PARTIAL FUNCTIONAL MATHEMATICAL MODEL OF NITROGEN TRANSFORMATION CYCLE

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ABSTRACT. The purpose of this paper is to investigate a system of parabolic equations with discrete time delays describing a nitrogen transformation cycle in aquatic environment, which consists of the 4 types living organisms (phytoplankton and microorganisms), the 4 types dissolved organic and inorganic nutrients and detritus. When the delays are relatively small, our predictions are also identical to the predictions given by the corresponding PDE. The system of parabolic equations is discretized by the finite difference method which yields a coupled system of nonlinear algebraic equations. Stability analysis of equilibria and some numerical examples are given. It is shown that Hopf bifurcation may occurs.

Keywords: nitrogen transformation cycle, partial functional differential equations, spatially constant equilibrium, stability analysis, Hopf bifurcation
AMS classification: 92D25, 92A10, 92A12, 92D05, 34K15

1. INTRODUCTION

The main purpose of this paper is to study the asymptotic behaviour of the nitrogen transformation cycle in an aquatic environment presented by [10].

Mathematical models of increasing complexity that describe the dynamics of material recycling in closed ecosystem were constructed by [1], [7] [8], [9], [11] and [14]. The common property of these models is that a total level of recycling material of this trophic chain is assumed to be constant for the duration of the investigation.

The global asymptotic behavior of the similar models of n species of microorganisms competing exploitatively for a single growth-limiting nutrient was studied in [2], [6], [15] and [16], .

The aerobic transformation of nitrogen compounds includes:
- the decomposition of complex organic substances into simpler compounds, ammonium being the final nitrogen product,
- ammonium and nitrate oxidation,
- the assimilation of nitrates.

Specific groups of microorganisms participate in these processes. Heterotrophic bacteria (x_1) assimilate and decompose the soluble organic nitrogen compounds DON (x_6) derived from detritus (x_5). Ammonium (x_7), one of the final decomposition products undergoes a biological transformation into nitrate (x_9). This is carried out by aerobic chemoautotrophic bacteria in two stages: ammonia is first oxidized by nitrifying bacteria from the genus Nitrosomonas (x_2) into nitrites

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(x_8) that serve as an energy source for nitrating bacteria mainly from the genus Nitrobacter (x_3). The resulting nitrates may be assimilated together with ammonia and soluble organic forms of nitrogen by the phytoplankton (x_4), whereby the aerobic transformation cycle of nitrogen compounds is formed (Fig.1). The individual variables $x_1, \dots, x_9$ represent nitrogen concentrations contained in the organic as well as in inorganic substances and living organisms presented in a model.

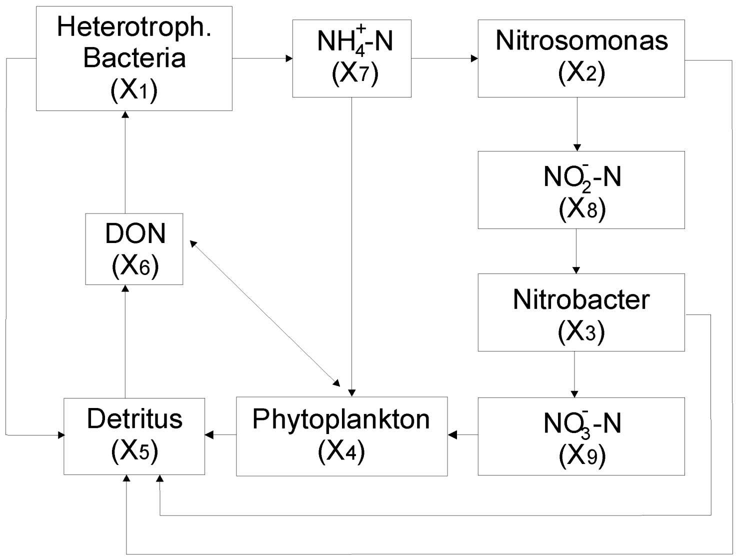

Figure 1. Diagram of the compartmental system modelled by (1).

The following system of partial functional differential equations is proposed as a model for the nitrogen transformation cycle:

$$
\begin{aligned}
\frac{\partial x_i(p,t)}{\partial t} &= d_i \frac{\partial^2 x_i(p,t)}{\partial p^2} + x_i(p,t-r_{ui})U_i(x(p,t-r_{ui})) \\
&\quad -x_i(p,t)E_i(x(p,t)) - x_i(p,t)M_i(x(p,t))) \\
\frac{\partial x_5(p,t)}{\partial t} &= d_5 \frac{\partial^2 x_5}{\partial p^2} + \sum_{i=1}^{4} x_i M_i(x) - K_5 x_5(t-r_{k5},p) \\
\frac{\partial x_6(p,t)}{\partial t} &= d_6 \frac{\partial^2 x_6}{\partial p^2} + K_5 x_5(t-r_{k5},p) - x_1(t,p)U_1(x(t,p)) + \\
&\quad x_4(t,p)E_4(x(t,p)) - x_4(t,p)P_6(x(t,p)) \\
\frac{\partial x_7(p,t)}{\partial t} &= d_7 \frac{\partial^2 x_7}{\partial p^2} + x_1(t,p)E_1(x(t,p)) - \\
&\quad x_2(t,p)U_2(x(t,p)) - x_4(t,p)P_7(x(t,p)) \\
\frac{\partial x_8(p,t)}{\partial t} &= d_8 \frac{\partial^2 x_8}{\partial p^2} + x_2(t,p)E_2(x(t,p)) - x_3(t,p)U_3(x(t,p)) \\
\frac{\partial x_9(p,t)}{\partial t} &= d_9 \frac{\partial^2 x_9}{\partial p^2} + x_3(t,p)E_3(x(t,p)) - x_4(t,p)P_9(x(t,p))
\end{aligned}
\tag{1}
$$

with Neumann boundary condition

$$\frac{\partial x_i}{\partial p}(t,0) = \frac{\partial x_i}{\partial p}(t,1) = 0 \tag{2}$$

and initial conditions

$$x_i\,(t,p) \quad = \quad \phi_i\,(t,p) \geq 0,\;\; 0 \leq p \leq 1,\;\; t \in \langle -r, 0\rangle \tag{3}$$

where $x_i(t,p)$ are the concentration of the recycling matter in microorganisms, the available nutrients and detritus, respectively. The constants r_{**} stand for the discrete time delays in uptake and excretion of nutrient and decomposition of detritus, $r = max\,\{r_{**}\}$ and $0 < p < 1$.

