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Mathematical models of lake Baikal ecosystem

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Abstract

A review is given of the mathematical models of lake Baikal existing today. Special attention is given to the models that take into account the influence of toxicants on the ecosystem components.

A model of ecosystem disturbances is described that may be used to forecast the ecosystem behaviour during various management conditions in the lake region. It is based on experimental data and the method of its informational provision is given. Model experiments showed that the lake ecosystem is more sensitive to chronic input of toxicants in low concentrations than to fluxes of their input resulting in a concentration of up to 1 mg l^{-1}. During ice-cover period the planktonic community is shown to be less resistant to disturbances than in summer.

Keywords: Disturbance; Lake ecosystems; Toxicology

1. Introduction

Studies of a complicated natural object usually bring to life an appreciable amount of models (Jørgensen, 1983). Their purpose is to explain the object behaviour, to forecast its changes with time. In this respect lake Baikal is not an exception. We shall not touch the models describing the dynamics of water, temperature conditions, individual ecosystem components, as well as statistical series, but consider such models of the lake ecosystem that could be employed to forecast its condition under the action of anthropogenic factors, as it is important to establish, even approximately, the self-purification potential of the lake for its managing (Uhlmann, 1982). The most realistic way to obtain such kind of forecast data in modern ecology is mathematical modelling (Straškraba and Gnauck, 1985).

2. Lake characteristics

Some general information on the lake is given in Table 1.

Life in the lake reaches its maximum depths, connected specifically with high oxygen content across the whole water depth. Photosynthesis takes place in the upper 50-m water layer, the richest in life. Beginning with 250 m depth the abiotic conditions in the lake are constant at any

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Table 1
Morphometrical characteristics of Lake Baikal

Volume	23 600 km^3
Area of surface	31 502 km^2
Depth	
average	730 m
maximum	1637 m
Elevation	455.6 m
Geographic coordinates	
Longitude	103° 47′ E-109° 54′ E
Altitude	51° 20′ N-55° 52′ N

season; there is no light and temperature is constant, 3.3–3.4° C.

Fauna and flora of the lake are marked by pronounced endemism (Kozhov, 1963; Galazy, 1978). Two peaks in the phytoplankton development are observed during the year. In spring diatomic plankton develops in abundance under the ice, at the end of summer blue-green and green algae. Periods of maximum quantities of zooplankton, as well as the highest development of the bacterial plankton follow the vegetation peaks. Zooplankton contains many species of Rotifera, rather abundant are *Cyclops kolensis*, predatory pelagic Amphipoda *Macrohectopus grewingki*, but the main component of the zooplankton is the endemic Copepoda *Epishura baicalensis* (Kozhova, 1987).

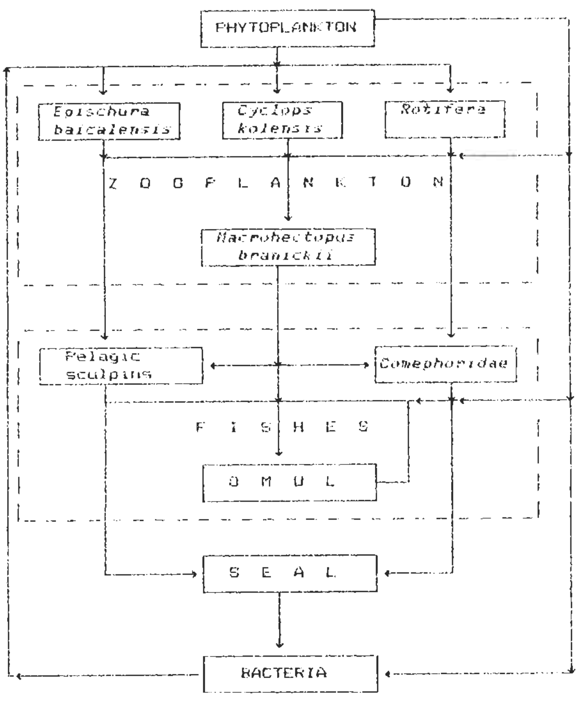

Fig. 1. Scheme of lake Baikal pelagial ecosystem.

The ichtyofauna of the lake is mainly represented by the sculpins and family of Comephorus, the endemics of Baikal. Pelagic sculpins (2 species), as well as Comephorus, feed on zooplankton and fish fry, being, in turn, the main food for *Coregonus migratorius* (omul) and seal (Fig. 1). In the lake there are also numerous benthos-feeding fishes, mostly species of sculpins, sigs, graylings and sturgeon.

3. Existing models

3.1. Models of "clean" lake

Model of seasonal dynamics

We begin our review of the lake ecosystem mathematical models with a model of seasonal dynamics of the lake Baikal pelagic community as developed by Aschepkova et al. (1978b).

The model consists of a number of sub-models: "Plankton community", "Macrohectopus", "Cottocomephorus grewingki", "Cottocomephorus inermis", "Omul", "Seal", "Benthos" (Fig. 2). A range of changes of each component is used in the model from 0 to +1, where 0 corresponds to "few, disappearing" and +1 to "unusually large". To the term "mean" accordingly applies magnitude 0.5. Mutual influences are reflected by a scale where "absence of influence" corresponds to the point 0, "the strongest negative influence" to −1, and "the strongest positive influence" to +1.

