

## A MINIMAL MODEL OF EUTROPHICATION IN FRESHWATER ECOSYSTEMS

A.A. VOINOV and Yu.M. SVIREZHEV

*Computer Center, U.S.S.R. Academy of Sciences, Moscow (U.S.S.R.)*

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### ABSTRACT

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A very simple model of eutrophication is presented. It includes several quite aggregated parameters and can be studied by analytical methods. Nevertheless, its dynamic behaviour reflects well real reservoir evolution as observed under the impact of increasing biogenic pollution. Such models, simple in construction but sensitive to the main trends of an ecosystem, are termed 'minimal'. The state variables in the model are the concentrations of: (1) phytoplankton; (2) biogenic elements (nutrients); (3) detritus; and (4) dissolved oxygen. Transformations among the substances are described by a system of four ordinary differential equations. Steady-state dynamics are studied (the so-called quasi-stationary process). The qualitative analysis undertaken shows that the total amount of substances in a reservoir (phytoplankton + detritus + nutrients) is a very important ecosystem control parameter. In fact, it is this parameter that determines the rate and the degree of eutrophication. It also turns out that the relations between some observed characteristics of the ecosystem may define beforehand the future behaviour of the reservoir.

### INTRODUCTION

With increasing anthropogenic load, more and more reservoirs are nowadays showing signs of eutrophication. By this term is usually meant nutrient enrichment of the water, accompanied by a rapid growth of living organisms, a decrease in the dissolved oxygen concentration, and a deterioration of water quality. Up till now we have failed to find any more precise and constructive biological definition. However, despite the gaps in theoretical as well as experimental biological data, the eutrophication process surely must be studied: the demand for clean fresh water is increasing constantly, while the anthropogenic influence is becoming more and more severe.

A fair number of simulation models of the process have been built already, based mainly on some intuitive notions about eutrophication.

Usually, when the simulation approach is used, either the ecosystem of the reservoir is modelled as a whole with more or less detail (Chen and Orlob, 1975; Jørgensen et al., 1978; Luckyanov, 1979), or the model deals with separate biochemical blocks (Imboden, 1974; Leonov, 1980). The main purpose of the modeller is to work out an adequate model in order to forecast quantitative changes in the ecosystem, occurring as a result of various exogenous and endogenous factors.

The other group of models consists mainly of mathematical models with a small number of variables, prepared usually for analytical and not computer analysis and devised for the purpose of qualitative study of general ecosystem dynamics. This approach has also been used in application to the eutrophication problem though not as widely as the simulation method (Svirezhev and Logofet, 1982; Suzuki and Fukuoka, 1979; Aponin and Bazykin, 1977; Arnold and Voss, 1981). The model presented here belongs to this second group. Our goal was to build a very simple model of eutrophication, that would include several quite aggregated parameters and permit an analytical study. Nevertheless, its dynamic behaviour should reflect real reservoir evolution as observed under increasing biogenic pollution. Following Moiseev and Svirezhev (1979), we call models which meet these requirements 'minimal models'. Our model was devised mainly in order to understand the eutrophication problem as a whole, to analyse the phenomenon qualitatively, and to establish the key control parameters of the ecosystem governing this process.

Finally, we selected four state variables, considering the dynamics of the reservoir's phytoplankton, nutrients, detritus and dissolved oxygen. The choice of these variables was based on common sense and general ecological ideas on the one hand, and on some asymptotic estimates on the other. Of course, to a great extent the choice is subjective; however, the good agreement of the model results with the processes observed in natural systems indicates that the variables chosen really do play an important role in eutrophicating ecosystems.

The so-called quasi-stationary process was studied, i.e., the steady-state dynamics. It is shown that when the model parameters are in some specific relations, an increase of biogenic pollution in the reservoir inevitably leads to a steady state of the system that corresponds to a state of eutrophication, and that further input of biogenic elements causes further progress in eutrophication.

#### BASIC VARIABLES OF A FRESHWATER ECOSYSTEM

In aggregated form, the state of a freshwater ecosystem is most commonly characterised by the following state variables:  $a(t)$ , concentration of pro-

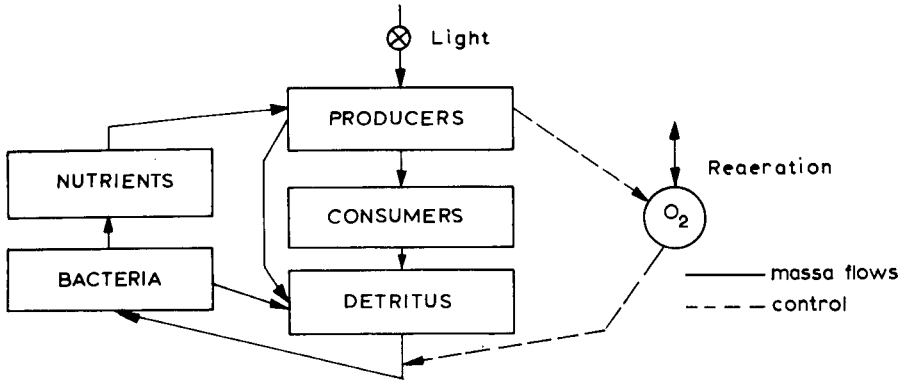


Fig. 1. Basic mass flows in a freshwater system. Broken lines indicate that there is no dry-material transformation.

ducers (phytoplankton);

$z(t)$ , concentration of consumers (zooplankton);

$n(t)$ , concentration of biogenic elements (nutrients);

$s(t)$ , concentration of detritus;

$b(t)$ , concentration of bacteria; and

$x(t)$ , concentration of dissolved oxygen.

