{pl}(\lambda, z)$ and input data of surface irradiance $E_d(\lambda, t, 0)$ using the formulas

$$E_d(\lambda, t, z) = E_d(\lambda, t, 0) \left\{ \exp\left[-\int_0^z K_d(\lambda, z) dz\right] \right\}, \quad (6)$$

$$\eta_{PAR}(z) = \int_{T_r}^{t_s} \int_{400 \text{ nm}}^{700 \text{ nm}} E_d(\lambda, t, z) d\lambda dt, \quad (7)$$

Table 2. continued

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

$$E_{PAR}(z) = \eta_{PAR}(z)/(t_s - t_r), \quad (8)$$

$$\eta_{PUR}(z) \approx 1.2 \int_{t_r}^{t_s} \int_{400 \text{ nm}}^{700 \text{ nm}} E_d(\lambda, t, z) K_{pl}(\lambda, z) d\lambda dt. \quad (9)$$

3. Daily values of vertical distributions of primary productions

$P(z)$ [atoms C m⁻³] and the total primary production in the water column

P_{tot} [atoms C m⁻²] are calculated on the basis of known $\eta_{PUR}(z)$,

$E_{PAR}(z)$, $C_a(0)$, eq. (6), and formulas:

$$P(z) = \Phi(z) \times \eta_{PUR}(z), \quad (10)$$

$$P_{tot} = \int_0^{z(P=0)} P(z) dz, \quad (11)$$

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

4. For use in the ecosystem model (1), the primary production value is recalculated to nutrient units in accordance with the procedure in subsection 2.2.

The initial conditions for the phytoplankton field are the January CZCS data for the surface, and the value 0.1 mgN m⁻³ for points where satellite data is unavailable. We reconstruct the vertical chlorophyll profiles according to the procedure in subsection 4.1 below (Tab. 3); they are used as initial values for the model.

There is an evident lack of global Baltic data for the winter zooplankton field. As a first approximation, the initial zooplankton concentration was left constant and equal to 0.1 mgN m⁻³ for the whole region. We hoped that the model would be stable and could then be integrated forward from suitable initial conditions with satellite data assimilation to obtain an adequate description of the annual phytoplankton variability.

4. Principles of assimilating remote sensing data

4.1. Model of vertical chlorophyll structure

One of the problems arising in the assimilation of remote sensing observations is to construct the vertical phytoplankton structure from *surface* data. However, this is not essential if we assume the chlorophyll profile to be constant in some layers, usually the upper mixed layer, as in Ishizaka (1990) and Semovski *et al.* (1995). This assumption may be valid in well-mixed waters, *e.g.* in the coastal zone. In a model with a vertical resolution one needs a ‘submodel’ to estimate vertical chlorophyll structure from surface data. A number of different models have been proposed (Platt *et al.*, 1991; review in Balch *et al.*, 1992). For example, the procedure of Platt *et al.* (1991) uses fixed forms of vertical chlorophyll profiles for a number of biogeographical provinces and for different seasons with a shift of the whole

profile in accordance with the corresponding value of surface chlorophyll. All these methods were developed for Waters Case 1 (see subsection 2.3).

Table 3. Model of the vertical chlorophyll profile (Woźniak *et al.*, 1992, 1995a)

For stratified dependences between vertical profiles of chlorophyll $C_a(z)$, its surface concentration $C_a(0)$ and the number of the day in this year n_d are as follows:

$$C_a(z) = C_a(0) \frac{C_{\text{const}} + C_m \exp\{ -[(z - z_{\text{max}})\sigma_z]^2 \}}{C_{\text{const}} + C_m \exp\{ -[(z_{\text{max}})\sigma_z]^2 \}}, \quad (12)$$

where for the North Atlantic:

$$z_{\text{max}} = 17.9 - 44.6Y + 38.1Y^2 + 1.32Y^3 + 10.7^4,$$

$$C_{\text{const}} = 10^{[-0.437 + 0.844Y - 0.00888Y^2]},$$

$$C_m = 0.269 + 0.245Y + 1.51Y^2 + 2.13Y^3 + 0.81Y^4,$$

$$\sigma_z = 0.048 + 0.217Y + 0.00239Y^2 + 0.0562Y^3 + 0.00514Y^4, \quad Y = \log C_a(0),$$

and for the Baltic:

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

$$\begin{aligned} C_m &= \frac{1}{2M} [(0.36)^{C_a(0)} + 1] \times [M + 1 + (M - 1) \times \cos(2\pi \times \frac{n_d - 120}{365})] - M = \\ &= 2.25(0.765)^{C_a(0)} + 1, \end{aligned}$$

$$z_{\text{max}} = 9.18 - 2.43Y + 0.213Y^2 - 1.18Y^3,$$

$$\sigma = 0.118 - 0.113Y - 0.0139Y^2 + 0.112Y^3,$$

$$Y = \log C_a(0).$$

Tab. 3 presents the algorithm (Woźniak *et al.*, 1992) for determining the vertical chlorophyll profile on the basis of the dependence of the whole profile shape on the surface chlorophyll content. In Baltic waters, as in Waters Case 2, the application of models to open ocean waters may not be suitable. In Woźniak *et al.* (1995a,b) there was an attempt to construct a first model of the chlorophyll vertical structure for the Baltic on the basis of over 1200 profiles. The formulas of this algorithm are presented in Tab. 3.

4.2. Methods of data assimilation in dynamical models

Methods of data assimilation in dynamic models can be referred to ‘fitting-dynamics-to-data’ procedures (see Thacker and Long, 1988). These methods are equivalent to a dynamic interpolation of data in accordance with our assumptions about the physical principles of the system under

study. Another use of such methods is parameter fitting for the best correlation between data and the model. The problem of unknown parameter estimation is essential for the ecological models – see studies of sensitivity in Fransz *et al.* (1991) – for these show substantial changes with parameter variations.

In recent years two main groups of data assimilation methods have become popular in meteorology and oceanology – the Kalman filter methods and the so-called ‘ajoint’, that is, an application of optimum control theory (see *e.g.* Ghil and Malanotte-Rizzoli, 1991; Thacker and Long, 1988). In our previous work (Semovski *et al.*, 1994a), assuming a constant concentration profile in the mixed layer, we used the Kalman filtering method for assimilating observed chlorophyll values in the column integrated model. This method requires an autocorrelation function computation, or its analytical representation. For the analytical approximation of the time autocovariance function for phytoplankton concentration C_1 , we have linearized (1) to allow the ‘slow’ variables C_2 and C_3 to be constant.

In eq. (1), the expressions for the autocovariance function become too complicated for analytical presentation. In this case we can use an expression for the autocovariance function estimated from field data as in Smith *et al.* (1988) for the California upwelling region and in Henderson and Steele (1993) for the North Sea.

