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SIMULATION MODEL OF PHOSPHORUS CYCLING IN THE EPILIMNION OF A EUTROPHIC LAKE*

ABSTRACT: The model describes time-related changes in six variables: concentration of dissolved orthophosphate phosphorus $P-PO_4$, phytoplankton, bacteria, detritus, nonpredatory zooplankton, and predatory zooplankton in the epilimnion of Lake Głębokie. The stability of the model was analysed, and it has been found that the variables show damped oscillations around equilibrium points. Results of numerical experiments are presented, simulating a cessation of fish farming in the lake, changes in the level and timing of phosphorus inflow to the epilimnion from deeper layers of the lake, and changes in temperature and light conditions. The results show that the inflow of phosphorus from deeper layers largely influences the values of the model variables.

KEY WORDS: Simulation model, phosphorus cycling, epilimnion, stability analysis, numerical experiments.

1. INTRODUCTION

The model of phosphorus cycling in the epilimnion of a deep eutrophic lake, presented in this paper, describes time-related changes in interrelated biological and chemical variables comprising the concentration of dissolved orthophosphate phosphorus $P-PO_4$ and the concentrations of phosphorus in the biomass of phytoplankton, nonpredatory and predatory zooplankton, bacteria, and detritus. The values of all these variables are expressed in $\mu g\ P \cdot l^{-1}$. Moreover, the model describes time-related changes in temperature at the surface, of water depth profiles of temperatures, light intensity at the surface, depth profiles of light intensity, coefficient of light absorption, and hypolimnion depth. The values of the variables generated by the

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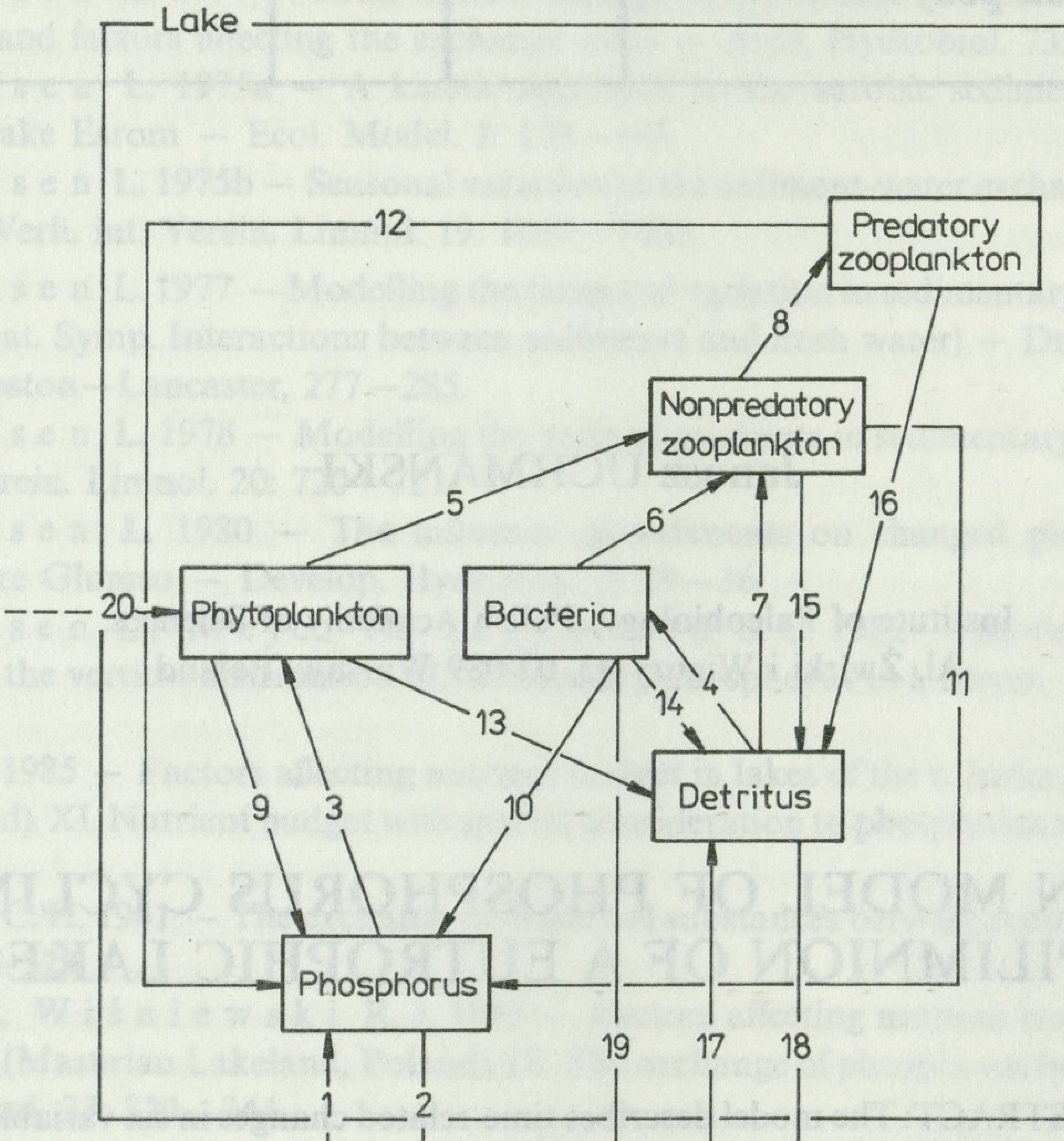

Fig. 1. Block diagram of the model of phosphorus cycling in the epilimnion of Lake Głębokie Processes described by the model are denoted as follows: 1 — epilimnion loading with phosphorus from deeper layers of the lake and from outside loading of the lake, 2 — sinking of phosphorus, 3 — utilization of phosphorus by phytoplankton in photosynthesis, 4 — utilization of detritus by bacteria, 5 — consumption of phytoplankton by nonpredatory zooplankton, 6 — consumption of bacteria by nonpredatory zooplankton, 7 — consumption of detritus by nonpredatory zooplankton, 8 — consumption of nonpredatory zooplankton by predatory zooplankton 9 — excretion of phosphorus by phytoplankton, 10 — excretion of phosphorus by bacteria, 11 — excretion of phosphorus by nonpredatory zooplankton, 12 — excretion of phosphorus by predatory zooplankton, 13 — phytoplankton mortality due to other factors than zooplankton grazing, 14 — bacterial mortality due to other factors than zooplankton grazing, 15 — mortality of nonpredatory zooplankton due to other reasons than consumption by predatory zooplankton and not digested remains of the food of nonpredatory zooplankton, 16 — mortality of predatory zooplankton and not digested remains of its food, 17 — loading of the detritus pool with food supplied for fish farming and with faeces of fish, 18 — detritus sedimentation, 19 — sedimentation of bacteria associated with detritus, 20 — solar radiation reaching the epilimnion. This diagram does not show that many of these processes depend on temperature

model are mean values for the top six metres of the lake depth in order to simulate the process of mixing in the epilimnion, on the one hand, and to approximate the model output to empirical data which were averaged in this way, on the other hand.

Figure 1 shows a block diagram of relationships among chemico-biological variables. The sources of dissolved phosphorus in the epilimnion involve loading from deeper layers of the lake, input connected with external loading of the lake, and excreta of the phytoplankton and the two trophic types of zooplankton. Also bacteria are involved in the process of detritus transformation into phosphorus. The nonpredatory zooplankton is feeding on phytoplankton, detritus, and bacteria. The predatory zooplankton lives on nonpredatory zooplankton. Detritus is formed from not digested remains of the food consumed by both trophic types of zooplankton and from dead parts of all the living components of the lake ecosystem. Also the food provided by man for fish stock is a source of detritus. The matter is lost from the system by sedimentation of particulate detritus and the associated bacteria, and by physical transport of dissolved phósphorus caused by water movements. Phytoplankton production depends on light intensity. Moreover, almost all the processes occuring in the lake depend on temperature.

Among various ways of constructing models of lake ecosystems, the one leading to a detailed model for a specific lake has been selected. The model presented here belongs to the group of more complicated models in terms of the description of biological and chemical processes occurring in lakes. It also contains some elements of the lake physics.

2. EMPIRICAL DATA

A mathematical model was fitted to the empirical data from Lake Głębokie located in the Mazurian Lakeland. This is a deep, stratified troughflow lake mixed twice a year. The river Jorka is flowing through this lake. The basic characteristics of this lake are as follows (B a j k i e w i c z-G r a b o w s k a 1985): volume — $5601 \cdot 10^6$ l, surface area — 47.3 ha, maximum depth — 34.3 m, mean depth — 11.8 m, and time of water retention — 0.8 — 1.5 years. This is a typical, lowland, eutrophic lake, the eutrophication of which is still increasing at a high rate. A large-scale cage aquaculture of the rainbow trout *Salmo gairdneri* Rich. has been developed in it. This and the other lakes located in the river Jorka basin were subject to intense studies, mostly from the point of view of phosphorus cycling.

Data on the concentration of dissolved orthophosphate phosphorus $P-PO_4$ were taken from H i l l b r i c h t-I l k o w s k a and Ł a w a c z (1983) and P l a n t e r el al. (1983). Data on the content of phosphorus in the biomass of phytoplankton are from S p o d n i e w s k a (1983). Data on the content of phosphorus in the biomass of both trophic types of the zooplankton are from W ę g l e ń s k a et al. (1983) and E j s m o n t-K a r a b i n et al. (1983). Information on the content of phosphorus in the biomass of bacteria is from G o d l e w s k a-L i p o w a (1983). Data on the content of phosphorus in detritus mass are from H i l l b r i c h t-I l k o w s k a (1983).

The following picture of changes in biological, chemical, and physical variables in the epilimnion of Lake Głębokie in 1976 emerged from these data.

The measurements of temperature profiles over the study period were started on 11 March, after the ice melted. The thermocline developed early in May, and stratification was maintained by mid-October. At the end of this month the thermocline disappeared.

Tables 1 and 2 show the results of measurements of the chemico-biological variables. These measurements were taken since the time of ice melting (11 March) at about two-week intervals throughout the growing season of 1976. The values of

Table 1. Data set concerning the concentration P of dissolved orthophosphate phosphorus $P-PO_4$ and the concentration of phosphorus in the biomass of phytoplankton F, nonpredatory zooplankton Z_{np}, and predatory zooplankton Z_p in the epilimnion of Lake Głębokie in 1976 (data after Ejsmont-Karabin et al. 1983, Hillbricht-Ilkowska 1983, Hillbricht-Ilkowska and Ławacz 1983, Planter et al. 1983, Spodniewska 1983, Węgleńska et al. 1983)

Date	Number of day	P μg P·l^{-1}	F μg P·l^{-1}	Z_{np} μg P·l^{-1}	Z_p μg P·l^{-1}
11 March	71	32	13.3	0.19	0.14
24 April	115	–	8.1	1.27	1.73
4 May	125	–	9.9	3.33	7.18
5 May	126	5	–	–	–
10 May	131	–	8.4	–	–
12 May	133	–	4.8	–	–
25 May	146	–	7.1	28.8	7.33
7 June	159	–	6.6	–	–
8 June	160	25	–	–	–
9 June	161	–	5.5	39.18	20.91
22 June	174	3	3.9	38.35	11.66
6 July	188	–	–	21.13	3.95
7 July	189	24	–	–	–
27 July	209	0	5.9	17.77	4.02
6 August	219	–	15.4	–	–
10 August	223	5	7.4	15.46	12.10
24 August	238	–	6.0	4.25	3.04
9 September	253	10	1.5	9.48	1.58
21 September	265	0	–	–	–
22 September	266	–	3.8	–	–
27 September	271	–	–	4.38	2.5
8 October	282	–	6.2	14.54	5.78
22 October	296	–	2.8	7.36	1.44
16 November	321	51	1.0	2.44	0.31

Table 2. Data set concerning the concentration of phosphorus in the biomass of bacteria B and detritus D in the epilimnion of Lake Głębokie in 1976 (data after Godlewska-Lipowa 1983, Hillbricht-Ilkowska 1983)

Month	B μg P·l^{-1}	D μg P·l^{-1}
April	42	–
May	61.9	–
June	101.4	1.32
July	134.4	5.91
August	181.2	2.67
September	124.8	0.78
October	–	1.06
November	78	–

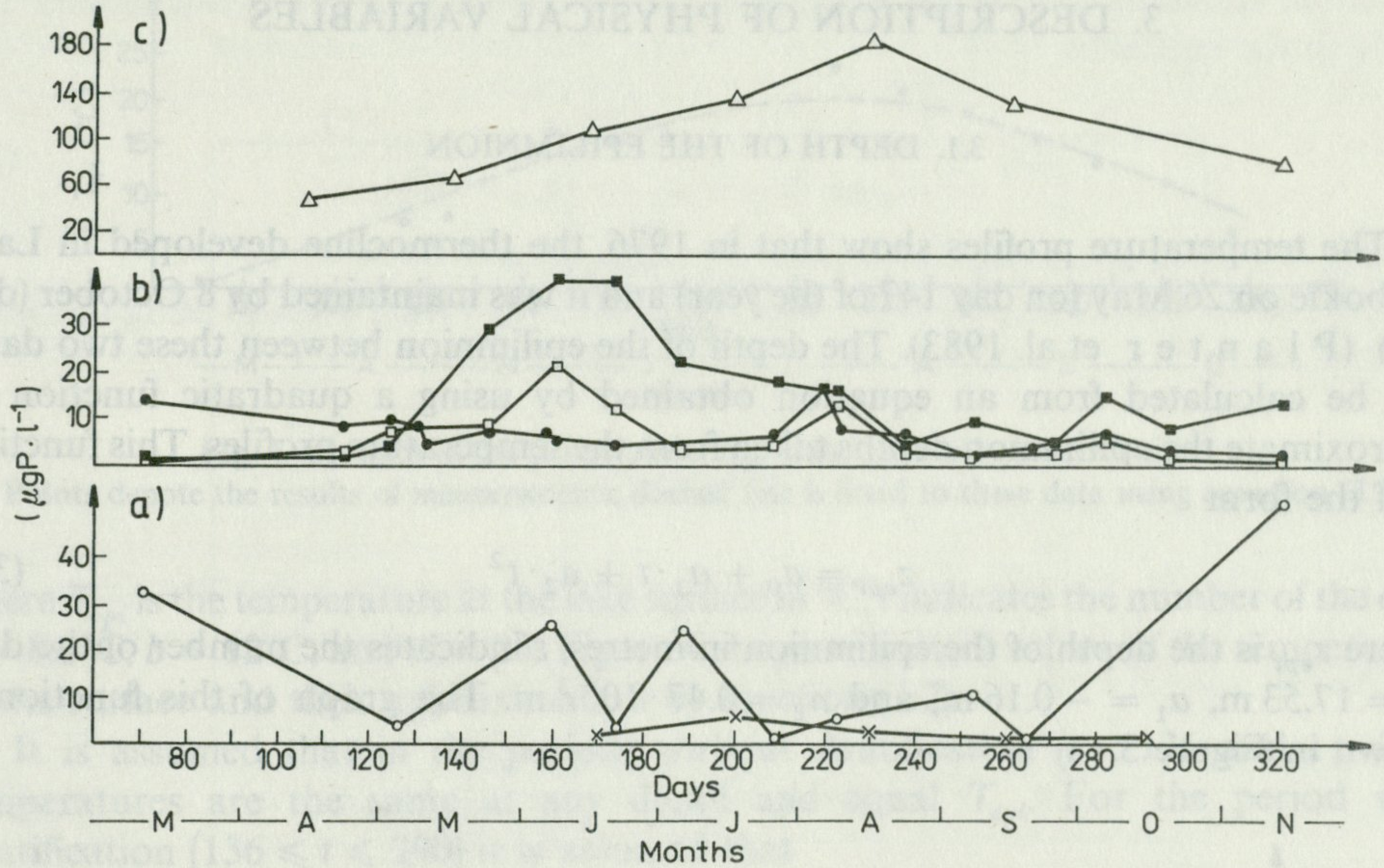

Fig. 2. Empirical values of chemico-biological variables as measured in the epilimnion of Lake Głębokie in 1976

a — open circles denots the concentration of dissolved phosphorus, crosses the concentration of detritus; b — closed circles denots the concentration of phytoplankton, closed squares the concentration of nonpredatory zooplankton, open squares the concentration of predatory zooplankton, c — concentration of bacteria

dissolved phosphorus and phytoplankton are means for samples taken at one-metre intervals from the lake surface to the depth of 6 m. The data concerning two trophic types of zooplankton are mean values over the epilimnion. The concentration of bacteria was measured only in the surface layer to the depth of 0.5 m. The mass of detritus was calculated as a difference between the mass of seston and the total biomass of phytoplankton, two trophic types of zooplankton, and bacteria in the epilimnion. Figure 2 shows the measured values of all the chemico-biological variables in relation to time.

It can be seen that there was no phytoplankton peak in spring, whereas a local peak of phytoplankton concentration appeared early in August, and it coincided with a decrease in the concentration of nonpredatory zooplankton in this period (Fig. 2). Maximum concentrations of the two trophic types of zooplankton were relatively high and they occurred concurrently. Bacteria reached very high concentrations, whereas detritus concentration was relatively low and approximately constant. The concentration of dissolved phosphorus largely increased in the period May-July (though a relatively low values was noted in mid-June), and in the same period the concentrations of the two trophic types of zooplankton were high.

3. DESCRIPTION OF PHYSICAL VARIABLES

3.1. DEPTH OF THE EPILIMNION

The temperature profiles show that in 1976, the thermocline developed in Lake Głębokie on 26 May (on day 147 of the year) and it was maintained by 8 October (day 282) (P l a n t e r et al. 1983). The depth of the epilimnion between these two dates can be calculated from an equation obtained by using a quadratic function to approximate the epilimnion depths taken from the temperature profiles. This function is of the form

$$z_{epi} = a_0 + a_1 \cdot t + a_2 \cdot t^2 \tag{3.1}$$

where z_{epi} is the depth of the epilimnion in metres, t indicates the number of the day, $a_0 = 17.53$ m, $a_1 = -0.16$ m, and $a_2 = 0.47 \cdot 10^{-3}$ m. The graph of this function is shown in Figure 3.

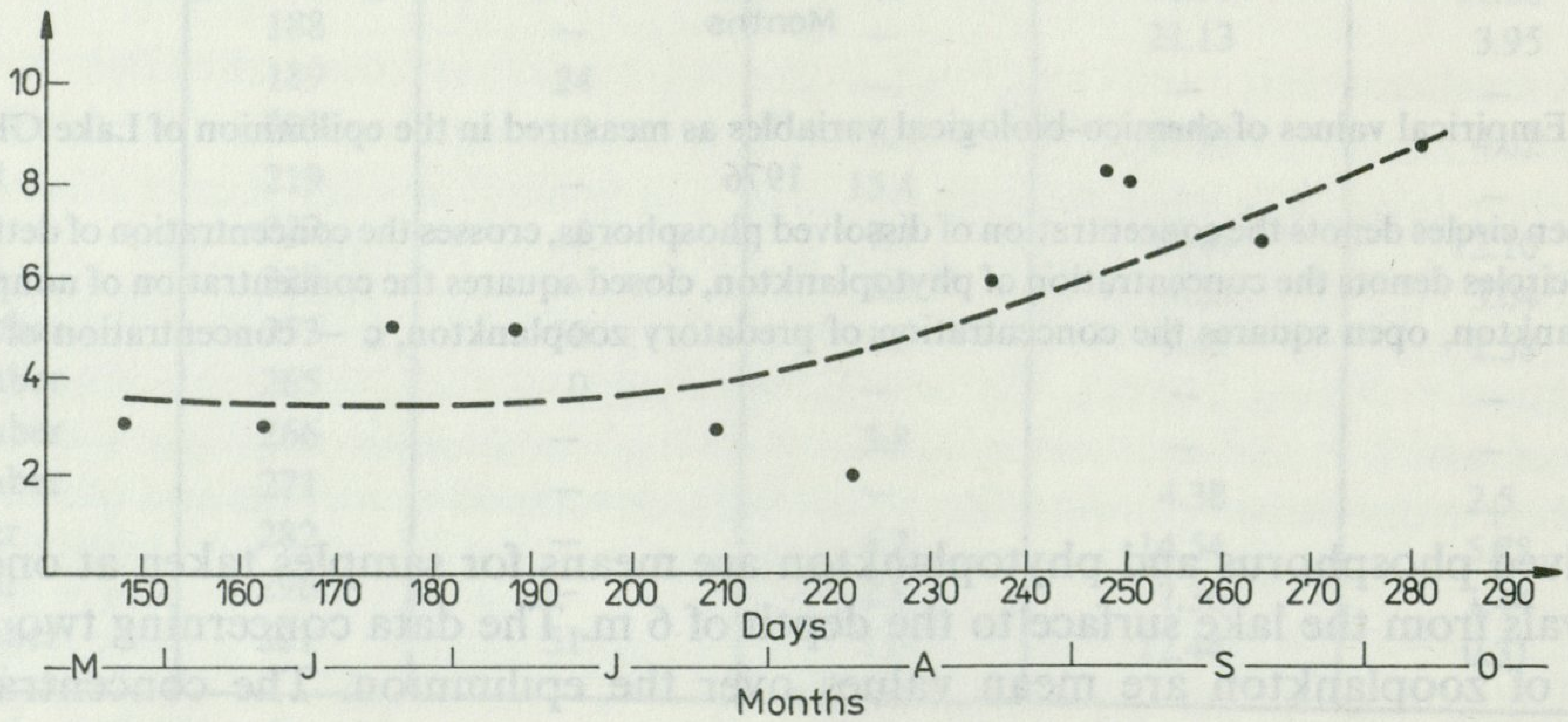

Fig. 3. Measured values of the epilimnion depth z_{epi} in relation to time
Points denote the results of measurements, dashed line is fitted to these data using euquation (3.1)

As the measurements could have been taken not exactly at the time of thermocline development and disappearance, it is assumed in the model that the thermocline developed a little earlier and disappeared a little later than observed. For this reason, the relationship (3.1) was applied for $136 \leqslant t \leqslant 290$. For $t < 136$ and $t > 290$ it is assumed that the lake was mixed to the bottom.

