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MATHEMATICAL MODELLING OF A FISH POND ECOSYSTEM

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ABSTRACT

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A mathematical model is constructed for a fish breeding pond for carp, silver carp and bighead. The model is a system of ordinary differential equations describing the material transformations in the ecosystem. It allows a choice of optimal regimes of the aeration, feeding and fertilization of a pond for different climatic conditions in order to maximize the yield.

1. INTRODUCTION

Fish ponds have long been used by man to meet his alimentary and—first of all—protein requirements. Fish breeding was highly developed in ancient China. A high efficiency is achieved only with optimum values of the control parameters, such as input of fodder and fertilizers, and re-aeration of the water body, and with an optimum choice of the seed piece characteristics. The management affects the entire fish pond ecosystem, resulting in unpredictable and, even more, not always desirable changes in the ecodynamics of the reservoir. A mathematical model permits an assessment to be made of the consequences of different control strategies and an estimation of all possible transformations in the whole complex of cause–effect relations in the ecosystem.

Attempts to model a fish pond have been made by Vinberg and Anisimov (1966), Borshev (1977), and others. However, the energy approach used by Vinberg and his successors, although providing an adequate qualitative ecosystem description, gives little insight into the management of an ecosystem. Therefore our model was based on the models of lake ecosystems (Jorgensen, 1980; Voinov et al., 1981).

This paper presents a fish pond simulation model. The food chain structure and the set of model phase variables are fixed. It is assumed a

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priori that the ecosystem in question already includes the biological species and that a management mode is envisaged that can result in the optimum yield. The model was identified for literature data and gives a quite reasonable response to changes in climatic factors and control parameters, thereby serving as a simulator for the analysis of all kinds of possible developments in a fish pond ecosystem. Suitable optimization techniques, derived on the basis of this model, allow one to define optimum control strategies for an ecosystem.

On the other hand, fish ponds may serve as useful models for the analysis of ecosystem properties in general, due to their relatively simple trophic structure and the high intensity of the biotic material and energy transformations. From this point of view the mathematical modelling of fish ponds is of some general ecological and theoretical significance.

2. MATERIAL CYCLES IN A FISH POND

When analyzing a concrete problem, it is necessary to choose a degree of generality that is ample for meeting the purposes of modelling. In our case, to model an optimum fish pond, we have to choose variables that would fully reflect the specificity of fish ponds giving stable high yields over long periods of time.

From experience, the joint breeding of carp and herbivorous fish (Bighead, Silver Carp, White Amur, etc.) is very effective. They complement each other well enough, as they occupy almost non-overlapping ecological niches. Although these species may compete for food, they prefer different natural feeds: benthos for Carp, phytoplankton for Silver Carp, zooplankton for Bighead, and macrophytes for White Amur. The last species has not been included into the model due to its relative independence from the other ecosystem components.

In describing the natural enrichment of the fodder supplies, it will be logical to take into account the concentrations of the two most usually limiting nutrients, i.e. nitrogen and phosphorus. They are supplemented by the bacterial destruction of dead organics—detritus—and also from the input of artificial fertilizers. Finally, the dissolved oxygen concentration is quite an important, and sometimes determining factor of the fish pond ecosystem.

Hence, the model includes the following phase variables: phytoplankton (F), zooplankton (Z), benthos (B), Carp (C), Bighead (H), Silver Carp (S), dissolved mineral phosphorus (P), dissolved inorganic nitrogen (N), dissolved oxygen (O), artificial fodder (A), detritus combined with bacteria(D). It is assumed that a concrete ecosystem can roughly be described by substituting the complex multi-species community structure with a simplified block pattern. In this case a separate block (for instance, F or Z) may contain dozens of species. Such a substitution may be considered correct if all the species within one block have close values of their prime ecological parameters (maximum growth rates, respiration coefficients, etc.). Later, certain variables can be disaggregated (e.g. F, Z, B, D); new variables can be added into the model (e.g. macrophytes, other fish species).

The interaction between the phase variables is described according to the scheme of the material cycle presented in Fig. 1. It is assumed that such a scheme comprehensively reflects the material transformation processes in the pond. Since the dissolved oxygen (DO) has a controlling, regulating effect upon different chemical and ecological processes, it is regarded as a special

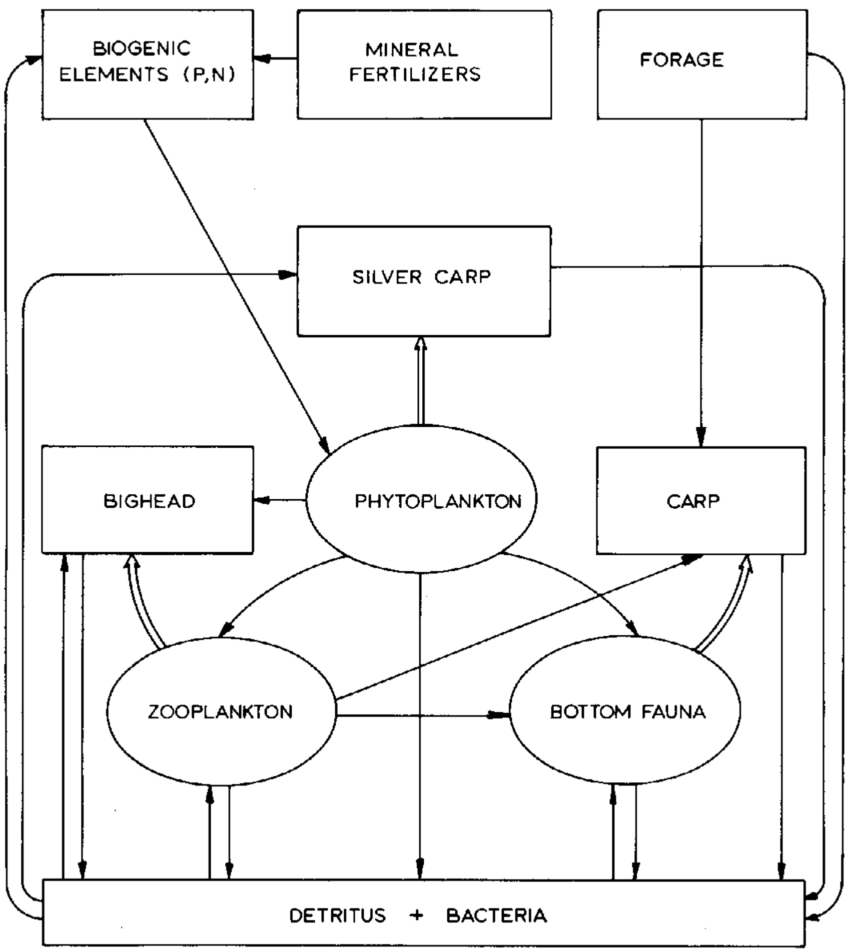

Fig. 1. Material cycle in the fish pond.