To analyse the space variability of the phytoplankton annual cycle, we can use this method with an exponential expression for the time autocovariance function $Q(t) = \exp(-\omega t)$, where the scale parameter ω depends on depth. The assimilation procedure now has a simple form:

$$C_1(\text{month}, \text{date}) = \alpha_1 C_{1,\text{model}}(\text{month}, \text{date}) + \alpha_2 \hat{C}_1(\text{month}, \text{date}),$$

$$\alpha_1 + \alpha_2 = 1, \alpha_2 = Q(\text{date} - 15). \quad (13)$$

The CZCS observed \hat{C}_1 was calibrated in accordance with the procedure in section 3 and pertains to the fifteenth day of every month.

The second method is based on the construction and numerical solution of ajoint equations describing the parameter variability in the fitting procedure for the main dynamic system. The ecosystem dynamics model can be interpreted as a model of non-conservative tracer diffusion and advection. It is possible to apply the method developed for diffusion-advection systems to the analysis, as in Nechayev and Yaremchuk (1992). In this study there was an analytical investigation of numerical methods convergence and a description of computation results for the simplest case.

The coefficients of turbulent vertical diffusion $K_{z,1}$ and $K_{z,2}$ for the upper and lower layers, the sinking rate w_z , the grazing rate R_m , and the nutrient chlorophyll ratio can be used as unknown parameters in the assimilation procedure.

The problem of determining the annual phytoplankton cycle in a model without advection (one-dimensional model) $\mathbf{P}^t = (P_o^t, \dots, P_M^t)$, $P_i^t = P(z_i, t)$ at regular time intervals $\Omega: \{t = 1, \dots, K\}$ from a set of phytoplankton profile observations (*e.g.* restored from the surface value as in the procedure in subsection 4.2) $\hat{\mathbf{P}}^{\tau_k} = (\hat{P}_i^{\tau_k} = \hat{P}(z_i, \tau_k), i = 0, \dots, M)$ for some regular time intervals $\Omega_k: \{\tau_k, k = 1, \dots, L\}$ can be described as the problem of determining the parameter values $\Theta = (\theta_1, \dots, \theta_N)$ minimizing the target function

$$J_0 = \sum_{i=1}^N \Gamma_i (\theta_i - \tilde{\theta}_i)^2 + \sum_{i=1}^M \sum_{t=1}^K \sum_{j=1}^L W_{ij} Q_i(t - \tau_j) (\hat{P}_i^{\tau_j} - P_i^t)^2, \quad (14)$$

with the dynamic conditions

$$\mathbf{P}^{t+1} - F(\mathbf{P}^t, \Theta) = 0, \quad t = 1, \dots, K, \quad (14.1)$$

where $F(\Theta)$ – dynamic operator of model (1). In eq. (14) $\tilde{\Theta}$ is an *a priori* estimation of the parameter vector, $\Gamma_i \geq 0$ is an inversion of the *a priori* estimation error, $\mathbf{W} = ((W_{ij}))$ is a positive definite matrix which is an inversion of the observation errors matrix and $\mathbf{Q}_i(t)$ is the covariance function of the phytoplankton field at depth z_i .

The extreme computation procedure of (14) under conditions (14.1) can be transformed to the minimization problem for the Lagrange target function

$$\mathbf{J} = \mathbf{J}_0 + \sum_{t=1}^K [\mathbf{P}^{t+1} - \mathbf{F}(\mathbf{P}^t, \Theta)] \wedge^t, \quad (15)$$

where $\wedge^t = (\lambda_0^t, \dots, \lambda_M^t)$ are Lagrange factors (or ‘ajoint functions’). The problem of minimizing expression (15) can be described as the solution of the linear differential equation system

$$\frac{\partial J}{\partial P_i^t} = 2 \sum_{j=1}^K W_{ij} Q(t - \tau_j) (P_i^t - \hat{P}_i^{\tau_j}) + \lambda_0^t - \wedge^t F_0^t = 0, \quad (16)$$

$$\frac{\partial \mathbf{J}}{\partial \mathbf{P}_0^{K+1}} = \lambda_0^t = 0, \quad (17)$$

$$\frac{\partial \mathbf{J}}{\partial \lambda_j^t} = P_j^{t+1} - \mathbf{F}_j^t = 0, \quad (18)$$

$$\frac{\partial J}{\partial \theta_0^t} = 2\Gamma_i (\theta_i - \tilde{\theta}_i) - \sum_{t=1}^K \wedge^t F_{(i)}^t = 0, \quad (19)$$

where the vector-functions of the partial derivatives are

$$F_j^t = \frac{\partial F}{\partial P_j^t}(\mathbf{P}^t, \Theta), \quad F_{(i)}^t = \frac{\partial F}{\partial \theta_i}(\mathbf{P}^t, \Theta).$$

The numerical methods of solving eqs. (15)–(19) as well as the convergence conditions have been studied in a number of papers (see *e.g.* Nechayev

and Yaremchuk, 1992) and are strictly dependent on the structure of the operators $\mathbf{F}^t, \mathbf{F}_j^t, \mathbf{F}_{(i)}^t$.

The most general way of solving the problem of minimizing function J is a direct search for its extremes with a minimization procedure that uses an antigradient vector direction of J . The gradient iteration procedure takes the form

$$\begin{aligned} \Theta_{(q+1)} &= \Theta_{(q)} - \alpha_q \Delta_{\Theta} J = \\ &= \Theta_{(q)} - \alpha_q \left[2\Gamma(\Theta_{(q)} - \tilde{\Theta}) - \sum_{t=1}^K \wedge_{(q)}^t \frac{\partial F(\mathbf{P}_{(q)}^t, \Theta_{(q)})}{\partial \Theta} \right]. \end{aligned} \quad (20)$$

The iteration step value α_q depends on q , and the expressions $\alpha_q \rightarrow 0, \sum \alpha_q \rightarrow \infty$ are usually partial conditions for convergence of the iteration procedure.

In our computations we use the method of gradient minimization (20), as it is equivalent to the direct ‘ajoint’ solution of (15)–(19). This was not so in the case of the simple advection-diffusion model of (Nechayev and Yaremchuk, 1992) because there it was possible to have an analytical expression for the partial derivatives of \mathbf{F}^t in (15)–(19). In our case we need to compute numerically the partial derivatives of this operator both for (15)–(19) and for (20).

5. Results

5.1. North Atlantic: simulation studies

Calculations on the model were performed for the region from the Equator to 65°N and from 82°W to 17°E, excluding the Baltic and Mediterranean Seas. Integration of eq. (2) over a period of one year with a time interval of 1 day was performed with a simple finite difference scheme for every point on a 1 × 1-degree grid. The time interval of one day was chosen because problems of diurnal variability are not dealt with in this article.