$$U_i(x) = \frac{K_i x_{i+5}}{1 + g_i x_{i+5}} \qquad \text{for i=1,2,3,4}$$

$$p = u_6 x_6 + u_7 x_7 + u_9 x_9$$

$$U_4(x) = \frac{K_4 p}{1 + g_4 p}$$

U - uptake rate

$$L_i(x) = \frac{a_{2i-1} U_i(x)}{1 + a_{2i} U_i(x)} + 1 - \frac{a_{2i-1}}{a_{2i}}$$

L - excretion activity

$$M_i(x) = g_{2i+3} + g_{2i+4} L_i(x)$$

M - mortality rate

$$E_i(x) = U_i(x) L_i(x) \qquad \text{for i=1,2,3,4}$$

E - excretion rate

$$P_i(x) = \frac{K_4 u_i x_i}{1 + g_4 p} \qquad \text{for } i = 6, 7, 9.$$

Note 1.1. *All coefficients occurring in these equations are nonnegative constants, further* d_{xi} $a_{2i}, g_i, g_{2i+3} > 0,$ $a_{2i-1} < a_{2i}$ *and* $a_{2i-1} > a_{2i}^2(g_{2i+3} + g_{2i+4})$ *for* $i = 1, 2, 3, 4$ *and represent relevant physical constants.*

2. Preliminary results

The following basic proposition is hold

Proposition 2.1. *The solution* $X(\Phi, .) = X\,(p,t) = (x_1\,(p,t)\,, \ldots, x_9\,(p,t))$ *of (1)-(3) exists for all* $\Phi \in C_+^9$, *defined by*

$$C_+^9 = \left\{\Phi \in C^9 | \phi_i(t,p) \geq 0, \quad t \in \langle -r, 0\rangle \;\; and \;\; p \in \langle 0,1\rangle \, and \;\; i = 1, \ldots, 9\right\}$$

remains nonnegative and for all $t > 0$

$$\int_0^1 \left(\sum_{i=1}^{4} x_i(p, t + r_{ui}) + \sum_{i=5}^{9} x_i(p, t)\right) dp = c$$

for all $t > 0$*, where* $c = \int_0^1 (\sum_{i=1}^{9} x_i(p, r_{ui}) + \sum_{i=5}^{9} x_i(p, 0))dp$.

Proof. Local existence is standard [17] p.37, 48. System of equations (1) describing the dynamic of nitrogen transformation can be written in the form:

$$\frac{d}{dt}x_i = d_{xi}\frac{\partial^2 x_i}{\partial p^2} + F_i(x) \text{ for } \ i = 1, \ldots, 9$$

Let us denote

$$R_+^9 = \{(x_1, \ldots, x_9)|x_i \geq 0 \text{ for } \ i = 1, \ldots, 9\}$$

By straightforward calculation we get that $F_i(x_1, \ldots, x_{i-1}, 0, x_{i+1}, \ldots, x_9) \geq 0$ for $i = 1, \ldots, 9$ and $x_j \geq 0$ for $j = 1, \ldots, i-1, i+1, \ldots, 9$. We obtain that the region R_+^9 is positively invariant for our system. By adding up of right-hand side of (1) we get $\sum_{i=1}^{9} F_i(x)) = 0$.

Let $\Phi \in C_+^9$ be given. We set

$$W(t) = \int_0^1 \left(\sum_{i=1}^{4} x_i(p, t + r_{ui}) + \sum_{i=5}^{9} x_i(p, t)\right) dp$$

for all $t \geq 0$, where $X(\Phi, t, p) = (x_1(\Phi, t, p), \ldots, x_9(\Phi, t, p))$ is the solution of (1) throught Φ.

It follows from model (1) that

$$\frac{dW(t)}{dt} = \frac{d}{dt}\left(\int_0^1 \left(\sum_{i=1}^{9} x_i(p, t + r_{ui}) + \sum_{i=5}^{9} x_i(p, t)\right) dp\right) =$$

$$\int_0^1 \frac{d}{dt}(\textstyle\sum_{i=1}^{9} x_i(p, t + r_{ui}) + \sum_{i=5}^{9} x_i(p, t))dp =$$

$$\int_0^1 (\textstyle\sum_{i=1}^{4} (\frac{d}{dt}x_i(p, t + r_{ui}) + \sum_{i=5}^{9} \frac{d}{dt}x_i(p, t + r_{ui}))dp =$$

$$\textstyle\sum_{i=1}^{9} \int_0^1 d_{xi}\frac{\partial^2 x_i(p, t)}{\partial p^2}dp = \sum_{i=1}^{9} d_{xi}(\frac{\partial x_i}{\partial p}(1, t) - \frac{\partial x_i}{\partial p}(0, t) = 0.$$

It follows easily that

$$W(t) = \int_0^1 \left(\sum_{i=1}^{4} x_i(p, t + r_{ui}) + \sum_{i=5}^{9} x_i(p, t)\right) dp = c \tag{4}$$

and $c = \int_0^1 (\sum_{i=1}^{9} x_i(p, r_{ui}) + \sum_{i=5}^{9} x_i(p, 0))dp$. That $X\,(p, t) = (x_1\,(p, t)\,, \ldots, x_9\,(p, t))$ is bounded follows immediately from (4). □

Note 2.1. *The nonnegative orthant is positively invariant for the model presented, and the initial value problem is well-posed in the sense that unique mild solutions* *exist for all $t > -r$ where $r = max\{r_{*i}\}$ and depend continuously on the initial data and parameters.*