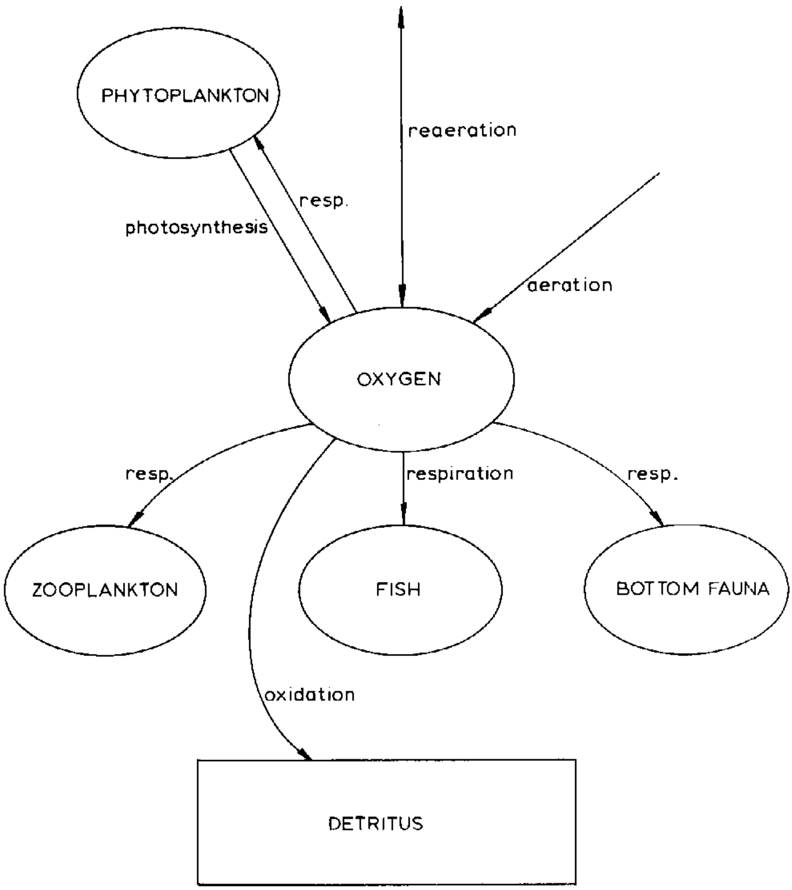

Fig. 2. Inflows and outflows of oxygen in the fish pond.

variable. Figure 2 shows the consumption and replenishment of *DO* in the ecosystem. It should be noted that the specific times inherent in the main *DO* transformations are shorter than the times of other ecosystem processes and, unlike the latter, should be measured in hours rather than in days. For instance, many scientists stress that fish kills in ponds are most common in the morning, i.e., the *DO* concentration definitely depends upon the hour of the day. This is quite natural, taking into account that the intensity of photosynthesis, the main source of *DO* in the ecosystem, is determined by the intensity of the solar radiation. Therefore, the *DO* concentration is analysed separately in the model with its own time step.

When modelling a shallow pond with depths of about 1 m and a small area (less than 1 ha) we may neglect the effects of the spatial distribution of organisms and material, as we are constructing a local, i.e. a point model. All the variables are regarded as concentrations and the unit of measurement is mg/l. By the concentration of living organisms we mean the ratio of their total biomass to the volume of the whole reservoir. Further, the square brackets [ ] will stand for the concentration of the respective ecosystem variables. The fish-breeding pond is modelled for five months (from April 15 to September 15).

The external forcing functions in the model are the climatic factors—water temperatures and the total solar radiation—as well as the control elements, such as the input of artificial feed, mineral fertilizers and the intensity of artificial water aeration.

3. BASIC MODEL EQUATIONS

(a) Nutrients uptake by phytoplankton

The phytoplankton growth is an important process, which depends on the presence of nutrients in the water and also on the external factors such as temperature (T) and illumination (L). The nutrients limiting the phytoplankton growth in a fish pond may be nitrogen or phosphorus. The cycles of these elements are closely related in the ecosystem. The uptake rates of the two elements may be viewed as synchronised according to the stoichiometric ratio, i.e. the N/P ratio in the living organic matter. For different estimates this ratio can be taken from N/P = 10/1 to N/P = 5/1. The phytoplankton growth is limited according to the stoichiometric ratio. Thus, accounting for the effect of external factors, we can represent the phytoplankton growth rate as follows:

$$\mu = \mu_F^{\max} \times FT(1) \times FF(L, [F], [D]) \times \min\left(\frac{[P]^n}{K_{PF}^n + [P]^n}, \frac{1}{m} \frac{[N]^n}{K_{NF}^n + [N]^n} \right) \times [F]$$

where $\mu_F^{\max}$ = phytoplankton maximum growth rate, K_{PF} = half-saturation constant for phosphorus uptake, K_{NF} = half-saturation constant for nitrogen uptake, and m = stoichiometric ratio.

The relationship between the phytoplankton growth rate and temperature is described by the modified Lehman function (Jorgensen, 1980) (Fig. 3):

$$FT(1) = \begin{cases} \exp\left(-4.6 \times \left(\dfrac{TO(1) - T}{Q1(1)} \right)^4 \right), & T < TO(1) \\ \exp\left(-4.6 \times \left(\dfrac{T - TO(1)}{Q2(1)} \right)^4 \right), & T \geqslant TO(1) \end{cases}$$

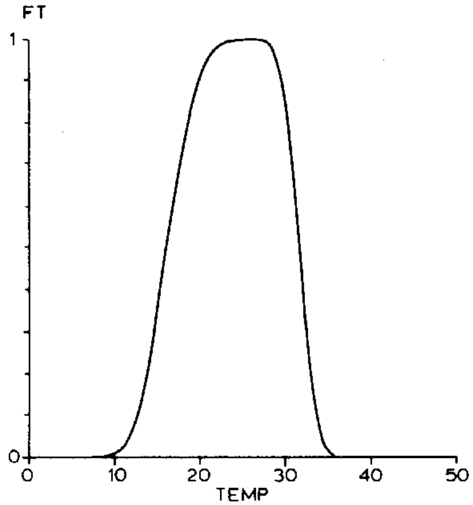

Fig. 3. Temperature limitation function for growth.

where $TO(1)$ is the optimum temperature for the phytoplankton development. $Q1(1) = T^1_{opt} - T^1_{min}$ is the difference between the optimum and minimum temperatures, $Q2(1) = T^1_{max} - T^1_{opt}$ is the difference between maximum and optimum temperatures.

Following Steele (1962), we represent the light limitation function for the

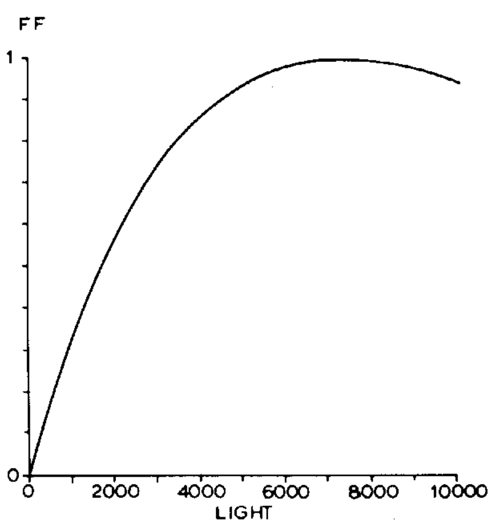

Fig. 4. Light limitation function for phytoplankton growth.