The first calculations with the model were made without data assimilation. The results of the simulation show the qualitative correlation of the vertical annual phytoplankton and primary production cycle with observations (see *e.g.* Platt *et al.*, 1992). Fig. 1 shows the typical annual variability of model variables during the year for points in the subarctic, temperate and tropical regions, and Fig. 2 shows the corresponding vertical sections of the phytoplankton concentration relative to time.

These figures show the best-known features of annual phytoplankton variability: the spring bloom, the later zooplankton bloom, the formation of the subsurface phytoplankton maximum, and the next bloom in the second half of summer. However, the duration of the spring bloom in the model

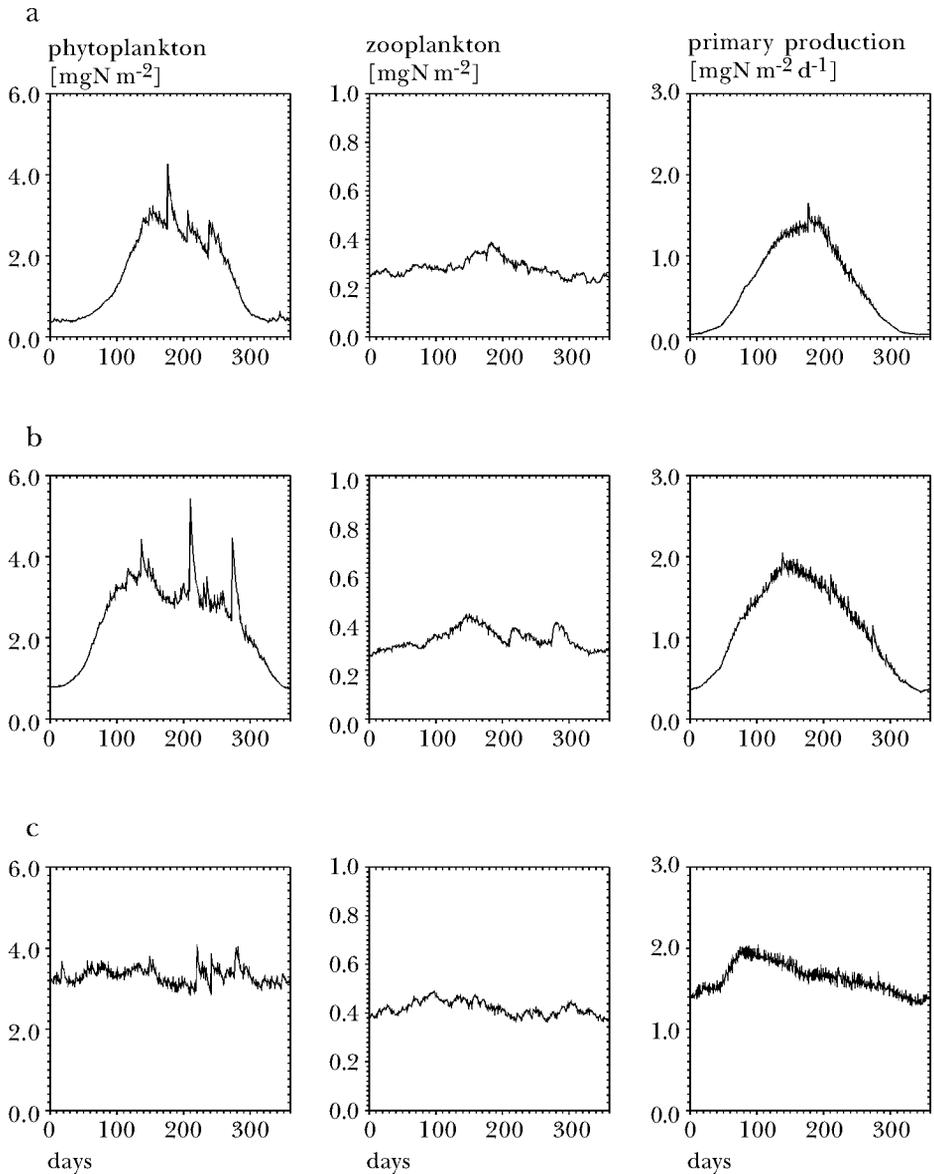


Fig. 1. North Atlantic model without data assimilation: annual variability of column-integrated model variables (phytoplankton, primary production, zooplankton); subarctic region (64°N, 32°W) (a), temperate region (45°N, 57°W) (b), tropical region (15°N, 77°W) (c)