3. Properties of the model

The first four equations describing the dynamics of the living organisms have the following structure:

$$\dot{x}_i = d_{xi}\frac{\partial^2 x_i}{\partial p^2} + x_i f_i(x, x_{ri}) \qquad \text{for } i = 1,2,3,4,$$

where $f_i(x, x_{ri}) = U_i(x, x_{ri}) - E_i(x, x_{ri}) - M_i(x, x_{ri})$. After algebraic modifications the functions $f_i(x, x)$ acquire the form

$$f_i(x) = \frac{d_i y_{i+5} - q_i}{a_{2i}(1 + y_{i+5}(g_i + a_{2i}K_i))},$$

where

$d_i = K_i(a_{2i-1} - a_{2i}^2(g_{2i+3} + g_{2i+4})) + g_i(a_{2i-1}g_{2i+4} - a_{2i}(g_{2i+3} + g_{2i+4}))$
$q_i = a_{2i}(g_{2i+3} + g_{2i+4}) - a_{2i-1}g_{2i+4}$ for $i = 1,2,3,4$
$y_{i+5} = x_{i+5}$ for $i = 1,2,3$
and $y_9 = u_6x_6 + u_7x_7 + u_9x_9$. Let us denote

$$\begin{aligned} K_i^* &= \frac{g_i(a_{2i}(g_{2i+3} + g_{2i+4}) - a_{2i-1}g_{2i+4})}{a_{2i-1} - a_{2i}^2(g_{2i+3} + g_{2i+4})} \\ b_{i+5} &= q_i/d_i \\ S_c &= \{x \in C_+^9 : x \geq 0 \int_0^1 \textstyle\sum_{i=1}^9 x_i(t,z)dz = c\} \\ S &= \{x \in S_c : x_i \text{ are spatially cons. and } x_1 = \cdots = x_5 = 0\} \\ S_0 &= \{x \in S : x_i < b_i \text{ for } i = 6,7,8\}. \end{aligned}$$

Proposition 3.1. *S_c is a positively invariant set of system (1)-(3).*

Proof. It follows from Proposition 1. □

Note 3.1. *If $K_4 < K_4^*$, then*

$$f_4(x) < -\frac{q_4}{a_8} < 0$$

for all $x \in S_c$

Let the functional $F : C_+^9 \to R^9$ be defined by

$$F = \begin{pmatrix} \phi_1(p,-r_{u1})U_1(\Phi(p,-r_{u1})) - \phi_1(p,0)E_1(\Phi(p,0)) - \phi_1(p,0)M_1(\Phi(p,0) \\ \phi_2(p,-r_{u2})U_2(\Phi(p,-r_{u2})) - \phi_2(p,0)E_2(\Phi(p,0)) - \phi_2(p,0)M_2(\Phi(p,0) \\ \phi_3(p,-r_{u3})U_3(\Phi(p,-r_{u3})) - \phi_3(p,0)E_3(\Phi(p,0)) - \phi_3(p,0)M_3(\Phi(p,0) \\ \phi_4(p,-r_{u4})U_4(\Phi(p,-r_{u4})) - \phi_4(p,0)E_4(\Phi(p,0)) - \phi_2(p,)M_4(\Phi(p,0) \\ \sum_{i=1}^4 \phi_i(p,0)M_i(\Phi(p,0) - K_5\phi_5(p,-r_{k5}) \\ K_5\phi_5(p,-r_{k5}) - U_1(\Phi(p,0))\phi_1(p,0) - P_6(\Phi(p,0))\phi_4(p,0) + E_4(\Phi(p,0))\phi_4(p,0) \\ E_1(\Phi(p,0))\phi_1(p,0) + U_2(\Phi(p,0))\phi_2(p,0) - P_7(\Phi(p,0))\phi_4(p,0) \\ \phi_2(p,0)E_2(\Phi(p,0)) - \phi_3(p,0)U_3(\Phi(p,0)) \\ \phi_3(p,0)E_3(\Phi(p,0)) - \phi_4(p,0)P_9(\Phi(p,0)) \end{pmatrix}$$

Let $\mathcal{X} = C([0,1];R^9)$. As the Laplace operator has eigenvalues $-k^2, (k = 0,1,\ldots)$ with corresponding eigenfunction $cos(k\pi x)$, λ is a characteristic value of (1) if and only if for some $k = 0,1,\ldots$ the characteristic equation

$$H(\lambda) \equiv \lambda I - k^2 D - J(\bar{x}) = 0,$$

where

$$J(\bar{x}) = \begin{pmatrix} j_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & j_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & j_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & j_4 & 0 & 0 & 0 & 0 & 0 \\ m_1 & m_2 & m_3 & m_4 & -K_5e^{-\lambda r_{k5}} & 0 & 0 & 0 & 0 \\ -u_1 & 0 & 0 & e_4 - p_6 & K_5e^{-\lambda r_{k5}} & 0 & 0 & 0 & 0 \\ e_1 & -u_2 & 0 & -p_7 & 0 & 0 & 0 & 0 & 0 \\ 0 & e_2 & -u_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & e_3 & -p_9 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

and $e_i = E_i(x^0)$, $m_i = M_i(x^0)$, $u_i = U_i(x^0)$, $s_i = u_i - e_i - m_i$, $j_i = e^{-\lambda r_{ui}}u_i - e_i - m_i$, $i = 1,\ldots,4$, and $p_i = P_i(x^0)$ $i = 6,7,9$.

Proposition 3.2. *If $K_4 < K_4^*$ and $r_{k5}K_5 < \zeta\sin(\zeta) - d_{x5}k^2\pi^2 r_{k5}\cos(\zeta)$ where ζ is the root of $\zeta = -a\tan\zeta$, $0 < \zeta < \pi$, if $d_{x5}k^2\pi^2 r_{k5} \neq 0$ and $\zeta = \dfrac{\pi}{2}$ if $d_{x5}k^2\pi^2 r_{k5} = 0$, then all points of the set S_0 are stable in S_c.*

Proof. Let $\bar{x} \in S_0$. With the translation $y = x - \bar{x}$ we can write the system (1) as

$$\dot{y} = D\frac{\partial^2 y}{\partial p^2} + DF(\bar{x})y + N(y),$$

$N(y)$ involves only the higher terms in $y_1, \dots y_9$. The perturbation system of (1) and its associated eigenvalue problem are, respectively, written as follows:

$$\dot{y} = D\frac{\partial^2 y}{\partial p^2} + DF(\bar{x})y \ ,$$

$$\lambda v = (-k^2\pi^2 D + J)v, \ k = 0, 1, \dots$$

The eigenvalues of $-k^2\pi^2 D + J(\bar{x})$ at $\bar{x} \in S_0$ are as follows

$$\begin{aligned} \lambda_{i,k} &= e^{-\lambda_{i,k} r_{ui}} u_i - e_i - m_i - d_{xi} k^2 \pi^2 && \text{for } i = 1, \dots, 4 \\ \lambda_{i,k} &= -d_{xi} k^2 \pi^2 && \text{for } i = 6, \dots, 9 \\ \lambda_{5,k} &= -K_5 e^{-\lambda_{5,k} r_{k5}} - d_{x5} k^2 \pi^2 \end{aligned}$$

