

LOCAL BIFURCATIONS IN A NONLINEAR MODEL OF A BIOREACTOR*

Neli Dimitrova

ABSTRACT. We consider a nonlinear model of a continuously stirred bioreactor and study the stability of the equilibrium points with respect to practically important model parameters. We determine regions in the parameter space where the steady states undergo transcritical and Hopf bifurcations. In the latter case, the stability of the emerged limit cycles is also studied. Numerical simulations in the computer algebra system *Maple* are presented to illustrate the theoretical results.

1. Introduction. The nonlinear model of a continuously stirred bioreactor based on one substrate and one biomass reaction is usually described by the system of ODEs [3]

$$\begin{aligned}\frac{dS}{dt} &= D(S_{in} - S) - \frac{1}{k} \cdot \mu(S)X \\ \frac{dX}{dt} &= (\mu(S) - D)X,\end{aligned}$$

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where the phase variables S and X are the substrate and biomass concentrations, S_{in} is the input substrate concentration, D is the dilution rate, $\mu(S)$ is a model function of the specific growth rate of the biomass and $k > 0$ is a yield coefficient.

Continuous cultures of some microorganisms like *Saccharomyces cerevisiae* and *Zymomonas mobilis* have long been known to exhibit oscillatory behaviour under suitable operating conditions (see [1] and the references there). Unfortunately the above model is not able to predict this type of behaviour by sudden changes in the model parameters. Instead, the following nonlinear model of the continuous growth of the yeast strain *Saccharomyces cerevisiae* has been proposed in [7], see also [1],

$$(1) \quad \begin{aligned} \frac{dS}{dt} &= D(S_{in} - S) - \frac{1}{k(S)} \cdot \mu(S) \cdot X \\ \frac{dX}{dt} &= (\mu(S) - D) \cdot X, \end{aligned}$$

where

$$k(S) = k_0 + k_1 S$$

presents the yield as a function of the substrate concentration S ; k_0 and k_1 are real positive constants. For physical evidence the following constraints on the phase variables and the model parameters are assumed [3]

$$D > 0, \quad S_{in} > 0, \quad 0 < S \leq S_{in}, \quad X \geq 0.$$

This model is investigated in [1], assuming that $\mu(S)$ is modelled by the Haldane law; it is shown there that under certain conditions the system undergoes Hopf bifurcations of the steady states with respect to the parameter D . It is known that Hopf bifurcations of the equilibrium points lead to the emergence of limit cycles, which can be stable or unstable. For practical applications, the knowledge of the stability/unstability of the limit cycle is very important, because unstable oscillations can destroy the proper operation of the bioreactor process. In [1] only the existence of limit cycles is demonstrated numerically, but their stability type is not studied.

In this paper we study the same model, assuming that the function for the specific growth rate of the microorganisms is described by the Monod law [3]

$$\mu(S) = \frac{\mu_{\max} S}{k_S + S};$$

μ_{\max} is a positive real constant called maximum specific growth rate of the biomass, $k_s > 0$ is a saturation constant. In Section 2 we transform the model into a dimensionless form keeping some practically important coefficients. In Sections 3 and 4 we investigate the local one-parameter bifurcations of the steady states, where D is considered as a bifurcation parameter. We show that under certain conditions the system undergoes a transcritical and a Hopf bifurcation of the equilibrium points. In the latter case we also investigate the stability type of the limit cycle. The computer algebra system *Maple* is used to carry out symbolic and numeric computations as well as the graphic visualization.

2. Analysis of steady states. In practical applications, the input concentration S_{in} and the dilution rate D are under the control of the experimenter. They can be changed to tune the bioreactor to work under desired conditions. In what follows we shall assume that S_{in} is constant, and the dilution rate D is the control (manipulated) variable.

The change of coordinates

$$\begin{aligned} s &= \frac{S}{S_{in}}, & x &= \frac{X}{k_0 S_{in}}, & u &= \frac{D}{\mu_{\max}}, \\ a &= \frac{k_1 S_{in}}{k_0}, & b &= \frac{k_s}{S_{in}}, & \tau &= \mu_{\max} t \end{aligned}$$

transforms the model (1) into the following dimensionless form

$$(2) \quad \dot{s} = u(1-s) - \frac{1}{k(s)} \cdot \mu(s) \cdot x$$

$$(3) \quad \dot{x} = (\mu(s) - u) \cdot x,$$

where \dot{s} and \dot{x} mean $\frac{ds}{d\tau}$ and $\frac{dx}{d\tau}$ respectively,

$$k(s) = 1 + as, \quad \mu(s) = \frac{s}{b+s}$$

with real positive constants a, b . Moreover,

$$0 < s \leq 1, \quad x \geq 0, \quad u > 0$$

are also assumed for biological reasons.

In what follows we shall study the open-loop system (2)–(3) considering u as a bifurcation parameter.

The equilibrium points (steady states) are solutions of the nonlinear algebraic system, obtained from (2)–(3) by setting the right-hand side functions equal to zero, that is

$$(4) \quad u(1-s) - \frac{1}{k(s)} \cdot \mu(s) \cdot x = 0$$

$$(5) \quad (\mu(s) - u) \cdot x = 0.$$

We are looking for nonnegative solutions of (4)–(5) as functions of u . Equations (4)–(5) possess a nontrivial solution

$$(6) \quad \begin{aligned} s(u) &= \frac{bu}{1-u}, \\ x(u) &= k(s(u))(1-s(u)) = \left(1 + \frac{abu}{1-u}\right) \left(1 - \frac{bu}{1-u}\right), \\ u &\in \left(0, \frac{1}{1+b}\right] \end{aligned}$$

and a trivial solution (called a wash-out state)

$$(7) \quad s(u) = 1, \quad x(u) = 0 \quad \text{for all } u > 0.$$

Denote

$$u^* = \frac{1}{1+b} = \mu(1) < 1.$$

Obviously, $u < u^*$ implies $x(u) > 0$ and $s(u) > 0$. Moreover, at $u = u^*$,

$$s(u^*) = 1, \quad x(u^*) = 0.$$

The steady states obviously satisfy the equality

$$s(u) + \frac{1}{k(s(u))}x(u) = 1, \quad u \in (0, 1).$$

Denote

$$\mathcal{L} = \{(s, x) \in \mathbb{R}^2 : s > 0, x \geq 0, s + \frac{1}{k(s)}x = 1\}.$$

It is straightforward to see that the curve \mathcal{L} is a weakly invariant set (manifold) for the system (2)–(3), that is for any initial point $(s(0), x(0)) \in \mathcal{L}$ there exists a

trajectory $(s(t), x(t))$ that remains in \mathcal{L} for all $t \in [0, +\infty)$, see [5]. As we shall see later, \mathcal{L} is a stable manifold of the system.

Denote for simplicity $y = (s, x)$ and by $G(y; u)$ the right-hand side functions of (2)–(3),

$$(8) \quad G(y; u) = \left(u(1-s) - \frac{1}{k(s)} \cdot \mu(s) \cdot x, \quad (\mu(s) - u) \cdot x \right)^T.$$

The linearization (Jacobian matrix) $DG(y; u) = D_y G(y; u)$ evaluated at an equilibrium point $y(u) = (s(u), x(u))$, $u \in (0, u^*)$, is easily seen to be

$$DG(y(u); u) = \begin{pmatrix} \frac{R(a, b; u)}{b(1-u(1-ab))} & -\frac{u(1-u)}{1-u(1-ab)} \\ \frac{(1-u(1+b))(1-u(1-ab))}{b} & 0 \end{pmatrix},$$

where

$$R(a, b; u) = (1+b)(1-ab)u^3 + ((1-b)(1+ab) - 4)u^2 + 3u - 1.$$

Note that $u \in (0, u^*]$ implies $u < \frac{1}{1-ab}$.