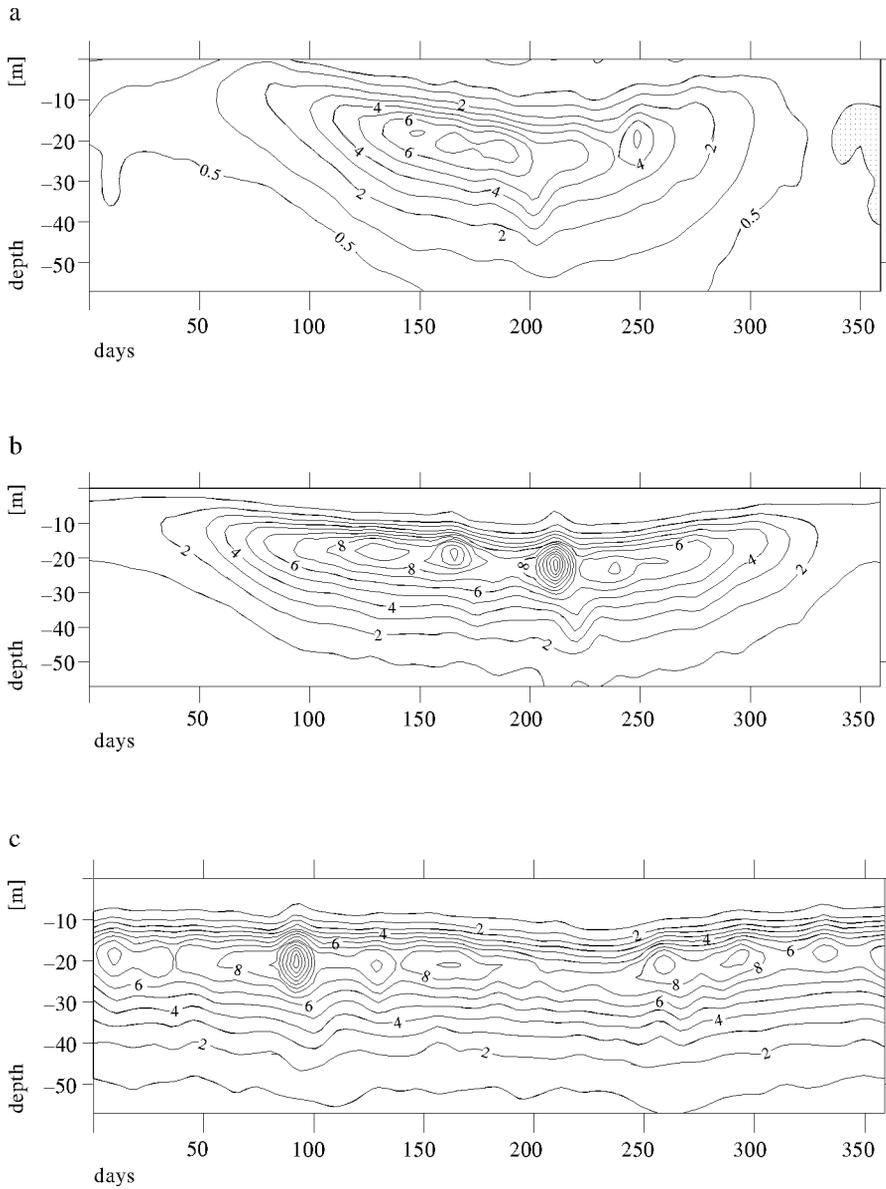


Fig. 2. North Atlantic model without data assimilation: depth-time section of annual variability of phytoplankton concentration [mgN m^{-3}]. (a), (b), (c) – the same points as in Fig. 1

without data assimilation is longer than in reality (see *e.g.* the discussion in Wroblewski, 1989). Also we need to note that the annual cycle in subtropical and tropical regions is not adequately resolved with the model because of the small annual variability in climatic surface irradiance.

5.2. North Atlantic: data assimilation and statistical analysis of the annual primary production cycle

For use in the assimilation procedure, the values of pixels on the CZCS mean monthly images (1024×1024 pixels on the whole of the Earth's surface – see Esaias *et al.*, 1986) were averaged to the centre of 1×1 -degree 'squares' and related to the fifteenth day of the corresponding month. For the computation scheme of assimilation we used a simple method (13). After assimilation in calculations, the results of simulation became closer to reality, although they were not smooth. This could have been, firstly, because the problems involved in stabilizing the assimilation procedure in such strictly non-linear models as population dynamics models are far from being *solved* at the present time. Another source of instability is the fact that CZCS chlorophyll estimations do not distinguish between chlorophyll and pheopigments on the one hand, and, in coastal regions, are nonselective with respect to suspended sediments and dissolved organic matter on the other (see the commentaries on this in Platt *et al.*, 1991). This could be the reason for the overestimation of the chlorophyll concentration in temperate coastal seas in winter on CZCS images (*e.g.* the North Sea). Now, with the new generation of satellite scanners, such as the SeaWiFS we hope it will be possible to solve part of this problem.

Nevertheless, we see the assimilation of CZCS data in a numerical model not only as the approval of available methods for new generation satellite information analysis, but also as a kind of 'dynamic interpolation' and 'dynamic smoothing' of global CZCS data over the whole ocean euphotic layer on the one hand and on a smaller time scale on the other. As in Platt *et al.* (1991) we used a set of 36 ten-day values of the column-integrated primary production for every geographical point involved in the model as they are more representative for this analysis.

In this formulation it may be of interest, for example, to build up a more accurate description of the North Atlantic spring bloom. Fig. 3a shows the distribution of the date of the maximum spring gradient in the annual North Atlantic column chlorophyll cycle. The results seem to confirm the conclusions of Wroblewski (1989), who showed that the spring bloom seems to progress from mid- to high latitudes, and from South to North. In our model, however, we can obtain a shorter and therefore more realistic spring bloom period (computed as the period from maximum positive to maximum