3.2. TEMPERATURE

The measurements of temperature at the surface of Lake Głębokie (P l a n t e r et al. 1983) were approximated by the function

$$T_{epi} = a - b\cos\left(\frac{2\pi(t-c)}{365}\right) \tag{3.2}$$

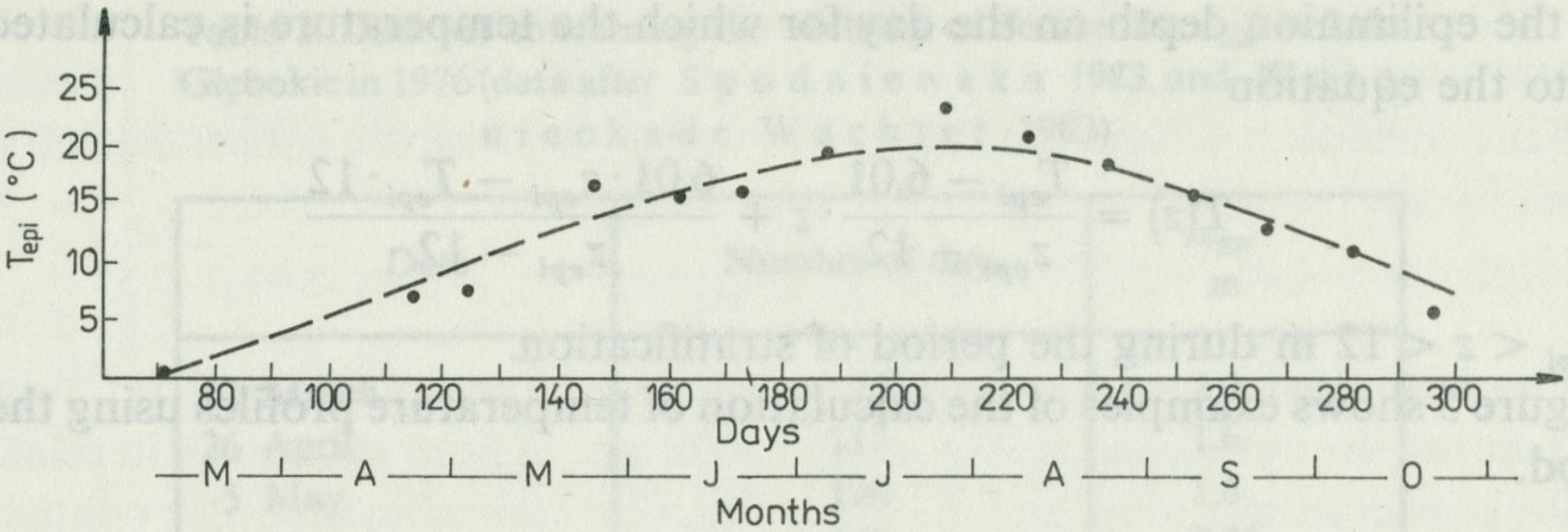

Fig. 4. Changes in the temperature T_{epi} of the surface layers over time
Points denote the results of measurements, dashed line is fitted to these data using equation (3.2)

where T_{epi} is the temperature at the lake surface in °C, t indicates the number of the day, $a = 8.2$°C, $b = 12$°C, and $C = 25$. Figure 4 shows empirical values of the temperature at the surface and their approximation by function (3.2).

It is assumed that in the periods without stratification ($t < 136$ and $t > 290$) temperatures are the same at any depth and equal T_{epi}. For the period with stratification ($136 \leqslant t \leqslant 290$) it is assumed that

$$T(z) = T_{epi} \quad \text{for} \quad z \leqslant z_{epi} \tag{3.3}$$

where $T(z)$ is water temperature at depth z. The temperature for $z > z_{epi}$ was calculated as follows. It is assumed that in this period the temperature at a depth greater than 12 m is constant and equal to 6.01°C. The latter value was obtained by averaging temperatures at depths not lower than 12 m during the period of stratification. For the depth $z_{epi} < z < 12$ m it is assumed that changes in temperature follow a straight line connecting the point $T = T_{epi}$ for z_{epi} with the point $T = 6.01$ for a depth of 12 m (where

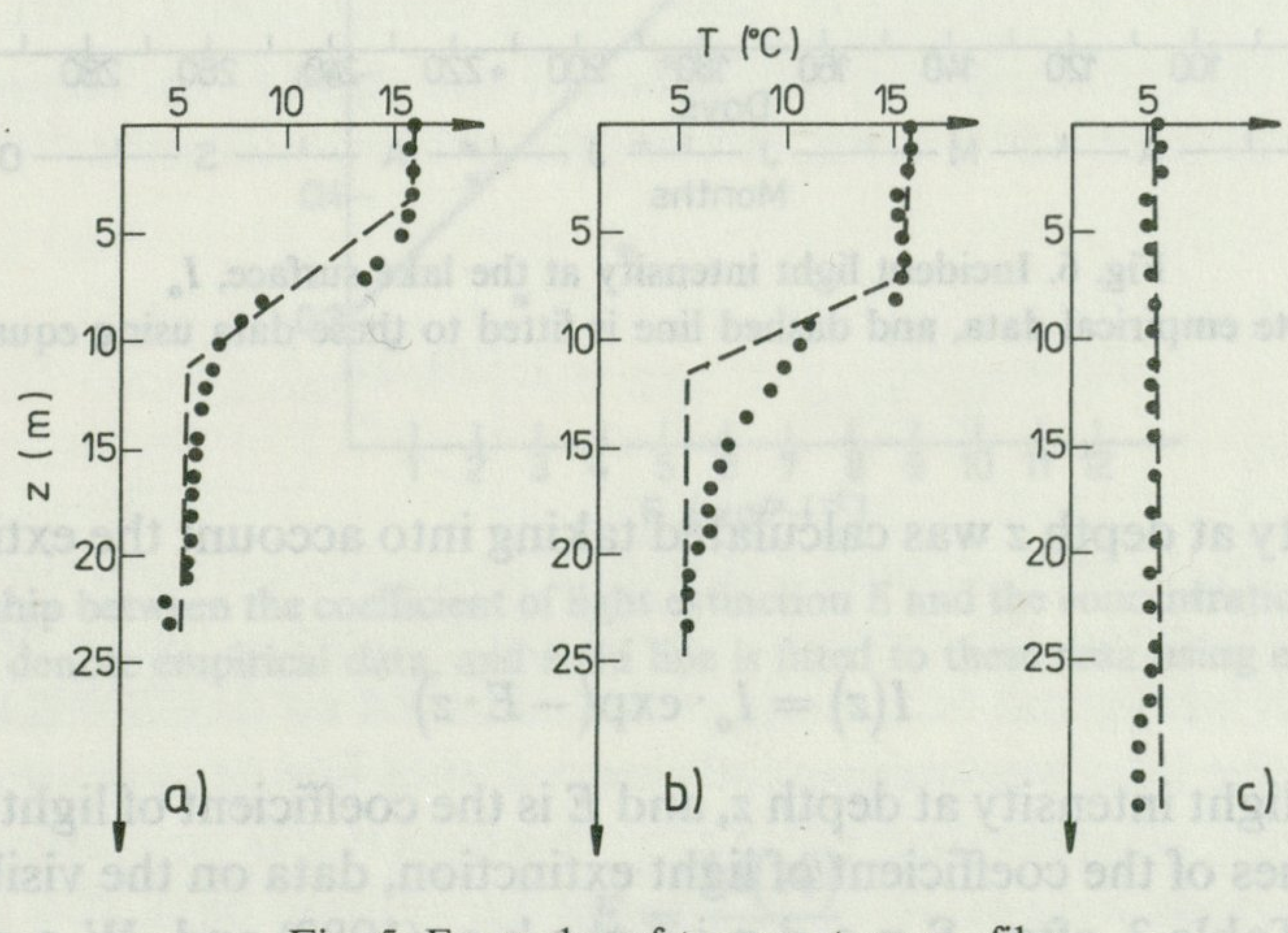

Fig. 5. Examples of temperature profiles
Points denote empirical data, and dashed lines are fitted to these data using equations (3.3) and (3.4), a — 22 June, 1976, b — 9 September, 1976, c — 22 October, 1976

z_{epi} is the epilimnion depth on the day for which the temperature is calculated). This leads to the equation

$$T(z) = \frac{T_{epi} - 6.01}{z_{epi} - 12} \cdot z + \frac{6.01 \cdot z_{epi} - T_{epi} \cdot 12}{z_{epi} - 12} \tag{3.4}$$

for $z_{epi} < z < 12$ m during the period of stratification.

Figure 5 shows examples of the calculation of temperature profiles using the above method.

3.3. LIGHT

The intensity of light measured at the surface of Lake Głębokie (data after W o r o n i e c k a-d e W a c h t e r 1983) is approximated by the function similar to the one used for calculating temperature at the surface

$$I_o = d - g\cos\left(\frac{2\pi(t-h)}{365}\right) \tag{3.5}$$

where I_o is the light intensity in $\mathrm{J \cdot cm^{-2} \cdot day^{-1}}$ at the lake surface, t is the number of the day, $d = 1046\ \mathrm{J \cdot cm^{-1} \cdot day^{-1}}$, $g = 1004.16\ \mathrm{J \cdot cm^{-2} \cdot day^{-1}}$, and $h = 5$. Figure 6 shows empirical values of light intensity and their approximation by function (3.5).

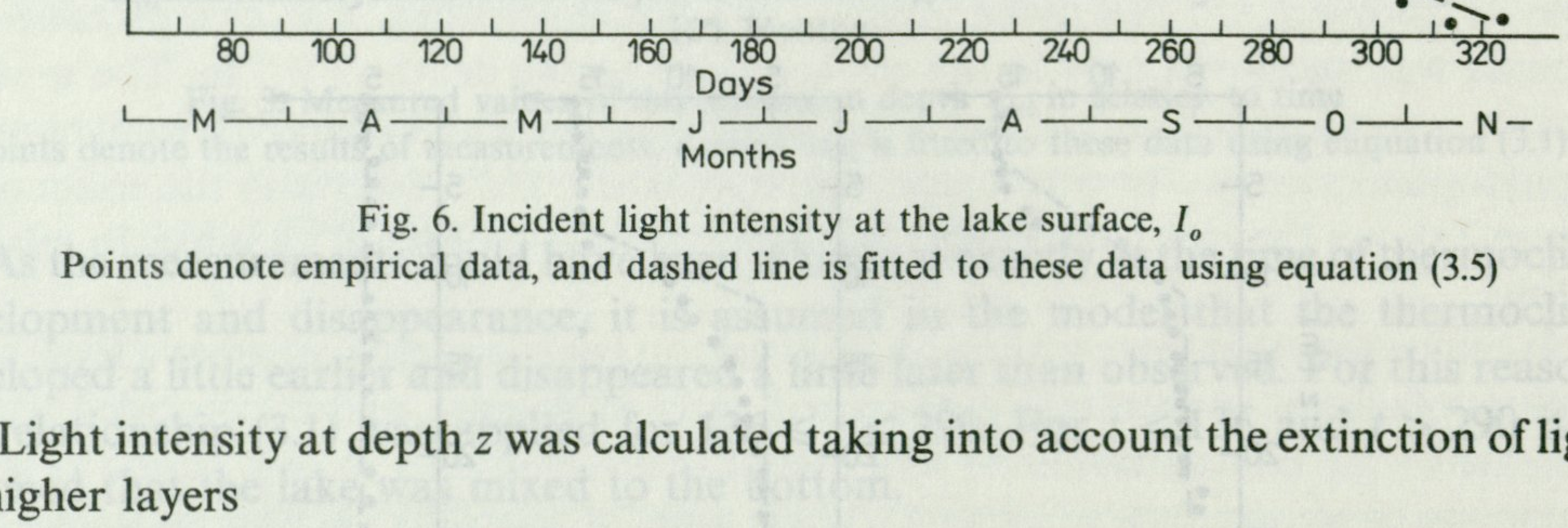

Fig. 6. Incident light intensity at the lake surface, I_o

Points denote empirical data, and dashed line is fitted to these data using equation (3.5)

Light intensity at depth z was calculated taking into account the extinction of light in higher layers

$$I(z) = I_o \cdot \exp(-E \cdot z) \tag{3.6}$$

where $I(z)$ is the light intensity at depth z, and E is the coefficient of light extinction. To estimate the values of the coefficient of light extinction, data on the visibility of Secchi disc were used (Table 3, after S p o d n i e w s k a (1983) and W o r o n i e c k a-d e W a c h t e r (1983)). It is assumed that the limit of the visibility of Secchi disc is at a depth from which 10% of the reflected light reaches the surface water. Then

Table 3. Data set concerning the visibility of Secchi disc z_{SD} in Lake Głębokie in 1976 (data after S p o d n i e w s k a 1983, and W o r o n i e c k a-d e W a c h t e r 1983)

Date	Number of day	z_{SD} m
12 March	72	2.0
26 April	117	1.6
5 May	126	1.6
26 May	147	2.25
10 June	162	2.6
23 June	175	2.6
10 August	223	1.2
25 August	239	1.45
8 September	252	2.3
21 September	265	3.6
8 October	282	3.2
22 October	296	2.8
16 November	321	4.1

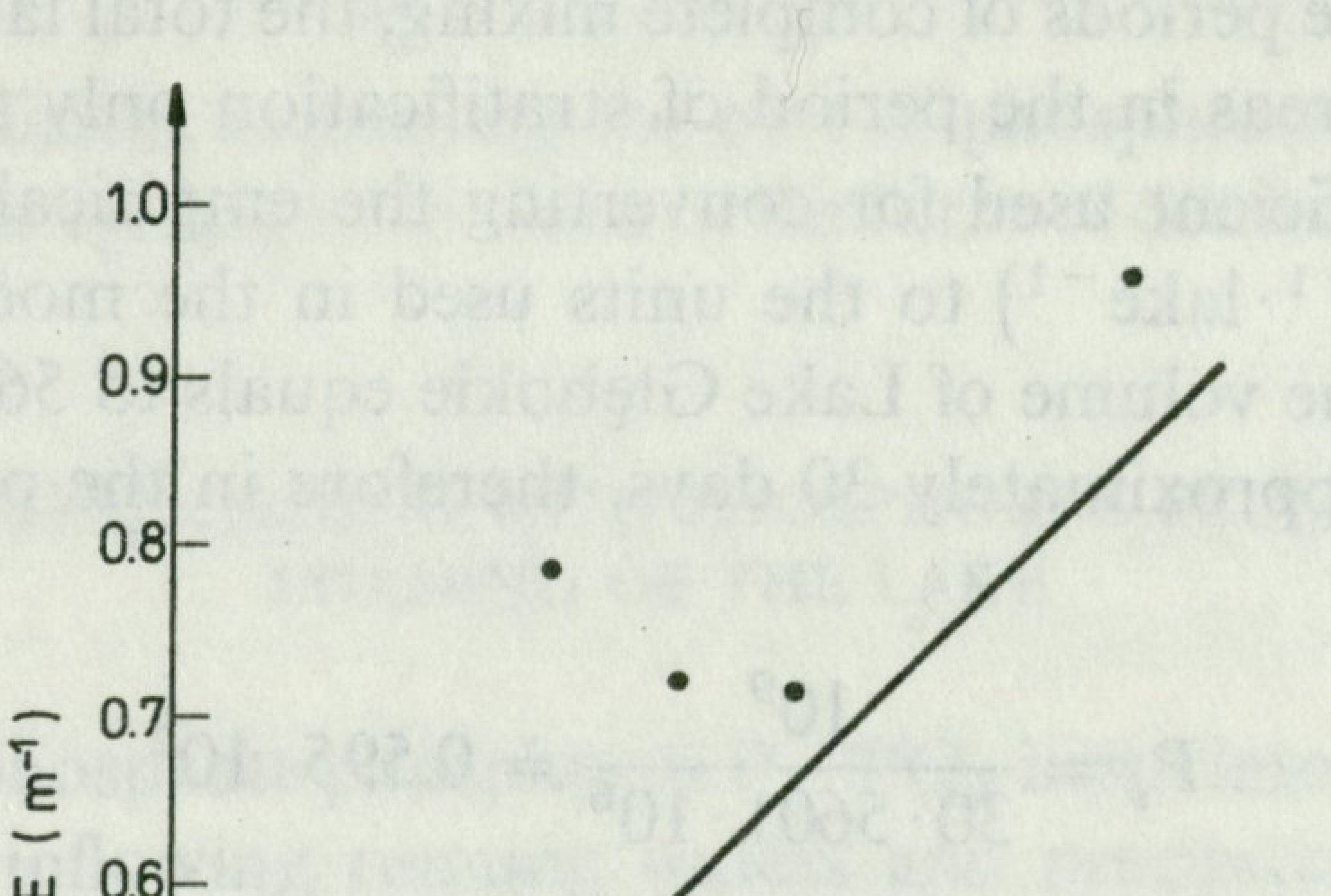

Fig. 7. Relationship between the coefficient of light extinction E and the concentration of phytoplankton F Points denote empirical data, and solid line is fitted to these data using equation (3.8)

$$E = \frac{\ln(10)}{2z_{sd}} \tag{3.7}$$

where z_{sd} is the depth of the visibility of Secchi disc.

It is assumed that the coefficient of light extinction depends on the concentration of phytoplankton (K r a m e r and N i x o n 1978). Then a linear relationship between the coefficient of light extinction and the phytoplankton concentration can be expressed by the formula

$$E = m_1 + m_2 \cdot F \tag{3.8}$$

where F is phytoplankton concentration, $m_1 = 0.30\,\mathrm{m}^{-1}$ and $m_2 = 0.101 \cdot \mathrm{m}^{-1} \cdot \mu\mathrm{g\,P}^{-1}$. Figure 7 shows the calculated values of the coefficient of light extinction in relation to phytoplankton concentration, and the linear function approximating this relationship.

4. DESCRIPTION OF PHOSPHORUS LOADING TO THE EPILIMNION

4.1. DISTRIBUTION OF PHOSPHORUS LOAD IN THE LAKE

Empirical values of phosphorus loading were given in kg per lake per month. In the mathematical model they are expressed in $\mu\mathrm{g} \cdot \mathrm{l}^{-1} \cdot \mathrm{day}^{-1}$. In further parts of Section 4 it is assumed that in the periods of complete mixing, the total lake volume was loaded with phosphorus, whereas in the period of stratification only the epilimnion.

Let P_v be the coefficient used for converting the empirical data on phosphorus loading ($\mathrm{kg\,P} \cdot \mathrm{month}^{-1} \cdot \mathrm{lake}^{-1}$) to the units used in the model ($\mu\mathrm{g\,P} \cdot \mathrm{l}^{-1} \cdot \mathrm{day}^{-1}$). Since 1 kg $= 10^9$ µg, the volume of Lake Głębokie equals to $5601 \cdot 10^6$ l, and because one month contains approximately 30 days, therefore in the period of total mixing

$$P_v = \frac{10^9}{30 \cdot 5601 \cdot 10^6} = 0.595 \cdot 10^2 \tag{4.1}$$

Let us assume that the epilimnion depth is constant and equals 5 m. The volume of this part of the lake is $2110 \cdot 7 \cdot 10^6$ l. Thus, in the period of stratification

$$P_v = \frac{10^9}{30 \cdot 2110 \cdot 7 \cdot 10^6} = 1.579 \cdot 10^{-2} \tag{4.2}$$

The calculations take into account a period of transition between the total mixing and stratification. In spring, the thermocline was introduced to the model for the first time on day 136 (24 May), and in autumn it was removed on day 290 (21 October). It was assumed that the lake was permanently mixed until five days prior to the spring data at the very latest, whereas since day 5 after this data it was permanently stratified. Similar five-day periods were established around the autumn data. It is assumed that the value of P_v changed linearly in these 10-day transition periods. Finally the value of P_v was thus calculated from the formula

$$P_v = \begin{cases} 0.595\cdot 10^{-2} & t < 131 \\ 0.984\cdot 10^{-3}\cdot t + 1.579\cdot 10^{-2} - 0.984\cdot 10^{-3}\cdot 141 & 131 \leqslant t < 141 \\ 1.579\cdot 10^{-2} & 141 \leqslant t \leqslant 285 \\ -0.984\cdot 10\cdot t + 1.579\cdot 10^{-2} + 0.984\cdot 10^{-3}\cdot 285 & 285 \leqslant t < 295 \\ 0.595\cdot 10^{-2} & 295 < t \end{cases} \tag{4.3}$$

4.2. LOADING DUE TO FISH FARMING

Fish stock in Lake Głębokie was supplied with food from May until the end of November, that is, from day 152 to day 334 of the year. It was assumed that monthly food ratios were constant and as expressed in phosphorus, they equalled to 87.86 kg·month^{-1}·lake^{-1} (Ławacz 1985, Penczak et al. 1985), and they loaded the pool of detritus. Thus the rate P_{fish} of the epilimnion loading from this source, as expressed in μg P·l^{-1}·day^{-1} can be obtained from the equation

$$P_{fish} = \begin{cases} O \text{ for } t < 152 \text{ or } t > 354 \\ A_{fish}\cdot P_v \cdot 87.86 \text{ for } 152 \leqslant t \leqslant 354 \end{cases} \tag{4.4}$$

where A_{fish} is the coefficient expressing the part of phosphorus from this source that entered the phosphorus cycling in the lake in the form of detritus, and P_v is defined by formula (4.3).