It is known that if an equilibrium point is hyperbolic, that is when the linearization $DG(y_0; u_0) = D_y G(y_0; u_0)$ at some equilibrium point y_0 for some value of $u = u_0$ does not possess eigenvalues on the imaginary axes, then $(y_0; u_0)$ is linearly stable or unstable. This means that varying u slightly in the neighbourhood of u_0 will not change the nature of stability of the steady state [4], [12]. When $(y_0; u_0)$ is not hyperbolic, that is when $DG(y_0; u_0)$ has eigenvalues on the imaginary axes, then for u close to u_0 new dynamical behavior can occur.

The characteristic equation of $DG(y(u); u)$ is

$$(9) \quad \lambda^2 - L(a, b; u)\lambda + K(a, b; u) = 0$$

with $L(a, b; u)$ and $K(a, b; u)$ being the trace and the determinant of $DG(y(u); u)$ respectively,

$$L(a, b; u) = \operatorname{tr}(DG(y(u); u)) = \frac{R(a, b; u)}{b(1-u(1-ab))},$$

$$K(a, b; u) = \det(DG(y(u); u)) = \frac{1}{b}u(1-u)(1-u(1+b)).$$

Denote by $\lambda_{1,2}(a, b; u)$ the roots of (9). The local stability of the equilibrium points depends on the signs of the real parts of the eigenvalues $\lambda_{1,2}(a, b; u)$; the signs can be easily determined using the well known relations

$$\lambda_1(a, b; u) + \lambda_2(a, b; u) = L(a, b; u), \quad \lambda_1(a, b; u) \cdot \lambda_2(a, b; u) = K(a, b; u).$$

If $\lambda_{1,2}(a, b; u)$ are real numbers, then their signs depend on both $\text{sign } L(a, b; u)$ and $\text{sign } K(a, b; u)$. If $\lambda_{1,2}(a, b; u)$ are complex conjugate numbers ($\lambda_1(a, b; u) = \overline{\lambda_2(a, b; u)}$) then $K(a, b; u) > 0$ is satisfied for all a, b, u ; in this case the sign of the real part depends on $\text{sign } L(a, b; u)$.

3. Local bifurcations of the equilibrium points with a single zero eigenvalue. In this section we shall consider the simplest way in which an equilibrium point can be nonhyperbolic, namely when the Jacobian matrix possesses a single zero eigenvalue. This means that the two eigenvalues $\lambda_{1,2}(a, b; u)$ should be real numbers.

The Jacobian matrix $DG(y(u); u)$ possesses a single zero eigenvalue if and only if

$$L(a, b; u) \neq 0, \quad K(a, b; u) = 0.$$

Obviously,

$$K(a, b; u) = 0 \iff u = u^* = \frac{1}{1+b}.$$

It is straightforward to see that

$$L(a, b; u^*) = \frac{b^2(a+1)}{(1+b)^2} > 0.$$

Thus the steady state $(s(u^*), x(u^*)) = (s^*, x^*) = (1, 0)$ is a nonhyperbolic equilibrium of the dynamic system (2)–(3). Our goal is to determine the nature of stability of $(s(u), x(u))$ for u near to the bifurcation value u^* . To do this we shall find the reduction of the system (2)–(3) at the nonhyperbolic point (s^*, x^*) to the corresponding center manifold [4], [12].

Proposition 1. *The system of ODEs (2)–(3) undergoes a transcritical bifurcation at the nonhyperbolic point $(s^*, x^*) = (1, 0)$.*

Proof. The following coordinate change

$$\xi = 1 - s, \quad \eta = x, \quad v = u^* - u$$

transforms $(s^*, x^*; u^*)$ into zero $(0, 0; 0) = (0; 0)$. Using Taylor approximations of $\mu(1 - \xi)$ and $\varphi(\xi) = \frac{\mu(1 - \xi)}{k(1 - \xi)}$ at $\xi = 0$,

$$\begin{aligned}\mu(1 - \xi) &= \mu(1) - \frac{d\mu}{ds}(1)\xi = u^* - m\xi, \\ \varphi(\xi) &= \varphi(1) + \frac{d\varphi}{ds}(1)\xi = \frac{u^*}{1+a} + \frac{m}{1+a}\xi - \frac{au^*}{(1+a)^2}\xi\end{aligned}$$

within

$$m = \frac{d\mu}{ds}(1) = \frac{b}{(1+b)^2} > 0,$$

system (2)–(3) is presented in the following form, where the parameter v has been included as a third dependent variable:

$$(10) \quad \begin{pmatrix} \dot{\xi} \\ \dot{\eta} \\ \dot{v} \end{pmatrix} = J^* \cdot \begin{pmatrix} \xi \\ \eta \\ v \end{pmatrix} + \begin{pmatrix} g_1(\xi, \eta; v) \\ g_2(\xi, \eta; v) \\ 0 \end{pmatrix},$$

in (10), J^* denotes the Jacobian matrix evaluated at $(s^*, x^*; u^*) = \left(1, 0; \frac{1}{1+b}\right)$,

$$J^* = \begin{pmatrix} -u^* & \frac{u^*}{1+a} \\ 0 & 0 \end{pmatrix}$$

and

$$\begin{aligned}g_1(\xi, \eta; v) &= v\xi + \frac{1}{1+a} \left(m - \frac{au^*}{1+a}\right) \xi\eta \\ g_2(\xi, \eta; v) &= v\eta - m\xi\eta.\end{aligned}$$

The eigenvalues λ_j and the corresponding eigenvectors p_j , $j = 1, 2$, of J^* are given by

$$\begin{aligned}\lambda_1 &= 0, & p_1 &= (1, 1+a)^T; \\ \lambda_2 &= -u^*, & p_2 &= (1, 0)^T.\end{aligned}$$

Obviously, $\lambda_2 < 0$ holds true. Forming a matrix P by taking as columns the eigenvectors p_j , $j = 1, 2$, and finding its inverse P^{-1} ,

$$P = \begin{pmatrix} 1 & 1 \\ 1+a & 0 \end{pmatrix}, \quad P^{-1} = \frac{1}{1+a} \begin{pmatrix} 0 & 1 \\ 1+a & -1 \end{pmatrix},$$

we make the coordinate change

$$\begin{pmatrix} \xi \\ \eta \end{pmatrix} = P \begin{pmatrix} \zeta \\ \varkappa \end{pmatrix}, \quad \begin{pmatrix} \zeta \\ \varkappa \end{pmatrix} = P^{-1} \begin{pmatrix} \xi \\ \eta \end{pmatrix}.$$

System (10) is transformed into

$$(11) \quad \begin{pmatrix} \dot{\zeta} \\ \dot{\varkappa} \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & -u^* \end{pmatrix} \cdot \begin{pmatrix} \zeta \\ \varkappa \end{pmatrix} + \begin{pmatrix} f_1(\zeta, \varkappa; v) \\ f_2(\zeta, \varkappa; v) \end{pmatrix}$$

$$\dot{v} = 0,$$

where

$$f_1(\zeta, \varkappa; v) = v\zeta - m\zeta^2 - m\zeta\varkappa,$$

$$f_2(\zeta, \varkappa; v) = v\varkappa + \left(2m - \frac{au^*}{1+a}\right)(\zeta^2 + \zeta\varkappa).$$

From the existence theorem for center manifolds [4], the stability of $(\xi, \eta) = (0, 0)$ near $v = 0$ is determined by studying a one-parameter family of first-order ODEs on the center manifold; the latter can be locally represented as a graph over ζ and v by

$$W^c(0) = \{(\zeta, \varkappa; v) \in R^3 \mid \varkappa = h(\zeta; v)\},$$

where $h(0; 0) = 0$ and $D_\zeta h(0; 0) = 0$ for ζ and v sufficiently small. Using the invariance of the graph of $h(\zeta; v)$ under the dynamics generated by (11), we have

$$\dot{\varkappa} = \frac{\partial}{\partial \zeta} h(\zeta; v) \dot{\zeta} + \frac{\partial}{\partial v} h(\zeta; v) \dot{v} = -u^* \cdot h(\zeta; v) + f_2(\zeta, h(\zeta; v); v).$$