The seasonal dynamics are reflected in a submodel "Plankton community". A year is divided into 6 periods. These are February–April, May–June, July–August, August–September, October–November and December–January. In the course of each season action is noted of abiotic factors of definite intensity, such as solar radiation, wind, ice and snow thickness and others that cause changes in warming of the water top layer, its agitation, evaporation, turbulence in the

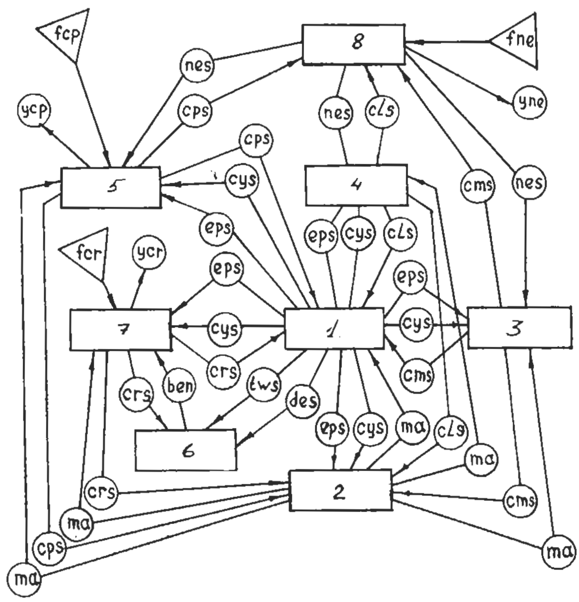

Fig. 2. Scheme of lake Baikal ecosystem model by Aschepkova et al., 1978b. 1, pelagic community; 2, *Macrohectopus*; 3, golomyanka; 4, 5 *Cottocomephorus grewingki*, *C. inermis*; 6, benthic community; 7, omul; 8, seal. Circles represent biotic interactions, triangles interactions regulated by economics values.

boundary layer water–air, heat-losses, dates of the lake ice breaking up and binding. Concentrations of the biogenic elements are defined by both hydrodynamic and biotic factors.

Annual dynamics take place under the action of the factors listed above of diatomic, *Peridinium* and other algae, bacteria on which feed rotifers, cyclops, successive stages of *Epishura* development and detritus.

The other sub-models have no seasonal dynamics. On sub-model "Macrohectopus" act sub-models "Plankton community" by average annual quantities of *Epishura* and *Cyclops* (eps, cys) serving as its food, and "Cottocomephorus grewingki", "Omul", "Cottocomephorus inermis" and "Comephorus" by average annual quantities of fish feeding on the crustaceans (cps, crs, cls, cms). Average annual quantity of *Macrohectopus* (ma) serves for these sub-models as a positively acting factor for fish accretion rates and negatively for plankton.

The sub-models of fish have age groups: 3 each for *Cottocomephorus grevingki* and *Cottocomephorus inermis*, 6 for *Comephorus* and 10 for omul. Each of them depends on plankton via (eps) and (cys), *Macrohectopus* via (ma), and omul, in addition, on benthos (ben). Omul and *Cottocomephorus grewingki* are objects of fishing (ycr, ycp) the catch being controlled by the magnitude of the fishing effort (fcr, fcp).

Cottocomephorus grewingki, *C. inermis* and *Comephorus* provide food for the seal (cps, cls, cms) whose quantity affects them (nes) and is determined by the hunting (yne) which depends on hunting efforts (fne). Seal has 16 age groups. Finally, benthos depends on temperature and food conditions via plankton block on consumption by omul (crs).

In the model there is a total of 120 variables, it is possible to modify 20 input variables, 3 variables being output in the form of fishing *Cottocomephorus grevingki* and omul, hunting for seal.

The model represents a system of linear equations:

$$X(t) = AX(t) + BX(t-1) + CU(t),$$

where $U(t) = (U(t),\ldots,U_{20}(t))$, $U_i(t) \in [0,1]$, vector of input variables for a year, t; $X(t) = (X(t),\ldots,X_{120}(t))$, $X_i(t) \in [0,1]$, vector of phase variables for the same year; A, matrix of influence coefficients within the year; B, matrix of interannual relations; C, matrix of dependence of the model variables on external conditions.

With this condition

$$\sum_{j=1}^{120} \left(|a_{ij}| + |b_{ij}|\right) + \sum_{k=1}^{20} |c_{ik}| = 1, \quad i = 1,2,\ldots,120.$$

At the stationary point of the system all the coordinates are equal to 0.5.

This model makes it possible to obtain only qualitative results, but its study permitted us to find a series of dependencies between abiotic factors, to discover that biotic components do not depend on air temperature, but depend strongly on conditions of insolation and winds, to isolate the community elements most sensitive to solar radiation (phytoplankton, bacteria, rotifers, *Cyclops*) and to wind activity (phytoplankton). This

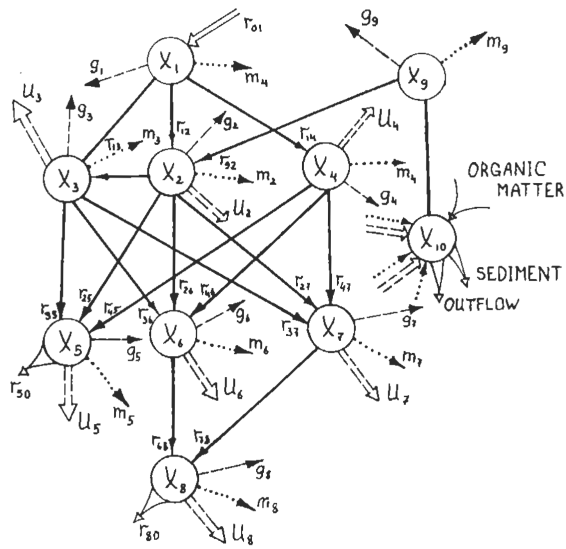

Fig. 3. Energy flows in model of pelagic community by Aschepkova et al., 1978a. For explanations see text.

model is considered by the authors themselves as an intermediate stage in the work.

Energy flow model

The next model is a energy flow model of the pelagic community of lake Baikal by Aschepkova et al. (1978a). This is a lumped model, i.e. the spatial structure of the lake is not considered, similarly to the previous model. Energy flows are reviewed in a 0–250 m layer, all values are expressed in kJ/m^3.