In most reservoirs it is the dynamics of these substances that exert the decisive influence on the state of the ecosystem and on water quality. The interactions among the variables chosen are described according to the flow diagram in Fig. 1. We consider this diagram to be sufficient for a qualitative description of eutrophication reservoirs. Evidently, the stratification actually existing will introduce some changes in this scheme. However, during the first stage of modelling, it is adequate to consider a local (one-point) model with average concentrations.

So far as light is not a limiting factor in most reservoirs, we do not take into consideration the dependence of photosynthesis rate upon illumination. The proposed scheme is now examined in more detail.

### Oxygen

It is considered that oxygen enters the system mainly due to reaeration and photosynthesis processes. These are the two greatest natural sources of oxygen and usually they are the ones taken into account when modelling the dissolved oxygen (DO) concentration. DO is consumed mostly in the oxidation of various organic substances, present as detritus (the classic biochemical oxygen demand, BOD). Moreover, the oxidation rate and accordingly the DO uptake rate depend on the degree of water saturation by oxygen: aerobic oxidation processes may prevail in the reservoir, or as a result of DO

shortage a switching to anaerobic mechanisms may take place. Thus, oxygen appears to be an important control parameter in the description of decomposition, i.e., the mineralisation rate of non-living organic matter. This role of oxygen in the detritus food chain has been analysed carefully by Rich and Wetzel (1978). In addition, the DO concentration determines the rate of phosphorus release from sediments. Although oxygen does not participate directly in the dynamics of the dry biomass in the system, it influences greatly the transformation rates among substances.

DO uptake in the form of respiration of consumers can be neglected, because the rate of this process is much less than those of photosynthesis and BOD. The respiration of phytoplankton may be accounted for when describing the photosynthesis process.

### *Phytoplankton*

Phytoplankton biomass accumulation results from the consumption of various biogenic substances. For a more adequate description, various plankton self-inhibitory effects resulting from self-shading, increase in competition for resources, etc., should be taken into consideration. Phytoplankton biomass decrease is determined by phytoplankton mortality as well as by consumption by predators.

### *Detritus*

Detritus represents dead organic matter suspended in the water body or sedimented to the bottom of the reservoir. The activity of various bacterial agents leads to its constant oxidation and mineralisation. The rate of this process depends upon the DO concentration in the water.

### *Bacteria*

Recently, most researchers have begun to stress the important role of bacterial destruction processes in the general ecodynamics of reservoirs. It should be noted that the bacterial biomass can be assumed not to limit the rate of biodestruction of organic matter, since the characteristic growth periods for microorganisms are less than the characteristic times for other processes. The bacterial population quickly adapts to all variations in the environment without delaying the decomposition process. Of course this assumption is correct only for average, approximate systems, where different effects such as temperature, light, toxic and other forms of inhibition are not taken into account.

### *Biogenic elements*

The term 'biogenic elements' indicates an aggregated variable which characterises the concentration of various available nutrients in the ecosystem that limit the growth of phytoplankton. The source of nutrients in a closed system is the decomposition of detritus, that is, the decay of organic matter and its transformation into more soluble and better digested inorganic compounds.

### *Consumers*

In this block we combine the biomasses of zooplankton, benthic organisms, fish, and so on. In most natural ecosystems the biomass of consumers is rather small compared with that of phytoplankton or bacterioplankton. (The only exception is that presented by so-called 'paradoxical' trophic chains (Svirezhev and Logofet, 1982).) At the same time, considerable quantities of matter pass through this block: phytoplankton are eaten, detritus is excreted. On the other hand, the biomass of consumers is usually a rather slowly varying component of the ecosystem. The reasons for this are the following: in the first place, the consumers are tied together into hierarchical food chains having a stable structure; and in the second, they have a sufficiently complicated trophic behaviour that they are independent of fluctuations in trophic resources.

### GENERAL MODEL STRUCTURE

The following flow equations correspond to the scheme in Fig. 1:

$$\begin{aligned}
 \dot{a} &= q_{na} - q_{az} - q_{as} \\
 \dot{z} &= q_{az} - q_{zs} \\
 \dot{s} &= q_{as} + q_{zs} + q_{bs} - q_{sb} - q_{sn} \\
 \dot{b} &= q_{sb} - q_{bs} \\
 \dot{n} &= q_{sn} - q_{na} \\
 \dot{x} &= k(x_n - x) + q_{xa} - q_{xb}
 \end{aligned} \tag{1}$$

where  $q_{ij}$  indicates the mass flow from block  $i$  to block  $j$ ,  $x_n$  is the saturation concentration of DO, and  $k$  is the reaeration coefficient.