Substituting $\dot{\zeta} = f_1(\zeta, h(\zeta; v); v)$ and $\dot{v} = 0$ we obtain

$$(12) \quad \frac{\partial}{\partial \zeta} h(\zeta; v) \cdot f_1(\zeta, h(\zeta; v); v) + u^* \cdot h(\zeta; v) - f_2(\zeta, h(\zeta; v); v) = 0.$$

In the next step we shall compute the center manifold $W^c(0)$ approximately and derive the dynamics on $W^c(0)$. Using Theorem 2.1.3 from [12], we assume that $h(\zeta; v)$ is of the form

$$h(\zeta; v) = a_1\zeta^2 + a_2\zeta v + a_3v^2 + O(\zeta^3, \zeta^2v, \zeta v^2, v^3)$$

with unknown coefficients a_1, a_2, a_3 . Substituting in (12) and equating terms with equal powers to zero we find

$$a_1 = \frac{2m}{u^*} - \frac{a}{1+a}, \quad a_2 = a_3 = 0,$$

thus

$$h(\zeta; v) = \left(\frac{2m}{u^*} - \frac{a}{1+a} \right) \zeta^2.$$

Hence the system of ODEs reduced on the center manifold is given by

$$(13) \quad \begin{aligned} \dot{\zeta} &= v\zeta - m\zeta^2 \\ \dot{v} &= 0. \end{aligned}$$

Since $m > 0$, we can set $m = 1$ in the first equation of (13) to obtain the normal form

$$\dot{\zeta} = \zeta(v - \zeta).$$

According to Theorem 5.4 in [8], the system (2)–(3) is locally topologically equivalent to the system

$$(14) \quad \dot{\zeta} = \zeta(v - \zeta)$$

$$(15) \quad \dot{\varkappa} = -\varkappa.$$

The two equations in (14)–(15) are decoupled. Obviously, $\zeta = 0$ and $\zeta = v$ are equilibrium points of (14), see Figure 1. It is straightforward to see, that for

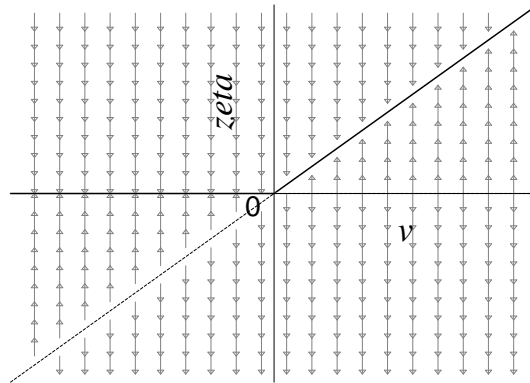


Fig. 1. Bifurcation diagram of (14)

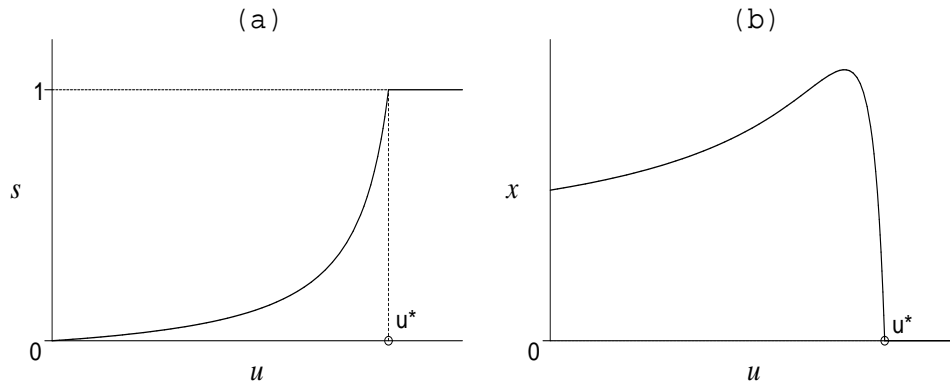


Fig. 2. Bifurcation diagrams of the steady states components: (a) $s(u)$ and (b) $x(u)$; stable branches are denoted by thick lines, unstable branches – by thin lines

$v < 0$ the point $\zeta = 0$ is linearly stable and $\zeta = v$ is unstable; these two points coalesce at $v = 0$ and, for $v > 0$, $\zeta = 0$ is unstable and $\zeta = v$ is stable. Thus, an exchange of stability between the two steady states occurs at the bifurcation value $v = 0$; the type of bifurcation is transcritical [12]. \square

In the (s, x) -plane, it is easy to see that for $u < u^*$, the nontrivial steady state $(s(u), x(u))$ is a stable equilibrium whereas $(s^*, x^*) = (1, 0)$ is unstable. At $u = u^*$, the steady states $(s(u), x(u))$ and $(s^*, x^*) = (1, 0)$ coalesces and exchange stability, thus for $u > u^*$, the unique equilibrium $(1, 0)$ is stable, see Figure 2.

Figure 3 presents phase portraits of (2)–(3) for fixed values of a, b and for different values of u near to u^* . The symbol circle denotes the corresponding steady state $(s(u), x(u))$, the boxes denote the initial points $(s(0), x(0))$ used to compute the system trajectories. The grey coloured curve presents the invariant set \mathcal{L} .

Figure 4 shows the plane $u = \frac{1}{1+b}$ in the parameter space (a, b, u) . For any fixed pair of values of (a, b) , changing u from 0 to 1, a transcritical bifurcation of the steady states occurs by crossing the plane, leading thus to a wash-out ($x = 0$) of the biomass in the bioreactor.

4. Hopf bifurcations of the equilibrium points. This type of bifurcation of an equilibrium point is named after E. Hopf, who was the first to prove (in 1942) an existence theorem for n -dimensional systems of ODEs [6], [9]. Historically, examples of such kind of bifurcations can be found in the work

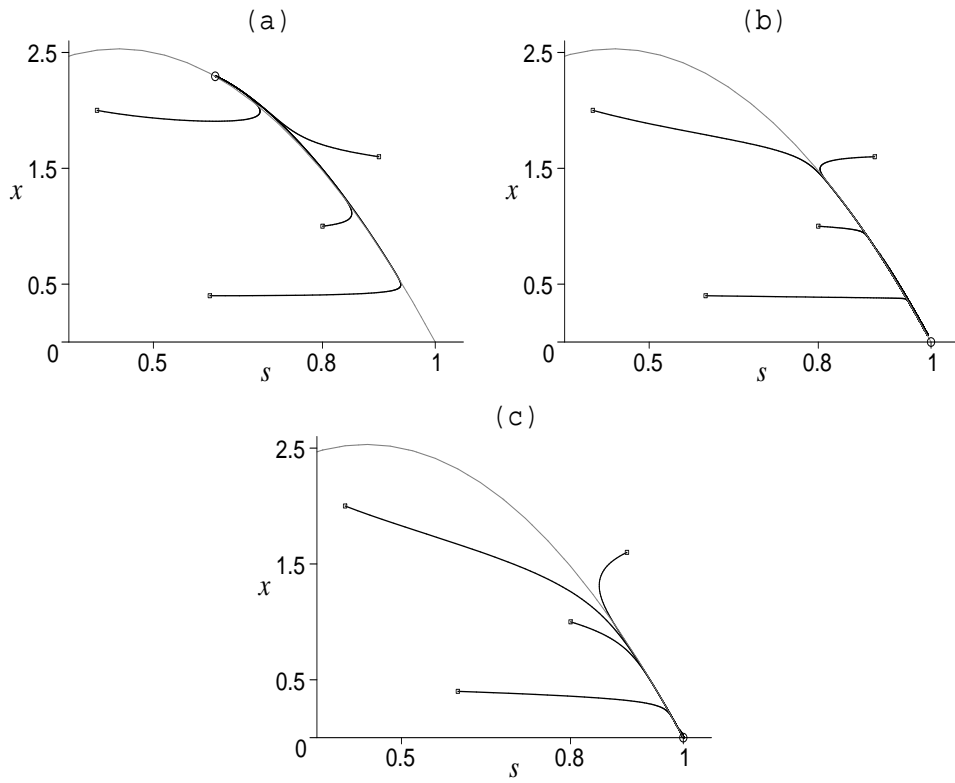


Fig. 3. Phase portraits in a neighborhood of the transcritical bifurcation value u^* : (a) $u < u^*$, (b) $u = u^*$, (c) $u > u^*$. The (grey) curve presents the invariant line \mathcal{L} .

