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EMERGENCE AND COLLAPSE OF LIMIT CYCLES IN THE GLYCOLYSIS MODEL

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ABSTRACT
The main question in this paper is to show that, for appropriated fixed values of the rate for the low activity state in the system modeling a type of glycolysis, a single limit cycle emerges after a supercritical Hopf Bifurcation as the bifurcation parameter increases, while continuously increasing the bifurcation parameter, this limit cycle collapses after a subcritical Hopf bifurcation. The motivation is in the study of Hopf bifurcations about the spatially homogeneous equilibrium in the reaction-diffusion system modeling glycolysis. To do so, we use Lyapunovs method.

KEYWORDS: non-degenerate Hopf bifurcation, pattern formation, asymptotic expansion, glycolysis model, reaction-diffusion.

MSC: 35B32, 35B36, 35C20, 92E20, 35K57, 35B40

RESUMEN
La cuestión principal en este artículo es mostrar que, para valores apropiados de la tasa para el estado de baja actividad en el sistema que modela un tipo de glicólisis, emerge un ciclo límite a partir de una bifurcación de Hopf supercrítica cuando el parámetro de bifurcación se incrementa, mientras que al continuar incrementando el parámetro de bifurcación, este ciclo límite colapsa producto de una bifurcación de Hopf subcrítica. La motivación está en el estudio de bifurcaciones de Hopf en torno al equilibrio espacialmente homogéneo en el sistema de reacción-difusión que modela el proceso de glicólisis. Para esto utilizamos el método de Lyapunov.

PALABRAS CLAVE: bifurcación de Hopf no degenerada, formación de patrones, desarrollo asintótico, modelo de glicólisis, reacción-difusión.

1. INTRODUCTION

An important example of two-species biological model describing oscillatory behavior is the glycolysis system. Glycolysis (or glucolysis) is the metabolic pathway entrusted to rust the glucose with the purpose to obtain energy for the cell. Its significance lies in that it can supply the energy with a rapid speed, but more importantly under oxygen-free conditions such as strenuous exercise and high-altitude hypoxia (see [14, 3, 4, 11, 13, 6, 2, 10] and [1]).
We shall represent the situation assuming that the chemicals concentrations u and v correspond to the glycolysis model for two species in reaction and diffusion in the plane (see [14])

$$\partial_t u = D_u \Delta_x u + \delta - \kappa u - uv^2, \qquad x \in \Omega,\ t > 0, \tag{1.1a}$$

$$\partial_t v = D_v \Delta_x v + \kappa u + uv^2 - v, \qquad x \in \Omega,\ t > 0, \tag{1.1b}$$

$$\partial_\nu u = \partial_\nu v = 0, \qquad x \in \partial\Omega,\ t > 0, \tag{1.1c}$$

with initial conditions

$$u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0, \qquad x \in \Omega. \tag{1.2}$$

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Here, the reactions occur in a bounded domain $\Omega \subset \mathbb{R}^2$ with smooth boundary $\partial\Omega$, where the functions $u(x,t)$ and $v(x,t)$ stand for the concentrations of two reactants in position x and time t. The positive constants D_u and D_v are the diffusion coefficients, meanwhile $\delta > 0$ is the dimensionless input flux and $\kappa > 0$ is the dimensionless constant rate for the low activity state. Moreover, Δ_x is the Laplace operator with respect to the spatial variable $x = (x_1, x_2)$. A no-flux boundary condition is assumed so that the chemical reactions occur in a closed reactor.
The chemical reaction represented in system (1.1) is autocatalytic of order 2 by the exponent of v in term uv^2 in the reaction part of both equations (1.1a) and (1.1b) (see [14], where the authors also consider an increasing smooth positive function $f(v)$ in a place of v^2).

We can obtain a proof of the existence and uniqueness of a solution $u(x,t)$, $v(x,t)$ to the evolution system (1.1) for $t \in (0,\infty)$, $x \in \bar{\Omega}$, if we apply a result in [7]. In this paper, we focus our attention on the question of existence and stability of steady-state solutions and periodic orbits emergent from a Hopf bifurcation in the steady-state.