The preceding considerations about the dynamics of bacteria and consumers may now be translated into formal terms. Since the consumers represent a slowly changing variable, in the ecosystem time hierarchy it may be assumed that  $z(t) \approx \hat{z} = \text{constant}$ , and consequently  $dz/dt$  is of the order of magnitude  $\epsilon$ , where  $\epsilon \ll 1$  is a small parameter; hence,  $q_{az} \approx q_{zs}$ , and

$q_{az} = V_a(a, z)z \approx V_a(a, \hat{z})\hat{z}$ , where  $V_a(a, z)$  is the trophic function for phytoplankton uptake by the consumers. Taking the Volterra trophic function and neglecting intraspecies competition among consumers:

$$q_{az} = m_1 a \hat{z} = m_a^1 a$$

The constant  $m_a^1$  describes here the additional 'mortality' of phytoplankton caused by consumers. Notice that an increase in complexity of the ecosystem food chains leads to an increase of  $m_a^1$  (as well as an increase in the biomass of consumers).

In contrast, bacteria represent a rapidly changing variable in the system. Taking the time hierarchy into account, the bacterial concentration can be considered to converge rapidly to its steady-state value:  $b(t) \rightarrow \hat{b} = \text{constant}$ . Therefore,  $db/dt \approx 0$ , and the flow  $q_{sb}$  can be considered approximately equal to  $q_{bs}$ . The bacterial decomposition of detritus is described in terms of enzyme kinetics: bacteria work as enzymes, and detritus is the substrate, which is transformed into the product—nutrients. The only difference is that a small fraction  $k_b$  of the substrate consumed by the bacteria is used by them to build up their own biomass. Therefore, the mass flow  $q_{sn}$  is in proportion to  $q_{sb}$  and may be expressed by the relation:

$$q_{sn} = q_{sn}(s, b, x) = (1 - k_b)\hat{\mu}(x)Q(s, b)$$

where  $\hat{\mu}(x)$  is the oxygen dependence, and  $Q(s, b)$  is the rate of mineralisation of organic matter. According to our assumptions,  $Q(s, b) \approx Q(s, \hat{b})$ , and as long as the bacterial populations can be considered not to limit the biodecomposition rate, it is possible to write that  $Q(s, \hat{b}) = \hat{\lambda}s$ . Finally:

$$q_{sn} = (1 - k_b)\hat{\lambda}\hat{\mu}(x)s = \mu(x)s$$

where  $\mu(x)$  is the rate of bacterial decomposition of detritus:  $\mu(x)$  depends upon the DO concentration (Fig. 2). Thus, variations in the biodecomposition rate when switching from aerobic to anaerobic conditions are reflected.  $x_{a1}$  and  $x_{a2}$  indicate threshold values of the DO concentration: those higher than  $x_{a1}$  correspond to aerobic, those lower than  $x_{a2}$  to anaerobic conditions. When  $x_{a2} < x < x_{a1}$ , certain intermediate regimes are established.

It should be noted here that if the ecosystem is phosphorus-limited, the function  $\mu(x)$  is to be taken in a somewhat different form to account for the release of nutrient (phosphates) from sediment under anaerobic conditions. In this case  $\mu(x)$  takes higher values for  $x < x_{a2}$  and lower ones for  $x > x_{a1}$ .

We now define more accurately the rest of the mass flows in system (1). Suppose that  $q_{na} = V_n(n, a)a$ , where  $V_n(n, a)$  is the trophic function for nutrient uptake by phytoplankton. In this minimal model we neglect the phenomena of self-inhibition for phytoplankton, and suppose that  $V_n = V_n(n)$ .

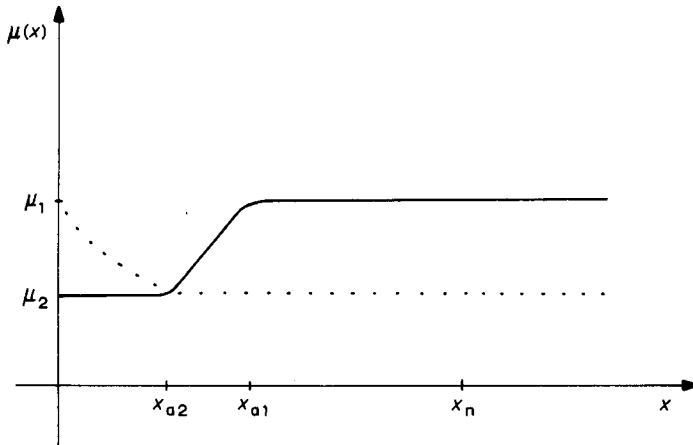


Fig. 2. Detritus mineralisation rate as a function of oxygen concentration. Points show the curve to be used in P-limited ecosystems.