4.3. EPILIMNION LOADING WITH PHOSPHORUS FROM EXTERNAL LOADING OF THE LAKE

Table 4 shows the phosphate phosphorus $P-PO_4$ input into the lake from external sources, that is, from inflowing running waters and precipitation, and phosphorus ouflow with river Jorka waters (data after Hillbricht-Ilkowska and Ławacz (1983) and Ławacz (1985)). Changes over time in the difference between phosphorus inflow from external sources and phosphorus outflow from the

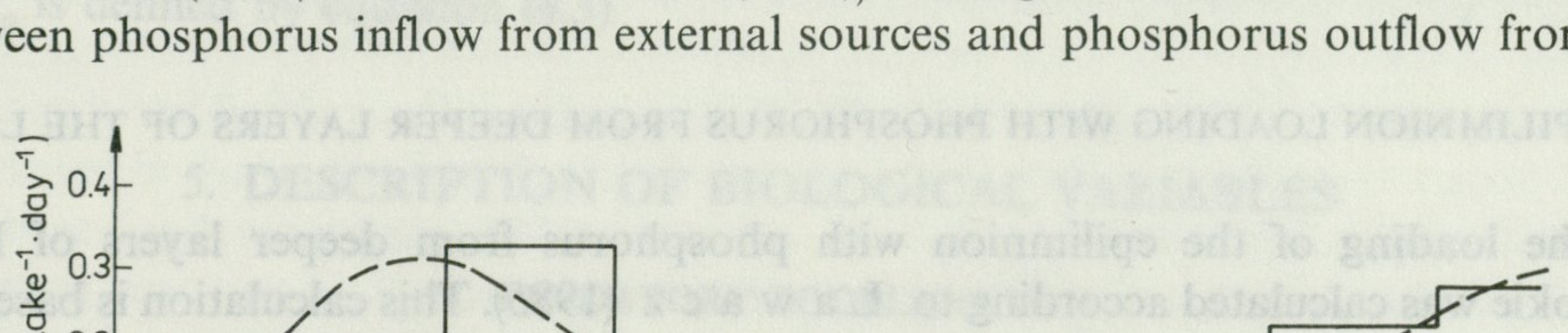

Fig. 8. Seasonal changes in the epilimnion loading with phosphorus as a result of external loading of the lake, P_e

Solid line illustrates empirical data, and dashed line is fitted to these data using equation (4.5) at $P_v = 1$ and $A_e = 1$ (original data characterized the phosphorus input to the lake over month, and here it is assumed that this input is evenly distributed on each day of one-month periods)

Table 4. Data set concerning the loading of Lake Głębokie in 1976 with dissolved orthophosphate phosphorus $P-PO_4$ from deeper layers of the lake and from the external loading of the lake, consisting of the phosphorus inflow with running waters and with air transport, and also the outflow of phosphorus with running waters (data after Hillbricht-Ilkowska and Ławacz 1985 and Ławacz 1985)

Month	Loading from deeper layers	External inflow	Outflow
	$kg\ P \cdot month^{-1} \cdot lake^{-1}$		
January	−29.6	9.2	8.4
February	7.1	9.7	8.4
March	11.8	17.6	14.0
April	770.7	24.0	18.0
May	337.25	26.9	17.0
June	214.55	9.99	6.0
July	102.25	12.79	13.0
August	192.95	3.59	3.5
September	111.75	5.59	5.0
October	85.35	9.89	3.0
November	319.65	11.19	3.0
December	55.8	2.4	2.0

lake can be approximated by a polynomial of degree four. The empirical data and their approximation by the polynomial are shown in Figure 8. Finally, the rate P_e ($\mu g\ P \cdot l^{-1} \cdot day^{-1}$) of the net loading of the epilimnion with phosphorus from external loading of the lake can be described by

$$P_e = A_e \cdot P_v \cdot (-77.434 + 2.065 \cdot t - 0.017 \cdot t^2 + 0.559 \cdot 10^{-4} \cdot t^3 - 0.631 \cdot 10^{-7} \cdot t^4) \quad (4.5)$$

where coefficient A_e informs of the proportion of the phosphorus from external sources entering the phosphorus cycling in the lake, and P_v is defined by formula (4.3).

4.4. EPILIMNION LOADING WITH PHOSPHORUS FROM DEEPER LAYERS OF THE LAKE

The loading of the epilimnion with phosphorus from deeper layers of Lake Głębokie was calculated according to Ławacz (1985). This calculation is based on phosphorus budgets at monthly intervals for the upper 5-m layer of the lake. The total phosphorus content was measured in this layer along with the external loading of this layer. By placing traps at the depth of 5 m, the monthly sedimentation was measured. Using these data it was possible to calculate the content of phosphorus in the upper 5-m layer of the lake at the beginning of the following month, and to compare this calculated value with the measured content of total phosphorus in the following month. The total phosphorus loading of the epilimnion from deeper layers of the lake was calculated as a difference between the measured and calculated contents of total phosphorus. The results are shown in Table 4.

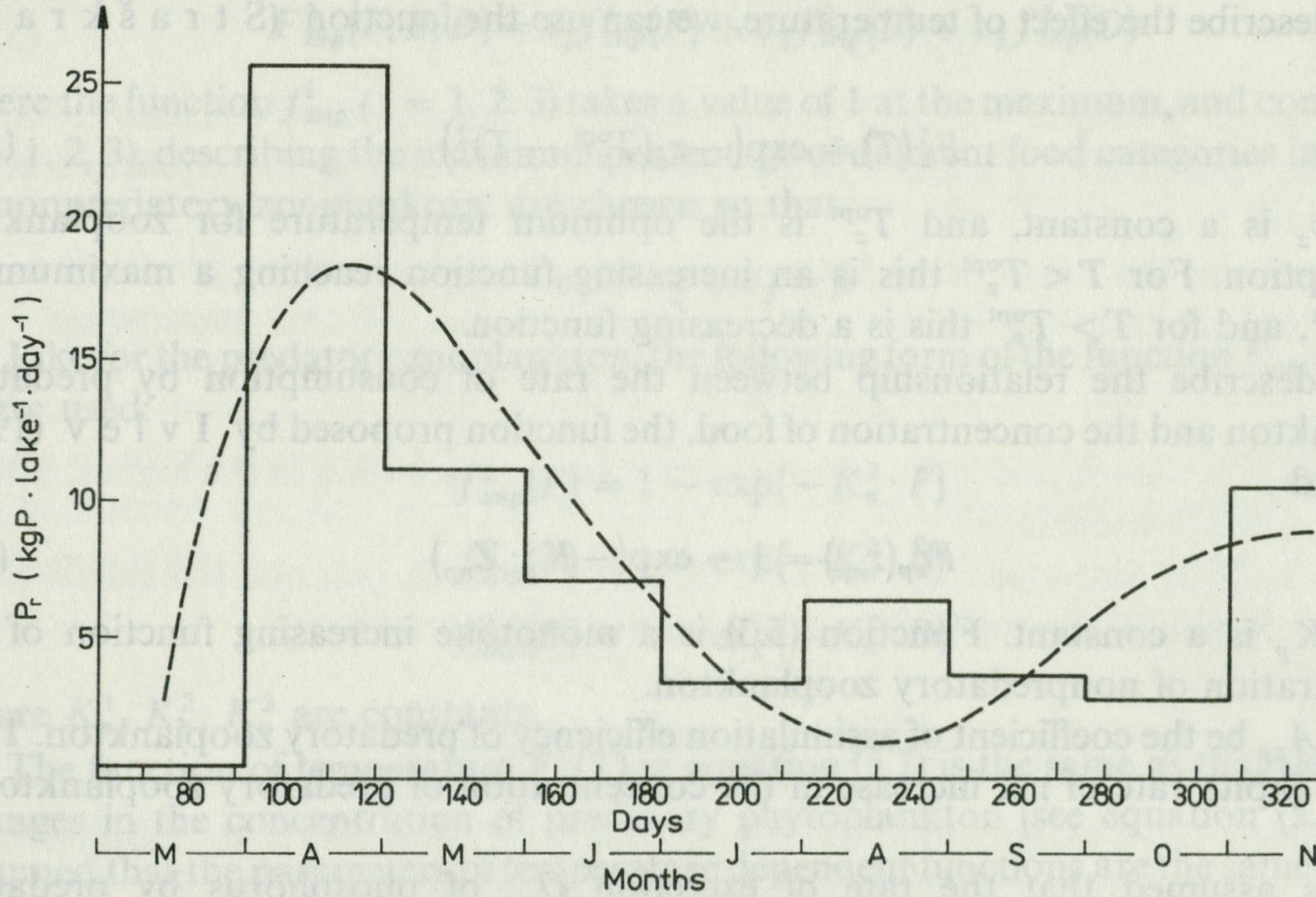

Fig. 9. Seasonal changes in the epilimnion loading with phosphorus from deeper layers of the lake, P_r. Solid line represents empirical data, and dashed line is fitted to these data using equation (4.6) at $P_v = 1$ and $A_r = 1$ (original data characterized the phosphorus input to the lake over month, and here it is assumed that this input is evenly distributed on each day of one-month periods)

The values of loading obtained in this way can be approximated by a polynomial of order four (Fig. 9). Finally, the rate of epilimnion loading from deeper layers of the lake, P_r (μg P·l^{-1}·day^{-1}) can be described by the function

$$P_r = A_r \cdot P_v \cdot (-5368.477 + 138.339 \cdot t - 1.222 \cdot t^2 + 0.368 \cdot 10^{-3} \cdot t^3 - 0.422 \cdot 10^5 \cdot t^4) \quad (4.6)$$

where A_r shows what proportion of phosphorus from this source is cycling in the lake, and P_v is defined by equation (4.3).

5. DESCRIPTION OF BIOLOGICAL VARIABLES

5.1. PREDATORY ZOOPLANKTON

It is assumed that predatory zooplankton, the concentrations of which are denoted by Z_p, is characterized by a maximum per capita consumption G_{zp}^{max}. The actual per capita consumption G_{zp} depends, however, on the concentration of food available to predatory zooplankton (which is nonpredatory zooplankton) and also on temperature

$$G_{zp} = G_{zp}^{max} \cdot F_z^1(T) \cdot F_{zp}^2(Z_{np}) \quad (5.1)$$

where Z_{np} is the concentration of nonpredatory zooplankton. The positive functions F_z^1 and F_{zp}^2 are chosen so that their maximum values equal 1. Thus, under optimum food and temperature conditions $G_{zp} = G_{zp}^{max}$.

To describe the effect of temperature, we can use the function (Straškraba 1976)

$$F_z^1(T) = \exp\left(-v_z\left(T_z^{\mathrm{opt}} - T\right)^2\right) \tag{5.2}$$

where v_z is a constant, and T_z^{opt} is the optimum temperature for zooplankton consumption. For $T < T_z^{\mathrm{opt}}$ this is an increasing function reaching a maximum at $T = T_z^{\mathrm{opt}}$, and for $T > T_z^{\mathrm{opt}}$ this is a decreasing function.

To describe the relationship between the rate of consumption by predatory zooplankton and the concentration of food, the function proposed by Ivlev (1955) was used

$$F_{zp}^2(z_{np}) = 1 - \exp\left(-K_p \cdot Z_{np}\right) \tag{5.3}$$

where K_p is a constant. Function (5.3) is a monotone increasing function of the concentration of nonpredatory zooplankton.

Let A_{zp} be the coefficient of assimilation efficiency of predatory zooplankton. Then the per capita rate of net increase in the concentration of predatory zooplankton is $A_{zp} \cdot G_{zp}$.

It is assumed that the rate of excretion Q_{zp} of phosphorus by predatory zooplankton is proportional to its concentration and dependent on temperature

$$Q_{zp} = q_{zp} \cdot F_z^1(T) \cdot Z_p \tag{5.4}$$

where q_{zp} is a constant and $F_z^1(T)$ is a function of temperature of the form (5.2).

It is also assumed that the mortality of predatory zooplankton is proportional to its concentration

$$M_{zp} = m_{zp} \cdot Z_p \tag{5.5}$$

where m_{zp} is a constant coefficient of the mortality of predatory zooplankton.

Finally, the rate of changes in the concentration of predatory zooplankton is described by a differential equation of the form

$$\frac{dZ_p}{dt} = G_{zp}^{\max} \cdot F_z^1(T) \cdot F_{zp}^2(Z_{np}) \cdot A_{zp} \cdot Z_p - Q_{zp} - M_{zp} \tag{5.6}$$

5.2. NONPREDATORY ZOOPLANKTON

Let $G_{znp}^{\max}$ denote the maximum per capita rate of consumption by nonpredatory zooplankton. The actual per capita rate of consumption G_{znp} by this zooplankton depends on temperature and on the concentration of food, which consists of phytoplankton, bacteria, and detritus. It is assumed that

$$G_{znp} = G_{znp}^{\max} \cdot F_z^1(T) \cdot F_{znp}^2(F, B, D) \tag{5.7}$$

where F is the concentration of phytoplankton, B is the concentration of bacteria, D is the concentration of detritus, and T denotes temperature. It is assumed that the function F_{znp}^2 is a sum of the terms describing consumption of different food categories

$$F_{znp}^2(F,B,D) = c_l f_{znp}^1(F) + c_2 f_{znp}^2(B) + c_3 f_{znp}^3(D) \tag{5.8}$$

where the function f_{znp}^i $(i = 1, 2, 3)$ takes a value of 1 at the maximum, and constants c_i $(i = 1, 2, 3)$, describing the maximum percentage of different food categories in the diet of nonpredatory zooplankton, are chosen so that

$$c_1 + c_2 + c_3 = 1 \tag{5.9}$$

Like for the predatory zooplankton, the following form of the function f_{znp}^i $(i = 1, 2, 3)$ are used:

$$f_{znp}^1(F) = 1 - \exp(-K_n^1 \cdot F) \tag{5.10}$$

$$f_{znp}^2(B) = 1 - \exp(-K_n^2 \cdot B) \tag{5.11}$$

$$f_{znp}^3(D) = 1 - \exp(-K_n^3 \cdot D) \tag{5.12}$$

where K_n^1, K_n^2, K_n^3 are constants.

The function of temperature $F_z^1(T)$ in equation (5.7) is the same as that describing changes in the concentration of predatory phytoplankton (see equation (5.2)). It is assumed that the parameters of temperature dependent functions are the same for both the trophic types of zooplankton.

The rate of phosphorus excretion Q_{znp} and the mortality M_{znp} of nonpredatory zooplankton are proportional to nonpredatory zooplankton concentration, and excretion also depends on temperature

$$Q_{znp} = q_{znp} \cdot F_z^1(T) Z_{np} \tag{5.13}$$

$$M_{znp} = m_{znp} \cdot Z_{np} \tag{5.14}$$

where q_{znp} is a constant and m_{znp} is a coefficient of mortality, and F_z^1 is a function given by equation (5.2).

When constructing a formula describing the rate of change in the concentration of nonpredatory zooplankton, we should consider the assimilation efficiency of the matter consumed by nonpredatory zooplankton, and also the fact that this concentration is reduced due to predatory zooplankton feeding on nonpredatory zooplankton. It is assumed in the model that the coefficient of assimilation efficiency is the same for all the three food categories (phytoplankton, bacteria, and detritus). This yields the following equation

$$\frac{dZ_{np}}{dt} = G_{znp}^{\max} \cdot F_z^1(T) \cdot F_{znp}^2(F,B,D) \cdot A_{znp} \cdot Z_{np} - G_{zp} \cdot Z_p - Q_{znp} - M_{znp} \tag{5.15}$$

where A_{znp} is the coefficient of assimilation efficiency for nonpredatory zooplankton.

5.3. PHYTOPLANKTON

Let $G_f^{\max}$ be the maximum rate of phytoplankton production. The actual rate of primary production G_f depends on the intensity of light, temperature, and phosphorus concentration:

$$G_f = G_f^{\max} \cdot F_f^1(T) \cdot F_f^2(I) \cdot F_f^3(P) \tag{5.16}$$

where T is temperature, I is light intensity, and P is phosphorus concentration. As earlier, the functions F_f^1, F_f^2, and F_f^3 are chosen in such a way that they equal to 1 at the maximum.

To describe the relationship between the rate of phytoplankton production and temperature, an equation similar to (5.2) is used but with different parameters

$$F_f^1(T) = \exp\left(-v_f \cdot (T_f^{\text{opt}} - T)^2\right) \tag{5.17}$$

where v_f is a constant, and T_f^{opt} is the temperature corresponding to the highest rate of phytoplankton production.

The function developed by Steel (1962) is used to describe the relationship between the rate of phytoplankton production and light intensity

$$F_f^2(I) = \frac{I}{I^{\text{opt}}} \exp\left(1 - \frac{I}{I^{\text{opt}}}\right) \tag{5.18}$$

This function has a maximum at the light intensity I^{opt}, thus this is an optimum light intensity at which phytoplankton production reaches the maximum rate.

To describe the relationship between the rate of primary production and phosphorus concentration, the Michaelis – Menten equation is used

$$F_f^3(P) = \frac{P}{K_f + P} \tag{5.19}$$

where K_f is a constant, K_f can be interpreted as the phosphorus concentration at which the mean rate of phytoplankton production reaches half of the maximum.

It is assumed that phytoplankton releases a small amount of phosphorus, and that the rate of phytoplankton excretion Q_f is proportional to the concentration of phytoplankton and it depends on temperature

$$Q_f = q_f \cdot F_f^1(T) \cdot F \tag{5.20}$$

where q_f is a constant and $F_f^1(T)$ is a function of the form (5.17).

The mortality of phytoplankton M_f (and the rate of sedimentation, which can be described by an identical equation) is, as assumed, proportional to the concentration of phytoplankton

$$M_f = m_f \cdot F \tag{5.21}$$

where m_f is a constant coefficient of mortality.

Finaly, the equation describing changes in phytoplankton concentration, after taking into account grazing by nonpredatory zooplankton, is of the form

$$\frac{dF}{dt} = G_f^{\max} \cdot F_f^1(T) \cdot F_f^2(I) \cdot F_f^3(P) - G_{znp}^{\max} \cdot F_z^1(T) \cdot c_1 \cdot f_{znp}^1(F) \cdot Z_{np} - Q_f - M_f \tag{5.22}$$

5.4. BACTERIA

The model assumes that detritus is the source of phosphorus for bacteria. The maximum per capita rate of detritus utilization by bacteria is denoted by G_b^{max}. The actual rate of this process G_b depends on temperature and detritus concentration

$$G_b = G_b^{max} \cdot F_f^1(T) \cdot F_b^2(D) \tag{5.23}$$

where $F_f^1(T)$ is the function (5.17), since it can be assumed that the relation to temperature for bacteria is the same as for phytoplankton. D is the concentration of detritus, and the function $F_b^2(D)$ has a maximum of 1, like in the preceding case.

To describe the rate of detritus utilization by bacteria, the Michaelis-Menten function is used

$$F_b^2(D) = \frac{D}{K_b + D} \tag{5.24}$$

where K_b is interpreted as the detritus concentration at which $F_b^2(D)$ reaches half of the maximum value.

As later attempts at simulation revealed, the mathematical model of bacterial growth should be much more constrained than function (5.23) with a constant K_b could do. For this reason in the final version at the model the parameter K_b is linearly related to bacteria concentration

$$K_b = g \cdot B \tag{5.25}$$

where g is a constant.

It can be assumed that the mortality of bacteria S_b is proportional to the concentration of bacteria

$$S_b = m_b \cdot B \tag{5.26}$$

where m_b is the mortality coefficient for bacteria.

It is assumed that a part of bacteria is permanently bound with detritus, and, consequently, is sedimented with it. The rate of this process S_b is given by

$$S_b^{sed} = s_{det} \cdot m \cdot B \tag{5.27}$$

where s_{det} is a constant characterizing the proportion of detritus sedimented per unit time.

We also assume an excretion of phosphorus by bacteria. The rate of this process Q_b is directly proportional to the concentration of bacteria and it depends on temperature

$$Q_b = q_b \cdot F_f^1(T) \cdot B \tag{5.28}$$

where q_b is a constant, and $F_f^1(T)$ is a function of temperature of the form (5.17).