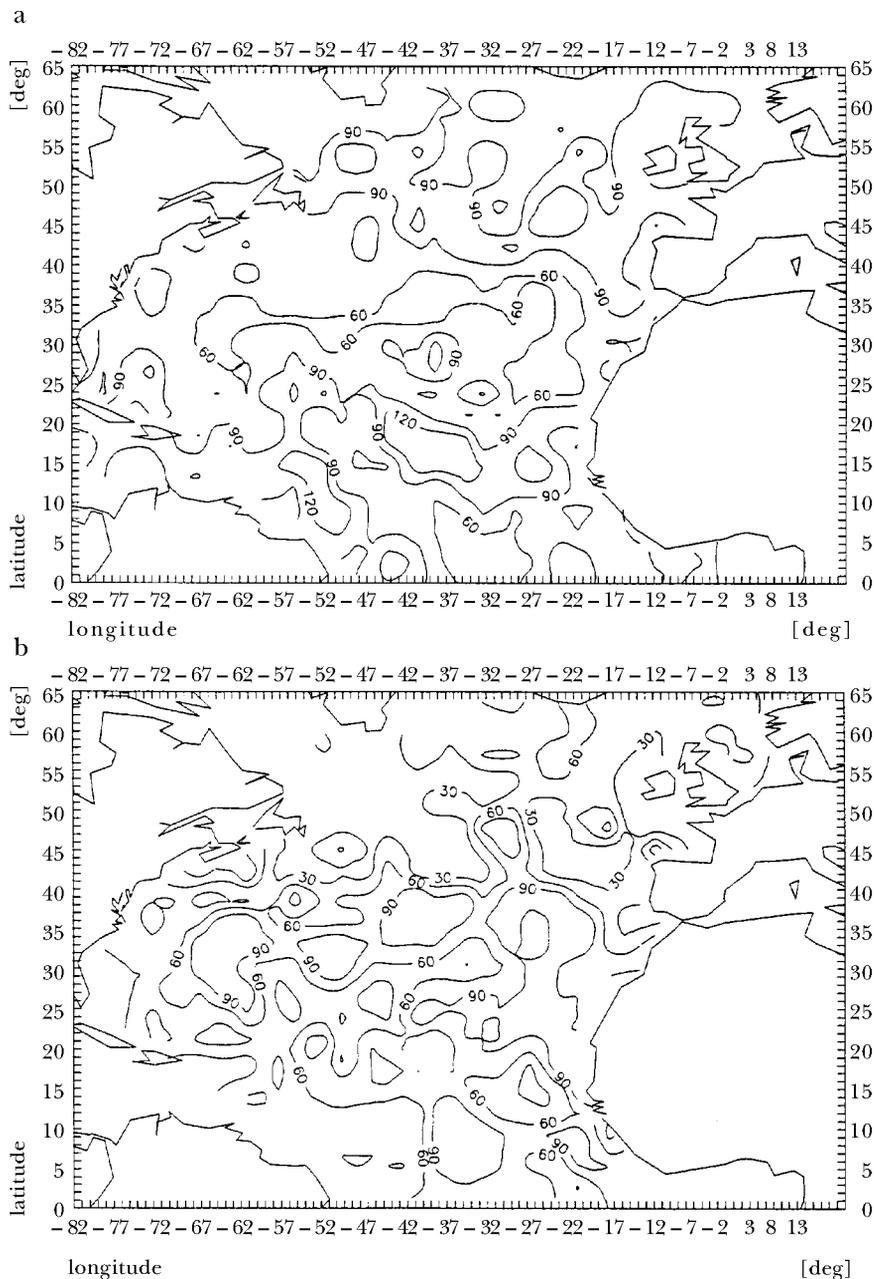


Fig. 3. North Atlantic model with CZCS data assimilation: distribution of the day number on which the spring bloom starts [d numb] (a), distribution of spring bloom duration [d] (b)

negative gradients) than in Wroblewski (1989), as can be seen in Fig. 3b, because we have used the vertical resolution model and data assimilation procedure.

As a basic statistical procedure for analysing annual variability we use the Empirical Orthogonal Functions (EOF) method (see *e.g.* Preisendorfer and Mobley, 1988). The method is based on the calculation of a multivariate cross-covariance matrix of observed vectors (in our case, in 36-dimensional space). Then the eigenvectors of the matrix need to be calculated, which are noncorrelated modes of data variability for the sample under analysis. The corresponding eigennumber value (as a percentage of cumulative dispersion) can be used as a weight for the mode impact in the formation of the annual primary production variability. The first few largest eigenvalues correspond to the main noncorrelated factors of variability.

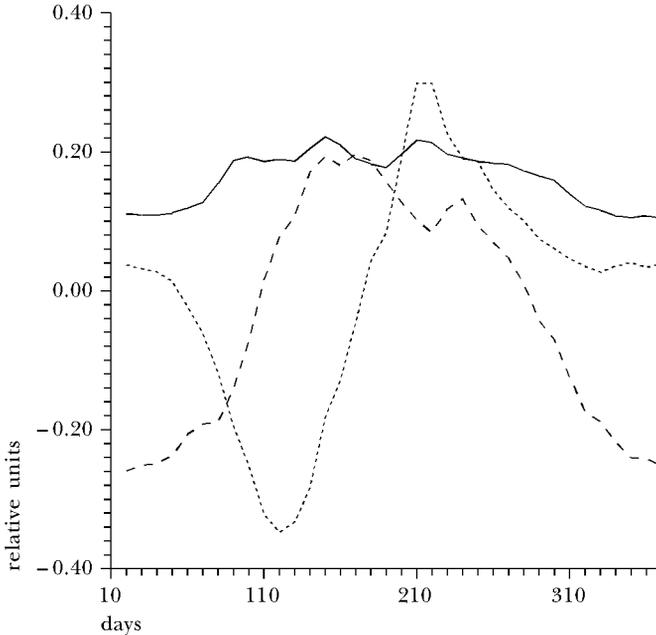


Fig. 4. North Atlantic model with CZCS data assimilation: the first three empirical orthogonal functions for the North Atlantic primary production cycle [rel. un.]. Solid line – first EOF, dashed line – second EOF, dotted line – third EOF

Fig. 4 shows the first three EOF of the annual North Atlantic column primary production. The first EOF (57.1% of the cumulative dispersion) is positive during the whole year. That means that this EOF corresponds to the annual integrated primary production at a point. The map of the corresponding principal component of annual variability (Fig. 5a) therefore

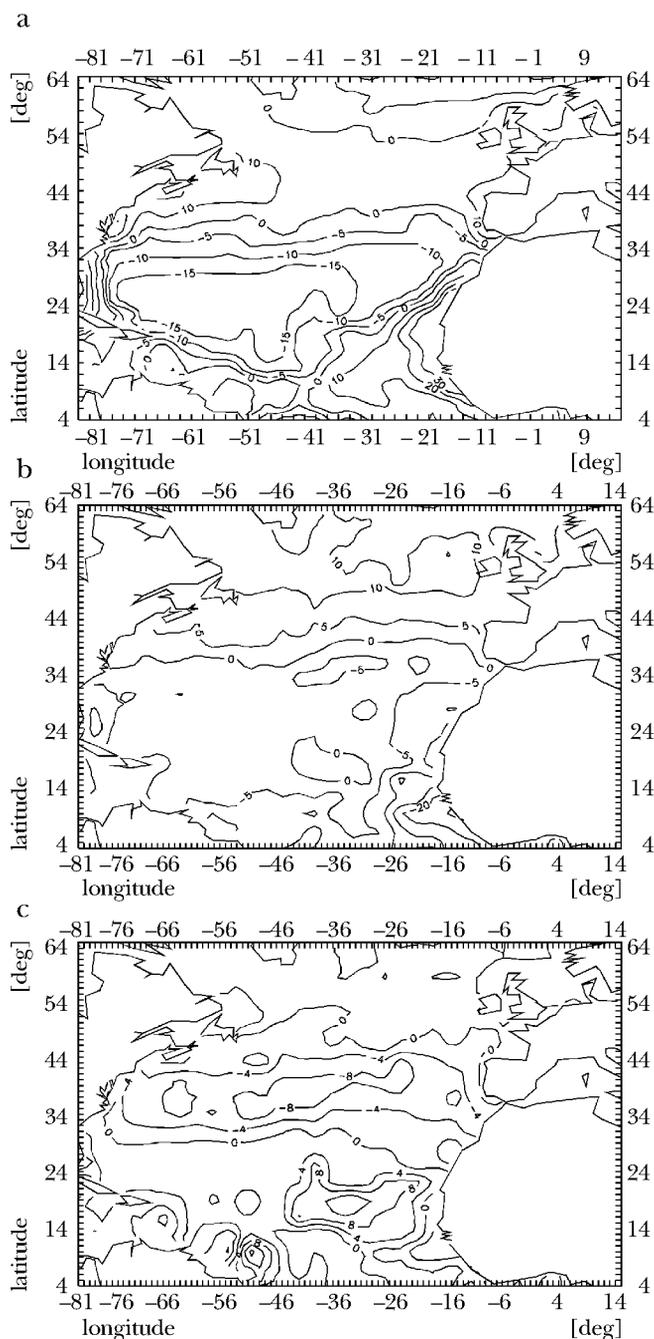


Fig. 5. North Atlantic model with CZCS data assimilation: Aerial distribution of the first three principal components of the annual North Atlantic primary production [mgN m^{-2}]; principal component 1 (a), principal component 2 (b), principal component 3 (c)

describes the distribution of the annual integrated column primary production of the North Atlantic. The second EOF (22.4%) changes sign twice – at the beginning of April (spring) and at the beginning of October (autumn). This means that the impact of this EOF describes the difference between winter and summer primary production, and the map of principal component distribution (Fig. 5b) displays zonal variability. The third EOF (8.0%) has a sinusoidal annual variability and can be interpreted as describing the difference between spring and summer production peaks. The map of corresponding principal component variability is presented in Fig. 5c.