The Monod function or its modifications are most widely used to represent  $V_n(n)$ :

$$q_{na} = [\alpha n / (\delta + n)] a$$

where  $\alpha$  is the maximum rate of nutrient uptake by algae, and  $\delta$  is the half-saturation constant.

We define the natural phytoplankton mortality as  $q_{as} = m_a a$ . Then the total phytoplankton biomass diminution is:

$$q_{as} + q_{az} = m_a a + m_a^1 a = \rho a$$

We suppose that photosynthetic oxygen has a linear dependence on phytoplankton biomass:  $q_{xa} = q_{xa}(a) = \beta a$ , where  $\beta$  is the photosynthetic rate of oxygen output. We suppose also that  $q_{xb} = \gamma q_{sb}$ , where  $\gamma$  is the coefficient of oxygen demand for decomposition of organic matter (BOD).

Finally, taking into account all the plausible assumptions mentioned, a minimal model can be constructed for the description of the dynamics of the freshwater reservoir ecosystem. The model is represented by the following system of ordinary differential equations:

$$\begin{aligned} da/dt &= \alpha n / (\delta + n) - \rho a \\ dn/dt &= -\alpha n / (\delta + n) + \mu(x) s \\ ds/dt &= \rho a - \mu(x) s \\ dx/dt &= k(x_n - x) + \beta a - \gamma \mu(x) s \end{aligned} \quad (2)$$

We now turn to the analysis of this system.

MODEL STABILITY ANALYSIS AND STUDY OF QUASI-STATIONARY BEHAVIOUR

For the first three variables of system (2) the mass conservation law is fulfilled: thus  $a + n + s = A$ , where  $A$  is a constant. Thus, system (2) can be reduced to a system of three equations:

$$\begin{aligned} \dot{a} &= a[B - (\alpha - \rho)s - (\alpha - \rho)a]/(\delta + A - s - a) \\ \dot{s} &= \rho a - \mu(x)s \\ \dot{x} &= k(x_n - x) + \beta a - \gamma\mu(x)s \end{aligned} \quad (3)$$

where  $B = \alpha A - \rho A - \rho\delta$ .

This system has two points of equilibrium:

$$a_1^* = 0; s_1^* = 0; x_1^* = x_n; n_1^* = A \quad (4)$$

and

$$a_2^* = B\mu/(\alpha - \rho)(\rho + \mu); s_2^* = B\rho/(\alpha - \rho)(\rho + \mu) \quad (\mu = \mu(x_2^*))$$

$x_2^*$  is the solution of the equation:

$$\begin{aligned} k(x_n - x) + \beta B\mu(x)/(\alpha - \rho)(\rho + \mu(x)) \\ - \gamma\mu(x)B\rho/(\alpha - \rho)(\rho + \mu(x)) = 0 \end{aligned} \quad (5)$$

and

$$n_2^* = \rho\delta/(\alpha - \rho).$$

The second point of equilibrium has a biological interpretation only if  $a_2^*$ ,  $s_2^*$ ,  $x_2^*$  and  $n_2^*$  are not negative.  $a_2^*$  and  $s_2^* > 0$  if  $A > \rho\delta/(\alpha - \rho)$ . Moreover, it is necessary that  $\alpha > \rho$ , because otherwise if  $\alpha < \rho$  then  $n_2^* = \rho\delta/(\alpha - \rho) < 0$ . Strictly speaking,  $V_n(n)$  is defined as:

$$V_n(n) = \begin{cases} \alpha n/(\delta + n) & \text{if } n \geq 0 \\ 0 & \text{if } n < 0 \end{cases}$$

and the equation for the steady state  $n^*$ , i.e.,  $V_n(n) = \rho$ , has no solutions for negative  $n$ . In this case the only point of equilibrium would be the point given by the relations (4).

Stability analysis of these points of equilibrium (using linear approximation) proves that if  $\alpha > \rho$  and  $A < \rho\delta/(\alpha - \rho)$ , the first point (4) is stable and the second point (5) is unstable, and when  $A > \rho\delta/(\alpha - \rho)$ , the first point becomes unstable and the second one stable. Thus the stability condition for the second point coincides with one of the conditions for its existence. When  $\alpha < \rho$ , the first point (4) is the only steady state, and is stable. This case may be considered to represent destruction of the ecosystem. We now examine the case  $\alpha > \rho$  in detail.

Let  $A$  be now a slowly varying function of time,  $A = A(t^*)$ , i.e.,  $A$  varies so slowly that the system is always able to reach its steady state. Consider the quasi-stationary process thus obtained.  $A$  can be interpreted as the total amount of substances in the ecosystem, provided that the algae, detritus and nutrient biomasses are measured in the same units. Then, for example, nutrient entry into the ecosystem, or partial burying of detritus in the bottom sediment, can be treated respectively as an increase or decrease in the  $A$  value.