The differential equation describing the rate of changes in the concentration of bacteria, after taking into account the consumption of bacteria by nonpredatory zooplankton, is finally of the form

$$\frac{dB}{dt} = G_b^{\max} F_f^1(T) F_b^2(D) \cdot B - G_{znp}^{\max} F_z^1(T) f_{znp}^2(B) \cdot Z_{np} - S_b - S_b^{sed} - Q_b \quad (5.29)$$

5.5. DETRITUS

Detritus gains and losses are partly due to the processes described above, that is, it is produced from not digested food remains of the two zooplankton trophic groups, from dead remains of all living components of the system, and from food provided for fish by man, and it is lost because of its consumption by nonpredatory zooplankton and as a result of its utilization by bacteria. So far only the process of detritus sedimentation has not been described.

Let us assume that a fixed proportion of detritus is sedimented per unit of time, which in this case means that it is lost from the system. This gives a directly proportional relationship between the rate of detritus sedimentation S_{det} and the concentration of detritus

$$S_{det} = s_{det} \cdot D \quad (5.30)$$

where s_{det} is a constant.

The differential equation describing changes in the concentration of detritus is thus of the form

$$\frac{dD}{dt} = S_f + S_b + S_{znp} + S_{zp} + (1 - A_{znp}) \cdot G_{znp} \cdot Z_{np} + (1 - A_{zp}) \cdot G_{zp} \cdot Z_p +$$

$$+ P_{fish} - G_{znp}^{\max} F_z^1(T) f_{znp}^3(D) Z_{np} - G_b \cdot B - S_{det} \quad (5.31)$$

where we have: S_f, S_b, S_{znp}, and S_{zp} — the mortality of phytoplankton, bacteria, nonpredatory zooplankton, and predatory zooplankton, respectively; A_{znp} and A_{zp} — coefficients of the assimilation efficiency on nonpredatory and predatory zooplankton, respectively, $G_{znp}^{\max} \ldots Z_{np}$ — the rate of detritus consumption by nonpredatory zooplankton, and $G_b \cdot B$ — the rate of detritus utilization by bacteria. The remaining symbols are defined in earlier sections.

5.6. DISSOLVED PHOSPHORUS

The source of dissolved phosphorus in the epilimnion are discussed in earlier sections. They involve the input with external loading of the lake, loading from deeper layers of the lake and the excretion of phosphorus by phytoplankton, bacteria, and the two trophic types of zooplankton. Phosphorus is lost from the system as a result of its utilization for phytoplankton production and also due to sinking. It is assumed that the rate of phosphorus sinking, S_p, is proportional to the concentration of phosphorus

$$S_p = s_p \cdot P \quad (5.32)$$

where s_p is a constant.

Thus, the equation describing the changes in phosphorus concentration is of the form

$$\frac{dP}{dt} = P_e + P_r + Q_f + Q_{zp} + Q_{znp} + Q_b - G_f \cdot F - S_p \tag{5.33}$$

where P_e is the rate of epilimnion loading connected with external loading of the lake, P_r is the rate of epilimnion loading from deeper layers of the lake, Q_f, Q_b, Q_{znp}, and Q_{zp} denote the excretion by phytoplankton, bacteria, nonpredatory zooplankton, and predatory zooplankton, respectively, $G_f \cdot F$ describes the rate of phosphorus utilization for phytoplankton production, and S_p is the rate of phosphorus sinking.

6. DESCRIPTION OF THE FUNCTIONING OF THE MODEL

For simulation purpose, calculations for each time step were started with computing temperature at water surface, the epilimnion depth, light intensity at the water surface, and coefficient of light extinction. Further computations involved the amounts of phosphorus reaching on the same day one litre of epilimnion water from deeper layers, from outside sources, and the loading of detritus due to fish farming. Then, using these values and the actual concentrations of phosphorus, phytoplankton, nonpredatory zooplankton, predatory zooplankton, bacteria, and detritus, we calculated the concentrations of phosphorus, phytoplankton, the two trophic types of zooplankton, bacteria, and detritus in the surface layer of the epilimnion in the next time step, by solving the respective sets of differential equations. Then we calculated the temperature and light intensity at a depth of 1 m and, like for the surface layer, using the values of the state variables from the current time step we computed the values of these variables in the next time step at a depth of 1 m.

Similarly, we calculated the values of the state variables at depths of 2, 3, ..., 6 m. Then we computed mean concentrations of phosphorus, phytoplankton, two trophic types of zooplankton, bacteria, and detritus at these seven depths. This was to simulate the process of natural mixing in the epilimnion and artificial mixing of the samples from the epilimnion, which were taken at 1-m intervals to the depth of 6 m and then put together into one container. These mean state variables were then used for calculating the values of state variables in the successive time step.

7. RESULTS OF THE SIMULATION

7.1. SELECTION OF PARAMETERS

Most of the over 20 parameters of this model were not directly known. Preliminary information on the values of these parameters was taken from J ø r g e n s e n (1979). But this was information on the ranges of these parameters rather than on their exact values.

Ultimately, the trial and error method was used to find the parameter values, paying attention that they lie within the originally assumed ranges. Parameter fitting was started at the lowest trophic level. First the equation describing changes in the concentrations of phytoplankton and phosphorus was solved. The parameters were fitted so that equilibrium concentrations were reached after a certain number of time steps. We attempted to get a certain excess of phytoplankton so that it could be used later by zooplankton. Then detritus and bacteria were added and treated in the same way, and again an attempt was made to reach an equilibrium state after some time. Finally, the two types of zooplankton were added to the set of equations. Final corrections to the parameter values were introduced when a complete set of equations

Table 5. Parameters of the model of the epilimnion of Lake Głębokie, estimated by simulation

Phosphorus:	Predatory zooplankton:
$A_f = 1.0$	$G_{zp}^{\max} = 0.65\,(\text{day}^{-1})$
$A_e = 1.0$	$K_p = 0.04\,(\text{l}\cdot\mu\text{g P}^{-1})$
$A_r = 0.65$	$A_{zp} = 0.6$
$S_p = 0.1\,(\text{day}^{-1})$	$q_{zp} = 0.04\,(\text{day}^{-1})$
	$m_{zp} = 0.01\,(\text{day}^{-1})$
Phytoplankton:	Bacteria:
$G_f^{\max} = 1.3\,(\text{day}^{-1})$	$G_b^{\max} = 2.5\,(\text{day}^{-1})$
$K_f = 8.0\,(\mu\text{g P}\cdot\text{l}^{-1})$	$g = 2.0$
$I^{\text{opt}} = 1464.4\,(\text{J}\cdot\text{cm}^{-2}\cdot\text{day}^{-1})$	$q_b = 0.005\,(\text{day}^{-1})$
$T_f^{\text{opt}} = 16\,(°\text{C})$	$m = 0.03$
$v_f = 0.004\,(°\text{C}^{-2})$	$m_b = 0.05\,(\text{day}^{-1})$
$q_f = 0.001\,(\text{day}^{-1})$	
$m_f = 0.15\,(\text{day}^{-1})$	
Nonpredatory zooplankton	Detritus:
$G_{znp}^{\max} = 1.25\,(\text{day}^{-1})$	$s_{det} = 0.3\,(\text{day}^{-1})$
$C_1 = 0.6$	
$C_2 = 0.3$	
$C_3 = 0.1$	
$K_n^1 = 0.05\,(\text{l}\cdot\mu\text{g P}^{-1})$	
$K_n^2 = 0.01\,(\text{l}\cdot\mu\text{g P}^{-1})$	
$K_n^3 = 0.2\,(\text{l}\cdot\mu\text{g P}^{-1})$	
$T_z^{\text{opt}} = 20\,(°C)$	
$v_z = 0.007\,(°\text{C}^{-2})$	
$A_{znp} = 0.5$	
$q_{znp} = 0.03\,(\text{day}^{-1})$	
$m_{znp} = \begin{cases} 0.01\,(\text{day}^{-1}) \text{ at } t < 136 \text{ i } t > 290 \\ 0.05\,(\text{day}^{-1}) \text{ at } 136 \leqslant t \leqslant 290 \end{cases}$	

was obtained. At each stage of the choice of parameters the results of simulation were compared with empirical data. This is a long and labour-consuming procedure. It required several hundreds runs of the model.

The ultimate set of the parameters of the model of phosphorus cycling in the epilimnion of Lake Głębokie is shown in Table 5. The characteristic propertities of this parameter set are as follows.

The whole dissolved phosphorus reaching the epilimnion from external loading of the lake and detritus from fish farming are cycling in the system ($A_e = 1, A_{fish} = 1$), but it is assumed that only 65% of the phosphorus coming from deeper layers is in the form that can be cycle in the system ($A_r = 0.65$). It is assumed that 10% of the dissolved phosphorus is lost from the epilimnion ($s_p = 0.1$ day^{-1}).

The maximum daily $P:B$ for the phytoplankton equals 1.3 ($G_f^{max} = 1.3$ day^{-1}). One-half of the maximum phytoplankton growth rate is reached at the concentration of dissolved phosphorus equal to 8 μg P·l^{-1} ($K_f = 8$ μg P·l^{-1}). Phytoplankton mortality not due to the consumption by zooplankton and to sedimentation equals to 15% of the phytoplankton biomass per unit time ($m_f = 0.15$ day^{-1}). The excretion of phosphorus by living phytoplankton is low. In this way only 0.001 of the phytoplankton biomass is lost per unit of time ($q_f = 0.001$ day^{-1}). The optimum light intensity ($I^{opt} = 1464.4$ J·cm^{-2}·day^{-1}) has such a value that the actual incident light intensity exceeds this value during the period from May to August.

The maximum daily rate of consumption by nonpredatory zooplankton equals 1.25 of its biomass ($G_{znp}^{max} = 1.25$ day^{-1}). At the maximum concentrations of all food categories, the diet of zooplankton will be made up of the phytoplankton in 60%, detritus in 30%, and bacteria in 10% ($c_1 = 0.6, c_2 = 0.1, c_3 = 0.3$). Proportions among maximum concentrations of bacteria, phytoplankton, and detritus are approximately such that bacteria > phytoplankton > detritus (bacteria of the order of several hundreds, phytoplankton several tens, and detritus several μg·l^{-1}), thus the values of $K_n^1 = 0.05$ l·μg P^{-1}, $K_n^2 = 0.01$ l·μg P^{-1}, and $K_n^3 = 0.2$ l·μg P^{-1} are so selected that the consumption by nonpredatory zooplankton is equally sensitive to changes in these three sources of food. It is assumed that nonpredatory zooplankton assimilated 50% of the food consumed ($A_{znp} = 0.5$). A time-dependent mortality of nonpredatory zooplankton is assumed. The ratio of the maximum to minimum mortality over the season equals 5 (see Table 5). It is assumed that the zooplankton of this trophic type looses a maximum of 3% of the biomass per unit time due to excretion ($q_{znp} = 0.03$ day^{-1}).

The maximum per capita rate of consumption by predatory zooplankton equals about half of that for nonpredatory zooplankton ($G_{zp}^{max} = 0.65$ day^{-1}). Predatory zooplankton has a slightly higher food assimilation ($A_{zp} = 0.6$), a constant mortality whis is equal to the lowest mortality of nonpredatory zooplankton ($m_{zp} = 0.01$ day^{-1}), and a slightly higher maximum excretion per unit biomass ($q_{zp} = 0.04$ day^{-1}).

Bacteria are characterized by the highest per capita rate of gross increase ($G_b^{max} = 2.5$ day^{-1}). The rate of bacterial growth rather strongly depends on the concentration of bacteria, as the parameter $g = 2.00$. The bacterial mortality not due to consumption by zooplankton equals 5% ($m_b = 0.05$ day^{-1}). Only 3% of the bacterial biomass is permanently bound with particulate detritus, and, consequently, is sedimented ($m = 0.03$). Merely 0.5% of the living bacterial biomass is lost due to phosphorus excretion ($q_b = 0.005$ day^{-1}).

It is assumed that 30% of the detritus is lost from the system per unit time due to sedimentation ($s_{det} = 0.3$ day^{-1}).

Optimum temperatures in the temperature-dependent functions are assumed to be such that in the middle of the season (from May-June to September-early October) water temperatures in the epilimnion are higher than the optimum ($T_f^{opt} = 16°C$ and $T_z^{opt} = 20°C$). The values of the parameters $v_f = 0.004°C^{-2}$ and $v_z = 0.007°C^{-2}$ (occurring in the temperature-dependent functions are assumed after S t r a š k r a b a 1976).

7.2. SOLVING THE EQUATIONS OF THE MODEL

The set of differential equations describing state variables of the model was solved by the Runge-Kutta method of order four. The initial values are the concentrations of dissolved phosphorus, phytoplankton, and two trophic types of zooplankton measured on 11 March, 1976 (day 71 of the year, see Tab. 1). The initial concentration of bacteria is assumed to be 20 μg P·l^{-1}, and that of detritus 2.35 μg P·l^{-1}, the latter being the annual mean.

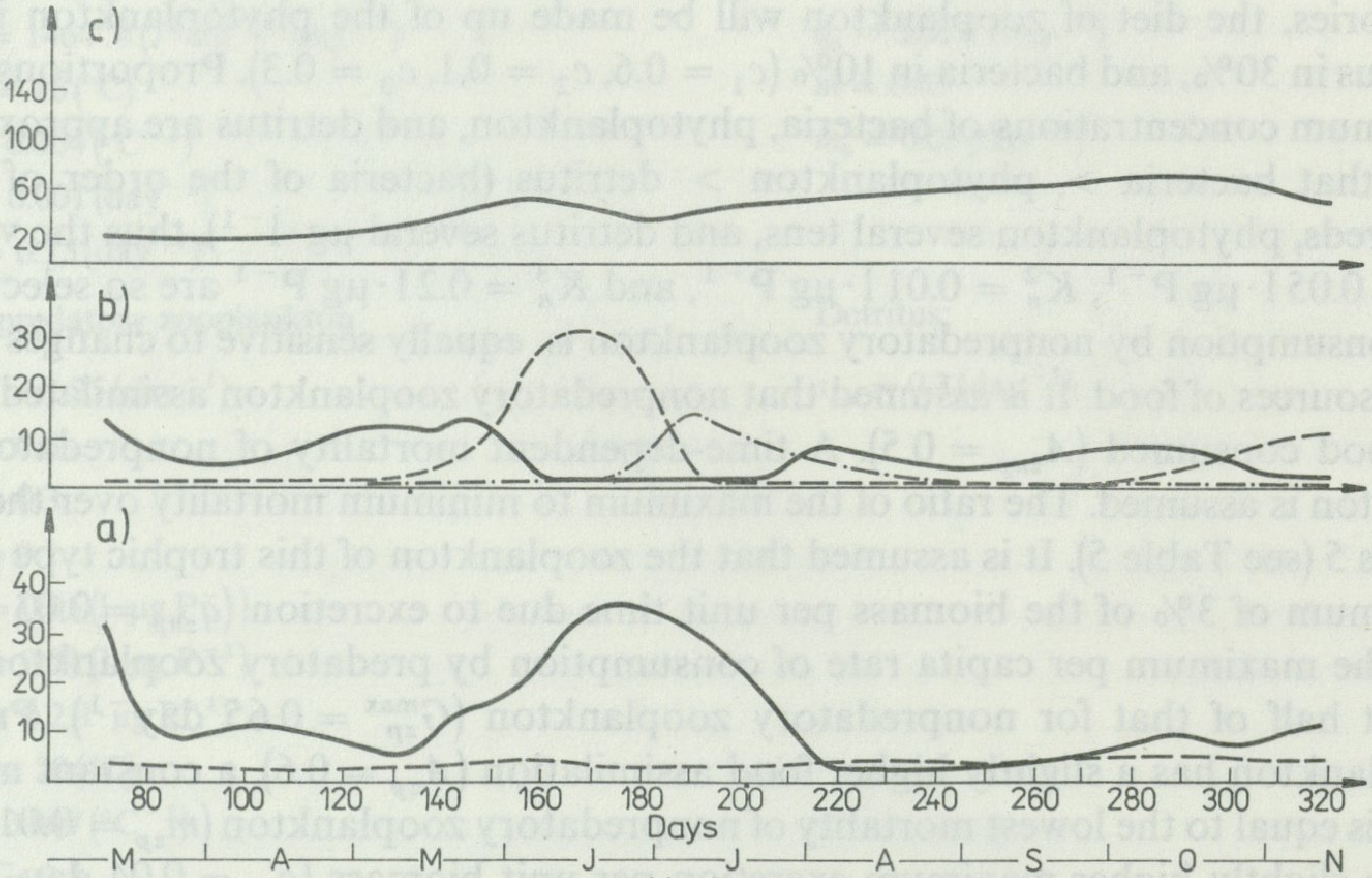

Fig. 10. Results of simulation

a — solid line illustrates the concentration of dissolved phosphorus, and dashed line the concentration of detritus; b — solid line represents the concentration of phytoplankton, dashed line the concentration of nonpredatory zooplankton, and dashed and dotted line is the concentration of predatory zooplankton; c — concentration of bacteria

Figure 10 shows changes over time in the values of all the variables of the system, as calculated from equations of the model. These are mean values at the depths of 0 m, 1 m, ..., 6 m. In Figures 11 – 17, empirical data are compared with the results of simulation for successive state variables.

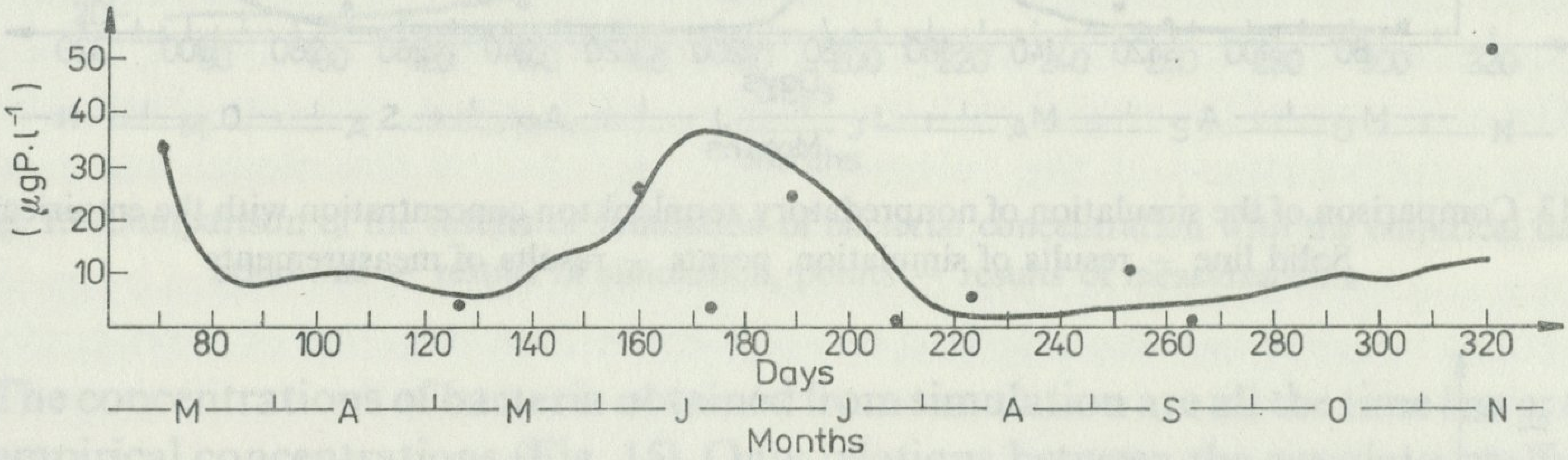

Fig. 11. Comparison of the simulation of phosphorus concentration with the empirical data
Solid line – results of simulation, points – results of measurements

The model simulates rather well the empirical values of the concentration of dissolved phosphorus (Fig. 11). Initially low concentrations are increased in May, June, and July, following the empirical data. The model does not simulate a violent decrease in the concentration of phosphorus that took place on 22 June, as indicated by the measurements, that is, in the period when the simulated phosphorus concentrations reached the highest value. In the second half of the season, small concentrations measured in the lake correspond to small concentrations obtained from the simulation. At the end of the season, the concentration of dissolved phosphorus measured in the lake considerably increased. The results of the simulation also increased at the end of the season but to a lower degree, and, consequently, the simulated concentration of dissolved phosphorus is much lower than the empirical value.