Upon simplification, the characteristic equation becomes

$$H(\lambda) = H_1(\lambda) H_2(\lambda) H_3(\lambda),$$

where

$$\begin{aligned} H_1(\lambda) &= \prod_{i=1}^{4} (\lambda_{i,k} - e^{-\lambda_{i,k} r_{ui}} u_i + e_i + m_i + d_{xi} k^2 \pi^2), \\ H_2(\lambda) &= \prod_{i=6}^{9} (\lambda_{i,k} + d_{xi} k^2 \pi^2) \\ H_3(\lambda) &= (\lambda_{5,k} + K_5 e^{-\lambda_{5,k} r_{k5}} + d_5 k^2 \pi^2). \end{aligned}$$

Denoted the three factor of $H(\lambda)$ by $H_1(\lambda)$, $H_2(\lambda)$ and $H_3(\lambda)$, respectively. The location of the roots of the quasi-polynomials $H_1(\lambda)$ and $H_3(\lambda)$ is accomplished by using the Pontryagins theorem, [4] contains a brief introduction of the Pontryagin's results, together with a proof of $Theorem$ 5.1, (see appendix $Theorem$ 5.1).

To apply the $Theorem$ 5.1 to the quasi-polynomial $H_3(\lambda)$, we first let $\omega = r_{k5}\lambda$ so that ω and λ have real parts of the same sign. Multiplying both side of $H_3(\lambda)$ by $r_{k5} e^{\lambda_{5,k} r_{k5}}$ yields

$$\left(\omega + d_5 k^2 \pi^2 r_{k5}\right) e^{\omega} + r_{k5} K_5 = 0$$

All roots of the equation

$$\left(\omega + d_5 k^2 \pi^2 r_{k5}\right) e^{\omega} + r_{k5} K_5 = 0$$

have negative real parts if and only if

$$d_{x5} k^2 \pi^2 r_{k5} > -1,$$
$$d_{x5} k^2 \pi^2 r_{k5} + r_{k5} K_5 > 0$$

and

$$r_{k5} K_5 < \zeta \sin(\zeta) - d_5 k^2 \pi^2 r_5 \cos(\zeta)$$

where ζ is the root of $\zeta = -d_{x5} k^2 \pi^2 r_5 \tan\zeta$, $0 < \zeta < \pi$, if $d_5 k^2 \pi^2 r \neq 0$ and $\zeta = \frac{\pi}{2}$ if $d_5 k^2 \pi^2 r_{k5} = 0$.

If $K_5 < min\left\{k^2\pi^2 d_{x5}, \frac{\pi}{2r_5}\right\}$ inequalities are satisfied and $H_3(\lambda)$ has roots with negative real parts.

If $\bar{x} \in S_0$ then $u_i - e_i - m_i < 0$ and by the similar way it can be shown, that all the roots of the following transcendental equations given by $H_1(\lambda)$ have negative real parts for all i=1,...,4.

The equation $H_1(\lambda) = 0$ is treated similarly by multiplying both sides by $r_{ui}e^{\lambda_{i,k}r_{ui}}$ to obtain

$$\lambda_{i,k} - e^{-\lambda_{i,k}r_{ui}}u_i + e_i + m_i + d_{xi}k^2\pi^2 \ = 0 \ \text{ for } \ \text{i=1,...,4}$$
$$\left(\omega + \left(d_{xi}k^2\pi^2 + e_i + m_i\right) r_{ui}\right) e^{\omega} - r_{ui}u_i = 0.$$

We can apply *Theorem* 5.1.All roots of the equation

$$\left(\omega + \left(d_{xi}k^2\pi^2 + e_i + m_i\right) r_{ui}\right) e^{\omega} - r_{ui}u_i = 0.$$

have negative real parts if and only if

$$\left(d_{xi}k^2\pi^2 + e_i + m_i\right) r_{ui} > -1,$$
$$\left(d_{xi}k^2\pi^2 + e_i m_i\right) r_{ui} - r_i u_i > 0$$

and

$$-r_{ui}u_i < \zeta\sin(\zeta) - \left(d_{xi}k^2\pi^2 + e_i + m_i\right) r_{ui}\cos(\zeta)$$

where ζ is the root of $\zeta = -\left(d_i k^2\pi^2 + e_i + m_i\right) r_{ui}\tan\zeta$, $0 < \zeta < \pi$, if $\left(d_i k^2\pi^2 + e_i + m_i\right) r_{ui} \neq 0$ and $\zeta = \frac{\pi}{2}$ if $\left(d_{xi}k^2\pi^2 + e_i + m_i\right) r_{ui} = 0$. The condition of *Theorem* 5.1 are satisfied that means all roots of $H_1(\lambda) = 0$ have negative real parts. This prove the result.

□

If $k = 0$ then $\zeta = \frac{\pi}{2}$ and

$$r_{k5}K_5 < \frac{\pi}{2}.$$

i.e. for

$$K_5 > \frac{\pi}{2\ r_{k5}}$$

all spatially constant $\bar{x} \in S_0$ are unstable.

Let us consider $H_3(\lambda)$ as a complex function of two complex variables

$$\mathcal{F}(\omega, K_5) = \left(\omega + d_{x2n+1}k^2\pi^2 r_{k5}\right) e^{\omega} + r_{k5}K_5$$

If we let $\omega = \alpha + i\beta$ and setting $\alpha = 0$. By *Theorem* 5.1 we get that there exists

$$K_5^* = \frac{\pi}{2\ r_{k5}}$$

for which $H_3(\lambda)$ has root with zero real part. Let $\omega_0(K_5^*)$ is a simple eigenvalue, therefore $\dfrac{\partial\mathcal{F}(\omega_0, K_5^*)}{\partial\omega} \neq 0$, by the implicit function theorem we get that

$$R_e\left(\frac{\partial\omega(K_5^*)}{\partial K_5}\right) = R_e\left(-\frac{\frac{\partial\mathcal{F}(\omega_0, K_5^*)}{\partial K_5}}{\dfrac{\partial\mathcal{F}(\omega_0, K_5^*)}{\partial\omega}}\right) =$$
$$\frac{r_{k5} * (\pi/2 - \cos(\omega_0))}{\|e^{i\beta} + i\beta e^{i\beta}\|^2} > 0.$$

Real part of eigenvalue $\omega = \alpha + i\beta$ crosses the imaginary axis transversely at K_5^*. For $k = 0$ 0 is the eigenvalue with multiplicity n which is a dimension of the family of equilibria set S_0. According to *Proposition* 3.1 the rest eigenvalues have been found to have real parts negative.