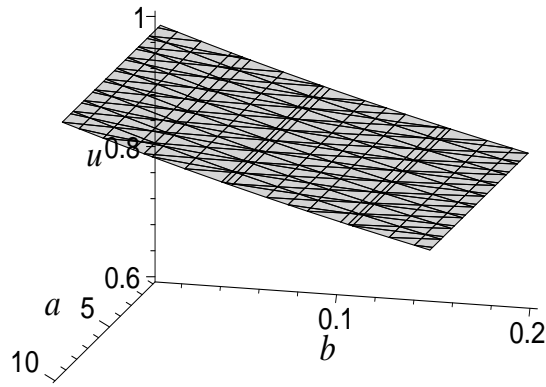


Fig. 4. The plane $u = \frac{1}{1+b}$

of Poincaré [10]. The first specific study and formulation of a theorem is due to Andronov [2]. The works of Poincaré and Andronov are concerned with two-dimensional systems, but before the discovery of the center manifold theory [4]. For that reason some authors call this type of bifurcations Poincaré–Andronov–Hopf [12] or Andronov–Hopf ones [8]. In the literature they are known only as Hopf bifurcations.

4.1. Theoretical background. The presentation here follows [8]. Consider a system

$$(16) \quad \dot{x} = f(x, \alpha), \quad x = (x_1, x_2)^T \in \mathbb{R}^2, \quad \alpha \in \mathbb{R}^1,$$

with a smooth vector function f . Without loss of generality assume that $x = 0$ is an equilibrium point of the system, such that the Jacobian matrix $Df(x; \alpha) = D_x f(x; \alpha)$ evaluated at $x = 0$ has for sufficiently small $|\alpha|$ a pair of complex conjugate eigenvalues, which degrade at $\alpha = 0$ in pure imaginary conjugate numbers. Then the system can be written in the following form

$$(17) \quad \dot{x} = Df(0; \alpha)x + F(x; \alpha),$$

where the function F is a smooth vector function whose components have Taylor expansions in x starting with at least quadratic terms, $F = O(\|x\|^2)$. The components of the Jacobian matrix $Df(0; \alpha)$ are smooth functions of α . Denote by $\lambda(\alpha)$ and $\overline{\lambda(\alpha)}$ the pair of complex conjugate eigenvalues,

$$\lambda(\alpha) = \lambda_R(\alpha) + i\lambda_I(\alpha), \quad \overline{\lambda(\alpha)} = \lambda_R(\alpha) - i\lambda_I(\alpha),$$

where

$$\lambda_R(\alpha) = \frac{1}{2}(\operatorname{tr} Df(0; \alpha)), \quad \lambda_I(\alpha) = \frac{1}{2}\sqrt{4(\det Df(0; \alpha)) - (\operatorname{tr} Df(0; \alpha))^2}.$$

The necessary conditions for a Hopf bifurcation of the steady state $x = 0$ at $\alpha = 0$ to occur is

$$\lambda_R(0) = 0, \quad \lambda_I(0) > 0.$$

Proposition 2 [8]. *By introducing a complex variable, system (17) can be written for sufficiently small $|\alpha|$ in the form*

$$(18) \quad \dot{z} = \lambda(\alpha)z + g(z, \bar{z}, \alpha),$$

where $g = O(|z|^2)$ is a smooth function of (z, \bar{z}, α) .

Sketch of the proof. We give below the main steps of the proof, because they propose a method for practical computation of the Hopf bifurcation.

Let $q(\alpha)$ be an eigenvector of $Df(0; \alpha)$ corresponding to the eigenvalue $\lambda(\alpha)$,

$$Df(0; \alpha) \cdot q(\alpha) = \lambda(\alpha) \cdot q(\alpha),$$

and let $p(\alpha)$ be the eigenvector of the transposed Jacobian matrix $Df(0; \alpha)^T$ corresponding to the eigenvalue $\overline{\lambda(\alpha)}$,

$$Df(0; \alpha)^T \cdot p(\alpha) = \overline{\lambda(\alpha)} \cdot p(\alpha).$$

Normalize $p = p(\alpha) = (p_1, p_2)^T$ with respect to $q = q(\alpha) = (q_1, q_2)^T$, so that

$$\langle p(\alpha), q(\alpha) \rangle = 1,$$

where $\langle p, q \rangle = \bar{p}_1 q_1 + \bar{p}_2 q_2$. Any vector $x \in R^2$ can be uniquely presented as

$$x = zq(\alpha) + \bar{z}\bar{q}(\alpha)$$

for some complex z ; actually, z is determined by $z = \langle p(\alpha), x \rangle$. The complex variable z obviously satisfies the equation

$$\dot{z} = \lambda(\alpha)z + \langle p(\alpha), F(zq(\alpha) + \bar{z}\bar{q}(\alpha), \alpha) \rangle,$$

having the required form with $g(z, \bar{z}, \alpha) = \langle p(\alpha), F(zq(\alpha) + \bar{z}\bar{q}(\alpha), \alpha) \rangle$. \square

We write a formal Taylor series of g in two complex variables z and \bar{z} ,

$$g(z, \bar{z}, \alpha) = \sum_{j+k \geq 2} \frac{1}{j! k!} g_{jk}(\alpha) z^j \bar{z}^k,$$

where

$$g_{jk}(\alpha) = \left. \frac{\partial^{j+k}}{\partial z^j \partial \bar{z}^k} \langle p(\alpha), F(zq(\alpha) + \bar{z}\bar{q}(\alpha), \alpha) \rangle \right|_{(z, \bar{z})=(0,0)}$$

$$j + k \geq 2, \quad j, k = 0, 1, \dots$$

The next step is to simplify the nonlinear part $g(z, \bar{z}, \alpha)$.

Proposition 3 [8] (Poincaré normal form of the Hopf bifurcation). *The equation*

$$\dot{z} = \lambda(\alpha)z + \sum_{2 \leq j+k \leq 3} \frac{1}{j! k!} g_{jk}(\alpha) \cdot z^j \bar{z}^k + O(|z|^4)$$

with $\lambda(\alpha) = \lambda_R(\alpha) + i\lambda_I(\alpha)$, $\lambda_R(0) = 0$, $\lambda_I(0) = \omega_0 > 0$ can be transformed by an invertible parameter-dependent change of complex coordinate, smoothly depending on the parameter α , for all sufficiently small $|\alpha|$, into an equation with only the resonant cubic term $z^2\bar{z}$:

$$\dot{z} = \lambda(\alpha)z + c_1(\alpha) \cdot z^2\bar{z} + O(|z|^4). \quad \square$$

It follows from the proof [8] that

$$(19) \quad c_1(0) = \frac{i}{2\omega_0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2 \right) + \frac{g_{21}}{2},$$

$$g_{jk} = g_{jk}(0), \quad j, k = 0, 1, 2.$$

Definition 1. *The real constant*

$$l_1(0) = \frac{\operatorname{Re} c_1(0)}{\omega_0} = \frac{1}{2\omega_0^2} \operatorname{Re} (ig_{20}g_{11} + \omega_0 g_{21}), \quad \omega_0 = \lambda_I(0),$$

is called the first Lyapunov coefficient of the equilibrium point $x = 0$ at the bifurcation value $\alpha = 0$.