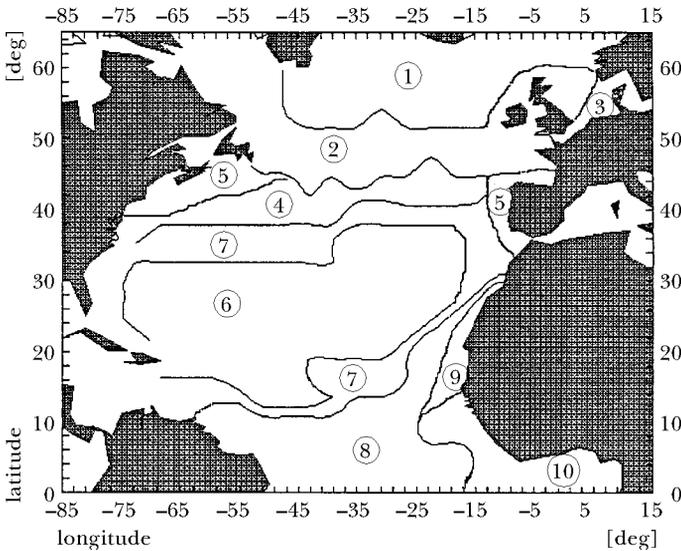


Fig. 6. North Atlantic model with CZCS data assimilation: delineation of the North Atlantic by main annual primary production variability types

Analysis of the scattering diagrams of EOF1 and EOF2 enable mean ‘clusters’ and hence main types of annual North Atlantic primary production to be found from which biogeochemical provinces can be delineated. The results of this procedure are presented in Figs. 6 and 7. These types of annual variability can be referred to as:

- | | |
|---------------------------|----------------------------------|
| 1 – subarctic, | 6 – mid-ocean gyre oligotrophic, |
| 2 – temperate open ocean, | 7 – transitional oligotrophic, |
| 3 – subarctic coastal, | 8 – transitional equatorial, |
| 4 – transitional coastal, | 9 – upwelling, |
| 5 – subtropical, | 10 – equatorial. |

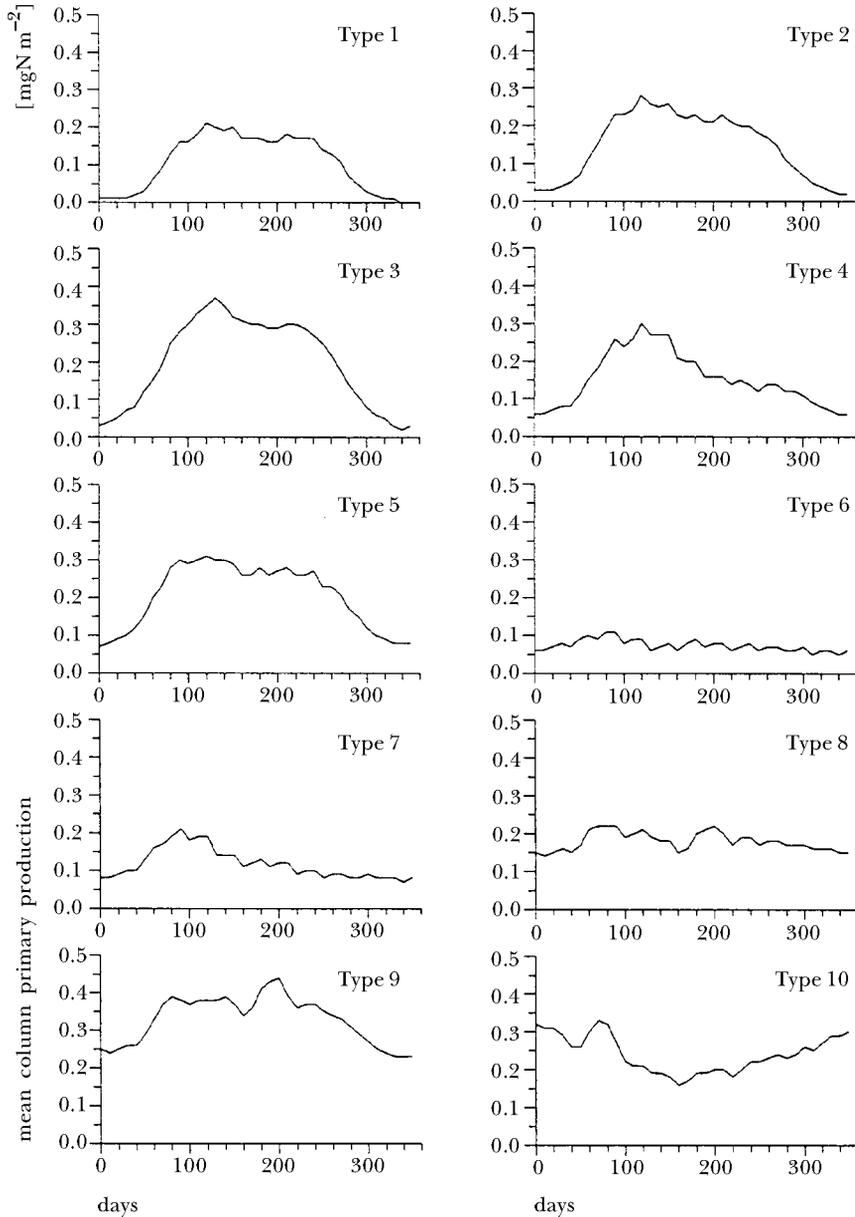


Fig. 7. North Atlantic model with CZCS data assimilation: main annual North Atlantic column-integrated primary production variability types [$\text{mgN m}^{-2} \text{d}^{-1}$]

The results of the procedure presented in Figs. 6 and 7 are generally close to those of Platt (1991), who delineated 12 types of annual primary production variability in four zonal regions: subarctic, temperate (transitional), subtropical, equatorial, and three zones describing the distance from the coast: shelf, slope, deep. Our types can be found in this zonal-coastal classification, but in our delineation one cannot see some of the types presented in the Platt scheme. One more difference is the strictly zonal character of Platt's boundaries between biogeographical provinces, which, in our opinion, are not always appropriate because of the well-known hydrological structure of the North Atlantic. We must note, however, that all such classifications and delineations are relative and can depend on the nature of the data.