Our numerical calculations are based on *Proposition* 3.1 and iterative schemes for numerical solution of system of nonlinear parabolic equations with discrete time delays presented by [12], [13]. The vector function $F = (F_1, \dots, F_9)$ given by right-hand side of (1) is mixed quasimonotone and the Jacobi iterative scheme, which is unconditionally stable with respect to the mesh sizes can be applied for numerical solution of (1). Decomposition rate of detritus K_5 and discrete time delay rate r_{k5} play a role of bifurcating parameters. For

$$K_5 > \frac{\pi}{2\ r_{k5}}$$

all spatially constant $\bar{x} \in S_0$ are unstable. Numerical calculations show that for K_5 near to K_5^* periodic solution occurs (Figure 2).

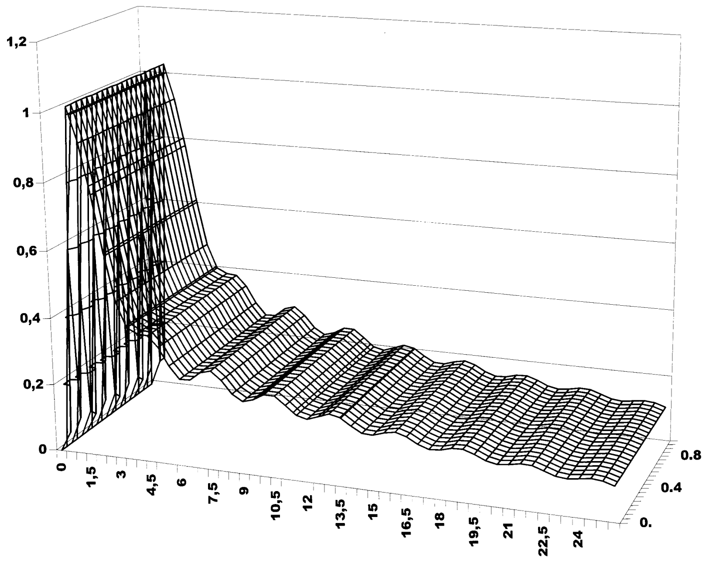

Figure 2. Numerical solution of (1) for $K_5 = 2.0$ and $r_{k5} = 0.8$ $(x_1(t,p))$.

If

$$K_5\ r_{k5} < \frac{\pi}{2}$$

all solutions converge to the set S_0 (Figure 3). If the time delay r_{k5} or the decomposition rate K_5 are relatively small ($K_5\ r_{k5} < \frac{\pi}{2}$), our predictions are identical to the predictions given by the corresponding PDE [9].

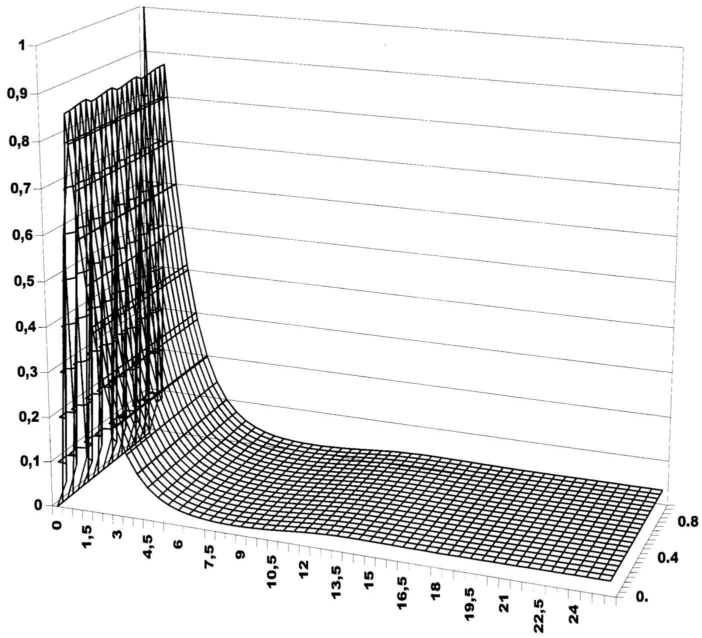

Figure 3. Numerical solution of (1) for $K_5 = 0.02$ and $r_{k5} = 0.8$ $(x_1(t,p))$.

4. Existence and stability of spatially constant equilibria

In this section we will suppose that $K_i > K_i^*$ for $i = 1, 2, 3, 4$. Under this assumption four possible kinds of spatially constant equilibria can exist :
- interior (large loop) spatially constant equilibrium with $x_i > 0$ for all $i = 1 \dots 9$
- medium loop spatially constant equilibria with $x_2 = x_3 = 0,\ x_1 > 0,\ x_4 > 0$
- small loop spatially constant equilibria with $x_1 = x_2 = x_3 = 0,\ x_4 > 0$
- a trivial spatially constant equilibria set S.

Now we now examine the existence and stability of equilibria of the particular loops. Let us denote

$$\begin{aligned}
b_9^* &= (b_9 - u_6 b_6 - u_7 b_7)/u_9 \\
b_7^* &= (b_9 - u_6 b_6)/u_7 \\
b_6^* &= b_9/u_6 \\
c_1 &= b_6 + b_7 + b_8 + b_9^* \\
c_2 &= b_6 + b_7^* \\
c_3 &= b_6^*.
\end{aligned}$$

It is evident that an equilibrium of a large and a medium loop can exist only for $b_9^* > 0$ and $b_7^* > 0$, respectively.