Finally, the following Theorem holds true:

Theorem 1 [8] (Topological normal form of the Hopf bifurcation). *Suppose the two-dimensional system (16) with smooth f , has for sufficiently small $|\alpha|$ the equilibrium $x = 0$ with eigenvalues $\lambda_{1,2}(\alpha) = \lambda_R(\alpha) \pm i\lambda_I(\alpha)$, where $\lambda_R(0) = 0$, $\lambda_I(0) = \omega_0 > 0$. Let the following conditions be satisfied:*

(H.1) $l_1(0) \neq 0$, where l_1 is the first Lyapunov coefficient;

(H.2) $\frac{d\lambda_R}{d\alpha}(0) \neq 0$.

Then there are invertible coordinate and parameter changes and a time reparametrization transforming the system into the following normal form with respect to a new complex variable $z = z_1 + iz_2$

$$\dot{z} = (\beta + i)z + \sigma \cdot z|z|^2,$$

or equivalently

$$(20) \quad \begin{pmatrix} \dot{z}_1 \\ \dot{z}_2 \end{pmatrix} = \begin{pmatrix} \beta & -1 \\ 1 & \beta \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} + \sigma \cdot (z_1^2 + z_2^2) \begin{pmatrix} z_1 \\ z_2 \end{pmatrix},$$

where $\beta = \beta(\alpha) = \frac{\lambda_R(\alpha)}{\lambda_I(\alpha)}$ is a new parameter, and $\sigma = \text{sign } l_1(0) = \pm 1$. \square

Using the representation $z = \varrho e^{i\varphi}$, $\varrho \geq 0$, we obtain the following polar form of the latter system (20)

$$(21) \quad \dot{\varrho} = \varrho(\beta + \sigma \cdot \varrho^2)$$

$$(22) \quad \dot{\varphi} = 1.$$

The equations for ϱ and φ are uncoupled. The first equation has the equilibrium point $\varrho = 0$ for all values of β . The equilibrium is linearly stable if $\beta < 0$; for $\beta > 0$ the equilibrium becomes linearly unstable.

Assume first that $\sigma = -1$, that is $l_1(0) < 0$. In this case the equilibrium point $\varrho = 0$ is nonlinearly stable at $\beta = 0$ (i. e, the rate of solution convergence to $\varrho = 0$ is no longer exponential). For $\beta > 0$ there is a second equilibrium of (21), $\varrho_0(\beta) = \sqrt{\beta}$, which is no more a point (due to the superposition of the motions defined by the two equations), but an isolated closed orbit, called a limit cycle, which is unique and stable; the cycle is a circle of radius $\varrho_0(\beta) = \sqrt{\beta}$. All orbits, starting outside or inside the cycle except at the origin tend to the cycle as $t \rightarrow \infty$. In this case the bifurcation is called supercritical (see Figure 5(a)).

In the opposite case $\sigma = +1$, that is $l_1(0) > 0$, the system undergoes the Hopf bifurcation at $\beta = 0$, but the limit cycle is unstable. The limit cycle exists for $\beta < 0$ and disappears when β crosses zero from negative to positive values.

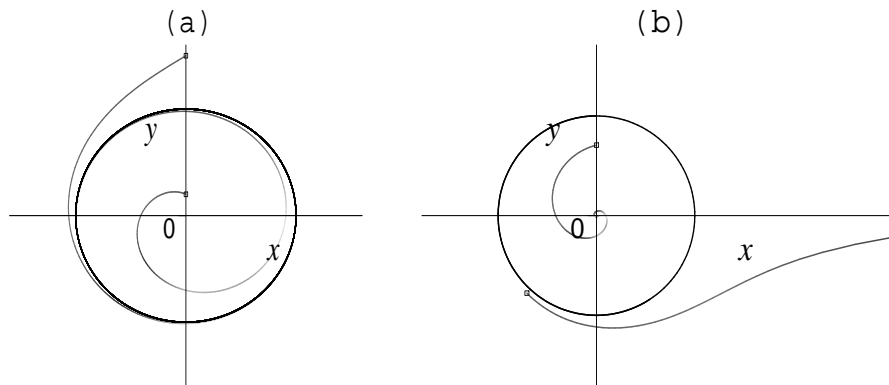


Fig. 5. Phase portrait of (21)–(22); (a) supercritical Hopf bifurcation ($l_1(0) < 0$); (b) subcritical Hopf bifurcation ($l_1(0) > 0$)z

The Hopf bifurcation is called subcritical (Figure 5(b)). The equilibrium $\varrho = 0$ is stable for $\beta < 0$, unstable for $\beta > 0$ and nonlinearly unstable at $\beta = 0$.

4.2. Hopf bifurcations in the bioreactor model. In practical applications we need to compute the first Lyapunov coefficient l_1 at the bifurcation parameter value. The value of l_1 depends on the normalization of the eigenvectors p and q , but we need only the sign of l_1 at the bifurcation parameter value and not the exact value of l_1 to detect stability of the limit cycle.

As we have seen in Section 2, the nontrivial steady states of (2)–(3) are $(s(u), x(u))$ and they exist for any $u \in \left(0, \frac{1}{1+b}\right]$, see (6). Let us recall that we shall study the Hopf bifurcations of the equilibrium points with respect to the bifurcation parameter u . Denote as before (see (8)) by G the right-hand side functions of (2)–(3). The necessary conditions for the existence of a Hopf bifurcation at $(s(u), x(u))$ are

$$(23) \quad L(a, b; u) = \operatorname{tr} DG(s(u), x(u); u) = \frac{R(a, b; u)}{b(1-u(1-ab))} = 0,$$

$$(24) \quad K(a, b; u) = \det DG(s(u), x(u); u) > 0.$$

Obviously, (23) and (24) are equivalent respectively to

$$(25) \quad R(a, b; u) \equiv (1+b)(1-ab)u^3 + ((1-b)(1+ab) - 4)u^2 + 3u - 1 = 0,$$

$$(26) \quad K(a, b; u) \equiv \frac{1}{b}u(1-u)(1-u(1+b)) > 0 \iff 0 < u < \frac{1}{1+b} < 1.$$

Condition (25), $R(a, b; u) = 0$, leads in general to solving a cubic equation with respect to the bifurcation parameter u ; if $ab = 1$, then $R(a, b; u) = 0$ reduces to a quadratic equation. We are looking for a solution u_0 of $R(a, b; u) = 0$ such that $0 < u_0 < \frac{1}{1+b}$ is satisfied. The discriminant $\Delta(a, b)$ of $R(a, b; u) = 0$ is given by

$$(27) \quad \Delta(a, b) = -4b^3(a^3b^3 + 3a^2(a-1)b^2 + 3a(a^2 + 7a + 1)b - (a-1)^3).$$

The cubic equation $R(a, b; u) = 0$ possesses three distinct real roots if $\Delta(a, b) > 0$ and a unique real root if $\Delta(a, b) < 0$. Denote

$$\Sigma = \{(a, b) \in \mathbb{R}^2 : a > 1, b > 0, \Delta(a, b) > 0\}.$$

Figure 6 presents the set Σ (grey coloured), bounded by the curve $\Delta(a, b) = 0$.

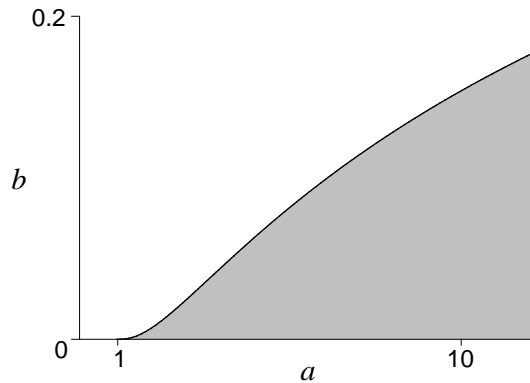


Fig. 6. The set Σ (grey coloured), bounded by $\Delta(a, b) = 0$

Proposition 4. For any point $(a, b) \in \Sigma$ there exist exactly two real roots u_1, u_2 of $R(a, b; u) = 0$ satisfying $u_i \in \left(0, \frac{1}{1+b}\right)$, $i = 1, 2$. The third real root u_3 for $(a, b) \in \Sigma$ as well as the unique real root u_3 in the case $\Delta(a, b) < 0$ satisfies $|u_3| > 1$.