phytoplankton growth as (Fig. 4):

$$FF(L, [F], [D]) = \frac{L}{L_{opt}} \exp\left(1 - \frac{L}{L_{opt}}\right)$$

where $L = L_0 \exp(-k \times h)$ is the illumination at a depth of h calculated by the Bur–Lambert empirical formula in terms of the total solar radiation L_0 and the extinction coefficient, k. The latter depends on the concentrations of phytoplankton and detritus in the water:

$$k = KW + KF \times [F] + KD \times [D] \times KPD$$

where KW = the light extinction coefficient for the water, KF = the phytoplankton self-shading parameter, KD = the shading parameter for suspended detritus, and KPD = a fraction of detritus suspended in water. The uptake of nutrients is presented by s-shaped trophic functions:

$$V([X]) = \frac{[X]^n}{K^n + [X]^n}$$

where $[X]$ = is the substrate concentration, n = a dimensionless quantity characterizing the steepness of the function (see Fig. 5). In our model $n = 2$. In this case the function vanishes with zero derivative, which is very important for the stability of the computer realisation of the model. Note that the experimental data cannot provide an objective criterion for the choice of n: near zero the s-shaped functions with $n = 1,2$ or 3 approximate the experimental results with practically the same accuracy.

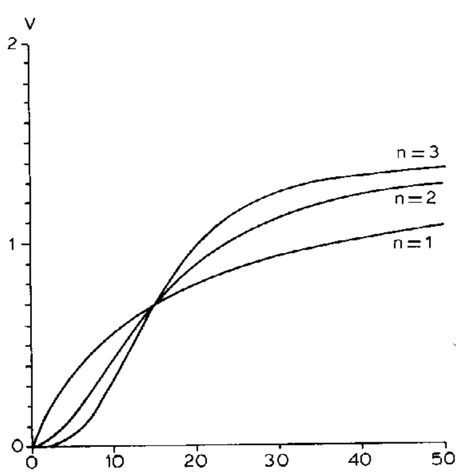

Fig. 5. Trophic functions.

(b) Feeding

Let us describe the feeding of higher trophic level organisms on organisms of lower levels with an example of zooplankton grazing on phytoplankton:

$$q_{FZ} = FT(2) \times FO(2) \times V(\mu_{FZ}^{\max}, K_{FZ}, [F]) \times [Z].$$

The temperature function $FT(2)$ is similar to $FT(1)$. The $FO(2)$ function of the logistic type (Fig. 6) accounts for the relationship between the zooplankton growth and the presence of DO in the water:

$$FO(2) = \frac{1}{1 + \exp(-\lambda(2) \times ([0] - m(2)))}$$

where $m(2)$ is the oxygen half-maintenance coefficient, i.e. the [0] value in which $FO(2) = 1/2$. $\lambda(2)$ is the parameter characterizing the steepness of the curve. The trophic function is determined by an s-shaped curve:

$$V(\mu_{FZ}^{\max}, K_{FZ}, [F]) = \frac{\mu_{FZ}^{\max} \cdot [F]^n}{K_{FZ}^n + [F]^n}$$

where $\mu_{FZ}^{\max}$ is the zooplankton maximum growth rate when grazing phytoplankton, K_{FZ} is the half-saturation constant for the phytoplankton uptake by zooplankton, and $n = 2$.

(c) Feeding with switching

It follows from the literature that some fish are characterized by the selectivity of feeding, i.e., feeding with switching. Carp, for instance, prefers

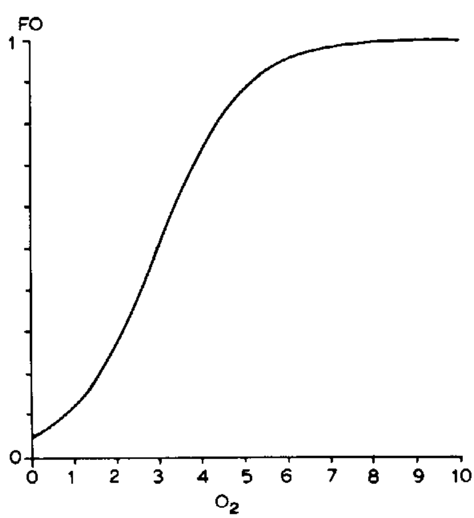

Fig. 6. Oxygen limitation function for growth.

to feed on benthic organisms, but, in the case of a deficit in benthos, it can switch to feeding on zooplankton. To describe feeding with switching we used the findings of W.S. Tan who analyzed the experimental data of Ivlev (1955) on the relationship between feeding and concentration of feed items for carp. The interpretation of the experimental data is impeded by the fact that model studies usually incorporate notions that give insight into the essence of the process. Their choice is arbitrary, to a great extent; whereas an experimentor uses only the empirically available values. Nevertheless, Tan has found a relationship between the probablility x_i of the uptake of the ith type feed item and the total concentration of feed $Q = \sum_{i=1}^{n} q_i$, where q_i is the concentration of the ith type prey. The feed items are listed according to the preference; q_1 is the favourite feed. Then the probability $x_1 = 1$ for any set $q = (q_1, q_2, \ldots, q_n)$, whereas the curves $x_i(Q)$ for $i = 2,3,\ldots,$have an inverted s-shaped form (Fig. 7), with $x_j < x_i$ for $j > i$ and $\lim_{Q \to 0} x_i(Q) = 1$, $\lim_{Q \to \infty} x_i(Q) = 0$.

This means that the transient regime is not clearly defined but covers an interval of Q-values. However, the dependence of x_i on Q with large Q values seems doubtful. Apparently, the functions $x_2(q_1)$, $x_3(q_1, q_2)$, etc. will be more appropriate. Thus the inverted s-shaped function in the model is used to characterize the feeding of carp with switching:

$$\eta([B], \lambda_B, m_B) = \frac{\exp(-\lambda_B([B] - m_B))}{1 + \exp(-\lambda_B([B] - m_B))}.$$

Here the λ_B and m_B parameters have the same meaning as for the s-shaped

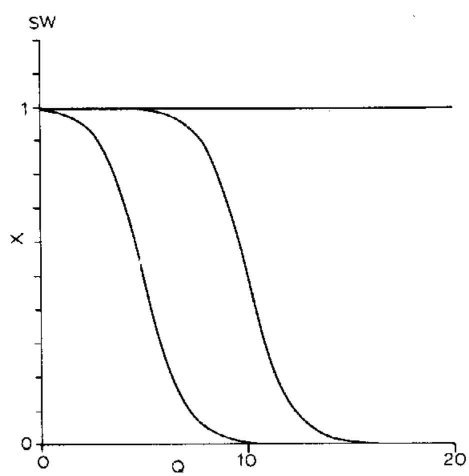

Fig. 7. Uptake probabilities, x_i, of the ith type of feed. Q = total concentration of feed.

function for oxygen. Therefore, the uptake of zooplankton by carp under a deficit of benthos can be written in the form:

$$q_{ZC} = FT(4) \times FO(4) \times \min([V(\mu_{BC}^{\max}, K_{BC}, B_{CR}) - V(\mu_{BC}^{\max}, K_{BC}, [B])],$$
$$[V(\mu_{ZC}^{\max}, K_{ZC}, [Z]) \times \eta([B], \lambda_B, m_B)]) \times [C].$$

Here $FT(4)$ is the carp growth rate as a function of temperature, $FO(4)$ is the carp growth rate as a function of DO concentration.