The following components are included in the model:

x_1: phytoplankton, x_2: *Epischura*, x_3: *Cyclops*, x_4: *Macrohectopus*, x_5: omul, x_6: pelagic sculpin, x_7: *Comephorus*, x_8: seal, x_9: bacteria, x_{10}: detritus (Fig. 3)

b_i biomass of i component
r_{ij} energy flow from component i to j
g_i energy exchange of i component
m_i energy loss with mortality of i component
U_i non-assimilated food remnants of component i
$æ_i$ tension of component i trophic relations
λ_{ij} share of component i in the food of j
c_{max} specific maximum ration
A annual influx of allochthonic organics
S_1 organic sedimentation
S_2 organic drainage via Angara

Energy flows representing biomass functions were calculated from formula proposed by Menshutkin (1971)

$$r_{ij}(b_i,b_j) = c^j_{\max} b_j \lambda_{ij} \frac{1 - e^{-\xi_j æ_i}}{æ_i},$$

where

$$c^j_{\max}(b_j) = \alpha_j e^{-\beta_j b_j}.$$

and

$$c^j_{\max}(b_j) = \alpha_j e^{-\beta_j b_j}.$$

Average correction of Menshutkin (1971), a fraction in the formula for $r_{ij}(b_i,b_j)$ was taken equal to 0.8. Coefficients ξ_i, α_j, and β_j were calculated on a condition that with $b_j \to 0$ specific maximum ration increases 2 times in comparison with the maximum ration for average value of the biomass. Values λ_{ij} were taken constant for each component.

Energy exchange and losses with mortality depended linearly on biomass components

$$g_i = \gamma_i b_i, \quad m_i = \delta_i b_i, \quad i = 1,\ldots,9,$$

as well as the non-assimilated rations linearly dependent on the summary ration

$$U_j = \rho_j \sum_i r_{ij}, \quad i = 2,\ldots,8.$$

Values γ_i and δ_i are taken constant for each component, values ρ_i are taken equal to 0.2.

The model is a system of ten differential equations

$$\frac{db_1}{dt} = r_{01} - g_1 - m_1 - \sum_j r_{1j};$$

$$\frac{db_i}{dt} = \sum_i r_{ij} - g_i - m_i - U_i - \Sigma r_{ij}, \quad i = 2,\ldots,9;$$

$$\frac{db_{10}}{dt} = \sum_{i=1} m_i + \sum_{i=2}^{8} U_i - r_{10,9} + A - S_1 - S_2,$$

where $S_1 = \chi b_{10}$, $S_2 = \mu b_{10}$. A value 6.7 was taken for χ and 20 for μ. In the equations for omul and seal, flows r_{50} and r_{80} were introduced representing their catch and connected linearly with corresponding biomasses by coefficients $r_{50} = \varphi_5 b_5$, $r_{80} = \varphi_8 b_8$.

Experiments with the model showed that increase in the inflow of allochthonic organics by 20% causes an increase in the primary production by 6%, decrease in the organic inflow by the same 20% results in the primary product decrease by 8%. But the authors themselves point out the hypothetic nature of many model parameters assigned by them and the necessity to define them more exactly experimentally at Baikal.

Box model of ecosystem dynamics

In a box model of the lake Baikal ecosystem dynamics by Menshutkin et al. (1981) the lake is already studied as an extended object. The water area is divided into 65 boxes of 484 km^2 each. A photosynthetic zone is located under each box (up to 50 m depth) and under 59 boxes also a destructive one (50 m bottom). Total number of boxes equals 124.

Concentrations of five components are accounted for in each box: $b_1(k,i)$, phytoplankton; $b_2(k,i)$, zooplankton; $b_3(k,i)$, detritus; $b_4(k,i)$, bacteria; $b_5(k,i)$, biogenic substances where $k =$ 1,2, numbers of photosynthetic and destructive zones; $i = 1,2,\ldots,65$, numbers of boxes.

All concentrations are given in kJ/m^3, $b_5(k,i)$ is understood as a hypothetic biogenic substance. The time step of the system is 1 day, the number of state vector components is 620.

The processes of biological nature are imitated by the same functions as the model just studied, temperature corrections are used for a number of them (optimum for algae growth is taken as 1.5° C, for zooplankton feeding 10° C according to Kozhov (1963)). If

$b_j(k,i)$ daily changes in concentrations,
P^k photosynthesis rate,
C_{jl}^k ration of l component on j,
Q_j^k losses of j on metabolism,
M_j^k mortality of j component, then

$$\Delta b_1(k,i) = P^k - C_{12}^k - Q_1^k - M_1^k;$$

$$\Delta b_2(k,i) = 0.9\left(C_{12}^k + C_{32}^k + C_{42}^k\right) - Q_2^k - M_2^k;$$

$$\Delta b_3(k,i) = 0.2\left(C_{12}^k + C_{32}^k + C_{42}^k\right) - C_{34}^k + M_1^k + M_2^k;$$

$$\Delta b_4(k,i) = C_{34}^k - C_{42}^k - Q_4^k;$$

$$\Delta b_5(k,i) = P^k + Q_1^k + Q_2^k + Q_4^k; \quad k = 1,2.$$

In the destructive zone $P^2 = 0$, P^1 is defined by the "Liebig's limitation principle".

Values obtained in the next half-step are converted in conformity with transfer coefficients between the boxes (currents imitation). In addition, sedimentation of detritus, bacteria and algae is accounted for by a formula:

$$V_j^k = \begin{cases} -V_j b_j(1,i), & k = 1 \\ -V_j b_j(1,i), & k = 2 \end{cases}$$

$j_k = 1,3,4; \quad i = 1,\ldots,65,$

where V_j^k = quantity of the component sedimented in a day; V_j = sedimentation coefficient.

$$V_j = \begin{cases} 0.05 & \text{for } j = 3,4 \text{ or } j = 1 \text{ and } t > 150, \\ 0 & \text{for } j = 1 \text{ and } t \leq 150, \end{cases}$$

where t is time, days.

The last entry means that phytoplankton begins to sedimentate only after the melting of ice. Bulk diffusion between vertical layers is also accounted for:

$$W_j(k,i) = \begin{cases} w_j(i)\left(b_j(2,i) - b_j(1,2)\right), & k = 1 \\ w_j(i)\left(b_j(1,i) - b_j(2,1)\right), & k = 2, \\ & i = 1,\ldots,65, \end{cases}$$

where $W_j(k,i)$ is diffusion; $w_j(i)$ is agitation coefficient in box i.