Proof. It follows directly from the Theorem of Budan–Fourier for the number of roots of a polynomial with real coefficients in a given interval, see e. g. [11]. \square

Let us fix $(a, b) \in \Sigma$ and let $u_1, u_2 \in \left(0, \frac{1}{1+b}\right)$ be the two Hopf bifurcation values, such that $u_1 < u_2$. To apply the normal form theorem to the analysis of the Hopf bifurcation at $(s(u_j), x(u_j))$, $j = 1, 2$, we have to check whether conditions (H.1) and (H.2) of Theorem 1 are fulfilled.

Denote by $\lambda_R(a, b; u) \pm i\lambda_I(a, b; u)$ the eigenvalues of the linearization $DG(s, x; u)$ for u close to u_1 or u_2 . Since $\lambda_R(a, b; u) = \frac{1}{2}L(a, b; u)$ holds true, we have for $j = 1, 2$,

$$\begin{aligned} \frac{d}{du}\lambda_R(a, b; u_j) &= \frac{1}{2} \frac{d}{du}L(a, b; u_j) = \frac{1}{2} \frac{d}{du}R(a, b; u_j) \cdot b(1 - u_j(1 - ab)) \neq 0 \\ \iff \frac{d}{du}R(a, b; u_j) &\neq 0 \iff \Delta(a, b) \neq 0. \end{aligned}$$

Therefore, condition (H.2) is satisfied.

Denote for convenience by u_0 any one of the bifurcation values u_1, u_2 ,

$$u_0 \in \{u_1, u_2\},$$

and let be $(s_0, x_0) = (s(u_0), x(u_0))$. To compute the first Lyapunov coefficient at $u = u_0$ we write system (2)–(3) in the form

$$\begin{pmatrix} \dot{s} \\ \dot{x} \end{pmatrix} = J_0 \cdot \begin{pmatrix} s - s_0 \\ x - x_0 \end{pmatrix} + \begin{pmatrix} g_1(s, x) \\ g_2(s, x) \end{pmatrix},$$

where

$$J_0 = \begin{pmatrix} 0 & -\frac{u_0(1-u_0)}{1-u_0(1-ab)} \\ \frac{1}{b}(1-u_0(1+b))(1-u_0(1-ab)) & 0 \end{pmatrix},$$

$$\begin{aligned} g_1(s, x) &= -\frac{a^2 s_0^3 - 3abs_0 - b(1+ab)}{(b+s_0)^3(1+as_0)^3} x_0 \cdot (s-s_0)^2 \\ &\quad - \frac{b - as_0^2}{(b+s_0)^2(1+as_0)^2} (s-s_0)(x-x_0) \\ &\quad - \frac{a^3 s_0^4 - 2a^3 s_0^3 + 6a^2 bs_0^2 + 4ab(1+ab)s_0 + b(a^2 b^2 + ab + 1)}{(b+s_0)^4(1+as_0)^4} x_0 \cdot (s-s_0)^3 \\ &\quad - \frac{a^2 s_0^3 - 3abs_0 - b(1+ab)}{(b+s_0)^3(1+as_0)^3} \cdot (s-s_0)^2(x-x_0), \end{aligned}$$

$$\begin{aligned} g_2(s, x) &= -\frac{b}{(b+s_0)^3} x_0 (s-s_0)^2 + \frac{b}{(b+s_0)^2} (s-s_0)(x-x_0) \\ &\quad + \frac{b}{(b+s_0)^4} x_0 (s-s_0)^3 - \frac{b}{(b+s_0)^3} (s-s_0)^2(x-x_0). \end{aligned}$$

Denote for simplicity $\omega_0^2 = \det J_0 = \lambda_I(a, b; u_0)^2 = \frac{1}{b} u_0(1-u_0)(1-u_0(1+b)) > 0$; the eigenvalues of J_0 are then $\pm i\omega_0$. Compute consecutively the eigenvectors $q = (q_1, q_2)^T$ and $p = (p_1, p_2)^T$,

$$J_0 \cdot q = i\omega_0 \cdot q, \quad J_0^T \cdot p = -i\omega_0 \cdot p$$

and normalize them so that $\langle p, q \rangle = 1$ (we use the same notations p, q for sim-

plicity):

$$p = \begin{pmatrix} \frac{i\omega_0}{2u_0(1-u_0)} \\ \frac{1}{2(1-u_0(1-ab))} \end{pmatrix}, \quad q = \begin{pmatrix} \frac{i}{\omega_0}u_0(1-u_0) \\ 1-u_0(1-ab) \end{pmatrix}.$$

Then $s - s_0$ and $x - x_0$ can be uniquely represented as

$$s - s_0 = zq_1 + \bar{z}\bar{q}_1, \quad x - x_0 = zq_2 + \bar{z}\bar{q}_2$$

for some complex variable z . Further construct the function

$$g(z, \bar{z}) = \bar{p}_1 g_1(s_0 + zq_1 + \bar{z}\bar{q}_1, x_0 + zq_2 + \bar{z}\bar{q}_2) + \bar{p}_2 g_2(s_0 + zq_1 + \bar{z}\bar{q}_1, x_0 + zq_2 + \bar{z}\bar{q}_2)$$

and find its Taylor expansion at $(z, \bar{z}) = (0, 0)$:

$$g(z, \bar{z}) = \sum_{2 \leq j+k \leq 3} \frac{1}{j!k!} g_{jk} \cdot z^j \bar{z}^k + O(|z|^4), \quad g_{jk} = g_{jk}(u_0).$$

Using the coefficients g_{20} , g_{11} and g_{21} we compute the first Lyapunov coefficient

$$l_1(u_0) = \frac{1}{2\omega_0^2} \operatorname{Re}(ig_{20} \cdot g_{11} + \omega_0 g_{21}).$$

If $l_1(u_0) < 0$ then there will be a stable limit cycle; if $l_1(u_0) > 0$ then the limit cycle will be unstable.

To understand the stability of (s_0, x_0) we consider the Taylor expansion of $\lambda_R(a, b; u)$ about u_0 :

$$\begin{aligned} \lambda_R(a, b; u) &= \lambda_R(a, b; u_0) + \frac{d}{du} \lambda_R(a, b; u_0) \cdot (u - u_0) + O((u - u_0)^2) \\ &= \frac{1}{2} \frac{d}{du} R(a, b; u_0) \cdot b(1 - u_0(1 - ab)) \cdot (u - u_0) + O((u - u_0)^2). \end{aligned}$$

The topological normal form of the Hopf bifurcation in polar coordinates (see (21)–(22)) is then given by

$$\begin{aligned} \dot{\varrho} &= \varrho(\beta - \sigma \cdot \varrho^2) \\ \dot{\varphi} &= 1 \end{aligned}$$

within $\sigma = \text{sign } l_1(u_0) = \pm 1$ and

$$\beta = \beta(u) = \frac{\frac{1}{2} \frac{d}{du} R(a, b; u_0) \cdot b(1 - u_0(1 - ab)) \cdot (u - u_0)}{\lambda_I(a, b; u)}.$$

Since $\lambda_I(a, b; u) > 0$ for sufficiently small $|u - u_0|$ and $1 - u_0(1 - ab) > 0$ hold true, it follows that the sign of $\beta(u)$ depends on the sign of $\frac{d}{du} R(a, b; u_0) \cdot (u - u_0)$. It is straightforward to see that at the bifurcation values u_1 and u_2 the following inequalities are valid:

$$\frac{d}{du} R(a, b; u_1) > 0, \quad \frac{d}{du} R(a, b; u_2) < 0.$$

Therefore, the equilibrium $(s(u), x(u))$ is a stable focus for $u \leq u_1$ and $u \geq u_2$. Limit cycles emerge for $u > u_1$ and $u < u_2$, whose stability depends on $\text{sign } l_1(u_j)$, $j = 1, 2$. The latter will be evaluated below numerically.