The $FT(4)$ and $FO(4)$ functions have forms similar to those for phyto- and zooplankton, B_{CR} is the critical value of the benthos concentration at which carp switches to feeding on zooplankton.

The difference between the two trophic functions under the minimum sign ensures that the growth rate of carp is no more than the one attained for B_{CR}, when switching to a new type of feed. The consumption of benthos by carp is represented as follows:

$$q_{BC} = FT(4) \times FO(4) \times V(\mu_{BC}^{\max}, K_{BC}, [B]) \times [C].$$

By analogy, we describe the feeding with switching for bighead, whose favourite feed according to the literature is zooplankton. Phytoplankton is the substituting feed, and detritus is the constrained feed. In this case we have a two-step switching.

(d) Metabolism

The excretion of the products of metabolism by the living organisms of the ecosytem may be considered to be approximately in proportion to the total uptake of food. Thus, the excretion of the products of metabolism and their transformation into detritus is represented in the following way (for zooplankton):

$$q_{ZD}^{(1)} = MB_Z \times (q_{FZ} + q_{DZ}),$$

where MB_Z is the metabolism parameter for zooplankton, q_{FZ} is the uptake function of the phytoplankton by zooplankton, q_{DZ} is the function of detritus uptake by zooplankton, $(q_{FZ} + q_{DZ})$ is the ration of zooplankton.

Energy losses are taken into account by the outflow

$$q_{ZE} = MBO_Z \times [Z]$$

where MBO_Z is the zooplankton respiration coefficient.

Moreover, the relationship between food assimilation and the ration values is taken into account for fish. For instance, in the abundant feeding of silver carp, the food is continuously swallowed and passes through the intestine so quickly that only 30–40% of it can be assimilated. With moderate feeding, almost twice as much food can be assimilated (Pushchina, 1975).

(e) Mortality

As we know from the literature, the mortality of living organisms depends on the *DO* concentration in the water. If this external factor is constant, mortality is in the first approximation proportional to the biomass or concentration of living organisms. This model accounts for mortality only for phyto- and zooplankton, and benthos. There should be no natural mortality of fish in the optimum conditions of a fish-breeding pond. Probable fish kills from oxygen deficit are described by another mechanism, depending on the *DO* concentration in the water. Artificial aeration is provided when oxygen concentration passes the threshold anaerobic value. Thus, the zooplankton mortality can be described in the following way:

$$q_{ZD}^{(2)} = FOX([0]) \times M_Z \times [Z]$$

Here *FOX* is the function of the mortality dependence on the *DO* concentration.

$$FOX([0]) = 1 + KA/[0],$$

M_Z is the mortality coefficient, *KA* is the coefficient of mortality increase under oxygen deficit.

(d) Destruction

The destruction process of the dead organic material, which produces the basic nutrients—phosphorus and nitrogen,—depends on the thermal conditions and on the presence of *DO* in the water. Therefore, the formation of, say, mineral phosphorus as a result of detritus destruction and dissolution can be described in the following way:

$$q_{DP} = UDP \times E1(T) \times E2([0]) \times [D].$$

Here the dependence of the destruction rate on temperature is given by the Vant-Hoff function

$$El(T) = 2^{(T-20)/10}$$

The oxygen function for this process is (Fig. 8):

$$E2([0]) = \exp[COP(M - [0])]/(1 + \exp[COP(M - [0])]),$$

where *COP* is the parameter of the steepness of the oxygen curve, *M* is the threshold between the aerobic and anaerobic conditions.

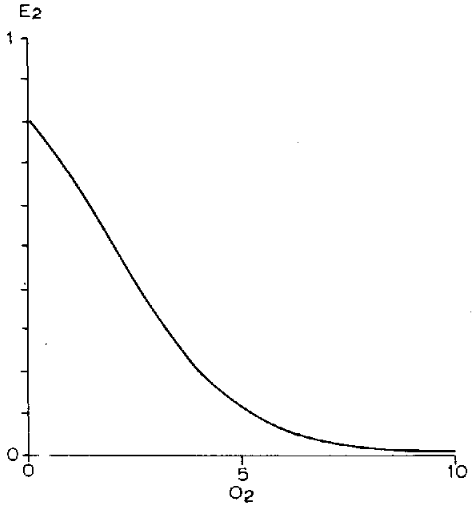

Fig. 8. Oxygen function for detritus destruction process.

Thus, under anoxic conditions, mineral phosphorus begins to flow intensively from sediments into the water. Under aerobic conditions, only the inflow of phosphates from detritus, decomposed in the water body, is worth considering; in the main, the process takes the opposite tendency: dissolved phosphates turn to insoluble forms and sink to the bottom.

$$q_{PD} = SEDP \times E3([0]) \times [P],$$

where

$$E3([0]) = \begin{cases} 0, & [0] < M \\ \dfrac{[0] - M}{[0] - COD}, & [0] \geqslant M \end{cases}$$

Here $COD = M - CK$, where CK is the steepness of the oxygen function, and $SEDP$ is the maximum sinking rate of phosphorus.

(h) Oxygen flows

The oxygen content in the fish pond water depends on the enrichment of water with oxygen and the rate of its consumption. The inflow of oxygen due to photosynthesis is proportional to the phytoplankton production and can be described by the function.

$$q_{FO} = PHOT \times \mu,$$

where $PHOT$ is the assimilation coefficient.

The exchange processes with atmospheric oxygen are characterized by the formula

$$R = RE \times (O_s - [0]),$$

where RE is the reaeration coefficient that is dependent on the wind velocity in the general case. O_s is the oxygen saturation concentration. Following Wang et al. (1978),

$$O_s = 14.61996 - 0.40420 \times T + 0.00842 \times T^2 - 0.00009 \times T^3.$$

Inflow of oxygen with artificial aeration is also taken into account.

The consumption of oxygen for the respiration of aqueous organisms and plants is proportional to their biomass, for example:

$q_{OZ} = RESP_Z \times [Z]$ for zooplankton,

TABLE I

Differential equations, level 1

$$\frac{dF}{dt} = q_{GF} - q_{FZ} - q_{FB} - q_{FS} - q_{FH} - q_{FD} - q_{FE}$$

$$\frac{dZ}{dt} = q_{FZ} + q_{DZ} - q_{ZB} - q_{ZC} - q_{ZH} - q_{ZD} - q_{ZE}$$

$$\frac{dB}{dt} = q_{FB} + q_{ZB} + q_{DB} - q_{BC} - q_{BD} - q_{BE}$$

$$\frac{dC}{dt} = q_{AC} + q_{BC} + q_{ZC} - q_{CD} - q_{CE}$$

$$\frac{dS}{dt} = q_{FS} + q_{DS} - q_{SD} - q_{SE}$$

$$\frac{dH}{dt} = q_{ZH} + q_{FH} + q_{DH} - q_{HD} - q_{HE}$$

$$\frac{dP}{dt} = q_{DP} + PU(t) - q_{PF} - q_{PD}$$

$$\frac{dN}{dt} = q_{DN} + NU(t) - q_{NF}$$

$$\frac{d[0]}{dt} = q_{FO} + RE \times (REA - [0]) + OU(t) - q_{OF} - q_{OZ} - q_{OB}$$
$$- q_{OC} - q_{OS} - q_{OH} - q_{OD}$$

$$\frac{dA}{dt} = AU(t) - q_{AC} - q_{AD}$$

$$\frac{dD}{dt} = q_{FD} + q_{ZD} + q_{BD} + q_{CD} + q_{SD} + q_{HD} + q_{AD}$$
$$- q_{DP} - q_{DN} - q_{DZ} - q_{DB} - q_{DS} - q_{DH} - SED \times D$$