Suppose that at first we have a reservoir containing a small amount of substances,  $A < \rho\delta/(\alpha - \rho)$ . It will soon reach a steady state at the first point of equilibrium. Accordingly, when the amount of substances in the reservoir is small, all of them become oxidised and transformed into inorganic compounds, or nutrients; algae die out, and the water becomes saturated with oxygen.

Suppose now that  $A$  slowly begins to increase. For a certain time the ecosystem will remain in the first steady state: all the substances are accumulated in the form of nutrients, but in a quantity insufficient to support life in the reservoir. Nevertheless, at some moment, when the amount of nutrients exceeds a definite critical value  $A > \rho\delta/(\alpha - \rho)$ , the ecosystem will switch to another steady state given by the second equilibrium point of the system:  $a_2^*$ ,  $s_2^*$ ,  $x_2^*$ ,  $n_2^*$ . From eqs. 5, then

$$\mu(x) = k(x_n - x)(\alpha - \rho)\rho / [(\gamma\rho - \beta)B - k(x_n - x)(\alpha - \rho)]$$

The right-hand side of this equation is a parabola  $f(x)$ ; on the left-hand side there is the function  $\mu(x)$ . By comparing their values,  $x_2^*$  can be defined as a function of the model parameters and the total amount of substances in the ecosystem (Fig. 3).

It can be seen that there are two possible paths for future ecosystem development. If  $\gamma\rho < \beta$ , then  $x_2^* > x_n$ , and the reservoir becomes a source of oxygen. When  $\gamma\rho > \beta$ ,  $x_2^* < x_n$ , and in the case of a continuing nutrient enrichment of the water (increase of  $A$ ), a typical eutrophication process begins to evolve:  $x_2^*$  decreases,  $a_2^*$  and  $s_2^*$  increase. Figure 4 illustrates the relation between the oxygen content in the water and the total amount of substances in the system.

When  $x_2^*$  becomes less than the value  $x_{a1}$ , the rate of increase of  $a_2^*$  begins to decline (Fig. 5), while  $s_2^*$  starts to increase more rapidly (Fig. 6). These phytoplankton and detritus growth-rate modifications continue until  $x_2^*$  exceeds  $x_{a2}$ . When  $x_2^* < x_{a2}$ , the changes of the variables become proportional again. From the biological point of view these rate variations are quite natural. When there is an oxygen deficit in the reservoir and the oxidation of organic matter switches to an anaerobic regime, the mineralisation rate diminishes, detritus accumulates more quickly, and meanwhile the phyto-

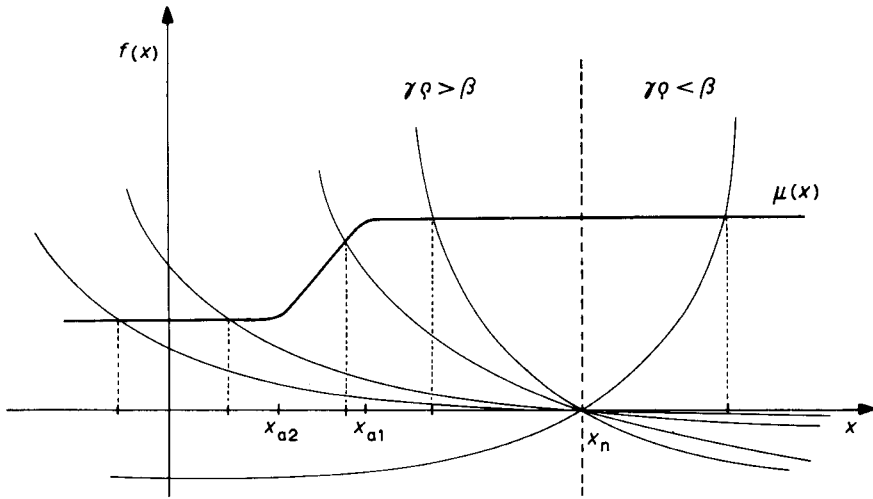


Fig. 3. Equilibrium dynamics for oxygen concentration  $x^*$ .

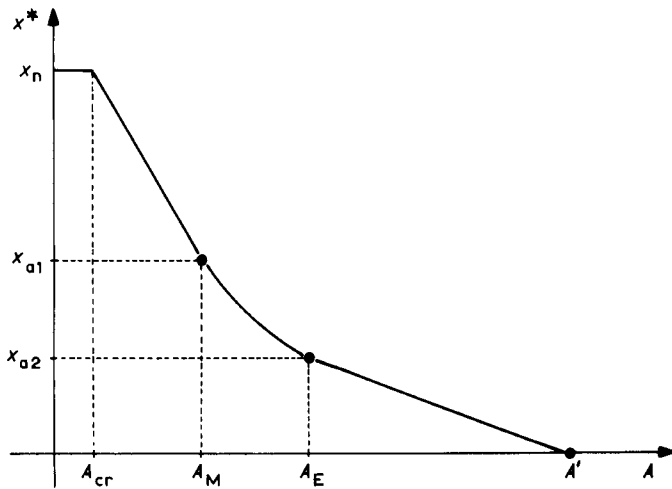


Fig. 4. DO concentration in water as a function of the total amount of material ( $A$ ) in the ecosystem:

$$A_{cr} = \rho\delta / (\alpha - \rho)$$

$$A_M = A_{cr} + k(x_n - x_{a1})(\rho + \mu_1) / \mu_1(\gamma\rho - \beta)(\alpha - \rho)$$

$$A_E = A_{cr} + k(x_n - x_{a2})(\rho + \mu_2) / \mu_2(\gamma\rho - \beta)(\alpha - \rho)$$

$$A' = \rho\delta / (\alpha - \rho) + kx_n(\rho + \mu_2) / \mu_2(\gamma\rho - \beta)(\alpha - \rho)$$

plankton biomass growth decreases because of the lack of nutrients.

If the content of substances in the reservoir is increased further, a time comes when  $x_2^*$  becomes less than zero. Practically this corresponds to death of the ecosystem, complete eutrophication and swamping of the reservoir. At

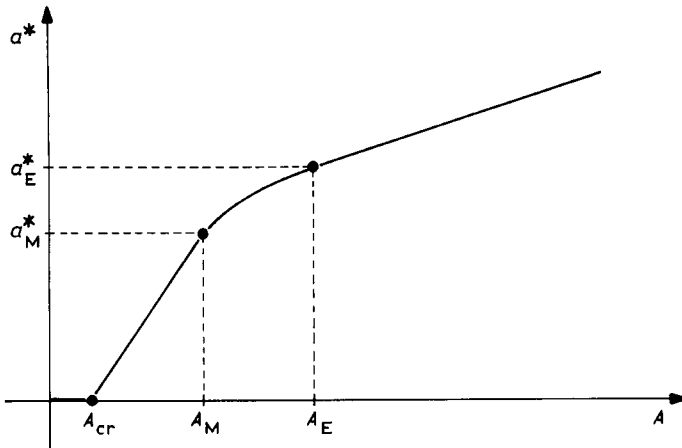


Fig. 5. Effect of enrichment on phytoplankton concentration:

$$a_M = k(x_n - x_{a1}) / (\gamma\rho - \beta)(\alpha - \rho)$$

$$a_E = k(x_n - x_{a2}) / (\gamma\rho - \beta)(\alpha - \rho)$$

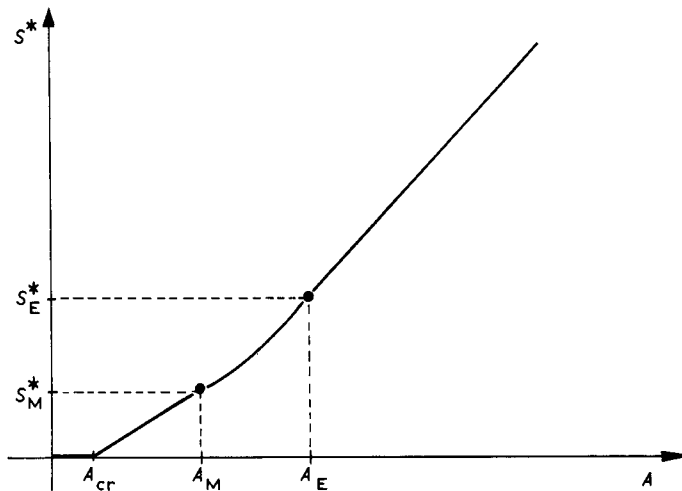


Fig. 6. Effect of enrichment on detritus concentration:

$$s_M = k(x_n - x_{a1})\rho / \mu_1(\gamma\rho - \beta)(\alpha - \rho)$$

$$s_E = k(x_n - x_{a2})\rho / \mu_2(\gamma\rho - \beta)(\alpha - \rho)$$

this stage another model is required. Thus using our minimal model it is possible to follow qualitatively the whole process of eutrophication.

If phosphorus release from sediment in phosphorus-limited systems is taken into account, then the dynamics are somewhat different, since under anaerobic conditions the flow of nutrients to the water will increase and, accordingly, the algal growth rate will also increase. The model supports the hypothesis that in phosphorus-limited systems, anaerobic conditions enhance algal 'blooming'. However, it is necessary to exercise caution with such conclusions, because phosphorus enrichment from sediment may easily switch the limiting factor and thus again call for a change in the form of the function  $\mu(x)$ . We may remark here that this delicate point well demonstrates the difficulties which appear when building a minimal model: it is very hard to outline the 'minimum' processes, which will ensure qualitatively realistic dynamics in a model that is still analytically solvable. For instance, no problems would arise with a switch of the limiting factor if several biogenic elements were considered in the model. However, it is extremely unlikely that such a version of the model could be tackled by analytical methods and analysed qualitatively.