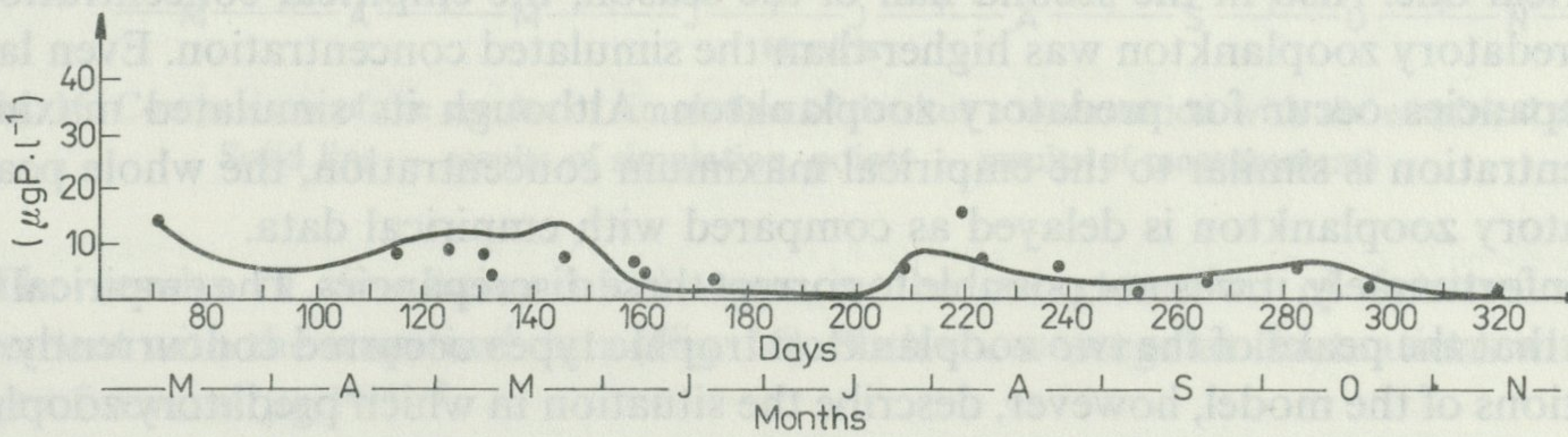

Fig. 12. Comparison of the simulation of phytoplankton concentration with the empirical data
Solid line – results of simulation, points – results of measurements

An equally good fit was obtained for changes in the concentration of phytoplankton (Fig. 12). In spring there was no clear phytoplankton bloom as indicated by both the simulation and the empirical results. A small increase in the phytoplankton concentration observed on the turn of July in the lake was successfully simulated, but the maximum phytoplankton concentration obtained from simulation was not so high as the empirical value.

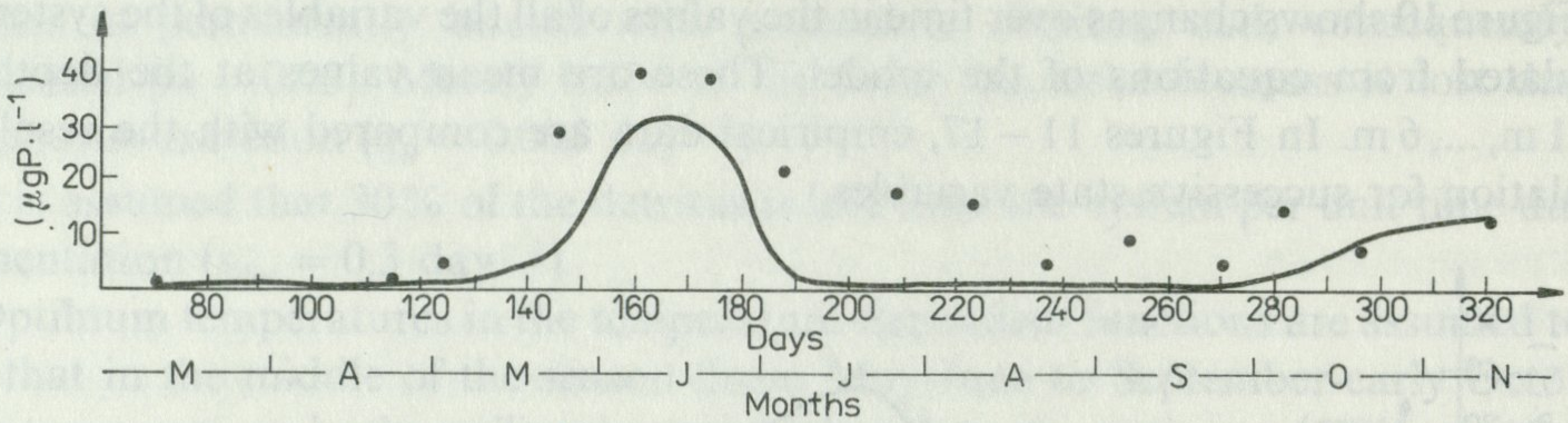

Fig. 13. Comparison of the simulation of nonpredatory zooplankton concentration with the empirical data
Solid line — results of simulation, points — results of measurements

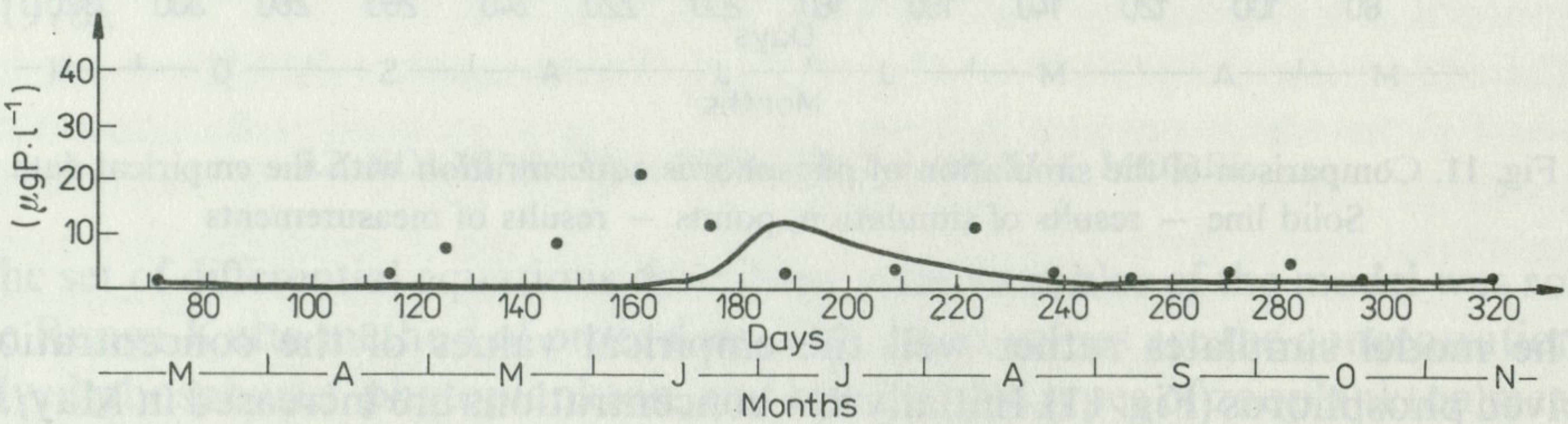

Fig. 14. Comparison of the results of simulation of predatory zooplankton concentration with the empirical data
Solid line — results of simulation, points — results of measurements

Larger discrepancies emerge when we compare the results of the simulation of changes in the concentrations of the two trophic types of phytoplankton with the empirical data (Figs. 13, 14). The simulated maximum of the concentration of nonpredatory zooplankton is lower and shorter in time than the empirical maximum. However, the simulated maximum appeared more or less at the same time as the empirical one. Also in the second half of the season, the empirical concentration of nonpredatory zooplankton was higher than the simulated concentration. Even larger discrepancies occur for predatory zooplankton. Although its simulated maximum concentration is similar to the empirical maximum concentration, the whole peak of predatory zooplankton is delayed as compared with empirical data.

Unfortunately, it was not possible to correct these discrepancies. The empirical data show that the peaks of the two zooplankton trophic types occurred concurrently. The equations of the model, however, describe the situation in which predatory zooplankton increases by consuming nonpredatory zooplankton, that is, like in a common prey-predator system, the peak of prey concentration has to precede the peak of predator concentration. During simulation an attempt was made to minimize discrepancies by obtaing the peak of predatory zooplankton as soon as only the results of simulations of other variables made this possible. The attempts to increase concentrations of the two zooplankton trophic types led, through increased excretion, to a considerable increase in the concentration of dissolved phosphorus, and to delaying the characteristic phytoplankton maximum on the turn of July. This produced a large discrepancy with respect to the empirical data.

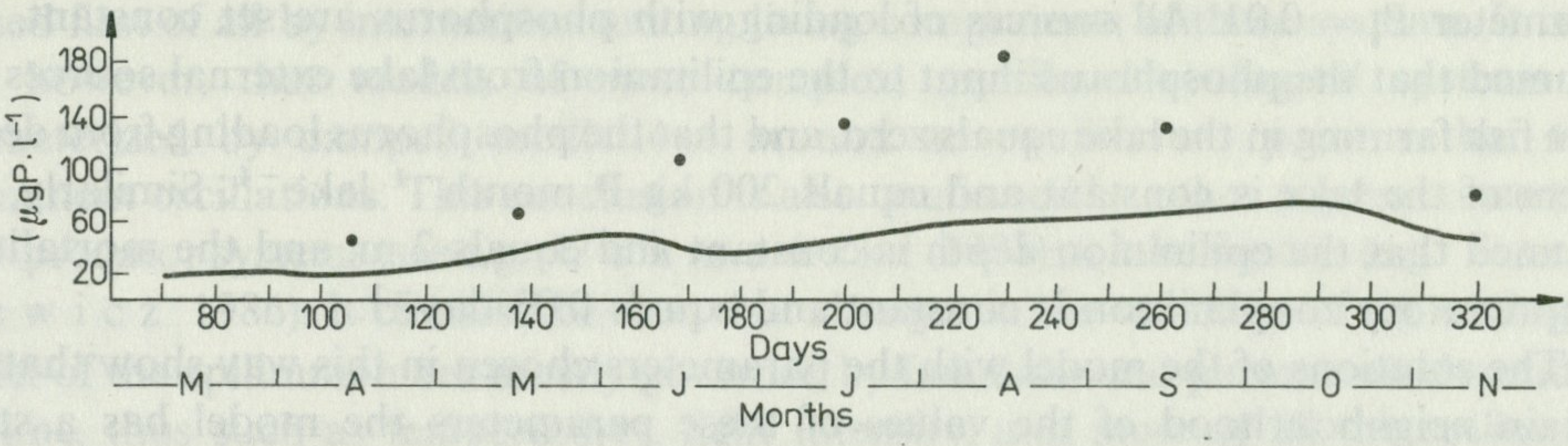

Fig. 15. Comparison of the results of simulation of bacterial concentration with the empirical data
Solid line — results of simulation, points — results of measurements

The concentrations of bacteria obtained from simulation are all the time lower than the empirical concentrations (Fig. 15). Only relations between the simulated values of bacterial concentration and concentrations of the other variables are similar to those between the empirical concentrations — concentrations of bacteria are the highest. Attempts at increasing the concentrations of bacteria introduced much disorder to the model. Practically, all the other variables failed to resemble the empirical data. The very smooth course of the empirical data for bacteria implies that they were almost independent on changes in the other components of the system. For this reason we resigned from continuing the attempts at increasing the importance of bacteria in the model by increasing their numbers.

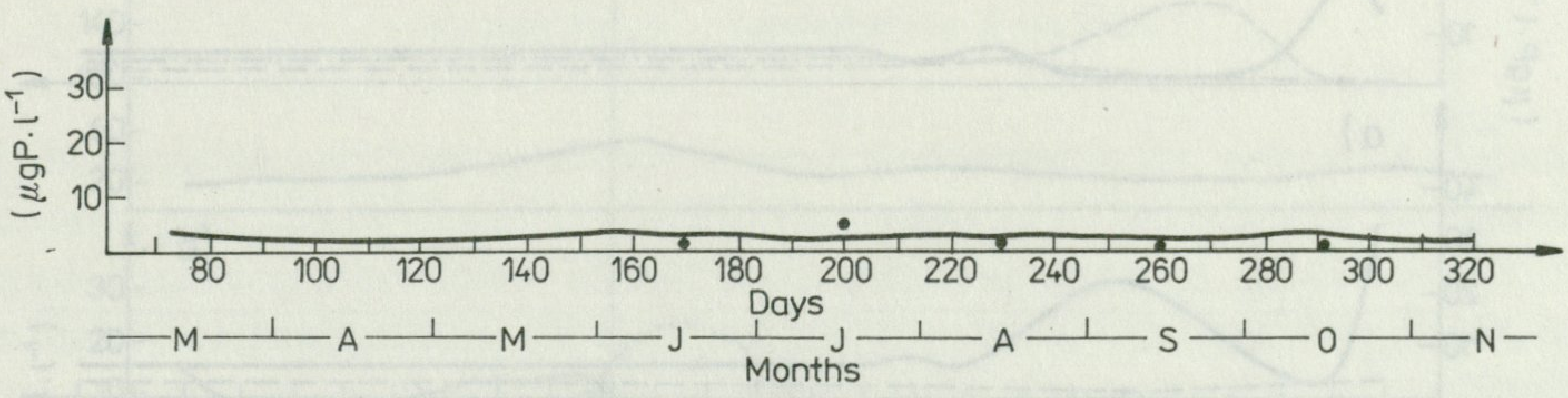

Fig. 16. Comparison of the results of simulation of detritus concentration with the empirical data
Solid line — results of simulation, points — results of measurements

The results of simulation of changes in the concentration of detritus are in agreement with the empirical data (Fig. 16). Both show irregular fluctuations within a range of several μg P·l^{-1}.

8. STABILITY ANALYSIS

The solutions of the model equations have been examined in the situation when all the time-dependent parameters and the other functions of time occurring in the model take constant values.

It is assumed that the epilimnion temperature is constant over the season and equals 16°C, also the incident light intensity is constant and equals 1673.6 J·cm^{-2}·day^{-1}, and parameter $P_v = 0.01$. All sources of loading with phosphorus are set constant. It is assumed that the phosphorus input to the epilimnion from lake external sources and from fish farming in the lake equals zero, and that the phosphorus loading from deeper layers of the lake is constant and equals 200 kg P month^{-1} lake^{-1}. Similarly, it is assumed that the epilimnion depth is constant and equals 2 m, and the mortality of nonpredatory zooplankton is constant and equals 0.03 day^{-1}.

The solutions of the model with the parameters chosen in this way show that in a certain neighbourhood of the values of these parameters the model has a stable equilibrium point of the focus type. All the variables are reaching stable values after damped oscillations (Fig. 17). The highest equilibrium value was reached by bacteria. The other variables are characterized by much lower equilibria. All of them, except for bacteria, have similar values. The simulation runs show that the equilibrium state is established after about 100 days.

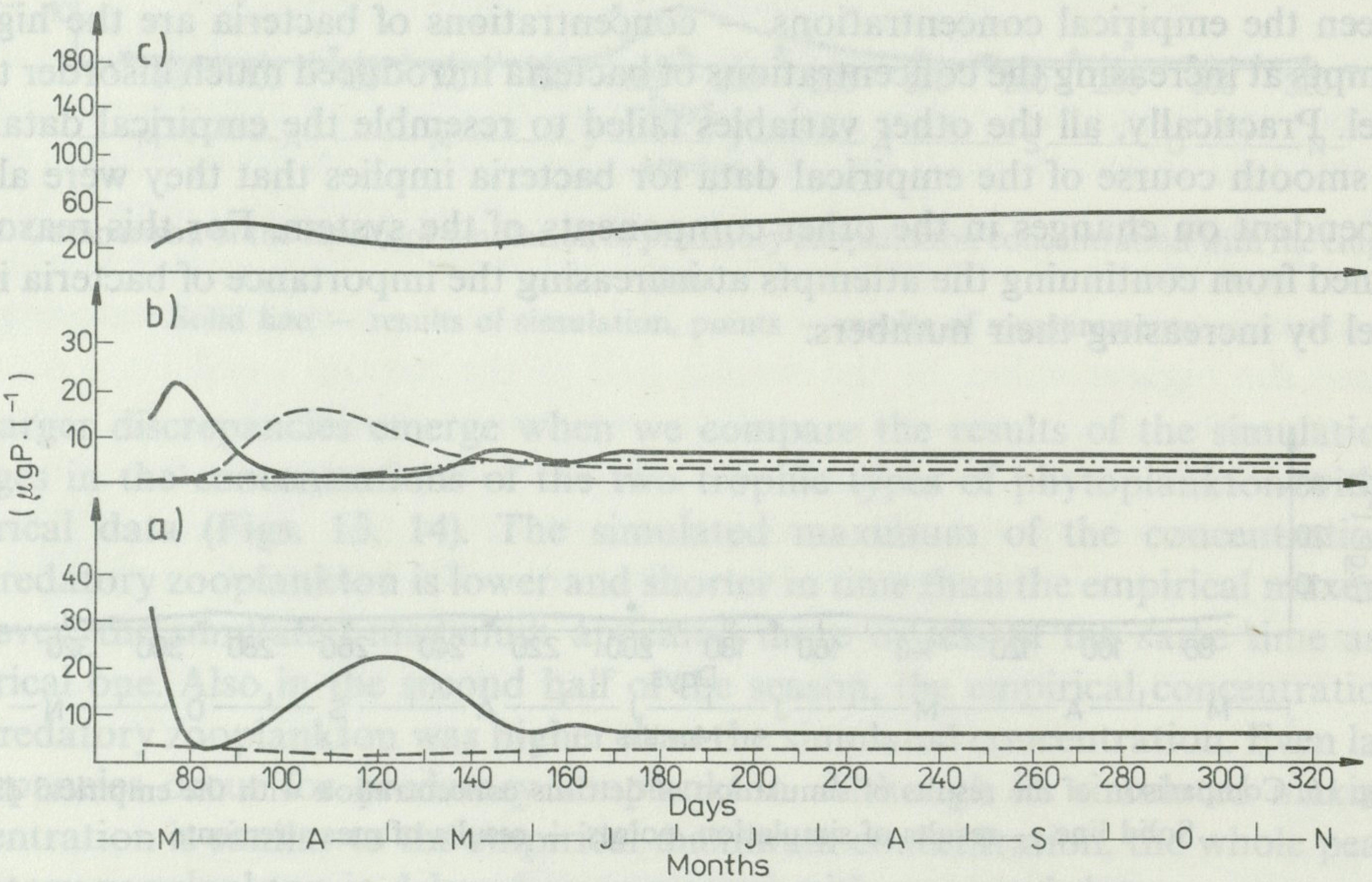

Fig. 17. Stability analysis: solutions to the equations of the model with constant values of all parameters and functions of time

a — continues line represents the concentration of dissolved phosphorus, dashed line the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

Equilibrium values depend on the parameters of the model. A reduction of the constant value of the epilimnion loading with phosphorus from deeper layers of the lake lowers the equilibrium values for all the variables, the greatest changes being observed for bacteria.

The analysis of stability allows the following more general conclusions. Intuition prompts that the prey-predator system should be characterized by permanent oscillations. It is also expected that changes in the variables of lake ecosystem should be caused first of all by interactions among living components of these systems. It turns out, however, that models of more complex, multilevel ecological systems are characterized by damped oscillations around an equilibrium point rather than permanent oscillations. This conclusion is also confirmed by other papers concerning prey-predator systems (see e.g. Uchmański 1983) or lake models (e.g. Szeligiewicz 1986). It can also be seen that changes in the variables of the ecological model of the epilimnion are mostly governed by functions and parameters dependent on time, thus such as temperatures, light intensity, and most of all the epilimnion loading from different sources. Changes in these factors over time account for modifying equilibrium values for variables of the system. As indicated by the results of simulation shown in Figure 17, the process of attaining the equilibrium state takes about three months. But since over a three-month period many parameters are changing their values, the variables of the model will "pursue" the permanently escaping equilibrium values, and, in addition, changes resulting from interactions among components of the system will be superimposed on these processes.

9. RESULTS OF SOME NUMERICAL EXPERIMENTS

9.1. ELIMINATION OF FISH FARMING IN THE LAKE

The solutions of the model equations at $P_{fish} = 0$ for all t are shown in Figure 18.