TABLE II

Flows, level 2

$$q_{GF} = FT(1)\times FF(L, F, D)\times \mu_F^{\max} \times \min\left(\frac{P^2}{K_{PF}^2 + P^2}, \frac{1}{5}\frac{N^2}{K_{NF}^2 + N^2}\right)\times F$$

$$q_{PF} = \tfrac{1}{106} \times q_{GF}$$

$$q_{NF} = \tfrac{5}{106} \times q_{GF}$$

$$q_{FZ} = FT(2)\times FO(2)\times V(\mu_{FZ}^{\max}, K_{FZ}, F)\times Z$$

$$q_{DZ} = FT(2)\times FO(2)\times V(\mu_{DZ}^{\max}, K_{DZ}, D)\times Z$$

$$q_{FB} = FT(3)\times V(\mu_{FB}^{\max}, K_{FB}, F)\times B$$

$$q_{ZB} = FT(3)\times V(\mu_{ZB}^{\max}, K_{ZB}, Z)\times B$$

$$q_{DB} = FT(3)\times V(\mu_{DB}^{\max}, K_{DB}, D)\times B$$

$$q_{AC} = FT(4)\times FO(4)\times V(\mu_{AC}^{\max}, K_{AC}, A)\times C$$

$$q_{BC} = FT(4)\times FO(4)\times V(\mu_{BC}^{\max}, K_{BC}, B)\times C$$

$$q_{FS} = FT(5)\times FO(5)\times V(\mu_{FS}^{\max}, K_{FS}, F)\times S$$

$$q_{DS} = FT(5)\times FO(5)\times V(\mu_{DS}^{\max}, K_{DS}, D)\times S$$

$$q_{ZH} = FT(6)\times FO(6)\times V(\mu_{ZH}^{\max}, K_{ZH}, Z)\times H$$

$$q_{ZC} = FT(4)\times FO(4)\times \min([V(\mu_{BC}^{\max}, K_{BC}, B_{CR}) - V(\mu_{BC}^{\max}, K_{BC}, B)], \quad [V(\mu_{ZC}^{\max}, K_{ZC}, Z)\times \eta(B, \lambda_B, m_B)])\times C$$

$$Y1 = V(\mu_{ZH}^{\max}, K_{ZH}, Z_{CR}) - V(\mu_{ZH}^{\max}, K_{ZH}, Z)$$

$$Y2 = V(\mu_{FT}^{\max}, K_{FT}, F)\times \eta(Z, \lambda_Z, m_Z)$$

$$Y3 = V(\mu_{FT}^{\max}, K_{FT}, F_{CR})\times \eta(Z, \lambda_Z, m_Z)$$

$$q_{FH} = FT(6)\times FO(6)\times \min(Y1, Y2)\times H$$

$$q_{DH} = FT(6)\times FO(6)\times \min([\min(Y1, Y3) - \min(Y1, Y2)], \quad [V(\mu_{DH}^{\max}, K_{DH}, D)\times \eta(Z, \lambda_Z, m_Z)\times \eta(F, \lambda_F, m_F)])$$

$$q_{FD} = \begin{cases} MB_F \times q_{GF}, & F < F_0 \\ MB_F \times q_{GF} + M_F \times F, & F > F_0 \end{cases}$$

$$q_{BD} = MB_B \times (q_{FB} + q_{ZB} + q_{DB})$$

$$q_{ZD} = MB_Z \times (q_{FZ} + q_{DZ}) + FOX([0])\times M_Z \times Z$$

$$q_{CD} = \left(MB_C + MBB_C \times \frac{RC}{RC_{\max}}\right)\times RC$$

$$q_{SD} = \left(MB_S + MBB_S \times \frac{RS}{RS_{\max}}\right)\times RS$$

TABLE II (continued)

$q_{HD} = (MB_H + MBB_H \times \frac{RH}{RH_{max}}) \times RH$
$RC = q_{AC} + q_{BC} + q_{ZC}$
$RS = q_{FS} + q_{DS}$
$RH = q_{ZH} + q_{FH} + q_{DH}$
$q_{FE} = MBO_F \times F$
$q_{ZE} = MBO_Z \times Z$
$q_{BE} = MBO_B \times B$
$q_{CE} = MBO_C \times C$
$q_{SE} = MBO_S \times S$
$q_{HE} = MBO_H \times H$
$q_{DP} = UDP \times E1(T) \times E2([0]) \times D$
$q_{PD} = SEDP \times E3([0]) \times P$
$q_{DN} = UDN \times E1(T) \times E2([0]) \times D$
$q_{FO} = PHOT \times q_{GF}$
$q_{OF} = RESP_F \times F$
$q_{OZ} = RESP_Z \times Z$
$q_{OB} = RESP_B \times B$
$q_{OC} = RESP_C \times C$
$q_{OS} = RESP_S \times S$
$q_{OH} = RESP_H \times H$
$q_{AD} = ALPHA \times A$

where $RESP_Z$ is the [0] consumption coefficient for the zooplankton respiration.

The oxygen consumption for oxidation of dissolved and suspended organic material in water is proportional to the detritus amount involved in the cycle

$$q_{OD} = OK \times [D],$$

where OK is the oxidation coefficient.

Thus, we have presented the main flows of the material necessary for the description of the fish pond ecosystem. It should just be added that an input of feed for fish and an input of mineral fertilizers are given by external

TABLE III

Functions, level 3

$$FT(I) = FT(T, TO(I), Q1(I), Q2(I)) = \begin{cases} \exp\left(-4.6 \times \left(\dfrac{TO(I) - T}{Q1(I)}\right)^4\right), & T < TO(I) \\ \exp\left(-4.6 \times \left(\dfrac{T - TO(I)}{Q2(I)}\right)^4\right), & T \geqslant TO(I) \end{cases}$$

$$FF(L, F, D) = \frac{L}{L_{\mathrm{opt}}} \exp(-k \times h) \times \exp[1 - \frac{L}{L_{\mathrm{opt}}} \exp(-k \times h)]$$

$$k = KW + KF \times F + KD \times D \times KPD$$

$$FO(I) = 1/(1 + \exp(-\lambda(I)([0] - m(I))))$$

$$\eta(X, \lambda, m) = \mathrm{e}^{-\lambda(X-m)}/(1 + \mathrm{e}^{-\lambda(X-m)})$$

$$V(\mu^{\max}, K, X) = \frac{\mu^{\max} \times X^2}{K^2 + X^2}$$

$$FOX([0]) = 1 + KA/[0]$$

$$E1(T) = 2^{(T-20)/10}$$

$$E2([0]) = \exp[COP(M - [0])]/(1 + \exp[COP(M - [0])])$$

$$E3([0]) = \begin{cases} 0, & [0] < M \\ \dfrac{[0] - M}{[0] - COD}, & [0] \geqslant M \end{cases}$$

inflows, while the sedimentation process of detritus and the settling of phosphorus (losses from the material cycle) are characterized by outflows. All the model equations are given in Table I. The flows they include and the functional relationships are listed in Tables II and III respectively.