A work session in the computer algebra system *Maple* is designed to carry out all the symbolic and numeric computations as well as the graphic visualizations.

Figure 7 presents a set of Hopf bifurcation points in the 3-dimensional parameter-phase space $(u, s(u), x(u))$. The paraboloid surface is constructed in the following way: on a grid of points $\{(a_i, b_j)\} \in \Sigma$, $i = 1, \dots, n$, $j = 1, \dots, m$, the two bifurcation values $u_1^{(i,j)}$, $u_2^{(i,j)}$ are computed and the steady states $s(u_k^{(i,j)})$, $x(u_k^{(i,j)})$, $k = 1, 2$, are evaluated.

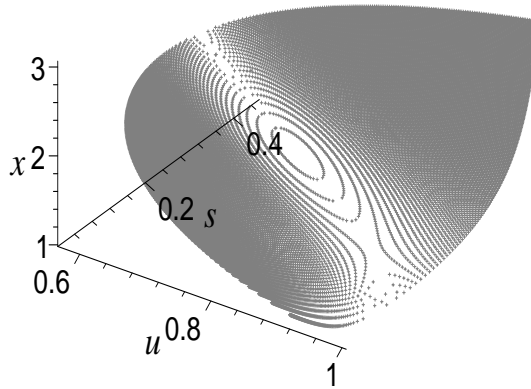


Fig. 7. Hopf bifurcation in the parameter-phase space (u, s, x)

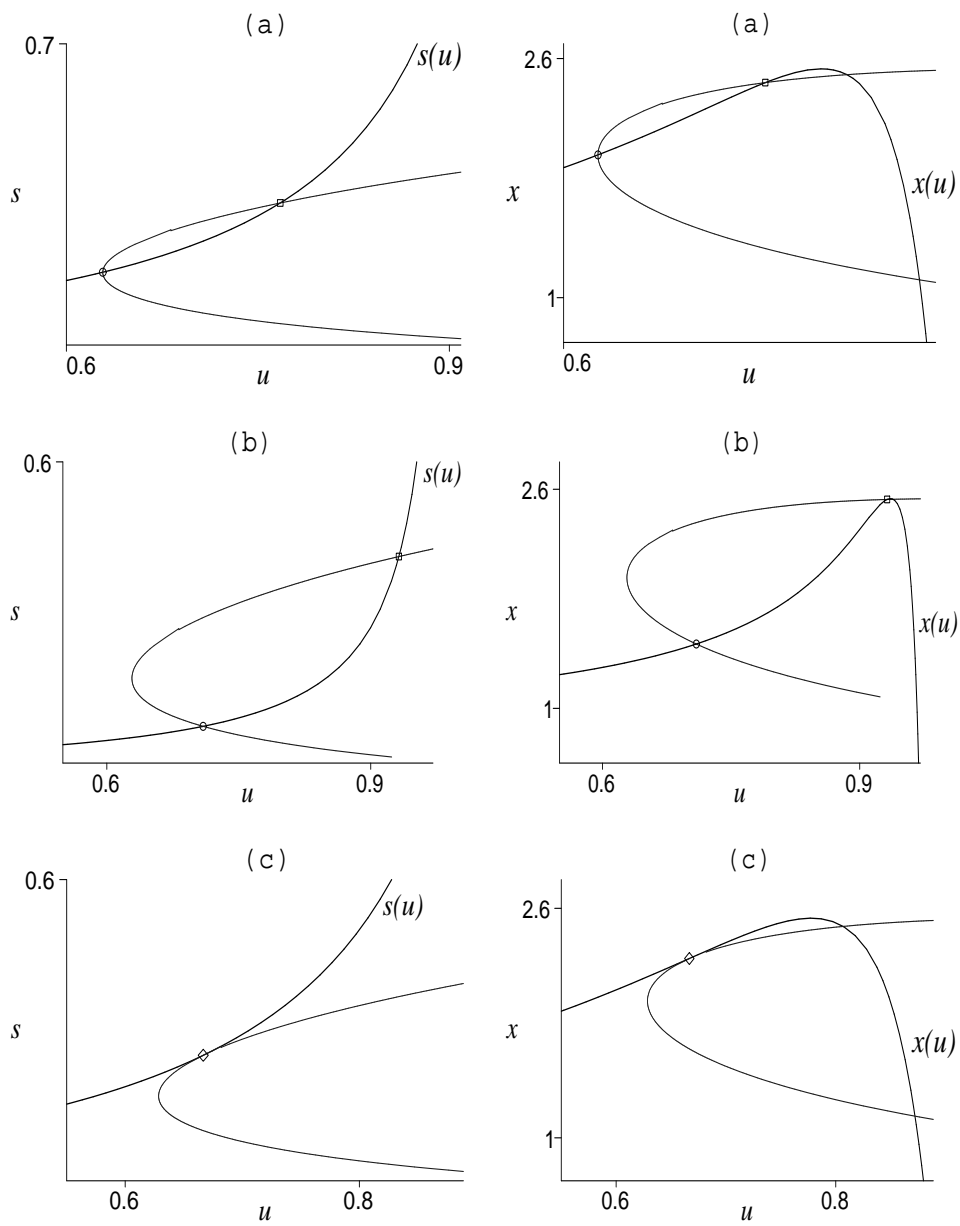


Fig. 8. Hopf bifurcations of the steady state components $s(u)$ and $x(u)$, $u \in (0, u^*)$ for $a = 8$; the graphics of $s(u)$ and $x(u)$ are visualized for (a) $b = 0.1$, (b) $b = 0.03$, (c) $b = 0.125$.

Figure 8 visualizes a projection of the Hopf bifurcation surface from Figure 7 on the plane (u, s) (left column) and (u, x) (right column). This projection is presented by the parabola on all plots, computed for fixed $a = 8$ and a mesh of points b such that $(a, b) \in \Sigma$. For three different values of b , the graphics of the steady states $s(u)$ and $x(u)$, $u \in (0, u^*)$ are also presented. The crossing points of the parabola and the graphics of $s(u)$ and $x(u)$ (denoted by a circle and a box) on plots (a) and (b) correspond to the two different Hopf points $(u_1, s(u_1))$ and $(u_2, s(u_2))$, respectively $(u_1, x(u_1))$ and $(u_2, x(u_2))$; plot (c) shows the case $\Delta(a, b) = 0$, i. e. when $u_1 = u_2$.

Figure 9 presents the first Lyapunov coefficient l_1 as a function of the Hopf bifurcation values u_j . The visualization is based on the numerical computations used in Figure 8 for fixed $a = 8$ and the same mesh of points b such that $(a, b) \in \Sigma$. As one can see, l_1 is negative on the set of the Hopf bifurcation values.