For bounded spatial domains and natural boundary conditions it is known from [5] and [9] that the non-constant spatially homogeneous periodic solution to Eqs.(1.1) is orbitally stable if (D_u, D_v) belongs to a certain open neighborhood of the bisectrix of the first quadrant in the Cartesian product of diffusion coefficients while the non-zero Flocquet's exponent of the linearized system is negative. But the periodic solution would be unstable for any pair of diffusion coefficients if the non-zero Flocquet's exponent is negative.

The scalar parameters δ and κ in the reaction part of the system (1.1) will govern the Hopf bifurcation. If we consider the steady-state equation associated with (1.1),

$$D_u\Delta_x u + \delta - \kappa u - uv^2 = 0, \qquad x \in \Omega, \tag{1.3a}$$

$$D_v\Delta_x v + \kappa u + uv^2 - v = 0, \qquad x \in \Omega, \tag{1.3b}$$

$$\partial_\nu u = \partial_\nu v = 0, \qquad x \in \partial\Omega, \tag{1.3c}$$

we can get the unique positive spatially homogeneous steady-state solution of system (1.1),

$$(u,v) = \left(\frac{\delta}{\alpha},\, \delta\right), \tag{1.4}$$

where $\alpha := \delta^2 + \kappa$. For convenience, in our bifurcation analysis we will occasionally use the unique parameter α as a bifurcation parameter.

We do not impose any restriction either to the shape of the bidimensional domain Ω, but it is well known that practical limitations would arise if one looks for eigenvalues and eigenvectors to the Laplacian operator in general domains. However we can denote by $0 = \mu_0 < \mu_1 \le \mu_2 \le \cdots \le \mu_n \le \cdots$, the eigenvalues of the operator $-\Delta_x$ with homogeneous Neumann boundary conditions in Ω. In this paper we will analyze the presence of Hopf bifurcations in the spatially homogeneous equilibrium for reaction-diffusion system (1.1) with Neumann boundary conditions just considering the solutions u, v to the eigenvalue problem asociated to $\mu_0 = 0$. This last condition signifies that $\Delta_x u = \mu_0 u = 0$ and $\Delta_x v = \mu_0 v = 0$ in system (1.1), then we obtain from (1.1a) and (1.1b),

$$\partial_t u = \delta - \kappa u - uv^2, \tag{1.5a}$$

$$\partial_t v = \kappa u + uv^2 - v. \tag{1.5b}$$

One of the main results in [14] about the glycolysis system (1.1) is that the constant steady-state solution $(\delta/\alpha, \delta)$ is globally asymptotically stable when $\kappa > 4\delta^2$ and $\kappa \ge (\max_{x\in\bar{\Omega}} v_0(x))^2$ (see [14, Theorem 2.4]). In this case, we obtain more accurate condition that guarantee the global asymptotic stability of the steady-state solution, so we expect a supercritical bifurcation when the condition fails.

In this paper we use the bifurcation theory from the book [8] to analyse the Hopf bifurcation of the planar system 1.5 and the appearance of a limit cycle after or before the critical value of the bifurcation parameter. We also suggest as a next work in this direction with the same system using the classification of the of the bifurcation on the basis of the number of emerging limit cycles at bifurcation (see [12]).

The plan of the paper is as follows. In Section 2. we give the outline of the results. In Section 3. elementary results about the stability analysis of the spatially homogeneous equilibrium and Hopf bifurcation curves in the parameter space are found. Section 4. is devoted to the analysis of Hopf bifurcations and the appearance of limit cycles.

2. OUTLINE OF RESULTS

Our main results for the glycolysis system (1.1) are:

1. We found two bifurcation curves that determine the regions for the stability of the unique spatially homogeneous steady-state solution.
2. One bifurcation curve corresponds to a supercritical Hopf bifurcation for all admissible κ while the other curve corresponds to a subcritical Hopf Bifurcation. In the region between the two curves a unique limit cycle appears surrounding the equilibria.