Experiments with the model showed that it reflects sufficiently well the real dynamics of the ecosystem, permits to follow the distribution path of a substance entering the lake, to evaluate the influence of the ecosystem condition changes in one location on other lake regions.

3.2. *Model of "polluted" lake*

All the models studied above have no connection at all with the action of pollutants on the ecosystem. But the next model includes the polluting substances. It was developed by a group of authors from Rostov University and the Institute of Hydrochemistry under guidance of A.B. Gorstko (Gorstko et al., 1978).

The ecosystem state is described by a vector $X(t)$, each coordinate of which is a numerical characteristic of a certain component of the ecosystem (for hydrobionts biomass; for biogens, pollutants etc. concentration). The model step t equals 5 days. Exogenic external factors (water temperature, wind velocity, solar radiation intensity etc.) are included in the vector $S(t)$. The model studies only one region of Baikal (southern), whose surface is divided into 9 regions (Fig. 4) and by depth: two layers are allotted for hydrological parameters, 0–200 m and 200 m–bottom; four for phytoplankton, 0–25 m (divided in turn into 5 layers), 25–50, 50–200, and 200–bottom. All this leads to an increase in the vector dimensions. General view of the model may be presented by an equation

$$X(t+1) = G(S(t))F(X(t),S(t)),$$

where F is the kinetic operator that converts the system state under the action of external factors, mutual conversions and influences; G is the linear operator for agitation.

The hydrodynamics block permits concentration calculations of the components in the cells at the next step, knowing the concentration for the present moment, velocity, force of wind, water roughness and level changes, and representing the water exchange as a successive water exchange between the surface cells, lifting and lowering of the water masses and water exchange between upper and lower cells.

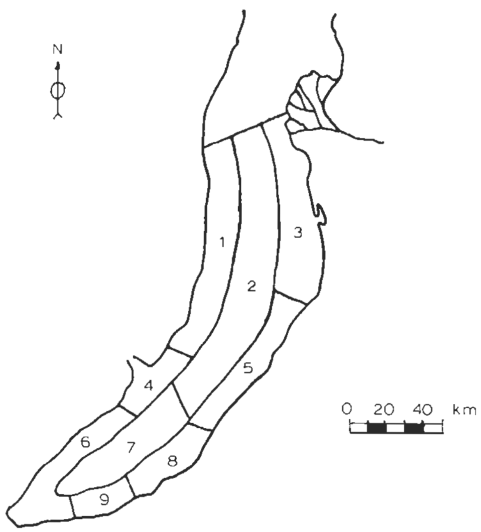

Fig. 4. Division of southern Baikal water body in model of Gorstko et al., 1978.

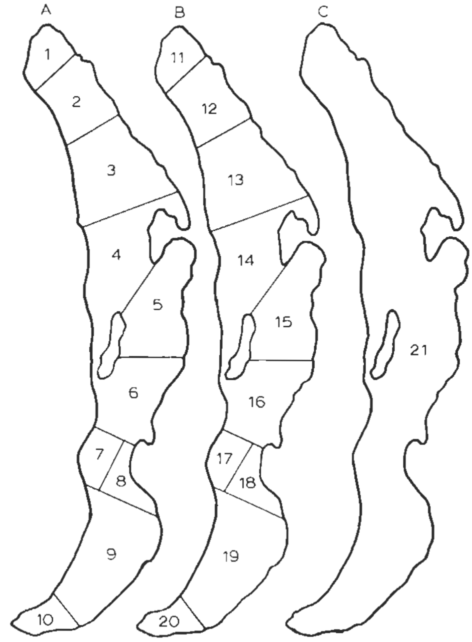

Fig. 5. Division of lake Baikal water body accepted by disturbances model. A, layer 0–50 m; B, layer 50–250 m; C, layer 250 m–bottom.

4. Ecosystem disturbances model

4.1. Description of model

The basic object of the model is optimization of interaction of the anthropogenic factors with the ecosystem of Lake Baikal, therefore the model was based on the method of disturbances also used by other authors (De Angelis et al., 1985). The lake water surface is divided into 10 regions, significantly differing by their conditions (Fig. 5).

In each region the water body is divided into three layers (0–50, 50–250), the layer 250 m–bottom was supposed to be homogenous. Thus 21 boxes are obtained and ecosystem dynamics within each box is described by an equation

$$\frac{dZ_k^i}{dt} = \sum_{j=1}^{N} Q_{ij} Z_k^i + \frac{1}{Vk}\left[\sum_{l\in L}\left(P_{lk} Z_l^i - P_{lk} Z_k^i + D_{kL}\left(Z_l^i - Z_k^i\right)\right)\right] + U_k^i,$$

where Z is vector of ecosystem deviation from unperturbed state; Q mutual influence matrix of ecosystem components; L aggregate of the neighbouring cells; P, D matrices of turbulence and diffusion; V vector of box volumes; U vector of external influences.

The scheme of ecosystem components interactions is given in Fig. 6. The number of the ecosystem condition indices studied by the model is 18. Coordinates of vector Z represent concentration deviations of mineral salts, biogenic elements, organic substance, main pollutants, quantities of phyto- and zooplankton, phyto- and zoobenthos, microflora, ichthyofauna and seals. Individual components listed above are represented by several coordinates (for example, zooplankton by *Epischura*, *Cyclops*, *Macrohectopus*; ichthyofauna by omul, *Comephorus*, pelagic sculpin).

Pollutants are introduced through vector U (excess of mineralization, biogenic elements, oil products, phenols, etc.), fishing of omul, seal hunting, introduction of fish fry are accounted for. To determine the elements of matrices P and D, a separate hydrodynamic block is formulated. Each element of the matrix Q–q_{ij} reflects the influence of component j on component i, i.e. demonstrates changes in component i in a unit of time during deviation of component j by a unit. Diagonal elements q_{ii} reflect the dynamics of returning component i to initial state during its single deviation, i.e. this is a constant for the population self-rehabilitation rate or a constant for the pollutant disintegration rate, etc.

The main problem usually ecologists are faced with (Straškraba and Gnauck, 1985; Tumeo and Orlob, 1988) is the informational provision of models.