4. SIMULATION EXPERIMENTS

The computer runs of the Fortran program for the model were carried out on BESM-6. The system of 11 ordinary differential equations is solved by the Runge–Kutta technique with an automatic choice of the step in the interval (0,150). To solve the system we had to specify 112 parameters, the arrays of temperature and illumination, the inflows of nitrogen and phosphorus fertilizers, of feed, and the regime of artificial aeration.

As with all simulation models of this kind, parameter estimation is quite a problem. Some of the parameters were determined from previous works

(Jorgensen et al., 1978; Wang et al., 1978), some can be estimated on the basis of the literature data, and others should be identified according to the variable dynamics. More difficulties arise because certain parameters characterize extremely aggregated processes; it is rather difficult to find unique quantitative values for them.

For model calibration we used the data of the Polish scientists (Opuszynski, 1978; Wasilewska, 1978; Grygierek, 1978, etc.), who carried out complex studies on a group of test ponds with carp as a monoculture (4,000 fish/ha.) and on three groups of ponds with the addition of silver carp (4,000, 8,000 and 1,200 fish/ha.). The fish ponds were regularly fertilized (by urea and superphosphate), and barley was used as the fodder for carp. The parameters resulting from the model identification are presented in Table IV.

TABLE IV

Ecological parameters

Notation	Ecological meaning		Units
μ_F^{max}	Maximum growth rate of phytoplankton	3.0	1/day
μ_{FZ}^{max}	Maximum uptake rate of phytoplankton by zooplankton	1.4	1/day
K_{FZ}	The corresponding half-saturation parameter	15.0	mg/l
μ_{DZ}^{max}	Maximum uptake rate of detritus by zooplankton	0.5	1/day
K_{DZ}	The corresponding half-saturation parameter	60.0	mg/l
μ_{FB}^{max}	Maximum uptake rate of phytoplankton by benthos	0.2	1/day
K_{FB}	The corresponding half saturation constant	15.0	mg/l
μ_{ZB}^{max}	Maximum uptake rate of zooplankton by benthos	0.4	1/day
K_{ZB}	The corresponding half-saturation constant	1.0	mg/l
μ_{DB}^{max}	Maximum uptake rate of detritus by benthos	0.2	1/day
K_{DB}	The corresponding half saturation constant	60.0	mg/l
μ_{ZC}^{max}	Maximum uptake rate of zooplankton by carp	0.02	1/day
K_{ZC}	The corresponding half saturation constant	1.0	mg/l
μ_{BC}^{max}	Maximum uptake rate of benthos by carp	0.06	1/day
K_{BC}	The corresponding half-saturation constant	5.0	mg/l
μ_{AC}^{max}	Maximum uptake rate of artificial feed by carp	0.03	1/day
K_{AC}	The corresponding half saturation constant	0.2	mg/l
μ_{FS}^{max}	Maximum uptake rate of phytoplankton by silver carp	0.1	1/day
K_{FS}	The corresponding half-saturation constant	20.0	mg/l

(continued)

TABLE IV (continued)

Notation	Ecological meaning		Units
μ_{DS}^{max}	Maximum uptake rate of detritus by silver carp	0.07	1/day
K_{DS}	The corresponding half saturation constant	60.0	mg/l
μ_{FH}^{max}	Maximum uptake rate of phytoplankton by bighead	0.1	1/day
K_{FH}	The corresponding half-saturation constant	20.0	mg/l
μ_{ZH}^{max}	Maximum uptake rate of zooplankton by bighead	0.15	1/day
K_{ZH}	The corresponding half-saturation constant	1.0	mg/l
μ_{DH}^{max}	Maximum uptake rate of detritus by bighead	0.1	1/day
K_{DH}	The corresponding half-saturation constant	60.0	mg/l
MB_F	Metabolism parameter for phytoplankton	0.3	dimensionless
MB_Z	Metabolism parameter for zooplankton	0.3	dimensionless
MB_B	Metabolism parameter for benthos	0.3	dimensionless
MB_C	Minimum metabolism parameter for carp	0.3	dimensionless
MB_S	for silver carp	0.3	dimensionless
MB_H	for bighead	0.3	dimensionless
MBB_C	Additional metabolism parameter for carp	0.4	dimensionless
MBB_S	for silver carp	0.4	dimensionless
MBB_H	for bighead	0.4	dimensionless
RC_{max}	Maximum ration for carp	13.0	mg/l
RS_{max}	for silver carp	10.0	mg/l
RH_{max}	for bighead	10.0	mg/l
MBO_F	Respiration coefficient for phytoplankton	0.001	dimensionless
MBO_Z	for zooplankton	0.001	dimensionless
MBO_B	for benthos	0.001	dimensionless
MBO_C	for carp	0.001	dimensionless
MBO_S	for silver carp	0.001	dimensionless
MBO_H	for bighead	0.001	dimensionless
M_F	Mortaility coefficient for phytoplankton	0.09	1/day
M_Z	for zooplankton	0.005	1/day
M_B	for benthos	0.05	1/day
$RESP_F$	*DO* consumption parameter for *F* respiration	0.001	1/day
$RESP_Z$	for Z	0.11	1/day
$RESP_B$	for B	0.01	1/day
$RESP_C$	for carp	0.01	1/day
$RESP_S$	for silver carp	0.01	1/day
$RESP_H$	for bighead	0.01	1/day
UDP	Phosphorus destruction parameter	0.00004	
UDN	Nitrogen destruction parameter	0.002	
PHOT	Assimilation coefficient	1.0	
ALPHA	Transformation coefficient of fodder into detritus	0.2	
RE	Reaeration coefficient	0.3	
OK	Detritus oxidation parameter	0.085	
SED	Sedimentation parameter of detritus	0.05	

TABLE IV (continued)

Notation	Ecological meaning		Units
SEDP	Sedimentation parameter of phosphorus	0.1	
TO(1)	Optimum temperature for *F* growth	24.0	°C
TO(2)	for *Z*	24.0	°C
TO(3)	for *B*	24.0	°C
TO(4)	for *C*	26.0	°C
TO(5)	for *S*	26.0	°C
TO(6)	for *H*	26.0	°C
T^1_{min}	Minimum temperature for *F* growth	9.0	°C
T^2_{min}	for *Z*	9.0	°C
T^3_{min}	for *B*	9.0	°C
T^4_{min}	for *C*	10.0	°C
T^5_{min}	for *S*	13.0	°C
T^6_{min}	for *H*	13.0	°C
T^1_{max}	Maximum temperature for *F* growth	34.0	°C
T^2_{max}	for *Z*	34.0	°C
T^3_{max}	for *B*	34.0	°C
T^4_{max}	for *C*	35.0	°C
T^5_{max}	for *S*	35.0	°C
T^6_{max}	for *H*	35.0	°C
L_{opt}	Optimum illumination for photosynthesis	3000.0	
KW	Light extinction coefficient in water	0.2	
KF	Self-shading parameter for phytoplankton	0.03	
KD	Shading parameter of detritus	0.4	
KPD	Fraction of detritus suspended in water	0.5	
h	Mean photosynthesis depth	0.1	
m(2)	Oxygen half-maintainance parameter for *Z*	3.0	
m(4)	for *C*	3.0	
m(5)	Oxygen half-maintainance parameter for *S*	3.0	
m(6)	for *H*	3.0	
λ(2)	Steepness of the oxygen curve for *Z*	1.0	
λ(4)	for *C*	1.0	
λ(5)	for *S*	1.0	
λ(6)	for *H*	1.0	
B_{CR}	Critical value of benthos concentration	20.0	
Z_{CR}	Critical value of zooplankton concentration	5.0	
F_{CR}	Critical value of phytoplankton concentration	30.0	
m_B	Parameter of the switch function for *B*	10.0	
m_Z	for *Z*	3.0	
m_F	for *F*	15.0	
λ_B	Steepness of the switch function for *B*	1.0	
λ*Z*	for *Z*	1.0	
λ*F*	for *F*	1.0	
KA	Parameter of mortality increase at *DO* deficit	2.0	
m	Stoichiometric ratio	5.0	
COP	Parameter of the oxygen function	2.0	
M	Parameter of the oxygen function	1.0	
COD	Threshold between oxic and anoxic conditions	2.0	