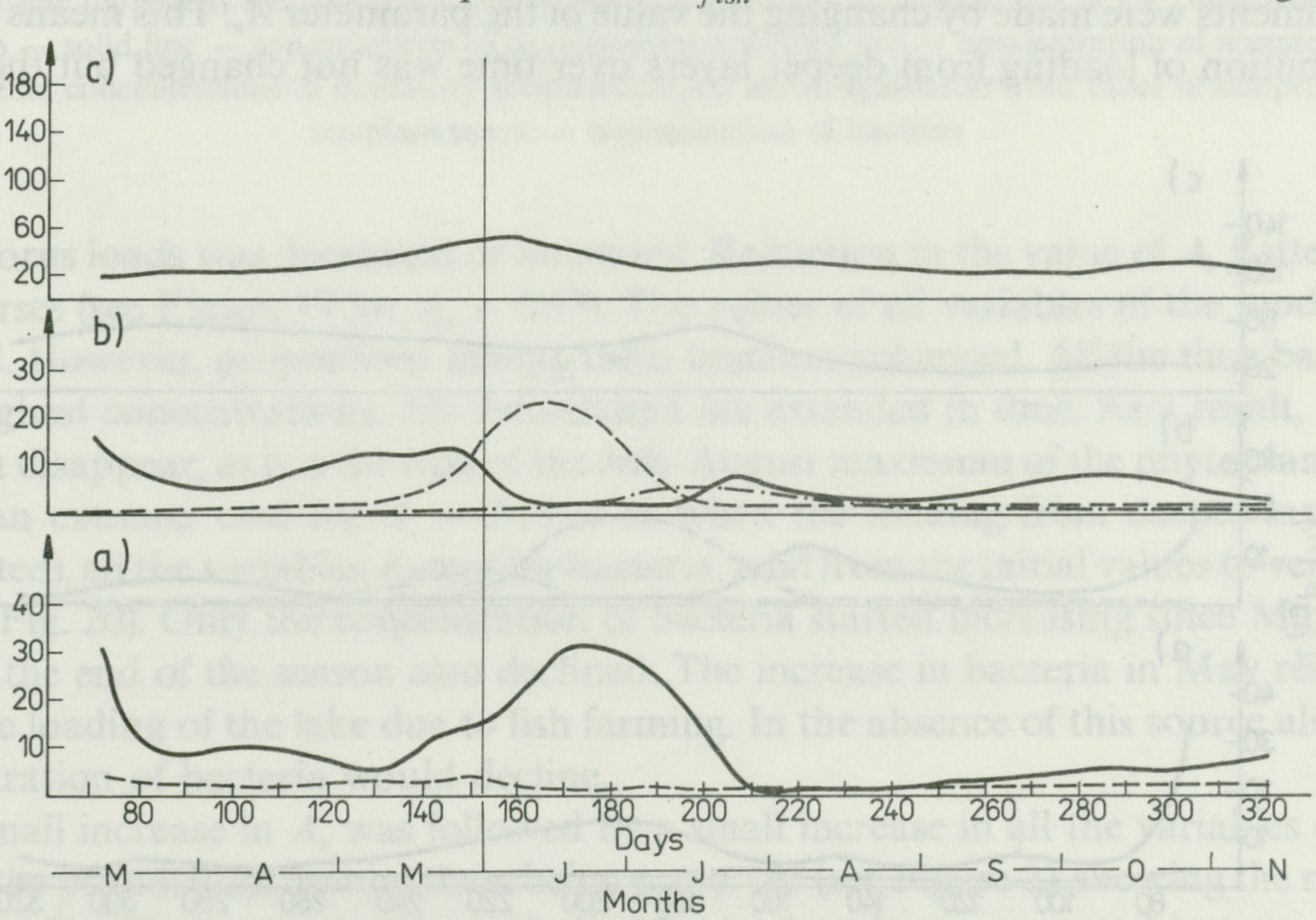

Fig. 18. Numerical experiments: consequences of the elimination of fish farming

Vertical line denotes the time when typically artificial food supplying for fish was started; it was continued beyond the simulation time. In the numerical experiment it was assumed that this source of detritus equals zero.

a – solid line represents the concentration of dissolved phosphorus, dashed line the concentration of detritus; b – solid line – concentration of phytoplankton, dashed line – concentration of nonpredatory zooplankton, dashed and dotted line – concentration of predatory zooplankton; c – concentration of bacteria

Phosphorus supplied to the lake from May to October in the form of food for fish and their faeces loads the detritus pool. The elimination of this source is thus followed, as Figure 18 shows, by a decline in the concentration of detritus, which persists until the end of the season.

The concentration of bacteria is largely reduced as detritus is the source of food for them. The first maximum of the bacteria concentration on the turn of May remains unchanged, but later the concentration of bacteria is reduced even to one-third. From July, practically it becomes fixed with only slight fluctuations around 20 μg $P \cdot l^{-1}$. There is no the second, wide peak of bacterial concentration, present in September and October in the simulation with real values of P_{fish}.

The concentrations of the two trophic types of zooplankton are reduced, especially those of the predatory zooplankton, and for this reason the summer peak of phytoplankton appears 10 days earlier, on the turn of July. Also the concentration of dissolved phosphorus slightly declines.

9.2. CHANGES IN THE EPILIMNION LOADING WITH PHOSPHORUS

In earlier simulations it is assumed that 65% of the phosphorus supply from lower layers of the lakes loads the pool of dissolved phosphorus ($A_r = 0.65$). Numerical experiments were made by changing the value of the parameter A_r. This means that the distribution of loading from deeper layers over time was not changed but the size of

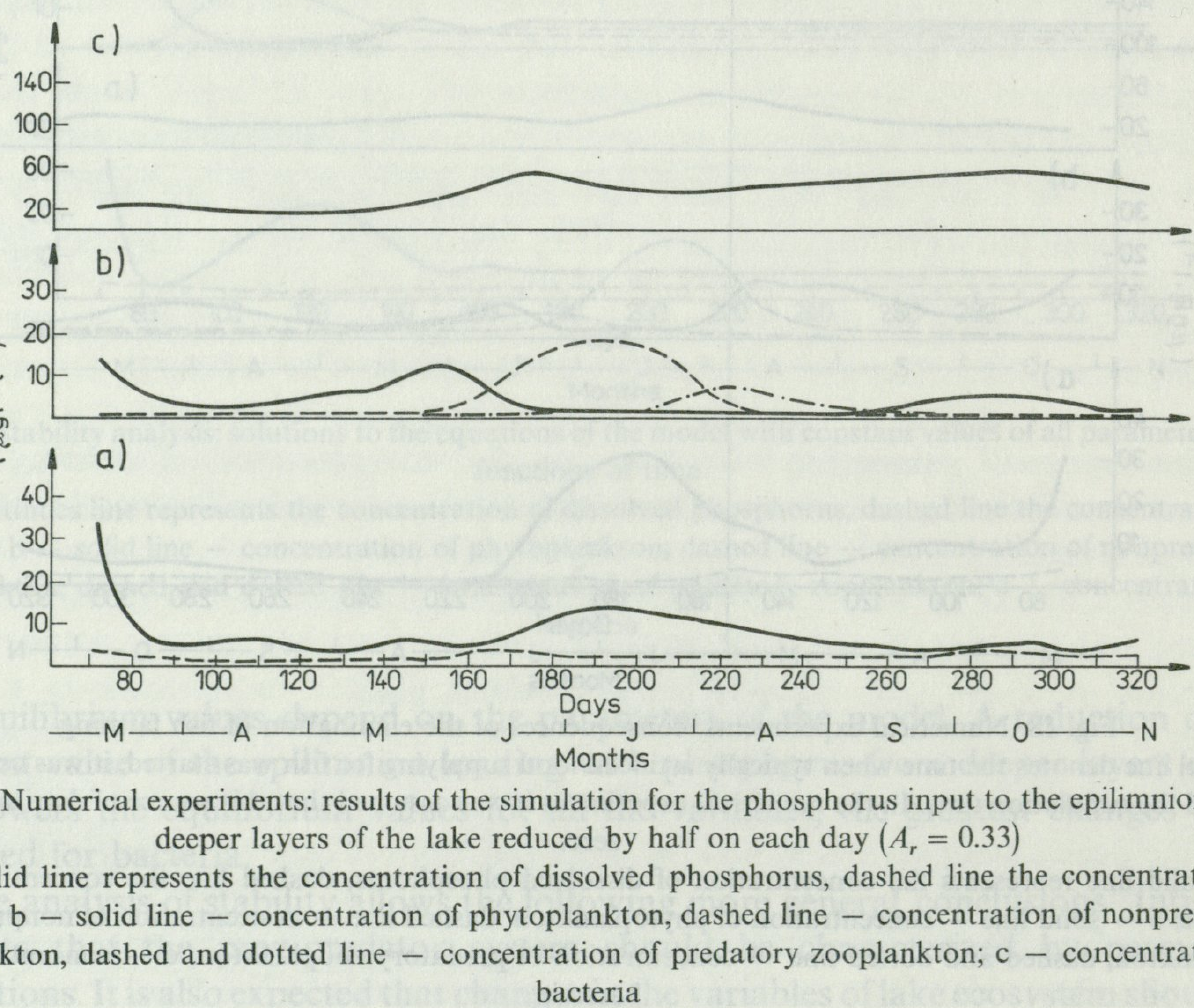

Fig. 19. Numerical experiments: results of the simulation for the phosphorus input to the epilimnion from deeper layers of the lake reduced by half on each day ($A_r = 0.33$)

a – solid line represents the concentration of dissolved phosphorus, dashed line the concentration of detritus; b – solid line – concentration of phytoplankton, dashed line – concentration of nonpredatory zooplankton, dashed and dotted line – concentration of predatory zooplankton; c – concentration of bacteria

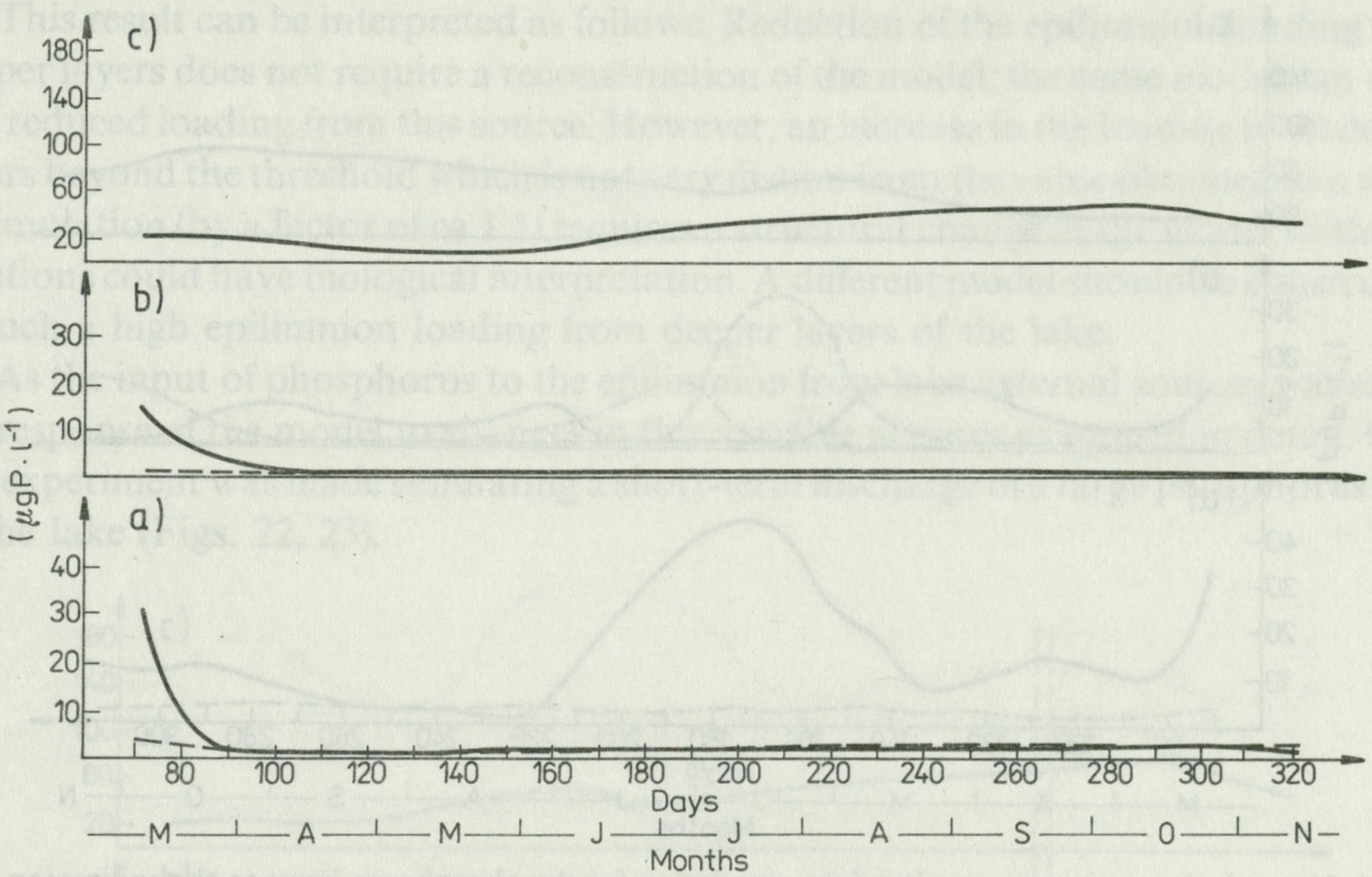

Fig. 20. Numerical experiments: results of simulation in the absence of epilimnion loading with dissolved phosphorus from deeper layers of the lake ($A_r = 0.0$)
a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton; concentrations of predatory zooplankton are indistinguishable from those of nonpredatory zooplankton; c — concentration of bacteria

phosphorus loads was decreased or increased. Reduction in the value of A_r flattens all the courses (see Figure 19 for $A_r = 0.33$). The values of all variables of the model are reduced. However, proportions among them remain unchanged. All the time bacteria have highest concentrations. All the maxima are extended in time. As a result, lower maxima disappear, as it is the case of the July-August maximum of the phytoplankton.

At an extreme case for $A_r = 0$ (that is, when the loading from deeper layers is eliminated), all the variables, except for bacteria, tend from the initial values to very low values (Fig. 20). Only the concentration of bacteria started increasing since May, but toward the end of the season also declined. The increase in bacteria in May resulted from the loading of the lake due to fish farming. In the absence of this source also the concentration of bacteria would decline.

A small increase in A_r was followed by a small increase in all the variables of the model, the proportions among them being preserved (see Figure 21 showing the results at $A = 0.8$). The concentration of dissolved phosphorus was subject to most remarkable changes. No larger shifts in time of the maximum values of the variables were observed.

But already at $A_r = 1.0$, that is, when the total phosphorus input from deeper layers is included to cycling, the solutions of the model start taking values without biological interpretation. First the concentration of phytoplankton and then of other variables becomes negative.

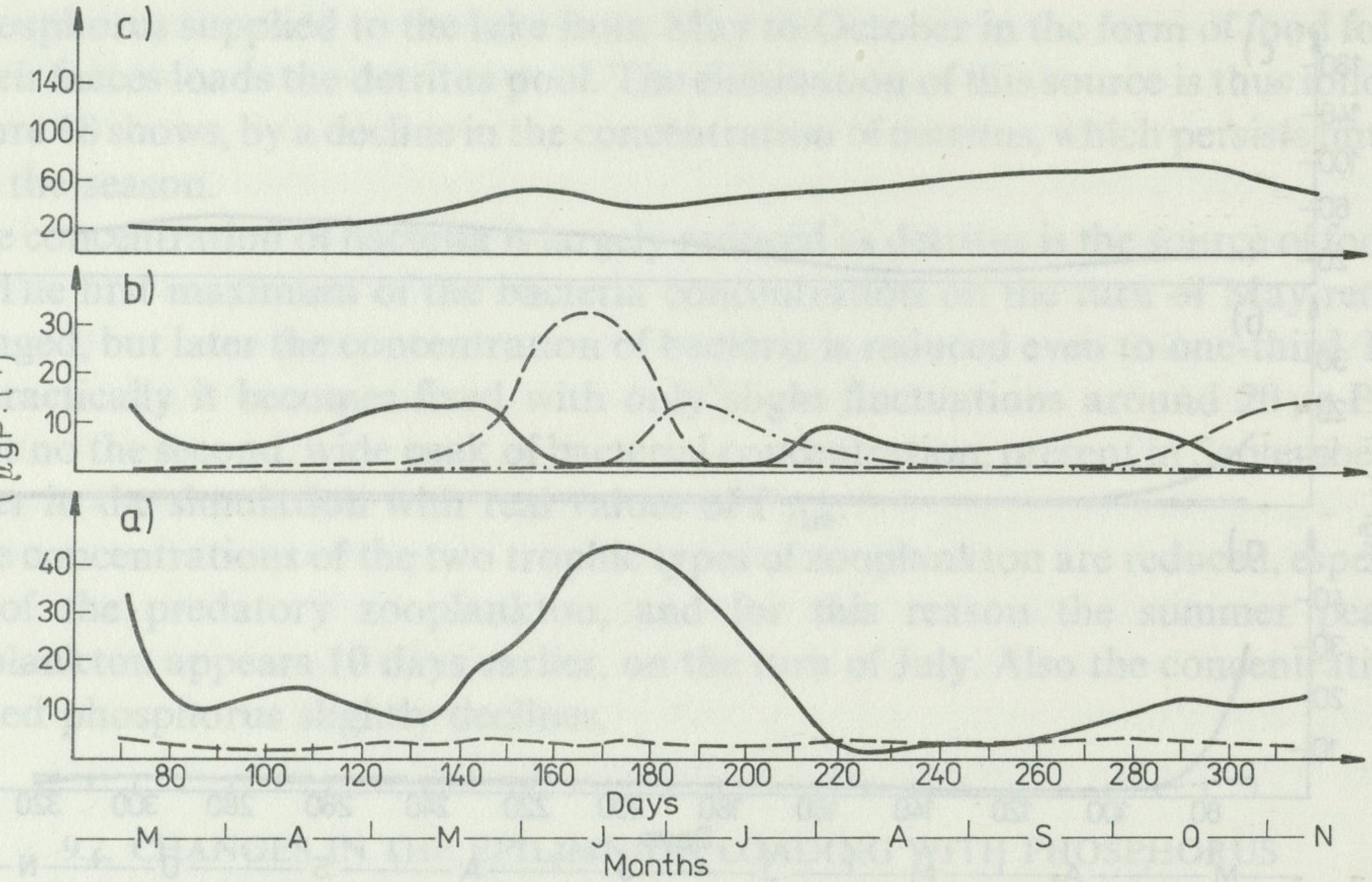

Fig. 21. Numerical experiments: results of the simulation for the phosphorus input to the epilimnion from deeper layers of the lake increased on each day ($A_r = 0.80$)
a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

Fig. 22. Numerical experiments: results of simulation of the effects of a three-day discharge of phosphorus on days 210 to 213 (the period of discharge is indicated by two perpendicular lines)
a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

This result can be interpreted as follows. Reduction of the epilimnion loading from deeper layers does not require a reconstruction of the model; the same model can work at a reduced loading from this source. However, an increase in the loading from deeper layers beyond the threshold which is not very distant from the value obtained as a result of simulation (by a factor of ca 1.5) requires a structural change in the model so that its solutions could have biological interpretation. A different model should be constructed at such a high epilimnion loading from deeper layers of the lake.

As the input of phosphorus to the epilimnion from lake external sources was small, the response of the model to changes in this variable was not examined in detail. Only one experiment was made simulating a short-term discharge of a large phosphorus load to the lake (Figs. 22, 23).

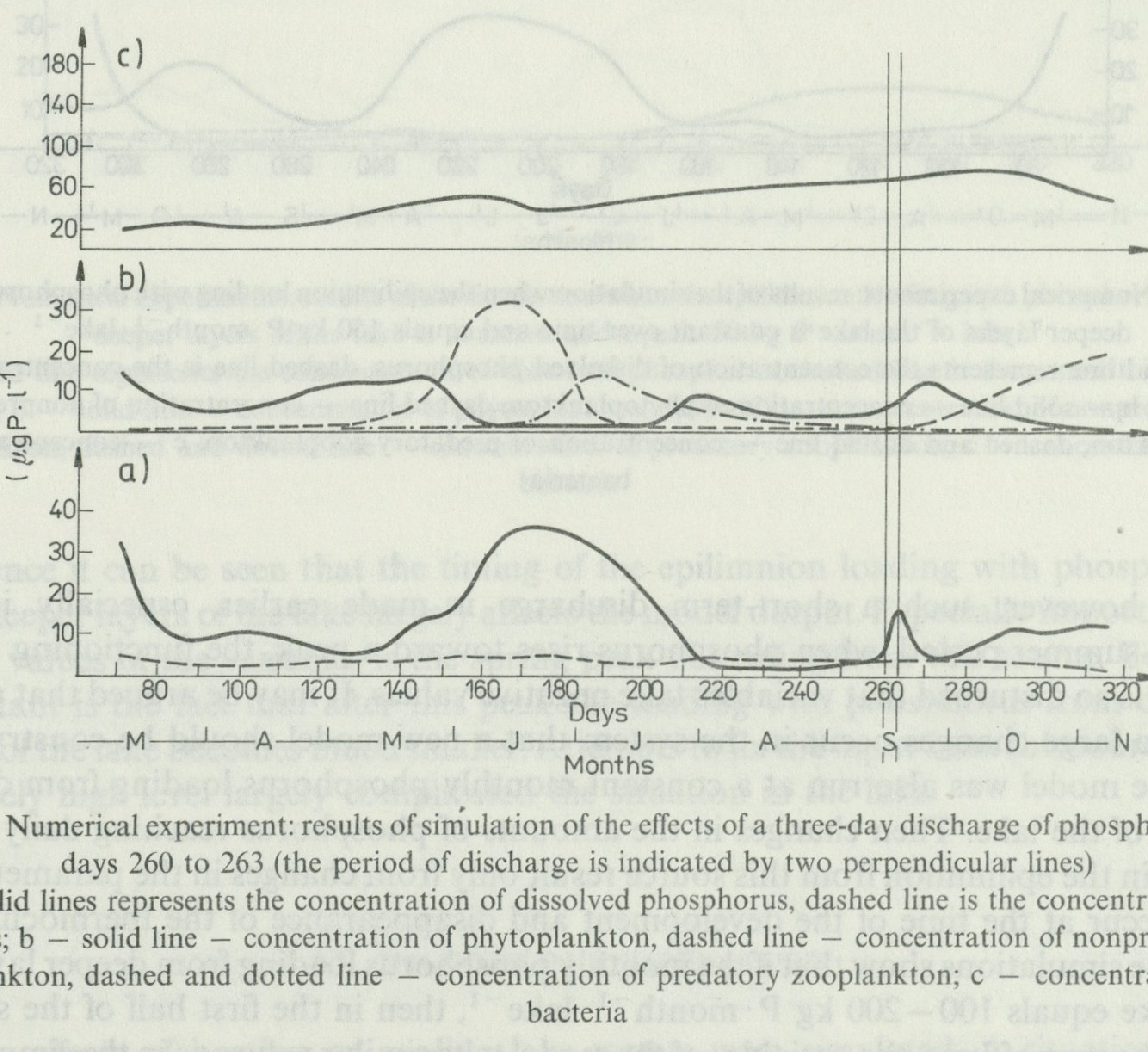

Fig. 23. Numerical experiment: results of simulation of the effects of a three-day discharge of phosphorus on days 260 to 263 (the period of discharge is indicated by two perpendicular lines)
a — solid lines represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

In this experiment a phosphorus load of 10 kg was supplied to the lake each day over three-day periods in different parts of the season. Simulations show that if this takes place in the second part of the season (starting with July — see Figures 22 and 23 showing the results of phosphorus discharge from days 210 and 260, respectively), then the concentration of dissolved phosphorus increases, this being followed by an increase in the concentrations of phytoplankton, bacteria, and then two trophic types of zooplankton. After about one month or earlier the concentrations of phytoplankton and dissolved phosphorus (the latter even sooner) decrease to the earlier values. The response of nonpredatory zooplankton is most delayed.