4.2. Identification method

To identify unknown parameters of perturbations of lake Baikal ecosystem mathematical

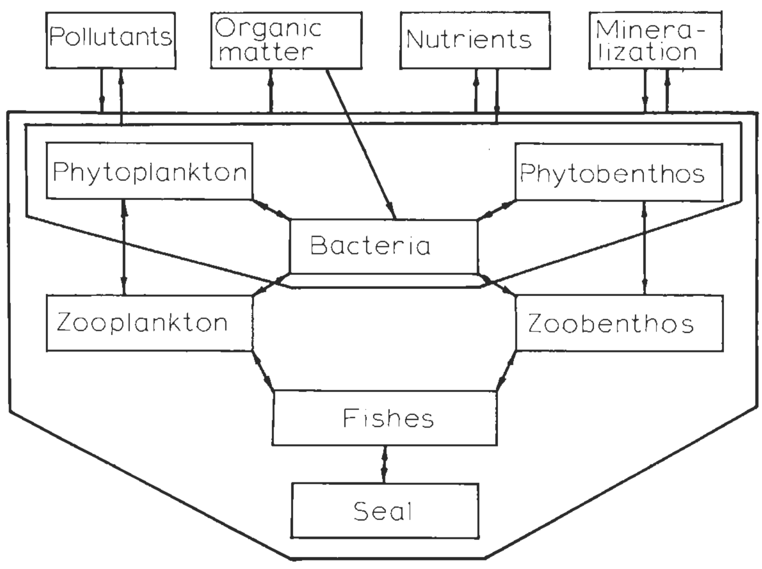

Fig. 6. Ecosystem components interactions in disturbances model.

model, a specific algorithm was developed and later implemented as a software complex on an IBM-compatible computer.

Let an object be described by the following mathematical model

$$\dot{z}=f(t,z,a) \tag{1}$$

where the functions $z(t)\in R^n$ characterize the state of the object; $a\in R^r$ is the vector of unknown parameters. The object is examined on some time-segments $T^i=[t_0^i,t_1^i]\subset T$, $i=\overline{1,p}$. On each time-segment T^i a vector-function $g^i(t,z,a)$ is known, describing the mathematical model of an operator of measurements over the object. So, input information of the model's identification unit may be composed not only of the state values of the ecosystem but of some state functions known in advance. For example, values of state change rates, and g^i describes these dependencies. The initial states vector $z^i(t_0)$ and the measurements operator values vector $\overline{g}^i(t)$ are given, as well as the mathematical model of measurements operator $\mathbb{C}^i(t_1,z,a)$ for $t=t_i$ and the vector of its values $\overline{\mathbb{C}}^i$.

The identification problem consists in seeking parameters of the vector a such that the mathematical model describe the objects behaviour in the best way, e.g. in the sense of the functional minimum

$$I=\sum_{i=1}^{P}\Big[\big(\mathbb{C}^i(t_1^i,z_1^i,a)-\overline{\mathbb{C}}^i\big)'\gamma^i\big(\mathbb{C}^i(t_1^i,z_1^i,a)-\overline{\mathbb{C}}^i\big) + \int_{t_0^i}^{t_1^i}\big(g^i(t,z,a)-\overline{g}^i(t)\big)'\beta^i(t) \times\big(g^i(t,z,a)-\overline{g}^i(t)\big)\mathrm{d}t\Big],$$

where $\beta^i(t)$ and γ^i are diagonal positive definite matrices.

The technique of deriving an improving algorithm in the problem of identification via a series of experiments is based on the construction of Krotov's theorem on sufficient conditions for optimality (Krotov and Gurman, 1973). We list these constructions, in view of the problem's specific properties.

Let the function $\varphi(t,z(t),a)$ be defined for every t, be continuous and continuously differentiable with respect to t and z. Introduce the constructions:

$$R^i(t,z,a)=\varphi_z^i(t,z,a)f(t,z,a)-f^0(t,z,a)+\varphi_t^i(t,z,a)$$

$$G^i(t_0^i,t_1^i,z_0^i,z_1^i,a)=\varphi^i(t_1^i,z_1^i,a)-\varphi^i(t_0^i,z_0^i,a)+F^i(t_1^i,z_1^i,a)$$

$$F^i(t^i,z^i,a)=\big(\mathbb{C}^i(t_z^1,z_1^i,a)-\overline{\mathbb{C}}^i\big)\gamma^i\times\big(\mathbb{C}^i(t_1^i,z_1^i,a)-\overline{\mathbb{C}}^i\big)$$

$$f^{0i}(t,z,a)=\big(g^i(t,z,a)-\overline{g}^i(t)\big)'\beta^i(t)\times\big(g^i(t,z,a)-\overline{g}^i(t)\big)$$

The functional L is formed thus

$$L(z,a)=\sum_{i=1}^{P}\Big[G^i(t_0^i,t_1^i,z_0^i,z_1^i,a)-\int_{t_0^i}^{t_1^i}R^i(t,z,a)\mathrm{d}t\Big]$$

Clearly, if the pair $(z(t),a)$ satisfies the model, then $I(a)=L(z,a)$; further it is evident that I_α coincides with the coefficient of the linear summand after factoring the functional L in terms of a.

Let a point a^0 and a corresponding set of trajectories $\{z^i(t)\}$ of solutions of Eq. 1 on segments T^i, $i=1,\dots,p$ be given. Consider the increment in the functional in the neighbourhood of the point $(a^0,z^i(t))$

$$\Delta L=\sum_{i=1}^{P}\Big[\Delta G^i-\int_{t_0^i}^{t_1^i}\Delta R^i\mathrm{d}t\Big]$$

The functions G^i and R^i are subjects to Taylor series expansion in terms of the variables (z,a) up to first-order terms. Further we have

$$\Delta G^i=G_{z_0}^{i\prime}\Delta z_0+G_{z_1}^{i\prime}\Delta z_1+G_\alpha^i\Delta a+o(\|\Delta z_0\|,\|\Delta z_1\|,\|\Delta a\|),$$

$$\Delta R^i=R_z^i\Delta z+R_\alpha^{i\prime}\Delta a+o(\|\Delta z\|,\|\Delta a\|),$$

$\|\cdot\|$ is the norm in corresponding euclidean spaces.