5. RESULTS, CONCLUSIONS AND DISCUSSION

The following graphs show different variants of the ecosystem development. When the nutrient concentration is maintained at a level of $P = 0.06 - 0.6$ mg/l, $N = 1 - 2$ mg/l (mostly due to fertilizers), it turns out that the phytoplankton growth is limited by the amount of phosphorus, and the phytoplankton dynamics clearly follows the dynamics of phosphates (in Fig. 10 the arrows indicate the moments of introducing the fertilizers).

Under other conditions, when the phytoplankton growth is not limited by nutrients, the natural fodder reserves are better developed. Fig. 11 shows the succession of the maxima of phytoplankton, zooplankton, and benthos concentrations. However, in this case the zooplankton and benthos concentrations once again drop sharply in the middle of the season, this being quite natural for such a dense fish population.

The next variant shows the ecosystem development in the conditions of a warmer climate (Fig. 12).

As a result of the simulations, we have derived the dynamics of the variables that adequately reflect the real picture of the development of the ecosystem for one season. The phytoplankton growth is limited by nutrients (mostly phosphorus). Fish consumes a lot of zooplankton, but its concentration may increase at the beginning of the season. A lot of benthos is consumed by carp. Carp begins to gain weight at the very beginning of the season, whereas bighead and silver carp begin to grow only in July, since their growth is to a greater extent limited by temperature. Right after their

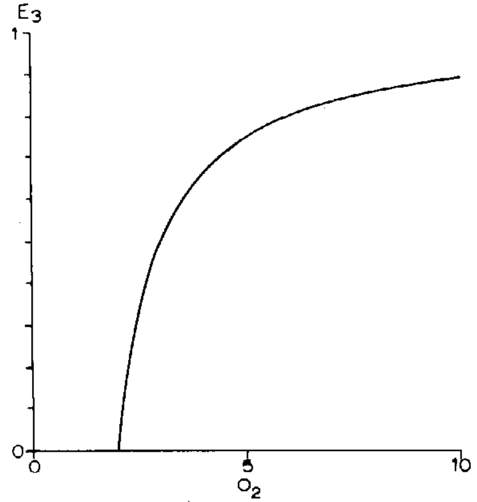

Fig. 9. Oxygen function for phosphorus sinking process.

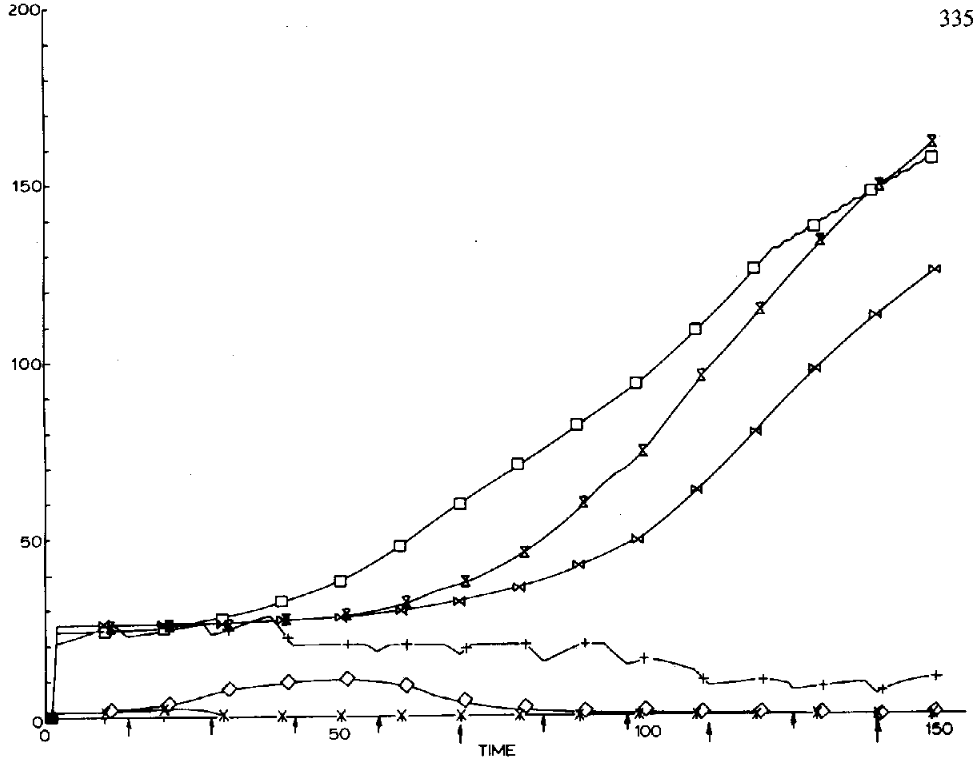

Fig. 10. Ecosystem development in phosphorus limited conditions. + = phytoplankton, × = zooplankton, ◇ = bethos, ⊡ = carp, ⧗ = silver carp, ⋈ = bighead.