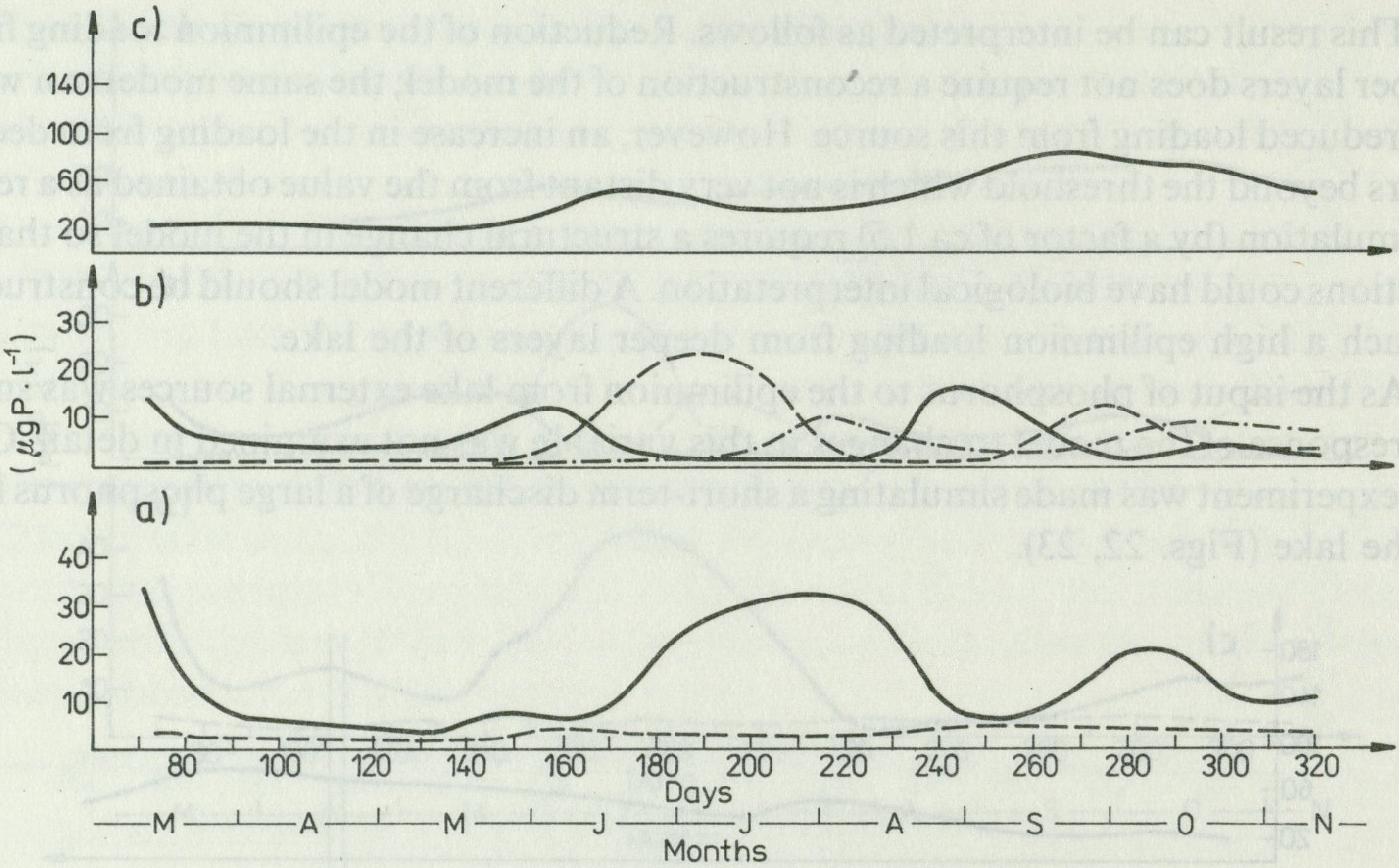

Fig. 24. Numerical experiments: results of the simulation when the epilimnion loading with phosphorus from deeper layers of the lake is constant over time and equals 150 kg P · month^{-1} · lake^{-1}. a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

If, however, such a short-term discharge is made earlier, especially in the spring-summer period, when phosphorus rises toward a peak, the functioning of the model is so disturbed that variables take negative values. It may be argued that at this time so large changes occur in the system that a new model should be constructed.

The model was also run at a constant monthly phosphorus loading from deeper layers of the lake. Then changes in the amounts of phosphorus reaching daily 1 l of water in the epilimnion from this source result only from changes in the parameter P_v, and occur at the time of the development and disappearance of the thermocline.

The simulations show that if the monthly phosphorus loading from deeper layers of the lake equals 100 – 200 kg P · month^{-1} · lake^{-1}, then in the first half of the season until the turn of June, the variables of the model take similar values as in the simulation with actual loading from this source (see Figure 24 for loading equal to 150 kg P · month^{-1} · lake^{-1}). This is due to the fact that such a loading of the epilimnion corresponds to the actual loading from deeper layers in this period. However, in the second part of the season, when the actual loading from this source is much lower and concentrations take small, almost fixed values, in simulations at constant loading from deeper layers, a new series of oscillations appears for all the variables, though with a little lower amplitudes. This picture becomes distorted at a low, fixed loading from deeper layers of the lake, for example, of the order of 50 kg P · month^{-1} · lake^{-1} (Fig. 25). Then the peaks of all the variables become wide and low.

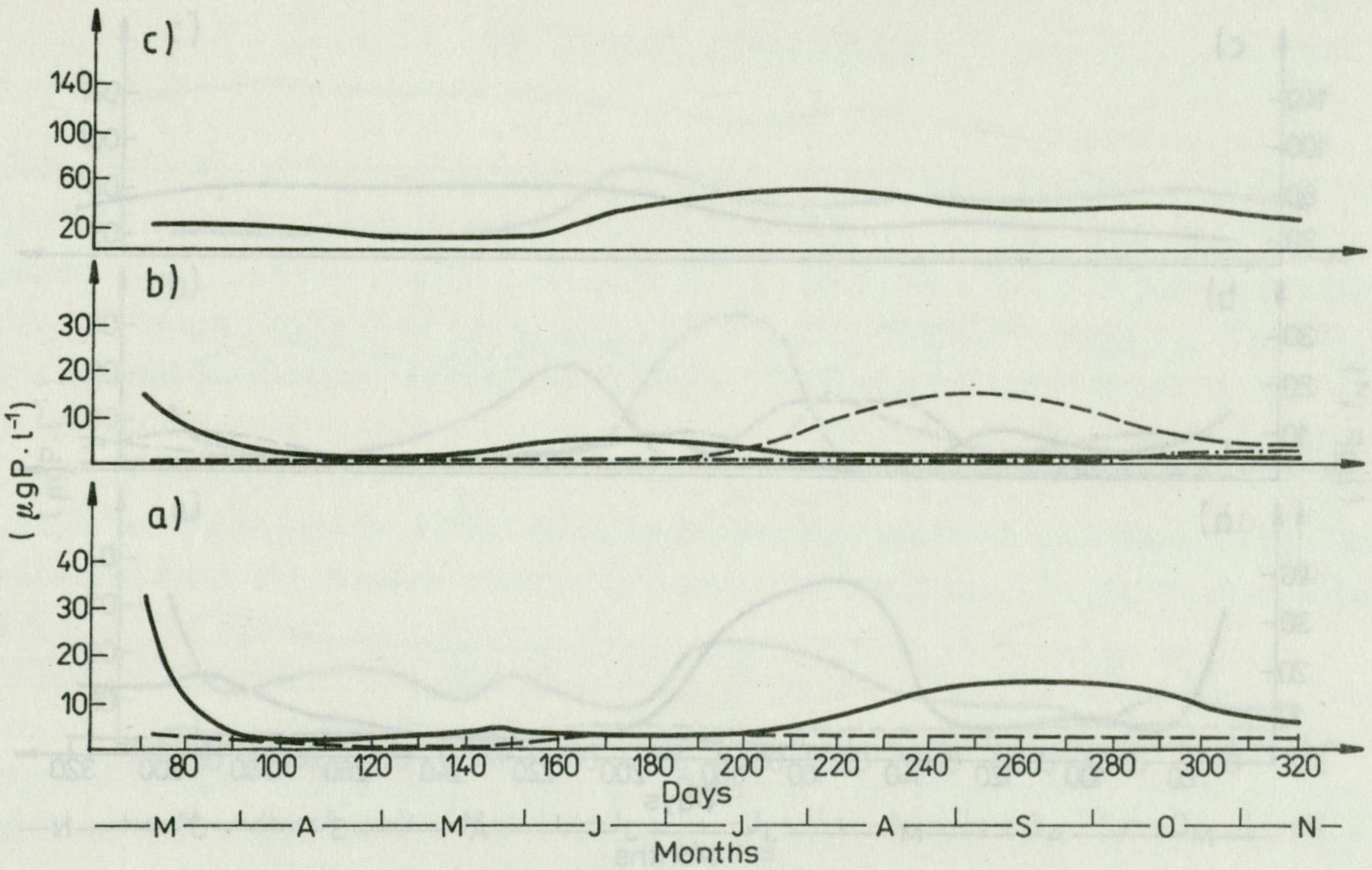

Fig. 25. Numerical experiments: results of the simulation when the epilimnion loading with phosphorus from deeper layers of the lake is constant and equals 50 kg P · month^{-1} · lake^{-1}

a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

Hence it can be seen that the timing of the epilimnion loading with phosphorus from deeper layers of the lake largely affects the model output. Especially important to actual values of the variables is the spring peak of loading from this source. Equally important is the fact that after this peak the loading with phosphorus from deeper layers of the lake becomes much smaller. Attempts to fix the input from this source at a relatively high level largely complicated the situation in the lake.

9.3. CHANGES IN TEMPERATURE

The effects of heating or cooling lake waters were simulated. A situation was considered when the temperature of the epilimnion changed by the same number of degrees throughout the season. The temperature of the epilimnion was increased or decreased by 4°C.

In the model developed here the terms describing increases of all the variables, and terms describing phosphorus excretion by living organisms depend on temperature. At a low concentration of nonpredatory zooplankton, however, an increase in temperature produces a relatively lower increase in excretion. For this reason, zooplankton appears earlier and markedly reduces the concentration of phytoplankton in spring (Fig. 26). But the parameters of the model are chosen in such a way that for higher

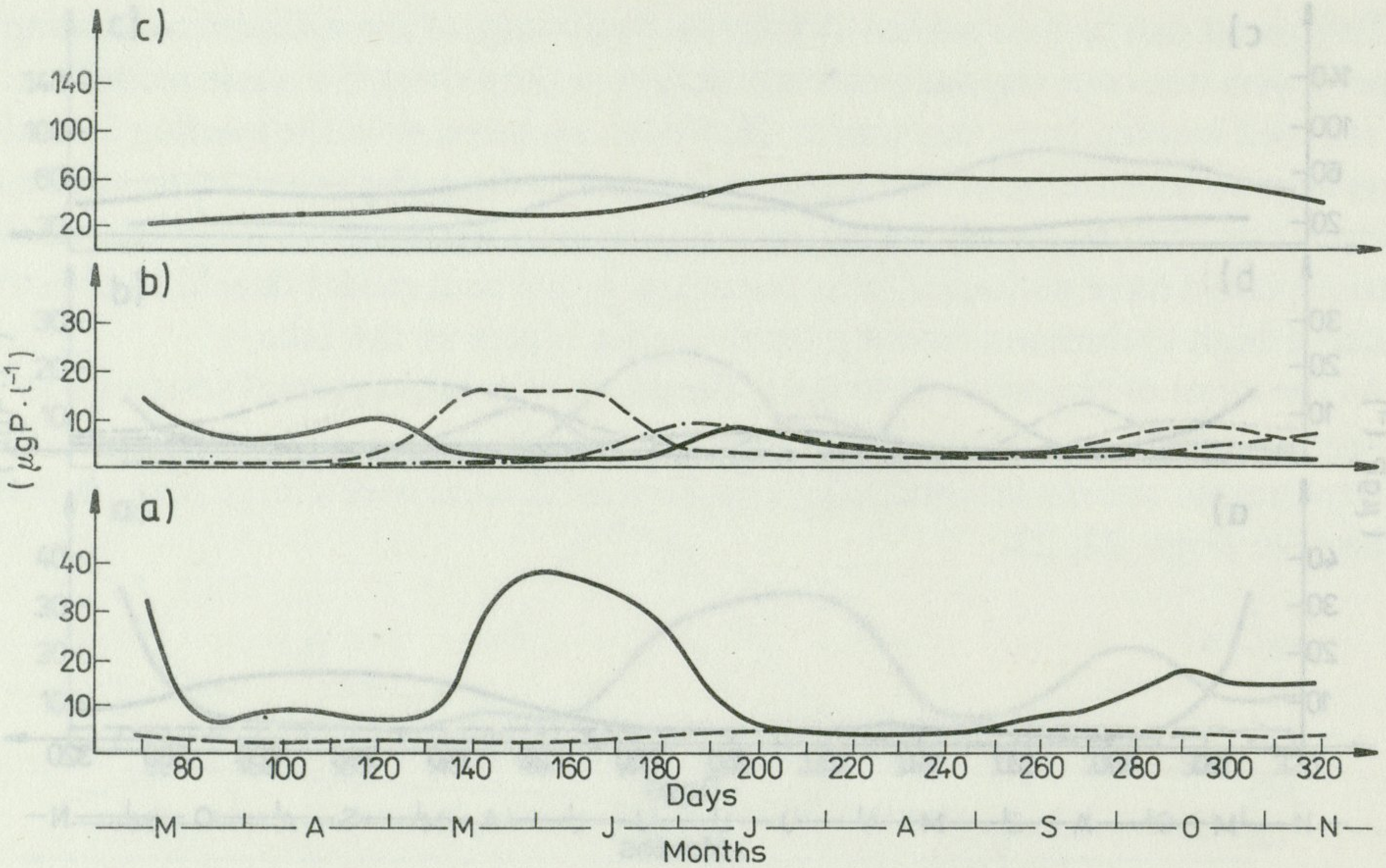

Fig. 26. Numerical experiments: results of the simulations at a temperature of the epilimnion increased by 4°C on each day

a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

values of the variables increasing temperature accounts for a relatively higher increase in phosphorus excretion. As a result, the peaks of all variables are flattened and the patterns are variable. Due to an increased excretion, only the concentration of dissolved phosphorus periodically increases (May-June and September). This produces an earlier phytoplankton peak in summer.

A more complicated pattern emerges when temperature is lowered (Fig. 27). Generally, the reduction in phosphorus excretion is relatively much higher now. Thus, the maxima of all the biological variables increase, and peaks are better pronounced. Instead, the concentration of dissolved phosphorus decreases. This is clear-cut during the May-June peak.

A different interpretation is needed only for a clear phytoplankton peak in spring, appearing on about day 150, and for the preceding increase in the concentration of phosphorus. In this system, phytoplankton is the only variable characterized by a very low phosphorus exretion (it is lower by about one order of magnitude than for other biological variables). In this relation a decrease in excretion does not compensate for a decrease in the rate of primary production, and by day 135 in spring phytoplankton is growing at a lower rate and utilizes less phosphorus at low temperature. However, the resulting increase in phosphorus concentration accounts for a clear phytoplankton peak a little later in spring.

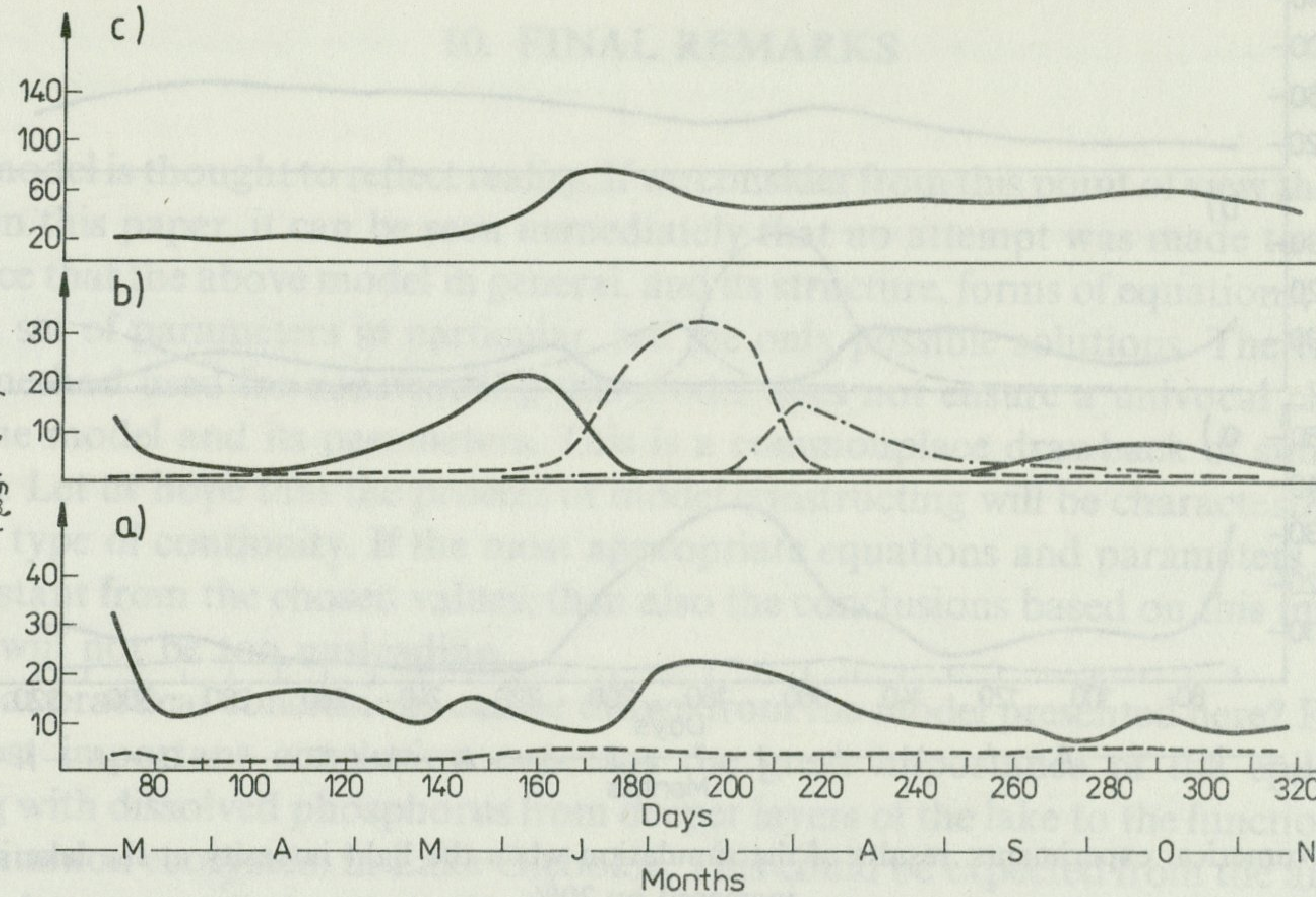

Fig. 27. Numerical experiments: results of the simulation at a temperature of the epilimnion decreased by 4°C on each day

a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

9.4. CHANGES IN LIGHT INTENSITY

The effects of changes in incident light intensity were simulated. The light intensity at the lake surface was increased or decreased by 20% throughout the season (Figs. 28, 29).

Generally the effect of such changes in light intensity is small. The response of the variables of the model is more pronounced when the light intensity is reduced than when it is increased. Presumably, this was due to the fact that in important periods of the season the intensity of incident light is insignificantly lower than the optimum light intensity.

The noticeable effects of changes in light intensity can be observed first of all for phytoplankton. In spring (April), however, phytoplankton does not respond to changes in light intensity. This is probably due to the fact that temperature and nutrients are main limiting factors in this period. The later phytoplankton peak, occurring on the turn of July is more conspicuous at a higher light intensity, and it almost totally disappears at a lower light intensity. In the latter situation, the reduction of this peak accounts for the extention of the phosphorus peak preceding the increase in phytoplankton. Some changes in concentrations are also observed for the two trophic types of zooplankton.