Henceforth we assume

$$G_{z_0}^i=0.$$

Introduce the notation

$$\phi^i(t) = \varphi_z^i(t,z^i(t),a^0)$$

$$\xi^i(t) = \varphi_\alpha^i(t,z^i(t),a^0)$$

$$H^i(t,z,a,\phi) = \phi^{i\prime}(t)f(t,z,a) - f^{0i}(t,z,a)$$

where $\phi^i(t)$ is a n-vector, and $\xi^i(t)$ is a k-vector.

Write down the derivatives of R^i and G^i through the derivatives of H^i and F^i. We have

$$G_{z_1}^i = \varphi_{z_1}^i + F_{z_1}^i,$$

$$G_\alpha^i = \varphi_\alpha^i(t_1^i,z_1^i,\cdot) - \varphi_\alpha^i(t_0^i,z_0^i,\cdot) + F_\alpha^i,$$

$$R_z^i = H_z^i + \frac{\mathrm{d}\phi^i}{\mathrm{d}t},$$

$$R_\alpha^i = H_\alpha^i + \frac{\mathrm{d}\xi^i}{\mathrm{d}t},$$

where the derivatives of H^i functions are calculated at the point $(t,z^i(t),a^0,\phi(t))$, and those of φ^i functions at the point $(t,z^i(t),a^0)$. Substitute the resulting expressions into the formula for the increment in the functional L and, due to the notation introduced and Newton–Leibnitz formula, we obtain

$$\Delta L = \sum_{i=1}^{P}\Bigg[\left(F_{z_1}^i + \phi^i(t_1)\right)'\Delta z_1 - \int_{t_0^i}^{t_1^i}(H_z^i + \phi^{i\prime})\Delta z\,\mathrm{d}t + \left(F_\alpha^i - \int_{t_0^i}^{t_1^i}H_\alpha^i\mathrm{d}t\right)'\Delta a\Bigg] + o(\|\Delta z\|,\|\Delta z_1\|,\|\Delta a\|).$$

Choose the functions $\phi^i(t)$ so that the first-order factorisation term does not depend on Δz_1, Δz. Then the formula for calculating the gradient $L_\alpha(\cdot)$, and hence $I_\alpha(\cdot)$ will take the form

$$I_\alpha(\cdot) = \sum_{i=1}^{P}\left[F_\alpha^i(t_1^i,z^i(t_1^i),\cdot) - \int_{t_0^i}^{t_1^i}H_\alpha^i(t,z^i(t),\cdot)\mathrm{d}t\right]$$

where $\phi^i(t)$ are the solutions of the system

$$\phi^{-i}(t) = -H_z^i(t,z^i(t),\cdot,\phi^i)$$

$$\phi^i(t_1^i) = -F_z^i(t_1^i,z^i(t_1^i),\cdot), \quad t \in T^i, \quad i = 1,\ldots,p$$

Knowing the value of I_α at the point a^0 one can construct the following approximation using familiar gradient-type schemes. For example, the sequence defined by

$$a^{k+1} = a^k - \alpha^k I_\alpha = (a^k)$$

prescribes a method of steepest descent, where α^k is found from the solution of a one-dimensional minimisation problem

$$\alpha^k = \underset{\alpha \geq 0}{argmin}\, I(a^k - \alpha I_\alpha(a^k))$$

The method of conjugate gradients is constructed after the following scheme

$$a^{k+1} = a^k - \alpha^k S_k,$$

$$S_0 = I_\alpha(a^0), S_k = I_\alpha(a^k) - \zeta_k S_{k-1},$$

$$\alpha^k = \underset{a \geq 0}{argmin}\, I(a_k - \alpha S_k).$$

The varieties of the conjugate gradients method differ in the way the parameter ζ is defined. Note that if $\zeta_k = 0$, the scheme degenerates into the method of steepest descent. For the calculations undertaken, ζ_k was assumed to be calculated by the formula

$$\zeta_k = \frac{-I_\alpha'(a^k)(I_\alpha(a^k) - I_\alpha(a^{k-1}))}{\|I_\alpha(a^{k-1})\|^2},$$

where $I_\alpha'(a^k)(I_\alpha(a^k) - I_\alpha(a^{k-1}))$ is a scalar product, $\|\cdot\|$ is the norm.

4.3. *In situ experiments*

Informational provision of the model is based on widely used microcosm approach (Uhlmann, 1985). Such laboratory and field experimental ecosystems are of great advantage for mathematical modelling (Andersen and Nival, 1987).

To determine coefficients, special experiments were conducted near the biological station of Scientific-Research Institute of Biology situated at the coast of the Southern Baikal from 1985 to 1990 during different seasons (from February to October). The main idea of experiments was to observe the dynamics of all parameters described by the model in almost natural conditions when one of them was artificially changed. To solve this task two series of mesocosms were placed simultaneously in the lake. One of them served as control, another as experimental mesocosm. Experimental mesocosms were treated in different ways. For example, in the course of these experiments substances included in the model as pollutants (biogenous elements, phenolic compounds, oil products, heavy metals, etc.) were filled into polyethylene bags of 2 m^3 in volume and placed in the lake; they contained lake waters and natural organisms. Then the changes in concentration of the added substances are traced during 2–3 weeks, connected with their decomposition or absorption by biota, changes in the number and activity of microorganisms, numbers, species composition and productivity of the phytoplankton, quantity and composition of the zooplankton, hydrochemical indices. The same measurements were made in control bags and in the lake outside mesocosms. Similar experiments were obtained with the additions of natural phytoplankton, zooplankton and bacterioplankton, suspended organic matter etc. Each series consisted of 8 control and 8 experimental mesocosms. It gave a possibility to obtain 8 measurements in lake, 8 in control and 8 in experiment for every parameter studied. Data obtained were recalculated in such way that resulting rows represented the differences between experimental ecosystems (treated bags) and control ecosystems (untreated ones), necessary to annihilate enclosure effects). These rows were later processed with the use of software developed on the basis of ideology described in previous part of the paper). To determine magnitudes of the coefficients q_{ij} at various seasons of the year, an original technique was developed for conducting experiments under ice. So, it became possible to calculate model coefficients for different months. To extrapolate these data on other parts of the lake we have used the results of almost 50 years observations of the lake Baikal ecosystem spatial dynamics obtained by Institute of Biology, Limnological Institute and other organisations. Data obtained were used for