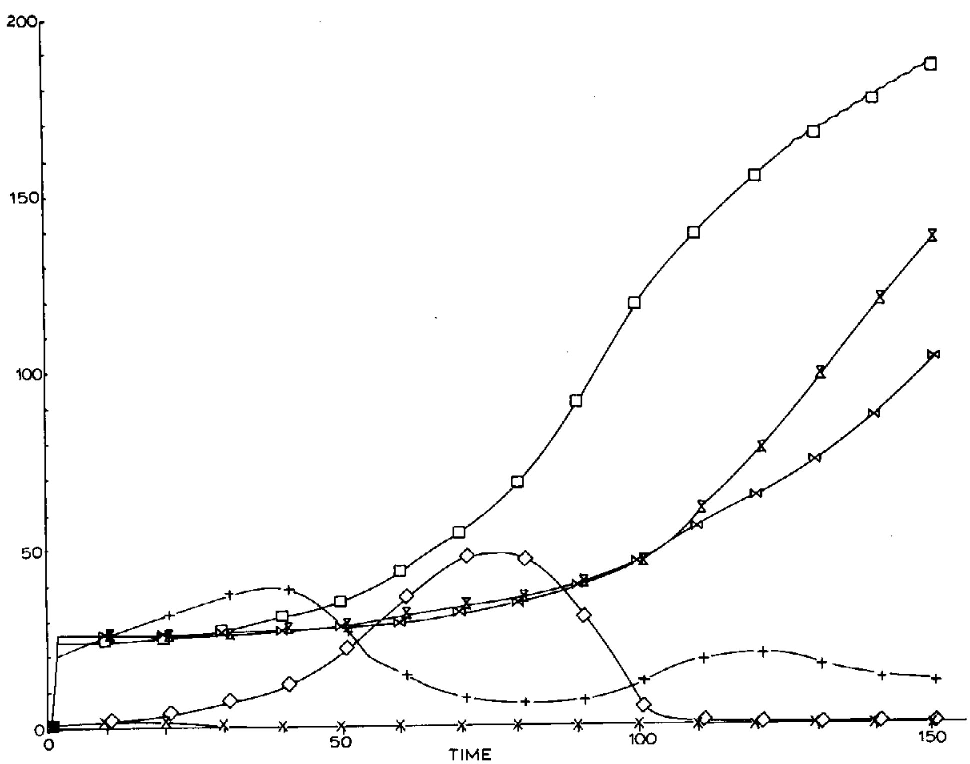

Fig. 11. Ecosystem development in the conditions of nutrient abundancy. + = phytoplankton, × = zooplankton, ◇ = bethos, ⊡ = carp, ⧗ = silver carp, ⋈ = bighead.

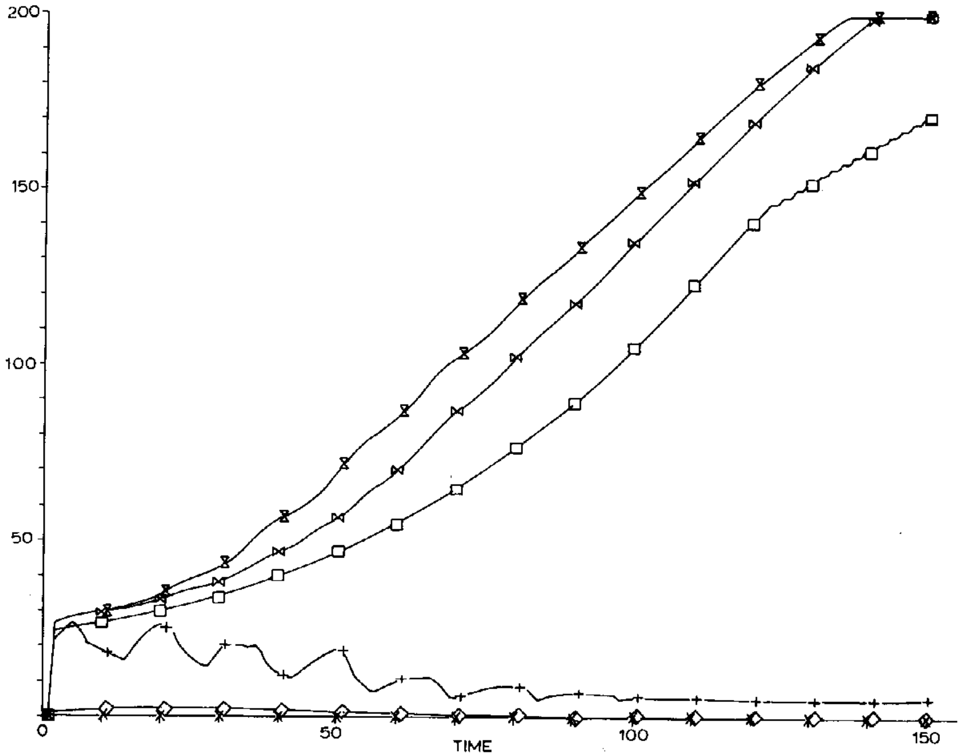

Fig. 12. Ecosystem development in the conditions of a warmer climate. ($T = T_0 + 4°C$). + = phytoplankton, × = zooplankton, ◈ = bethos, □ = carp, ⧗ = silver carp, ⋈ = bighead.

application, fertilizers are quickly consumed, and the phytoplankton concentration increases. The oxygen control unit is so designed that the oxygen content never drops below 3 mg/l. The artificial aeration is increased when this threshold is passed. The amount of detritus has increased by the middle of the season, and then begins to diminish due to its uptake by bighead and silver carp.

The next stage envisages the search for the optimum regimes of the fish pond. The control parameters are the inflows of fertilizers and fodder, the artificial aeration, and the density of implantation. The mathematical model allows one to find the operating modes that maximize the yield.

REFERENCES

Borshev, V.N., 1977. Mathematical modelling experience in a simple fishpond ecosystem. In: Fish Breeding in Ponds. VNIIPRH, 18: 260–281 (in Russian).

Grygierek, E., 1978. The influence of the silver carp on eutrophication of carp ponds. IV. Zooplankton. Rocz. Nauk rol., H, 99: 81–92.

Ivlev, V.S., 1955. Experimental ecology of fish nourishment. Pishchepromizdat, Moscow, 252 pp. (in Russian).

Januszko, M., 1978. The influence of the silver carp on eutrophication of carp ponds. III. Phytoplankton. Rocz. Nauk rol., H, 99: 55–80.

Jorgensen, S.E., Friis, M.B., Henriksen, J., Jorgensen, L.A. and Mejer, H.F. (Editors), 1978. Handbook of Environmental Data and Ecological Parameters. I.S.E.M., Væerløse, Denmark.

Jorgensen, S.E., 1980. Lake Management. Pergamon Press. Oxford, 167 pp.

Opuszynski, B., 1978. The influence of the silver carp on eutrophication of carp ponds. VII. Recapitulation. Rocz. Nauk rol., H, 99: 127–151.

Piotrowska, W., 1978. The influence of the silver carp on eutrophication of carp ponds. I. Physico-chemical conditions. Rocz. Nauk rol., H, 99: 7–32.

Pushchina, L.I., 1975. Phytoplankton of fishbreeding ponds in Krasnodar region under intensive management. Leningrad, 23 pp. (in Russian).

Steele, J.H., 1962. Environmental control of photosynthesis in the sea. Limnol. Oceanogr., 7: 137–150.

Vinberg, G.G. and Anisimov, S.I., 1966. Mathematical model of an aquatic ecosystem. In: Photosynthetic Systems of High Productivity, Nauka, Moscow (in Russian).

Vinberg, G.G. and Liachnovitch, V.P., 1965. Fertilization of the ponds. Pishchepromizdat, Moscow, 271 pp. (in Russian).

Wang, L.K., Vielkind, D. and Wang, M.H., 1978. Mathematical models of dissolved oxygen concentration in fresh water. Ecol. Modelling, 5: 115–123.

Wasilewska, W., 1978. The influence of the silver carp on eutrophication of carp ponds. V. Bottom fauna, Rocz. Nauk rol., H, 99: 93–108.

Voinov, A.A., Voronkova, O.V., Luckyanov, N.K. and Svirezhev, Yu.M., 1981. Lake ecosystems modelling. In: Ecological Monitoring Problems, IV. Gidrometeoizdat, Leningrad (in Russian).