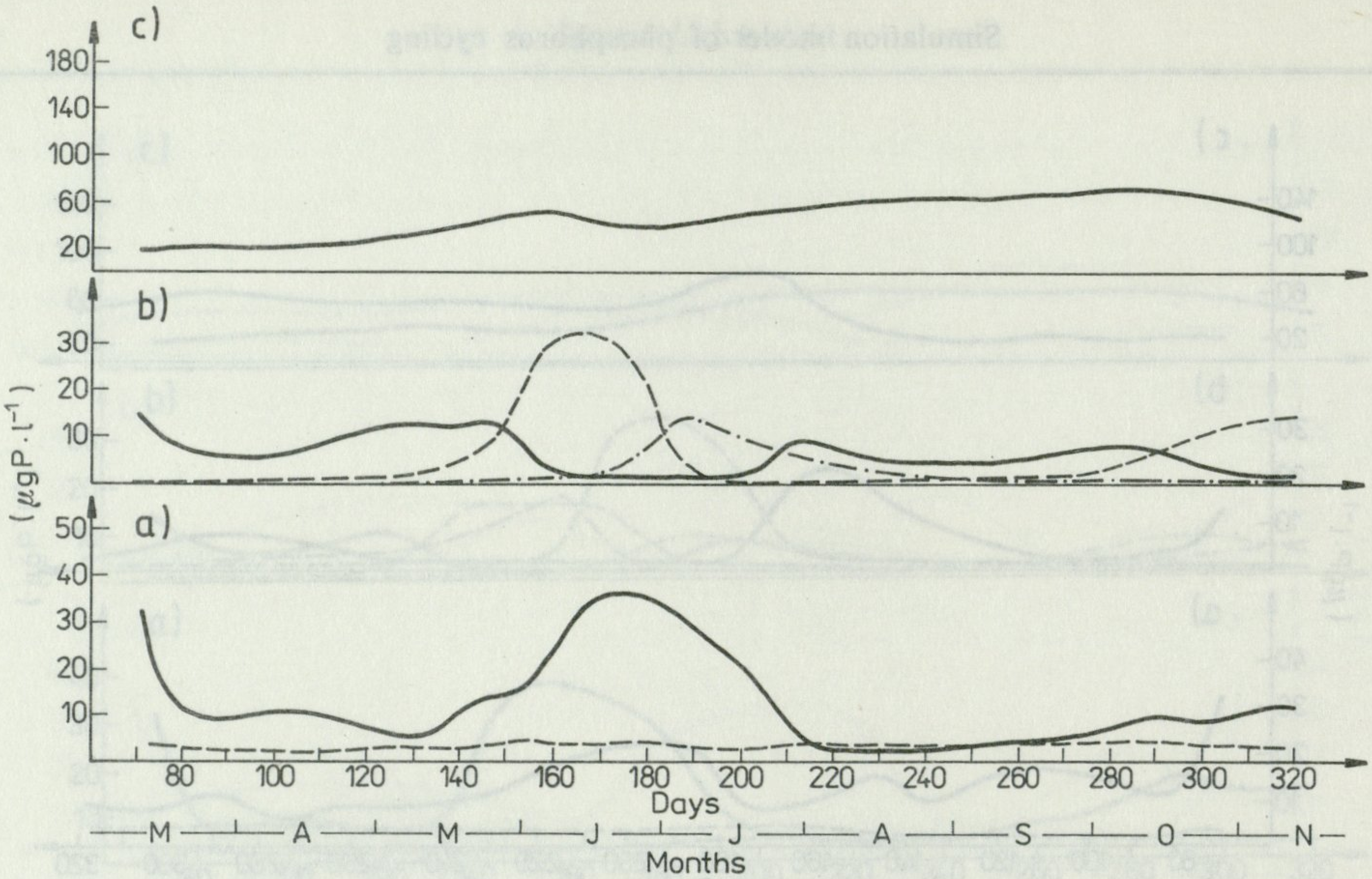

Fig. 28. Numerical experiments: results of the simulation when the light intensity at the lake surface is increased by 20%

a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

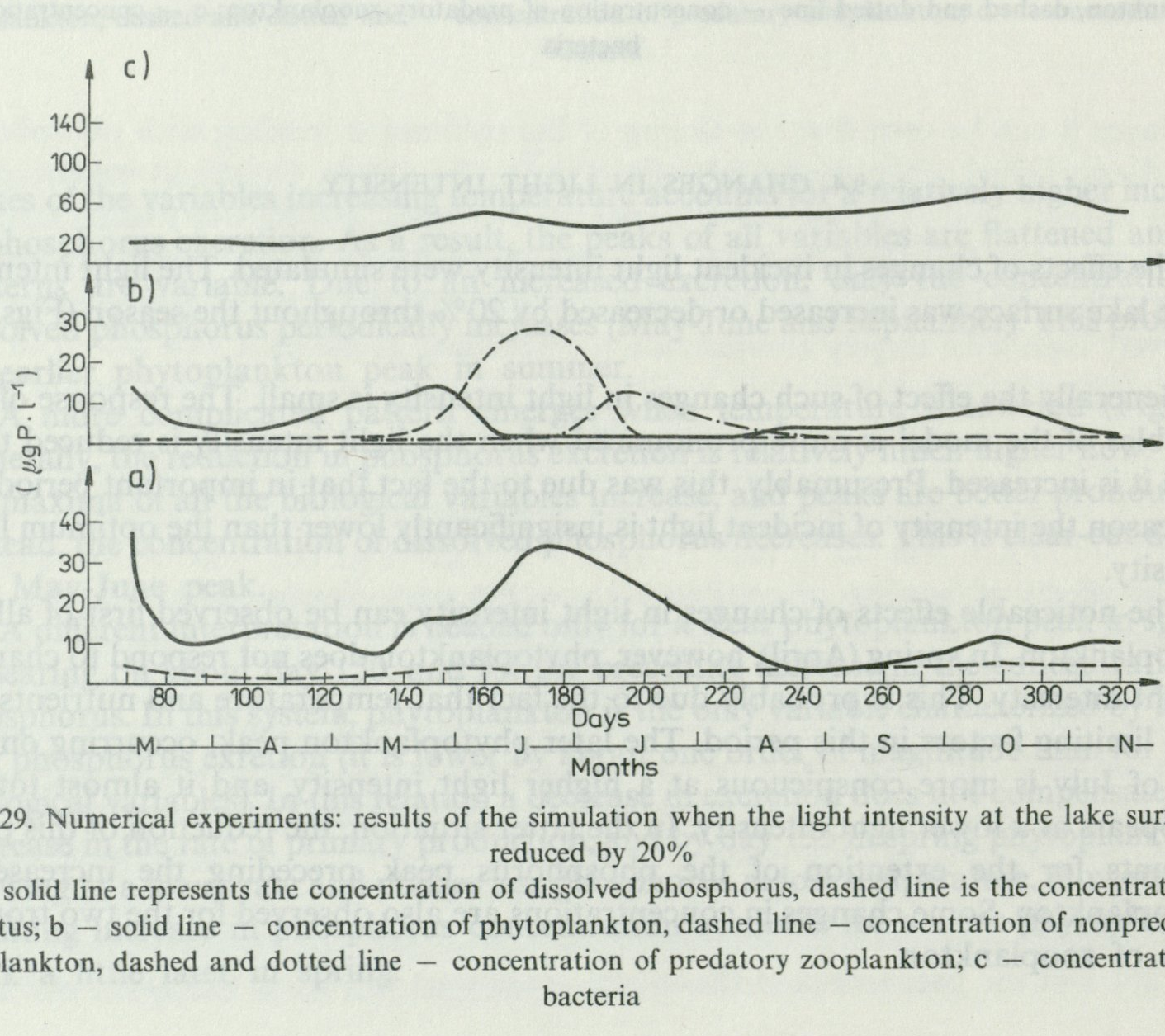

Fig. 29. Numerical experiments: results of the simulation when the light intensity at the lake surface is reduced by 20%

a — solid line represents the concentration of dissolved phosphorus, dashed line is the concentration of detritus; b — solid line — concentration of phytoplankton, dashed line — concentration of nonpredatory zooplankton, dashed and dotted line — concentration of predatory zooplankton; c — concentration of bacteria

10. FINAL REMARKS

A model is thought to reflect reality. If we consider from this point of view the efforts made in this paper, it can be seen immediately that no attempt was made to provide evidence that the above model in general, and its structure, forms of equations, and the chosen set of parameters in particular, are the only possible solutions. The trial and error method used for constructing this model does not ensure a univocal choice of both the model and its parameters. This is a commonplace drawback of simulation models. Let us hope that the process of model constructing will be characterized by a certain type of continuity. If the most appropriate equations and parameters are not very distant from the chosen values, then also the conclusions based on this imperfect model will not be too misleading.

What practical conclusions can be drawn from the model presented here? Perhaps the most important conclusion concerns the great importance of the epilimnion loading with dissolved phosphorus from deeper layers of the lake to the functioning of the epilimnion ecosystem in Lake Głębokie. This could be expected from the amounts of phosphorus supplied to the epilimnion in this way. However, only the model enables us numerical predictions of the consequences of changes in the epilimnion loading with phosphorus from this source. Also the other numerical experiments make possible quantitative predictions of the effects of different treatments in the lake. It is also shown that the ecosystem of Lake Głębokie consists of two subsystems. One involves bacteria and the other one the remaining biological variables. The exchange of matter between these two subsystems goes through detritus and dissolved phosphorus, but they are largely independent. This is implied by the fact that the elimination of fish farming, which enriches the lake with detritus, largely affects concentrations of bacteria, whereas the other variables are much less affected. And conversely, changes in the lake loading with phosphorus largely affect the phytoplankton and the two trophic types of zooplankton, whereas bacteria are considerably less affected.

Stability of such models is analysed on rare occasions. Some attempts were made to analyse the properties of sets of equations describing aquatic ecosystems (Arnold 1978, Arnold and Voss 1981). One of the results of the analysis of the model developed in this paper, showing that under constant environmental conditions the variables of the model tend to equilibrium values, emphasizes once again the importance of changes occurring outside the epilimnion to the patterns of processes in the epilimnion of Lake Głębokie.

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11. SUMMARY

The model presented in this paper describes the cycling of phosphorus in the epilimnion of a stratified, eutrophic lake. It simulates seasonal changes in six variables: concentration of dissolved orthophosphate phosphorus $P-PO_4$, concentration of phosphorus contained in the biomass of phytoplankton, bacteria, nonpredatory zooplankton, and predatory zooplankton, and concentration of phosphorus in detritus. A block diagram of the model is shown in Figure 1. The model also describes the pattern of seasonal changes in light intensity, temperature at the surface of the lake and its changes with depth, and changes in the epilimnion depth. The model also includes functions describing seasonal changes in the epilimnion loading with phosphorus from deeper layers of the lake, from external loading of the lake, and from fish farming in the lake.

The model has been calibrated from data from Lake Głębokie located in the Mazurian Lakeland, north-eastern Poland. A part of the data concerning this lake is shown in Tables 1 – 4. The results of the simulation of changes in the variables of the model and the results of measurements of these variables in the lake are shown in Figures 10 – 16.

The stability of the model was analysed. It has been found that the model has a stable equilibrium point of the focus type as the variables show damped oscillations around the equilibrium states at constant values of the parameters and functions of the model (Fig. 17).

Using this model, many numerical experiments were made. The behaviour of the system was examined in the case when fish farming was stopped in the lake. It has been found that this mainly affects the concentration of bacteria, and the response of other variables is much weaker (Fig. 18). The level, but not timing of the epilimnion loading with phosphorus from deeper layers of the lake, was changed. A decrease in the rate of phosphorus loading from this source largely reduced the values of all the variables of the model (Figs. 19 – 20). An increase in the loading from deeper layers readily produced negative values of the variables, which implies that the description of a system with such loading requires a different model. The model developed here cannot simulate processes generated by high loading. Also experiments were made with a constant loading from deeper layers of the lake. Loading of this kind largely changed the results of the simulation (Figs. 24, 25). All these results show that the loading of the epilimnion of Lake Głębokie with phosphorus from its deeper layers is extremely important. It seems that the timing of the epilimnion loading with phosphorus, rather than interactions among living components of the system, determines the values of all the variables of the model. Also the effects of a short-term discharge of a large amount of phosphorus to the epilimnion was simulated. It has been found that the system is more sensitive if this discharge is made in spring than in the second half of the season (Figs. 22, 23). Also the effects of heating and cooling lake water were simulated. The results of these experiments can be explained by relations between changes in the rate of increase in the concentration and in the rate of excretion of phosphorus in living components of the system (Figs. 26, 27). It has been found that changes in light intensity have small effect on variables of the model (Figs. 28, 29).

The ecosystem of the epilimnion of Lake Głębokie seems to be consisted of two subsystems. One is related with bacteria and the other one with the remaining biological variables. The exchange of matter between them goes through detritus and dissolved phosphorus.

12. POLISH SUMMARY

Model przedstawiony w tej pracy dotyczy krążenia fosforu w epilimnionie stratyfikowanego jeziora eutroficznego. Opisuje on zmiany w czasie jednego sezonu sześciu zmiennych: koncentracji rozpuszczongo fosforu ortofosforanowego $P-PO_4$, koncentracji fosforu zawartego w biomasie fitoplanktonu, bakterii, zooplanktonu niedrapieżnego, zooplanktonu drapieżnego oraz koncentracji fosforu zawartego w masie detrytusu. Schemat blokowy modelu przedstawiono na rys. 1. Model zawiera także opis zmian w sezonie natężenia światła, temperatury na powierzchni i jej rozkładu wraz z głębokością oraz głębokości epilimnionu. Dołączono także funkcje opisujące zmiany w sezonie zasilania w fosfor epilimnionu z głębszych

warstw jeziora, zasilania epilimnionu w wyniku zewnętrznego zasilania jeziora oraz zasilanie epilimnionu jako skutek sadzowej hodowli ryb prowadzonej w jeziorze.

Model ten został wykalibrowany dla danych pochodzących z Jeziora Głębokiego położonego na Pojezierzu Mazurskim. Część danych dotyczących tego jeziora przedstawiono w tab. 1–4. Wyniki symulacji zmian zmiennych występujących w modelu porównane z wynikami pomiarów tych wartości w jeziorze przedstawiono na rys. 10–16.

Przeprowadzono analizę stabilności modelu. Stwierdzono, że model charakteryzuje się punktem równowagi typu ognisko, gdyż dla ustalonych w czasie wartości parametrów i funkcji modelu zmienne wykazują zanikające oscylacje wokół położenia równowagi (rys. 17).

Wykonano wiele eksperymentów numerycznych z tym modelem. Badano zachowanie układu w przypadku wstrzymania hodowli ryb w jeziorze. Stwierdzono, że ma to głównie wpływ na koncentrację bakterii, pozostałe zmienne reagują znacznie słabiej (rys. 18). Zmieniano poziom, a nie rozkład w czasie zasilania epilimnionu w fosfor z głębszych warstw jeziora. Zmniejszenie szybkości dostarczania fosforu do epilimnionu tą drogą prowadziło do znacznego obniżenia wartości wszystkich zmiennych modelu (rys. 19–20). Zwiększanie natomiast zasilania z głębszych warstw powodowało bardzo łatwo to, że zmienne modelu zaczynały przyjmować wartości ujemne, co oznacza, że do opisu układu z takim zasilaniem należy użyć innego modelu, gdyż dotychczasowy nie jest w stanie odtworzyć procesów wywołanych dużym zasilaniem. Eksperymentowano także ze stałym w czasie zasilaniem z głębszych warstw jeziora. Taki rodzaj zasilania zmieniał bardzo wyniki symulacji (rys. 24, 25). Wszystko to wskazuje na ogromne znaczenie zasilania epilimnionu Jeziora Głębokiego z jego głębszych warstw. Wydaje się, że nie oddziaływanie między żywymi składnikami ekosystemu, lecz rozkład w czasie ładunków fosforu docierających do epilimnionu ma decydujące znaczenie dla wartości wszystkich zmiennych modelu. Naśladowano także skutki krótkotrwałego zrzutu dużej ilości fosforu do epilimnionu. Stwierdzono, że układ jest bardziej czuły, jeśli zrzutu tego dokonano na wiosnę niż w drugiej połowie sezonu (rys. 22, 23). Badano także skutki podgrzewania i ochładzania wód jeziora. Wyniki tych eksperymentów dają się wytłumaczyć relacjami między zmianami szybkości przyrostu koncentracji i szybkości ekskrecji fosforu żywych składników układu (rys. 26, 27). Stwierdzono, że zmiany oświetlenia na powierzchni jeziora mają niewielki wpływ na przebieg zmiennych modelu (rys. 28, 29).

Wydaje się, że ekosystem epilimnionu Jeziora Głębokiego składa się jak gdyby z dwóch podukładów. Jeden związany jest z bakteriami, drugi – z pozostałymi zmiennymi biologicznymi. Wymiana między nimi odbywa się poprzez detrytus i fosfor rozpuszczony.

13. REFERENCES

1. Arnold E. M. 1978 – Aspects of a zooplankton, phytoplankton, phosphorus system – Ecol. Model. 5: 293–300.
2. Arnold E. M., Voss D. A. 1981 – Numerical behaviour of a zooplankton, phytoplankton and phosphorus system – Ecol. Model. 13: 183–193.
3. Bajkiewicz-Grabowska E. 1985 – Factors affecting nutrient budget in lakes of the r. Jorka watershed (Masurian Lakeland, Poland) I. Geographical description, hydrographic components and man's impact – Ekol. pol. 33: 173–200.
4. Ejsmont-Karabin J., Bownik-Dylińska L., Godlewska-Lipowa W. A. 1983 – Biotic structure and processes in the lake system of r. Jorka watershed (Masurian Lakeland, Poland) VII. Phosphorus and nitrogen regeneration by zooplankton as the mechanism of the nutrient supplying for bacteria and phytoplankton – Ekol. pol. 31: 719–746.
5. Godlewska-Lipowa W. A. 1983 – Biotic structure and processes in the lake sytem of r. Jorka watershed (Masurian Lakeland, Poland) V. Biomass and production of bacterioplankton – Ekol. pol. 31: 667–678.
6. Hillbricht-Ilkowska A. 1983 – Biotic structure and processes in the lake system of r. Jorka watershed (Masurian Lakeland, Poland) XII. Productivity, structure and dynamics of lake biota (a synthesis of research) – Ekol. pol. 31: 801–834.

7. H i l l b r i c h t-I l k o w s k a A., Ł a w a c z W. 1983 — Biotic structure and processes in the lake system of r. Jorka watershed (Masurian Lakeland, Poland). I. Land impact, loading and dynamics of nutrients — Ekol. pol. 31: 539—585.
8. I v l e v V. S. 1955 — Eksperimentalnaja ékologija pitanija ryb — Piščepromizdat, Moskva, 250 pp.
9. J ø r g e n s e n S. E. (Ed.) 1979 — Handbook of environmental data and ecological parameters — International Society for Ecological Modelling, 1162 pp.
10. K r a m e r J. N., N i x o n S. W. 1978 — A coastal marine ecosystem. Simulation and analysis — Ecol. Stud. No. 24, Springer—Verlag, Berlin—Heidelberg—New York, 217 pp.
11. Ł a w a c z W. 1985 — Factor affecting nutrient budget in lakes of the r. Jorka watershed (Masurian Lakeland, Poland). XI. Nutrient budget with special consideration to phosphorus retention — Ekol. pol. 33: 357—381.
12. P e n c z a k T., M o l i ń s k i M., G a l i c k a W., P r e j s A. 1985 — Factors affecting nutrient budget in lakes of the r. Jorka watershed (Masurian Lakeland, Poland). VII. Input and removal of nutrient with fish — Ekol. pol. 33: 301—309.
13. P l a n t e r M., Ł a w a c z W., T a t u r A. 1983 — Biotic structure and processes in the lake system of r. Jorka watershed (Masurian Lakeland, Poland). II. Physical and chemical properties of water and sediments — Ekol. pol. 31: 587—611.
14. S p o d n i e w s k a I. 1983 — Biotic structure and processes in the lake system of r. Jorka watershed (Masurian Lakeland, Poland). IV. Structure and biomass of phytoplankton — Ekol. pol. 31: 635—665.
15. S t e e l J. H. 1962 — Environmental control of photosynthesis in the sea — Limnol. Oceanogr. 7: 137—150.
16. S t r a š k r a b a M. 1976 — Development of an analytical phytoplankton model with parameters empirically related to dominant controlling variables (In: Umweltbiophysik, Eds. R. Glaser, K. Unger, M. Koch) — Abhandlugen der Akademie der Wissenschaften der DDR, 33—65.
17. S z e l i g i e w i c z W. 1986 — Numeryczny model krążenia fosforu w jeziorze stratyfikowanym termicznie (Numerical model of phosphorus circulation in a thermally stratified lake) — Ph. D. Thesis, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, 287 pp.
18. U c h m a ń s k i J. 1983 — Stabilność układów ekologicznych (Stability of ecological systems) — Wiad. ekol. 29: 231—269.
19. W ę g l e ń s k a T., B o w n i k-D y l i ń s k a L., E j s m o n t-K a r a b i n J. 1983 — Biotic structure and processes in the lake system of r. Jorka watershed (Masurian Lakeland, Poland). VI. Structure and dynamics of zooplankton — Ekol. pol. 31: 679—717.
20. W o r o n i e c k a-d e W a c h t e r U. 1983 — Biotic structure and processes in the lake system of r. Jorka watershed (Masurian Lakeland, Poland). III. Production and photosynthesis efficiency of phytoplankton — Ekol. pol. 31: 613—633.

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