5.3. Baltic: simulation studies, data assimilation and statistical analysis of the annual primary production cycle

We begin our simulation studies with a model without assimilation. Computation results show good qualitative correlation between simulation results and our knowledge of the annual chlorophyll cycle (Fig. 8a). General features of the annual primary production cycle are close to those for the same latitudes in the North Atlantic. This fact is in accordance with observations (see Esaias *et al.*, 1986), but the small aerial variability of model input factors (climatic downwelling irradiance, climatic mixed layer depth) cannot provide us with the possibility of describing the details in annual chlorophyll cycles in different regions (West-East shift of the beginning of the spring bloom, the difference in summer chlorophyll concentration between the open sea and coastal waters).

The application of CZCS data assimilation procedures to the model was performed in the next stage of the studies. At first we tested the applicability of the method of directly minimizing the target function (20) of subsection 4.2 to the model (1). The results of the computation are presented in Fig. 8b for a typical position in the central Baltic. As the parameter vector for the optimization procedure we use the coefficients of vertical mixing in the upper and lower layers $K_{z,1}$, $K_{z,2}$ and the vertical sinking rate of phytoplankton cells w_s .

The result in Fig. 8c shows the application of a simple interpolation scheme (13) with model parameters defined in procedure (20). One can see that here we have the best correlation between data and model results, but the zooplankton annual cycle changes dramatically. These changes are due to an additional 'artificial' biomass in the numerical model added by the data assimilation procedure.

We used a third method for the statistical analysis of general features in the Baltic annual primary production cycle, because this procedure gave us

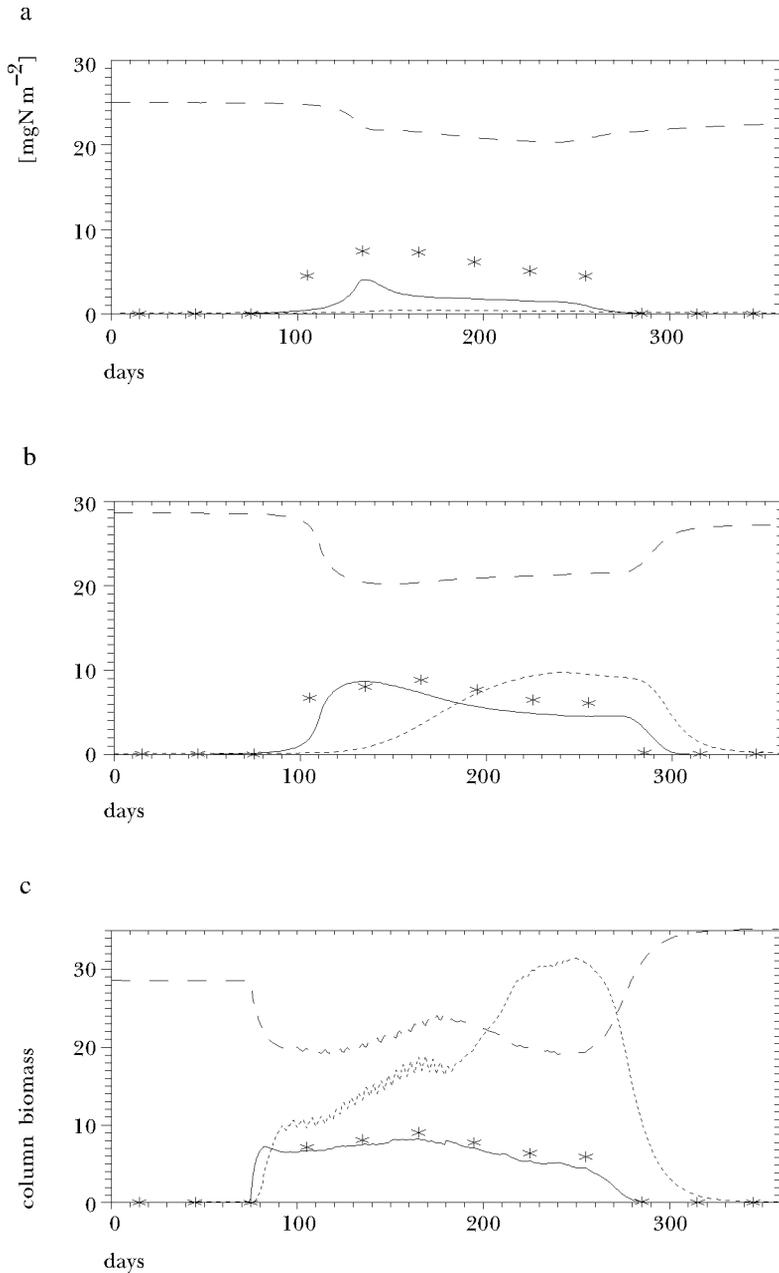


Fig. 8. CZCS data assimilation in the Baltic phytoplankton annual cycle model. initial parameter values (a), assimilation using method 2 (target function min) (b), assimilation using method 1 (covariance function) (c). Solid line – phytoplankton column biomass [mgN m^{-2}], dashed line – nutrient column concentrations [mgN m^{-2}], dotted line – zooplankton column biomass ($\times 50$) [mgN m^{-2}], asterisks – column phytoplankton biomass reconstructed from CZCS data [mgN m^{-2}]

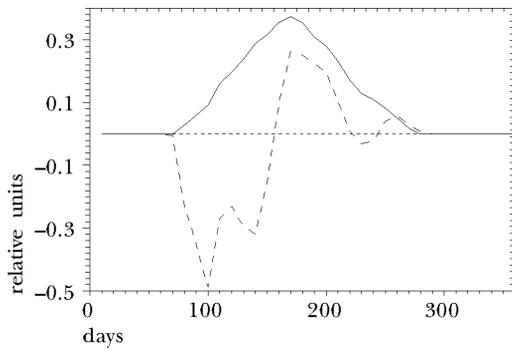


Fig. 9. EOF analysis of the Baltic primary production annual cycle. Solid line – EOF 1 [rel. un.] (91.3% of cumulative dispersion), dashed line – EOF2 [rel. un.] (3.7%)