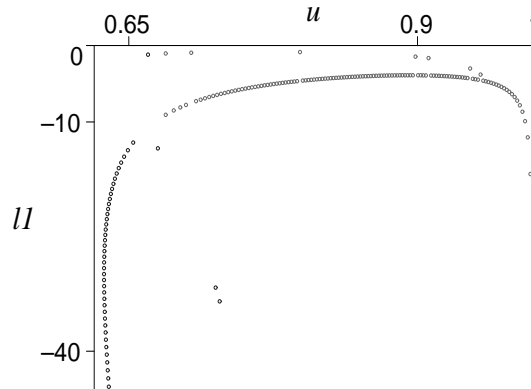


Fig. 9. The first Lyapunov coefficient l_1

The next example visualizes the solution of (2)–(3) in neighbourhoods of the two Hopf bifurcation points for concrete values of the model coefficients $a = 8$ and $b = 0.03$. The cubic equation $R(a, b; u) = 0$ possesses the following two roots u_1 and u_2 in the interval $(0, 0.9708)$,

$$u_1 = 0.7095, \quad u_2 = 0.93204.$$

As mentioned before, the first Lyapunov coefficient computed at u_1 and u_2 is negative,

$$l_1(u_1) < 0, \quad l_1(u_2) < 0.$$

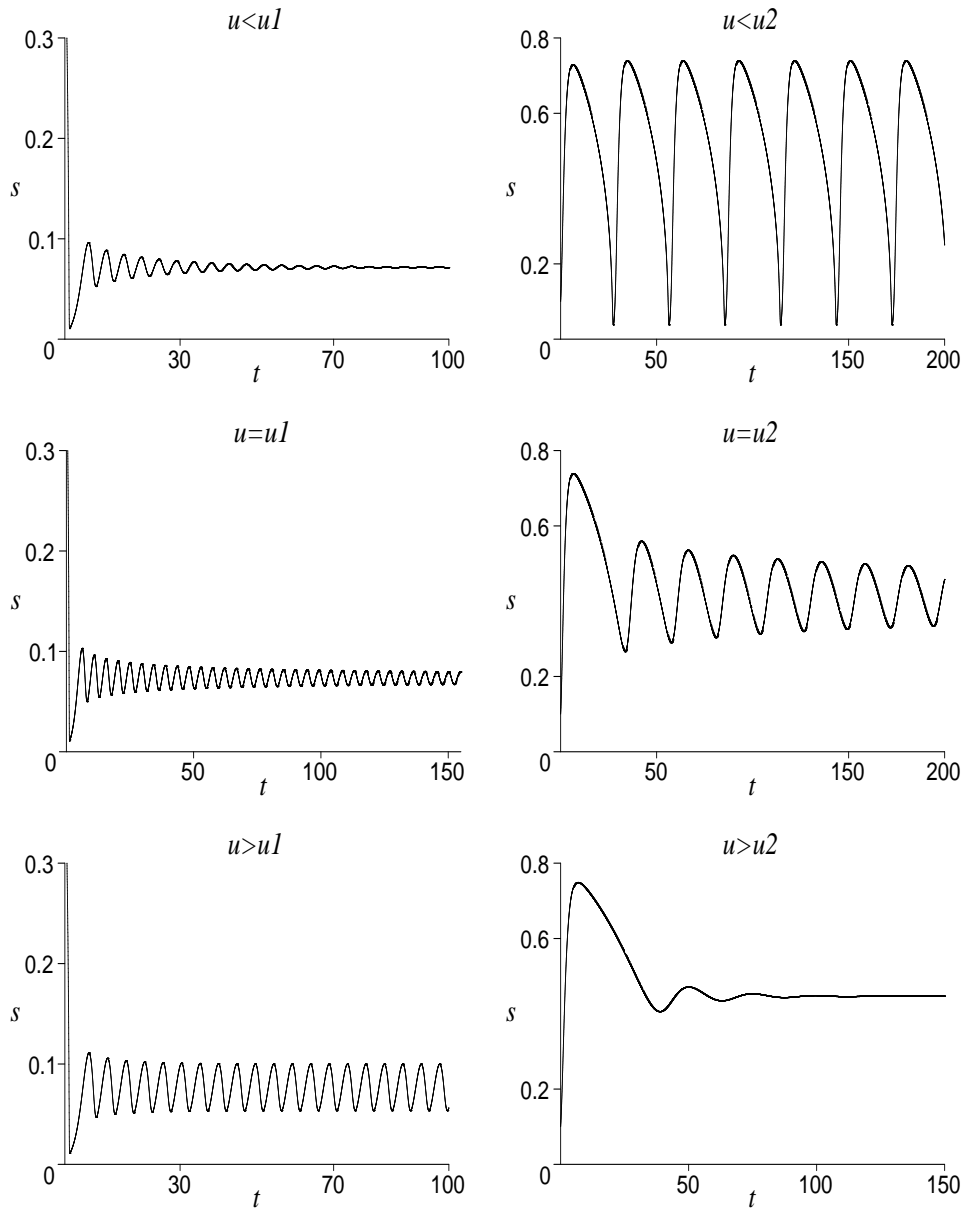


Fig. 10. The phase curve $s(t)$ computed for different values of u near to u_1 (left column) and u near to u_2 (right column)

In both cases the periodic orbits are stable, that is, the Hopf bifurcations are supercritical. Figure 10 presents the solution $s(t)$ when u undergoes small changes near u_1 (left column) and near u_2 (right column). One can see the damped oscillations of $s(t)$ when $u \leq u_1$ that correspond to the stable focus $(s(u), x(u))$ and the fixed oscillations in the case $u > u_1$, when the limit cycle emerges. In the right column the transition from fixed ($u < u_2$) to damped ($u \geq u_2$) oscillations is clearly observable.

5. Discussion and future work. Figure 11 presents the surface $R(a, b; u) = 0$ and the plane $u = \frac{1}{1+b}$. The surface and the plane, do not intersect. For fixed coefficient values (a, b) , when the bifurcation parameter u changes from 0 to 1, the steady states $(s(u), x(u))$ might undergo two Hopf bifurcations and one transcritical bifurcation.

The presence of a transcritical bifurcation leads to biomass wash-out ($x = 0$) and the bioprocess breaks down.

The numerical simulations show that the dynamic model undergoes supercritical Hopf bifurcations of the steady states. The supercritical Hopf bifurcation (with $l_1(u_0) < 0$) of the steady state (s_0, x_0) is also called soft or noncatastrophic [8]; in this case the stable equilibrium at $u = u_0$ goes into a stable limit cycle and all system trajectories spiral towards it (see Figure 5(a)). The system “remains” in a neighbourhood of the equilibrium (s_0, x_0) and is “controllable” in the sense that small changes of the control input u will return it into the stable equilibrium.

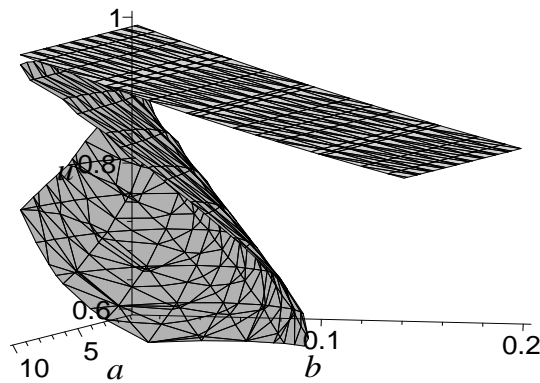


Fig. 11. The surface $R(a, b; u) = 0$ and the plane $u = \frac{1}{1+b}$

The violation of condition (H.2) in Theorem 1 means that the two bifurcation values u_1 and u_2 coincide; in this case the eigenvalues do not cross the imaginary axis as the parameter passes through the bifurcation value $u_1 = u_2$. This results in the same local phase portrait for either sub- or supercritical parameter values depending on the sign of l_1 .

If condition (H.1) of Theorem 1 is not satisfied, that is if the first Lyapunov coefficient vanishes at a bifurcation point, then at this point the Hopf bifurcation turns into the Bautin bifurcation, also called a generalized (or degenerate) Hopf bifurcation. To unfold this type of bifurcation, a second bifurcation parameter should be involved; this leads to the so-called co-dimension two bifurcations. Such bifurcations will be a subject of a further study.

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Institute of Mathematics and Informatics
Bulgarian Academy of Sciences
Acad. G. Bonchev Str., Bl. 8
1113 Sofia, Bulgaria
e-mail: nelid@bio.bas.bg

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