#### MODEL STUDY FOR SOME REAL EXPERIMENTAL DATA

In this section we test the relationships derived above against experimental data observed for various ecological systems. The goal is not to carry out model identification or verification: models of this type are not intended to provide quantitative conclusions; they are built basically for qualitative analysis. Rather, the aim is to investigate whether the relationships derived have any ecological sense (for instance, and primarily, the relationship between  $\gamma\rho$  and  $\beta$ ), whether the highly aggregated model parameters can be estimated quantitatively in principle, and whether and to what extent the approximate model results correspond to ecological reality.

The phytoplankton growth rate  $\alpha$  depends greatly upon the external inputs to the ecosystem. This might be the reason for the high dispersion among data taken from different sources. According to the data of Jørgensen et al. (1978b),  $\alpha$  can vary from 0.01 to 5.65  $\text{d}^{-1}$ . However, in most ecosystems,  $\alpha = 2-3 \text{ d}^{-1}$ . (In our model we study long-term, qualitative ecosystem dynamics: this is the reason for the neglect of all dependences of process rates upon time of day, the choice of average values and the use of days (d) and  $\text{mg l}^{-1}$  as the units for the parameters.)

The phytoplankton biomass decrease rate, as well as its growth rate, is subject to considerable variations. In his model, Nyholm (1978) also used a generalised function for phytoplankton mortality and consumption to describe its biomass decrease, and set  $\rho$  equal to 0.1–0.6  $\text{d}^{-1}$ . However, his

function had the form  $\rho a / (K + a)$ , where  $K = 4.0 \text{ mg l}^{-1}$ . Therefore in the first stage of ecosystem development, when  $a$  is small, it would be reasonable to consider  $\rho$  equal to  $0.025\text{--}0.15 \text{ d}^{-1}$  in our model. On the other hand, Jørgensen proposed  $0.1 \text{ d}^{-1}$  for phytoplankton mortality, while its maximum rate of biomass decrease due to zooplankton feeding was  $0.36 \text{ d}^{-1}$ . Consequently, for 'juvenile' ecosystems, we take  $\rho = 0.1 \text{ d}^{-1}$ ; for 'older' reservoirs, with settled food chains and a sufficient phytoplankton population,  $\rho = 0.4\text{--}0.6 \text{ d}^{-1}$ .

The reaeration parameter  $k$  also depends greatly upon external factors, primarily wind rate and existing water currents. It is rather difficult to find any average value for this coefficient. In the literature the minimum value of  $k$  appears to be  $0.17 \text{ d}^{-1}$ . Obviously  $k$  may be greater by a factor of 100 or even 1000 if there is a strong wind. According to Hutchinson's (1957) data, the average reaeration coefficient for lakes is  $300 \text{ d}^{-1}$ . Such a dispersion of values surely renders analysis more complicated.

The saturation oxygen concentration depends upon water temperature. Assuming that the reservoir considered has an average water temperature of  $15^\circ\text{C}$ , we take  $x_n = 10 \text{ mg l}^{-1}$ . Following the data of Wang et al. (1978), aerobic conditions prevail if the DO concentration is not less than  $4 \text{ mg l}^{-1}$  ( $x_{a1} = 4 \text{ mg l}^{-1}$ ). When the DO concentration is less than  $1 \text{ mg l}^{-1}$ , anaerobic oxidation processes dominate ( $x_{a2} = 1 \text{ mg l}^{-1}$ ). Analysing the data collected by Jørgensen et al. (1978b), we reached the conclusion that the aerobic oxidation rate is approximately twice the anaerobic rate, and we thus set  $\mu_1 = 0.4 \text{ d}^{-1}$  and  $\mu_2 = 0.2 \text{ d}^{-1}$ .

The photosynthesis rate coefficient  $\beta$  varies from  $0.012$  to  $0.108 \text{ mg O}_2$  per  $\text{mg}$  phytoplankton per day in various sources (Jørgensen et al., 1978b). A similar dispersion is typical of data for the parameter  $\gamma$ , for which the range is  $0.018\text{--}0.09 \text{ mg O}_2$  per  $\text{mg}$  substrate. (Usually the oxygen uptake rate coefficient for decomposition,  $\gamma'$ , is given in the literature. In the present case  $\gamma' = \gamma\mu$ , and so estimates of  $\gamma$  were made according to the relation  $\gamma = \gamma' / \mu$ , where  $\gamma'$  and  $\mu$  are taken for aerobic conditions.)

We now consider whether there is any sense in the resulting quantitative relations. First of all, of course, it would be interesting to analyse the correlation between  $\gamma\rho$  and  $\beta$ , which determines the oxygen regime in the reservoir. When the evolution of the freshwater ecosystem begins,  $\rho = 0.1 \text{ d}^{-1}$  and  $\gamma\rho < \beta$  for all available  $\gamma$  and  $\beta$ . In this case an increase of  $A$  turns the reservoir into a source of oxygen. However, this situation cannot last for a long time. Food chains begin to appear: as a result of phytoplankton consumption by zooplankton, its biomass decrease rate grows:  $\rho$  increases. When  $\rho > 0.14 \text{ d}^{-1}$ , for the chosen ranges of  $\gamma$  and  $\beta$ , the relation  $\gamma\rho > \beta$  already becomes possible, and as  $\rho$  increases further, the reservoir ecosystem more and more probably becomes a consumer of oxygen. Nevertheless, even

for the maximum value of  $\rho$ ,  $1.2 \text{ d}^{-1}$ , the relation  $\gamma\rho < \beta$  cannot be excluded, although its occurrence would be very doubtful (supposing that smaller values of oxygen consumption for BOD decomposition correspond to smaller values of photosynthesis rates).