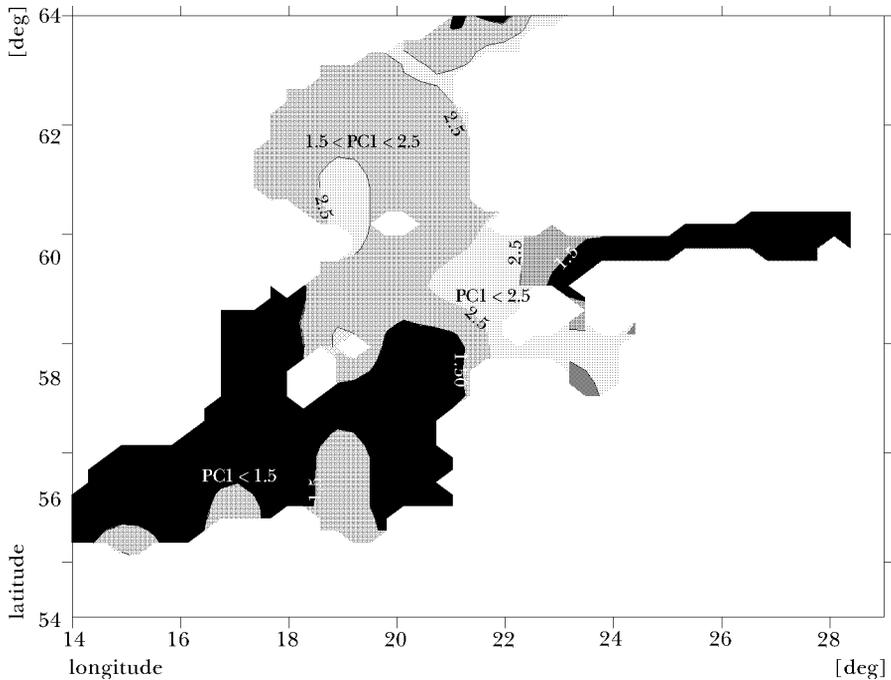


Fig. 10. Map of the first principal component of the Baltic annual column primary production distribution [mgN m^{-2}]. Black area – $\text{PCI} < 1.5$, dark grey area – $1.5 < \text{PCI} < 2.5$, light grey area – $\text{PCI} > 2.5$

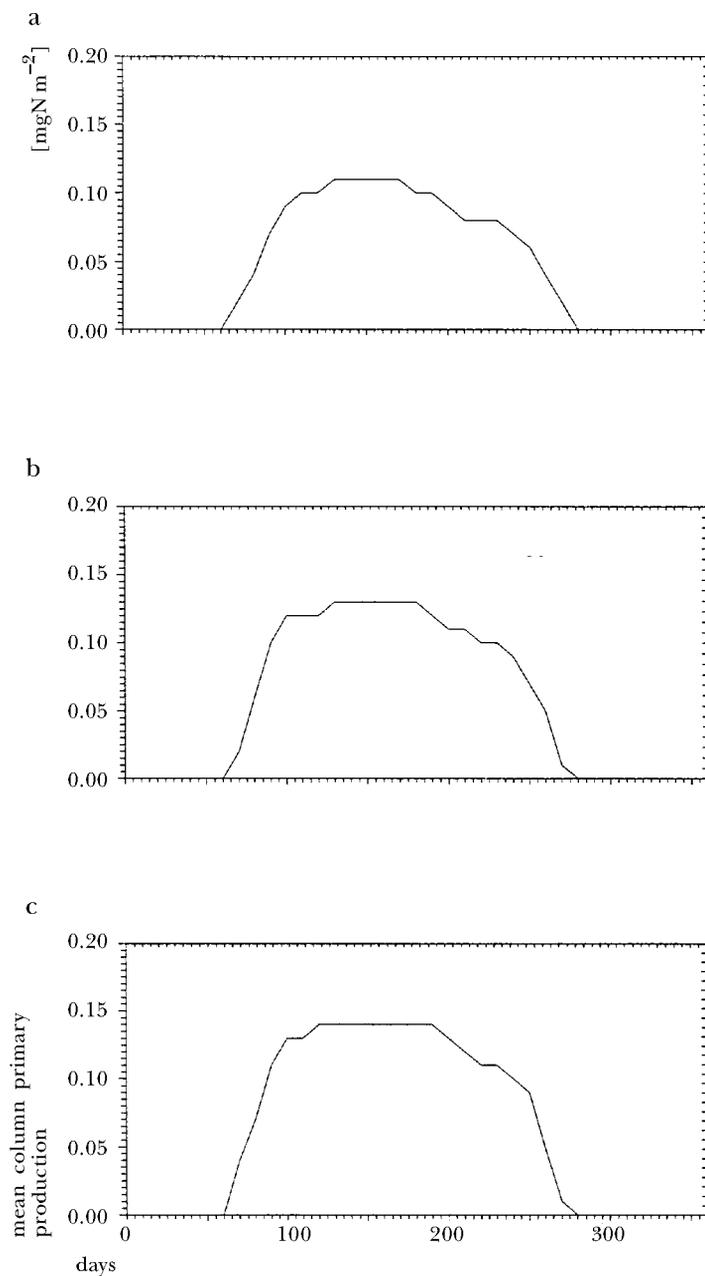


Fig. 11. Main types of Baltic annual column integrated phytoplankton concentration variability [$\text{mgN m}^{-2} \text{d}^{-1}$]. $\text{PC1} < 1.5$ (a), $1.5 < \text{PC1} < 2.5$ (b), $2.5 < \text{PC1}$ (c)

the best correlation with observations. We calculated the empirical orthogonal functions of the Baltic annual primary production cycle in the same way as for the North Atlantic (Fig. 9).

The first EOF corresponds to 91.3% of the cumulative dispersion. For the main types of primary production annual cycles the Baltic can be delineated using the aerial distribution of the first principal component (Fig. 10). The main types of annual Baltic primary production cycles are presented in Fig. 11.

6. Discussion

Chlorophyll CZCS data are now well-known and have been used in a number of studies of ocean phytoplankton variability. Models close to those described here could be useful for a better assimilation of new satellite-based scanner data (*e.g.* SeaWiFS) in statistical procedures and numerical models. But, in fact, it is not the first example in oceanology where the same data source has served as a database for a number of researchers.

The following comments refer to the use of numerical models in ecosystems analysis. Much experience in constructing ecosystem models shows that an unlimited increase in model complexity does not mean an improvement in suitability. A simpler one corresponding to the data can often describe reality more adequately than a very complex one. Numerical models of such complex nonlinear processes as the processes of population dynamics should be developed in accordance with the development of observational instruments. For example, a block of dissolved organic matter (DOM) dynamics can be added for future assimilation of DOM remote detected data.

We must note that modelling results for the Baltic can be presented here only as a preliminary study. At the present time we have no adequate procedure for CZCS data interpretation in Case 2 Baltic Waters (*cf.* Sturm, 1993; analysis of CZCS observations for the North Sea). This approach can be used successfully only for the databases of new generation scanners like the future SeaWiFS.

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