Proposition 4.1. *Let $K_i > K_i^*$ and $b_9^* > 0$ and $c > c_1$ then there a unique positive spatially constant equilibrium $\bar{x}$ on S_c exists.*

Proof. See [7]. □

Let us consider the stability of small loop spatially constant equilibria with $x_1 = x_2 = x_3 = 0, \; x_4 > 0$

For $x_1 = x_2 = x_3 = 0$ *and* $r_{*i} = 0$ system (1) - (3) has the following form:

$$\begin{aligned} \frac{\partial x_4(p,t)}{\partial t} &= d_{x4}\frac{\partial^2 x_4(p,t)}{\partial p^2} + x_4(p,t)U_4(x(p,t)) - \\ (5) \qquad & \quad x_4(p,t)E_4(x(p,t)) - x_4(p,t)M_4(x(p,t))) \\ \frac{\partial x_5(p,t)}{\partial t} &= d_{x5}\frac{\partial^2 x_5}{\partial p^2} + x_4(p,t)M_4(x(p,t) - K_5 x_5(p,t-r_{k5}) \\ \frac{\partial x_6(p,t)}{\partial t} &= d_{x6}\frac{\partial^2 x_6}{\partial p^2} + K_5 x_5(p,t-r_{k5}) + E_4(x(p,t))x_4(p,t) - P_6(x(p,t))x_4(p,t) \end{aligned}$$

with boundary conditions

$$\frac{\partial x_i}{\partial p}(0,t) = \frac{\partial x_i}{\partial p}(1,t) = 0$$

for $i = 4, 5, 6$ and initial conditions

$$x_i\,(p,t) = \phi_i\,(p,t) \geq 0 \text{ for } 0 \leq z \leq 1, t \in \langle -r, 0)$$

and $i = 4, 5, 6$

For $d_i = 0$ and $r_i = 0$ we have the following result:

Proposition 4.2. *Let* $\Gamma(t) = (x_(t), x_5(t), x_6(t)$ *be an arbitrary periodic orbit of (5) with period* $T > 0$, *then* $\Gamma(t)$ *is asymptotically stable.*

Proof. Substituting into the system (5) $x_5 = c - x_4 - x_6$ we get

$$\begin{aligned} \dot{x}_4 &= x_4(U_(x_6) - E_4(x_6) - M_4(x_6)) \\ (6) \qquad \dot{x}_6 &= K_5(c - x_4 - x_6) - x_4(U_4(x_6) - E_4(x_6)) \end{aligned}$$

Consider the fundamental matrix $U(t)$ defined as a solution of

$$\dot{U}(t) = P(t)U(t), \qquad U(0) = I,$$

where $P(t)$ is a Jacobian matrix of (9) and

$$J(\bar{x}) = \begin{pmatrix} U_4(x_6) - E_4(x_6) - M_4(x_6) & (U_4(x_6) - E_4(x_6) - M_4(x_6))' \; x_4(t) \\ -K_5 - U_4(x_6) + E_4(x_6) & -K_5 - (U_4(x_6) - E_4(x_6))' \; x_4(t) \end{pmatrix}$$

The Floqouet exponents of (6) are 0 and γ, where

$$\gamma = -\int_0^T (K_5 - (U_4(x_6) - E_4(x_6))' \; x_4(t))dt < 0,$$

i.e. $\Gamma(t)$ is asymptotically stable. □

By the help of the last Proposition we can show that the equilibrium point $(\bar{x}_4, \bar{x}_5, \bar{x}_6)$ is globally asymptotically stable in int S_c^3.

Proposition 4.3. *The critical point* $\bar{\Theta} = (\bar{x}_4, \bar{x}_5, \bar{x}_6)$ *is globally asymptotically stable w.r.t. the interior* S_c^3.

Proof. We linearize to study the behaviour of (1) near the equilibrium $\bar{\Theta}$. The behaviour of the solution of a linearized system depends on the eigenvalues of P which are the roots of the characteristic equation det $(\lambda I - P) = 0$ or

$$\lambda^2 + \lambda(K_5 + (U_4(x_6) - E_4(x_6))^{'})\ x_4(t)) +$$
$$(U_4(x_6) - E_4(x_6) - M_4(x_6))^{'}\ x_4(t)(K_5 + U_4(x_6) - E_4(x_6)) = 0.$$

$$U_4(x_6) - E_4(x_6),\quad (U_4(x_6) - E_4(x_6) - M_4(x_6))^{'},$$
$$(U_4(x_6) - E_4(x_6))^{'}\ >\ 0$$

implies that every eigenvalue of the matrix P has a negative real part, i.e. $\bar{\Theta}$ is a locally asymptotically stable equilibrium of (1). Suppose that $\Gamma(t)$ is an arbitrary periodic orbit. By proposition 4.2 it must be asymptotically stable - a contradiction since an asymptotically stable equilibrium mandates at least one periodic orbit being unstable. Thus there are no periodic orbits and the local asymptotic stability of $\bar{\Theta}$ is global by the Poincare-Bendixon Theorem. □

Let the functional $F : C^3_+ \to R^3$ be defined by

$$F = \begin{pmatrix} \phi_4(p,0)U_4(\Phi(p,0)) - \phi_4(p,0)E_4(\Phi(p,0)) - \phi_2(p,0)M_4(\Phi(p,0) \\ \phi_i(p,0)M_4(\Phi(p,0) - K_5\phi_5(p,-r_{k5}) \\ K_5\phi_5(p,-r_{k5}) - P_6(\Phi(p,0))\phi_4(p,0) + E_4(\phi(p,0))\phi_4(p,0) \end{pmatrix}$$

As the Laplace operator has eigenvalues $-k^2, (k = 0, 1, \ldots)$ with corresponding eigenfunction $cos(k\pi x)$, λ is a characteristic value of (1) if and only if for some $k = 0, 1, \ldots$ the characteristic equation

$$H(\lambda) \equiv \lambda I + k^2 D - J(\bar{x}) = 0,$$

where

$$J(\bar{x}) = \begin{pmatrix} 0 & 0 & a_1x_4 \\ m_4 & -k_5q^{-\lambda r_{k5}} & a_2x_4 \\ -m_4 & k_5e^{\lambda r_{k5}} & x_4(-a_1 - a_2), \end{pmatrix}$$

where $a_1 = (U_4(x_6) - E_4(x_6) - M_4(x_6))^{'}$, $a_2 = M_4(x_6)^{'}$ and $m_4 = M_4(x_6)$

Stability of spatially constant equilibrium depends on the stability of linearization in $\bar{x}$.

Spatially constant equilibrium $\bar{x}$ is asymptotically stable if and only if all roots of characteristic equation have negative real parts.