Thus an important result is that in real-life ecosystems both relations between  $\gamma\rho$  and  $\beta$  are possible: it is most probable that  $\gamma\rho$  will be less than  $\beta$  in the earlier stages of ecosystem evolution, whereas  $\gamma\rho$  will be greater than  $\beta$  in systems with developed food chains. Nevertheless, even in old ecosystems, situations with  $\gamma\rho < \beta$ , due to changes in certain conditions (for example, in climatic factors), remain possible. This makes the system switch to another steady state when the water becomes oversaturated with oxygen. Further increase of  $A$  leads to an intensification of  $\text{O}_2$  output into the atmosphere. Meanwhile substances are still accumulating in the reservoir and hence eutrophication progresses. Such 'oxygenous' eutrophication, however, cannot continue for a long time. Even if  $\gamma\rho$  does not increase, sooner or later  $\beta$  will diminish as a result of the photosynthesis inhibition caused by phytoplankton self-shading effects, and the system will return to its usual evolution, characterised by DO deficit, phytoplankton growth, and detritus accumulation.

We now consider general ecosystem development. The critical total amount of substances in the reservoir,  $A_{\text{cr}} = \rho\delta/(\alpha - \rho)$ , for our parameters varies from 0.003 to  $0.026 \text{ mg l}^{-1}$  ( $\rho = 0.1 \text{ d}^{-1}$ ). Comparing these values with the total amount of substances even in such an oligotrophic lake as Lake Onega, where the value is 1.8–3.5  $\text{mg l}^{-1}$ , it can be seen that  $A_{\text{cr}}$  is much less. For this reason it can be considered that in practically all natural reservoirs  $A > A_{\text{cr}}$ , the corresponding ecosystems are in the steady state described by relations (5), and the algal and detritus biomasses are not zero.

Neglecting the small value  $A_{\text{cr}}$  yields  $A_{\text{M}} \approx 10.5 k/(\gamma\rho - \beta) \text{ mg l}^{-1}$  and  $A_{\text{E}} \approx 54 k/(\gamma\rho - \beta) \text{ mg l}^{-1}$ . Supposing that  $A_{\text{M}}$  refers to a mesotrophic and  $A_{\text{E}}$  to eutrophic reservoir state, it can be seen that in terms of the total amounts of substances, these two reservoir states differ by a factor greater than five. This agrees quite well with existing conceptions of eutrophication.

Thus the model, generally speaking, yields reasonable estimations, on the basis of which some conclusions can be drawn about the future development of the freshwater ecosystem.

## SUMMARY

We have considered a simple, minimal model of the eutrophication process in a water body. Having taken phytoplankton, detritus, nutrients and DO concentration as the model state variables, we obtained a qualitative picture of the freshwater system eodynamics. The total amount of subs-

tances,  $A$ , proved to be the most important control parameter. It is this parameter that determines the degree and the rate of eutrophication.

Using this model some concrete methods of eutrophication management may be developed. The most natural and most usual management measure is a reduction of nutrient enrichment, i.e., a decrease of  $A$ . This can be accomplished either by the extraction of detritus or by the withdrawal of phytoplankton biomass from the system. At the same time, it is shown that the correlations between some observed characteristics of the ecosystem (namely, the rate coefficients of phytoplankton biomass decrease, photosynthesis and BOD) may also considerably influence reservoir functioning. For example, by destroying existing food chains in the reservoir and thus diminishing  $\rho$  so that  $\gamma\rho$  becomes less than  $\beta$ , it is possible to change completely the oxygen regime of the ecosystem. Moreover, the model analysis shows that processes in the reservoir are greatly influenced by the reaeration rate. The values of  $A_M$  and  $A_E$  have a linear dependence upon the reaeration coefficient  $k$ , and it is actually just these parameter that determine the ecosystem carrying capacity. They define the threshold values of the total amount of substances which correspond to the switching points from aerobic to anaerobic processes of bacterial destruction. The oxygen regime of the ecosystem can be used for a sufficient objective classification of reservoirs into oligotrophic, mesotrophic and eutrophic. The values  $A_M$  and  $A_E$  that define to what class a reservoir belongs depend upon the individual characteristics and parameters of the ecosystem and may be different for different reservoirs.

The model is a very aggregated one and consequently all the results are only qualitative, and, of course, they cannot be used for concrete forecasts. However, the minimal model proposed gives a reasonable theoretical description of eutrophication process in a freshwater reservoir.

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