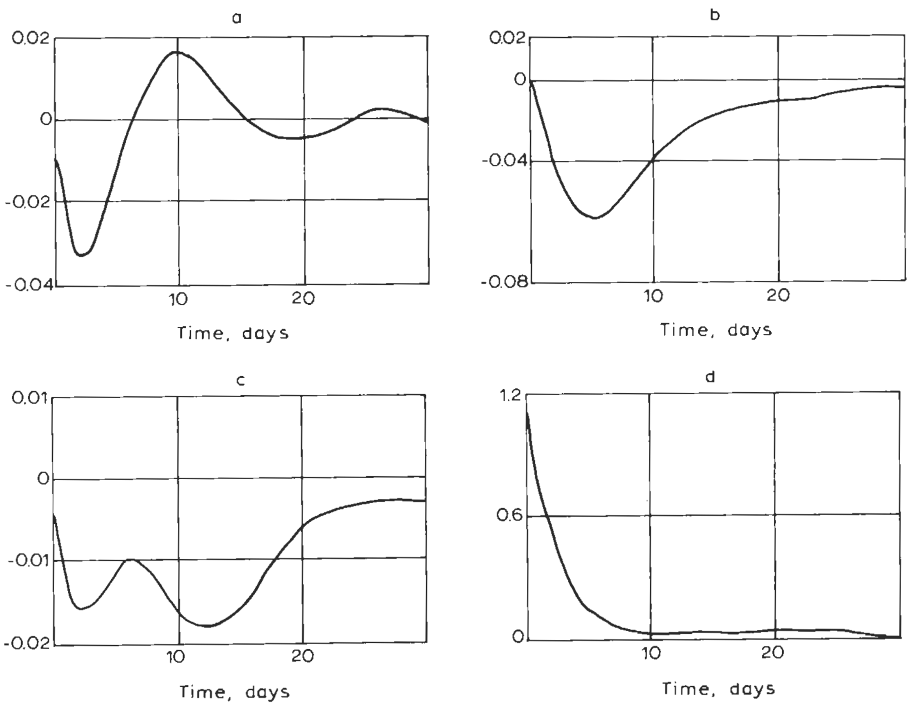

Fig. 7. Four ecosystem components absolute deviations (mg/l) dynamics after introducing of toxicants in summer. a, phytoplankton; b, zooplankton; c, nutrients (P); d, phenols (model results).

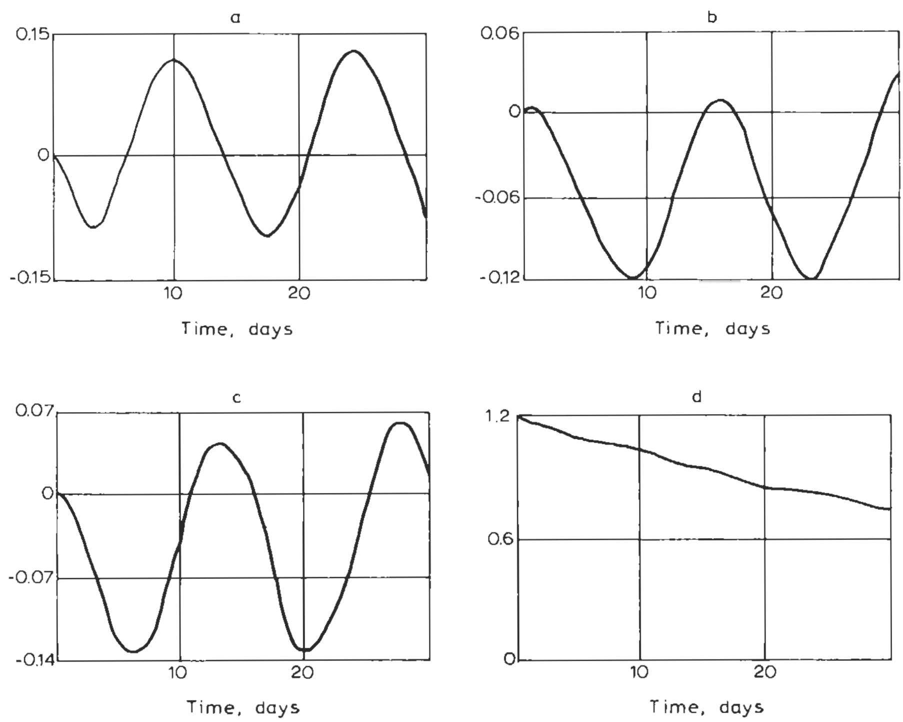

Fig. 8. Four ecosystem components absolute deviations (mg/l) dynamics after introducing of toxicants in winter. a, phytoplankton; b, zooplankton; c, nutrients (P); d, phenols (model results).