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = -e^{-\lambda r_{k5}}(B_1\lambda^2 + B_2\lambda + B_3) \tag{7}$$

where $A_1, A_2, A_3, B_1, B_2, B_3$ are positive numbers and
$A_1 = d_1k^2 + d_2k^2 + d_3k^2 + a_1x_4 + a_2x_4$
$A_2 = d_1d_2k^4 + d_1d_3k^4 + d_2d_3k^4 + a_1d_1x_4k^2 + a_2d_1x_4k^2 + a_1d_2x_4k^2 + a_2d_2x_4k^2 + a_1m_1x_4$
$A_3 = d_1d_2d_3k^6 + a_1d_1d_2x_4k^4 + a_2d_1d_2x_4k^4 + a_1d_2m_1x_4k^2$
$B_1 = K_5$
$B_2 = d_1K_5k^2 + d_3K_5k^2 + a_1K_5x_4$
$B_3 = d_1d_3K_5k^4 + a_1d_1K_5x_4k^2$

We set $\lambda = \alpha + i\beta$ and substituting into (7) similarly as in[6] we obtain the following equations :

$$
\begin{aligned}
&\alpha^3 - 3\alpha\beta^2 + A_1(\alpha^2-\beta^2) + A_2\alpha + A_3 = \\
(8)\qquad &\quad -e^{-\alpha r}\left[\left\{B_1\left(\alpha^2-\beta^2\right) + B_2\alpha + B_3\right\}\cos(\beta r) + \{2B_1\alpha\beta + B_2\beta\}\sin(\beta r)\right] \\
&\alpha^2\beta - \beta^3 + 2A_1\alpha\beta + A_2\beta = \\
&\qquad -e^{-\alpha r}\left[\left\{B_1\left(\alpha^2-\beta^2\right) + B_2\alpha + B_3\right\}\sin(\beta r) + \{2B_1\alpha\beta + B_2\beta\}\cos(\beta r)\right]
\end{aligned}
$$

Let r_{k5}^* be such that $\alpha(r_{k5}^*) = 0$. Substituting to (8) then equations (8) reduce to

$$
\begin{aligned}
(9)\qquad -A_1\beta^2) + A_3 &= -\left\{B_1\left(-\beta^2\right) + B_3\right\}\cos(\beta r) + B_2\beta\sin(\beta r) \\
-\beta^3 + A_2\beta &= \left\{B_1\left(-\beta^2\right) + B_3\right\}\sin(\beta r) + B_2\beta\cos(\beta r)
\end{aligned}
$$

Squaring and adding the equations (9) and simplifying we obtain at an equation for β^* of the form:

$$\beta^{*6} + (A_1^2 - 2A_2 - B_2^2)\beta^{*4} + (A_2^2 - 2A_1A_3 + 2B_1B_3 - B_2^2)\beta^{*2} + A_3^2 - B_3^2 = 0.$$

For $k = 0$ $A_3, B_3 = 0$ and we have the following form:

$$(10)\qquad \beta^{*2}(\beta^{*4} + (A_1^2 - 2A_2 - B_2^2)\beta^{*2} + (A_2^2 - B_2^2)) = 0,$$

where $A_2^2 - B_2^2 = a_1{x_4}^2(m_1^2 - K_5^2)$. If $m_1 < K_5$ there is a simple largest positive root β^* of equation (10).

We now show that for $\beta = \beta^*$ there is a r_{k5}^* such that $\alpha(r_{k5}^*) = 0$.

The equation (9) can be written in the form:

$$
\begin{aligned}
P\cos(\beta r_{k5}) + Q\sin(\beta r_{k5}) &= G, \\
Q\cos(\beta r_{k5}) + P\sin(\beta r_{k5}) &= H,
\end{aligned}
$$

where $G^2 + H^2 = P^2 + Q^2 = C_1^2$. The equations

$$
\begin{aligned}
P &= C_1\cos(\beta r_{k5}), \\
Q &= C_1\sin(\beta r_{k5})
\end{aligned}
$$

determine a unique $\delta \in <0, 2\pi)$ and

$$
\begin{aligned}
C_1\cos(\beta^* r_{k5} - \delta) &= G, \\
C_1\sin(\beta^* r_{k5} - \delta) &= H.
\end{aligned}
$$

As it follows from last equations there uniquely $r_{k5}^* \in < \delta/\beta^*, (2\pi+\delta)/\beta^*)$ exists for which $\alpha(r_{k5}^*) = 0$.

To calculate $d\alpha(r_{k5})/dr_{k5}$ let we consider equations (8). Differentiating with respect r_{k5}, setting $r_{k5} = r_{k5}^*, \beta = \beta^*$ and $\alpha = 0$ we obtain

$$\frac{d\alpha(r_{k5}^*)}{dr_{k5}} = \frac{3\beta^{*6} + (2A_1^2 - 4A_2 - 2B_2^2)\beta^{*4} + (A_2^2 - 2A_1A_3 + 2B_1B_3 - B_2^2)\beta^{*2}}{h_1^2 + h_2^2},$$

where

$$
\begin{aligned}
h_1 &= A_2 - 3\beta^{*2} + r_{k5}^*(-B_1\beta^{*2} + B_3)\cos(r_{k5}^*\beta^*) - \\
&\quad 2B_1 r_{k5}^*\sin(r_{k5}^*\beta^*) + B_2 r_{k5}^*\beta^*\sin(r_{k5}^*\beta^*) - B_2\cos(r_{k5}^*\beta^*)
\end{aligned}
$$

and

$$
\begin{aligned}
h_2 &= -2A_1 r_{k5}^* + 2B_1 r_{k5}^*\cos(r_{k5}^*\beta^*) + r_{k5}^*(-B_1\beta^{*2} + B_3)\sin(r_{k5}^*\beta^*) \\
&\quad -B_2\sin(r_{k5}^*\beta^*) - B_2 r_{k5}^*\beta^*\cos(r_{k5}^*\beta^*).
\end{aligned}
$$

Let $\eta = \beta^2$, then equation (10) we can reduce to

$$\Phi(\eta) = \eta(\eta^2 + (2A_1^2 - 2A_2 - 2B_2^2)\eta + (A_2^2 - -B_2^2)).$$

β^* is the largest positive simple root of equation (10), we have

$$\frac{d\Phi(\eta^*)}{d\eta} > 0.$$

Hence

$$\frac{d\alpha(r_{k5}^*)}{dr_{k5}} = \frac{\beta^{*2}\frac{d\Phi(\eta^*)}{d\eta}}{h_1^2 + h_2^2} > 0.$$

Let $k > 0$. We show that there exists K_5^* so that for all $K_5 < K_5^*$ the characteristic equation

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = -e^{\lambda r}(B_1\lambda^2 + B_2\lambda + B_3) \tag{11}$$

has eigenvalues with negative real parts. Coefficients $B_1,\ B_2$ *and* B_3 are linear function in K_5, A_1, A_2, A_3 are independent on K_5 and $B_1 = B_2 = B_3 = 0$ for $K_5 = 0$. Let we consider the characteristic equation for $K_5 = 0$.

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0 \tag{12}$$

It is convenient to use the Routh-Hurwitz criterion (see, [3]) to test the stability properties of (12). By this criterion the real part of the eigenvalues of (12) are negative if and only if $A_1, A_3 > 0$ and $A_1A_2 > A_3$. By straightforward computation we get

$$
\begin{aligned}
A_1A_2 - A_3 = ((d_1k^2 + d_3k^2 + (a_1 + a_2)x_4)(d_2^2k^4 + a_1m_1x_4 + \\
d_2k^2(d_3k^2 + (a_1 + a_2)x_4) + d_1k^2(d_2k^2 + d_3k^2 + (a_1 + a_2)x_4)) > 0
\end{aligned}
$$

Eigenvalues are continues functions of K_5 , i.e. there exists K_5^* that for all $0 < K_5 < K_5^*$, $m_1 \geq 0$ and $k > 0$ all eigenvalues of characteristic equation (11) has negative real parts.

According to [17] we proofed the following proposition:

Proposition 4.4. *Let be $x_1 = x_2 = x_3 = 0$ and $0 < m_1^* < K_5 < K_5^*$. Then system (1) has a family of periodic solutions bifurcating from spatially constant interior equilibrium $\bar{x}$, when r_{k5} is near r_{k5}^*.*

For numerical calculation of r_{k5}^* depending on K_5 we used a values of coefficients given in $TableI$.

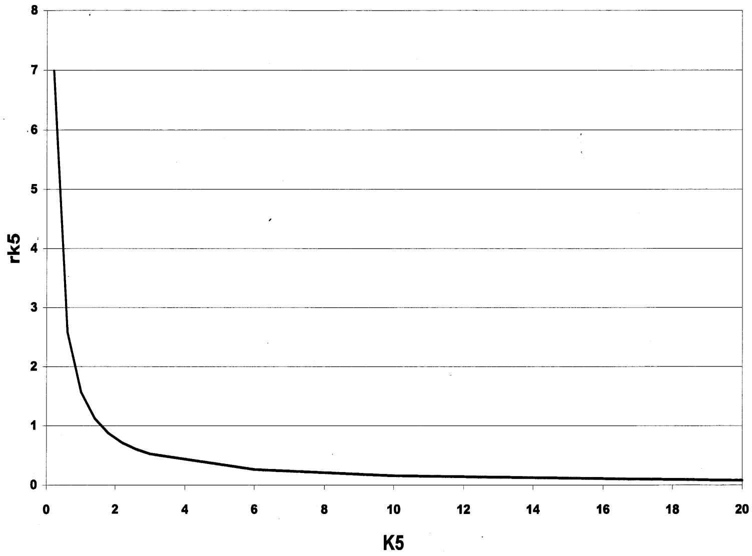

Figure 4. Numerical calculation of bifurcation parameter r^*_{k5} depending on K_5.

5. Discussion

In this paper, a functional partial mathematical model of nitrogen transformation cycle with discrete time delay is considered. The model incorporates discrete time delays in uptake, excretion of nutrient and decomposition of detritus. Decomposition rate of detritus K_5 and discrete time delay rate r_{k5} play a role of bifurcating parameters. For $K_4 < K_4^*$ and

$$K_5 > \frac{\pi}{2\ r_{k5}}$$

all spatially constant $\bar{x} \in S_0$ equilibriia are unstable. Numerical calculations show that for K_5 near to K_5^* periodic solution occurs (Figure 2,3). If $K_4 > K_4^*$, then system (1) has a family of periodic solutions bifurcating from spatially constant interior equilibrium $\bar{x}$, when r_{k5} is near r^*_{k5} (See Figure 4).

6. APPENDIX

Theorem 6.1. *All roots of the equation $(z+a)e^z + b = 0$, where a and b are real, have negative real parts if and only if*

$$\begin{aligned} a &> -1 \\ a+b &> 0 \\ b &< \zeta \sin\zeta - a\cos\zeta \end{aligned}$$

where ζ is the root of $\zeta = -a\tan\zeta$, $0 < \zeta < \pi$, if $a \neq 0$ and $\zeta = \frac{\pi}{2}$ if $a = 0$.

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Table I. Values of the constants used in the model

$a_1 = 0.007$	day	$K_4 = 3.4323$	$(mgN/l)^{-1}\ day^{-1}$
$a_2 = 0.0182$	day	$K_5 = 0.62$	day^{-1}
$a_3 = 0.5$	day	$g_1 = 0.14$	$(mgN/l)^{-1}$
$a_4 = 0.67$	day	$g_2 = 1.5$	$(mgN/l)^{-1}$
$a_5 = 1.$	day	$g_3 = 2.0$	$(mgN/l)^{-1}$
$a_6 = 1.39$	day	$g_4 = 1.5$	$(mgN/l)^{-1}$
$a_7 = 0.66$	day	$g_5 = 0.8$	day^{-1}
$a_8 = 0.67$	day	$g_6 = 0.4$	day^{-1}
$u_6 = 0.01$	$dimensionless$	$g_7 = 0.2$	day^{-1}
$u_7 = 0.03$	$dimensionless$	$g_8 = 0.$	day^{-1}
$u_9 = 0.2$	$dimensionless$	$g_9 = 0.15$	day^{-1}
$K_1 = 19.3$	$(mgN/l)^{-1}\ day^{-1}$	$g_{10} = 0.$	day^{-1}
$K_2 = 8.17$	$(mgN/l)^{-1}\ day^{-1}$	$g_{11} = 0.1$	day^{-1}
$K_3 = 71.28$	$(mgN/l)^{-1}\ day^{-1}$	$g_{12} = 0.$	day^{-1}

Figure description:
Figure 1. Diagram of the compartmental system modelled by (1).
Figure 2. Numerical solution of (1) for $K_5 = 2.0$ and $r_{k5} = 0.8$ $(x_1(t,p))$.
Figure 3. Numerical solution of (1) for $K_5 = 0.02$ and $r_{k5} = 0.8$ $(x_1(t,p))$.
Figure 4. Numerical calculation of bifurcation parameter r^*_{k5} depending on K_5.

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