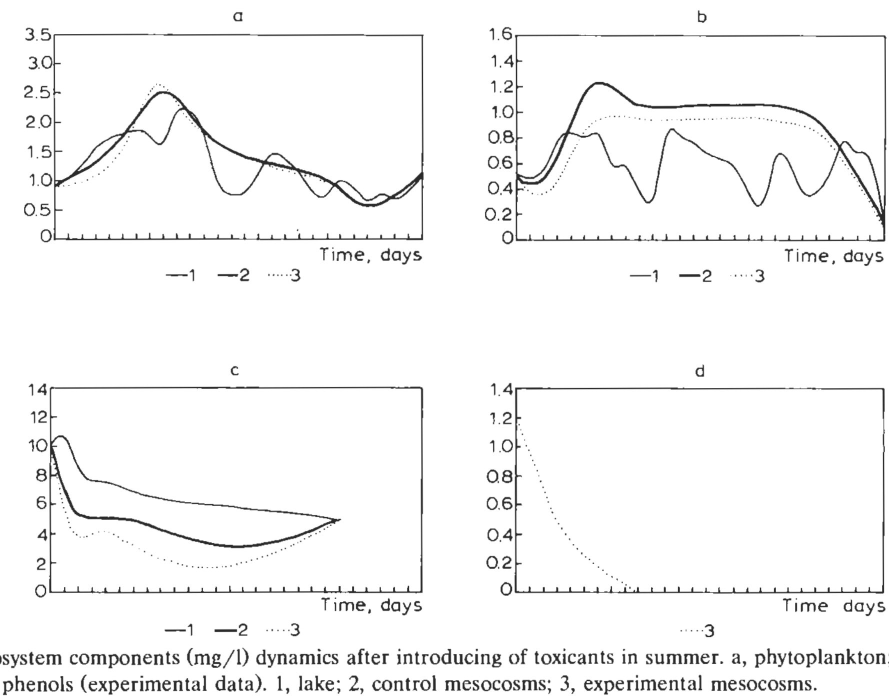

Fig. 9. Four ecosystem components (mg/l) dynamics after introducing of toxicants in summer. a, phytoplankton; b, zooplankton; c, nutrients(P); d, phenols (experimental data). 1, lake; 2, control mesocosms; 3, experimental mesocosms.

the evaluation of the model coefficients and for carrying out computation experiments.

4.4. Results of model experiments

Figs. 7 and 8 demonstrate the dynamics of some components of the pelagic ecosystem model during 1 month after phenols addition in summer and in conditions below ice-cover. Figs. 9 and 10 represent data obtained during experiments. Concentrations used were higher because otherwise it would be impossible to measure their changes. It is easy to see that under ice the species complex is much more sensitive to toxicants than in the summer. Amplitude of deviations in summer is 7–10 times less than under ice. Zooplankton in both cases is suppressed by phenolic compounds. Summer complex returns to natural state faster than the spring one, requiring 40–50 days to return. This can be explained by higher relative amount of more sensitive endemic species during ice-cover period.

This model can serve as a sensitive tool for forecasting of changes in ecosystem components behaviour under external influences. As exact prediction of ecosystem behaviour is still a very sophisticated and practically unsolved task, such models can be of great use in prediction of changes caused by anthropogenic pressure. The results demonstrated here are of illustrative character, as it is practically impossible to present the materials, obtained in calculation experiments with model, based on more than 400 series of field experiments in the paper, devoted mainly to overview of the lake Baikal ecosystem models. The model of the lake Baikal ecosystem disturbances described above was included as a model of a unique natural object into a widespread multi-level system of conceptional models, consisting of the top level models (interaction of production and resources on a regional level), models of the second level (components of the natural environment: water, air, soil, forests, minerals, biological resources) and a widening complex of particular models (river, steppe, forest etc.). Use of this complex of models makes it possible to evaluate expenditures that will secure the desired ecological situation, the large scale

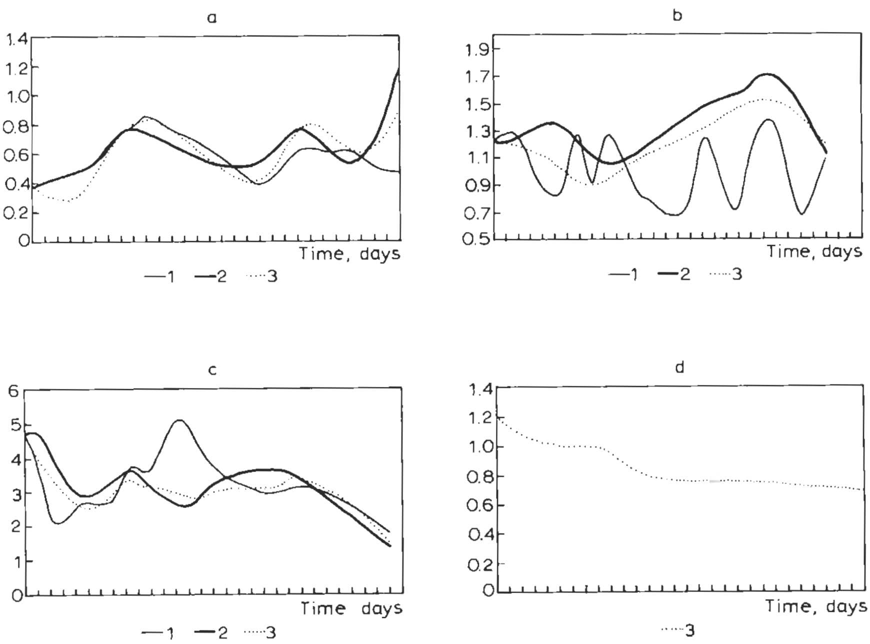

Fig. 10. Four ecosystem components (mg/l) dynamics after introducing of toxicants under ice. a, phytoplankton; b, zooplankton; c, nutrients (P); d, phenols (experimental data). 1, lake; 2, control mesocosms; 3, experimental mesocosms.

projects, substantiate the schemes of siting the production objects, recreation territories, etc.

5. Conclusion

It is seen from the review made that modelling of the lake Baikal ecosystem at present is quite a wide branch of science with rich traditions, but, although different approaches are used for model construction, the overwhelming majority of these models does not possess sufficient forecasting power as they are based on the magnitudes of coefficients that connect the ecosystem components taken mainly from literature referring to water bodies (Aschepkova et al., 1978a; Gorstko et al., 1978) or obtained by expert evaluation.

A disturbances model, in contrast to others, displays on the background of the natural dynamics its disturbances: biotic interactions, action of toxicants on hydrobionts, decomposition of the pollutants, hydrodynamic processes. Its purpose is to prevent the ecosystem condition during various situations of the use of Baikal, search of optimum rates of the economic activities that will reflect the least on the lake ecosystem. This, the latter, requires its amalgamation with a more general model of a natural economy system.

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