We summarize the above results in the following theorem:

Theorem 2.1 *Let $\delta > 0$ and $0 < \kappa \leq 1/8$, then for the unique equilibrium $(\delta/\alpha, \delta)$ of the ODE system* (1.5)*, there exists two Hopf bifurcation curves in the parameter space (δ, κ). Moreover both Hopf bifurcations are generics and the system* (1.5) *has a globally asymptotically stable periodic orbit if*

$$\left|\delta^2 + \kappa - \frac{1}{2}\right| < \sqrt{1 - 8\kappa} \qquad \textit{and} \qquad 0 < \kappa < 1/8.$$

In the following we first verify the fulfillment of the transversality condition for the existence of a generic Hopf bifurcation in the steady state using a standard procedure and we obtain regions of stability and instability limited by bifurcation curves. Then we use the method described in [8, Ch. 3] to compute the first Lyapunov coefficient and we finally apply the topological normal form theorem for the Hopf bifurcation in order to prove the theorem 2.1.

3. HOPF BIFURCATION IN GLYCOLYSIS SYSTEM

Here we consider the ODE system corresponding to (1.1),

$$\partial_t u = f(u, v), \tag{3.1a}$$
$$\partial_t v = g(u, v). \tag{3.1b}$$

with

$$f(u, v) = \delta - \kappa u - uv^2 \qquad \text{and} \qquad g(u, v) = \kappa u + uv^2 - v. \tag{3.2}$$

By (1.4) the unique stationary state for the system (1.5) is given by

$$E_0 = (u^{(0)}, v^{(0)}) = (\delta/\alpha, \delta), \qquad \text{where } \alpha := \delta^2 + \kappa > 0,$$

depending on the parameters δ and κ. In the following, we use α as the main bifurcation parameter. Note that the parameter α is equivalent to κ in the sense of that $\kappa > 0$ correspond to $\alpha > \delta^2$. The Jacobian matrix of the reaction part $(f(u,v), g(u,v))$ evaluated at E_0 is

$$\frac{\partial(f,g)}{\partial(u,v)}(u^{(0)}, v^{(0)}) \;=\; \begin{pmatrix} -(\delta^2+\kappa) & -\dfrac{2\delta^2}{\delta^2+\kappa} \\ & \\ \delta^2+\kappa & \dfrac{\delta^2-\kappa}{\delta^2+\kappa} \end{pmatrix},$$

wish we can write as

$$L_0(\alpha,\kappa) \;=\; \begin{pmatrix} -\alpha & \dfrac{2(\kappa-\alpha)}{\alpha} \\ & \\ \alpha & \dfrac{\alpha-2\kappa}{\alpha} \end{pmatrix}. \tag{3.3}$$

The Hopf bifurcation condition implies that the trace of $L_0(\alpha,\kappa)$ vanishes and the determinant is positive for some pair (α,κ). So, we first compute

$$\sigma(\alpha,\kappa) := \operatorname{tr} L_0(\alpha,\kappa) \;=\; -\alpha + \frac{\alpha-2\kappa}{\alpha}. \tag{3.4}$$

Now, we determine the neutral curve $\sigma(\alpha,\kappa) = 0$ in the corresponding parameter space by

$$\alpha^2 - \alpha + 2\kappa = 0, \tag{3.5}$$

reducing to a one-parameter dependence. Taking α as the bifurcation parameter for each fixed value of κ, the solutions to the equation (3.5) are

$$\alpha_0^{\pm} = \alpha_0^{\pm}(\kappa) \;=\; \frac{1}{2}(1 \pm \sqrt{1-8\kappa}) > 0, \tag{3.6}$$

provided $0 < \kappa \leq 1/8$.
Now, computing the determinant of the matrix $L_0(\alpha_0^{\pm})$ in 3.3, we obtain

$$\omega^2(\alpha_0^{\pm}) = \det L_0(\alpha_0^{\pm},\kappa) \;=\; \alpha_0^{\pm} = \frac{1}{2}(1 \pm \sqrt{1-8\kappa}) > 0. \tag{3.7}$$

Then, for α close enough to $\alpha_0^{\pm}$, the eigenvalues of $L_0(\alpha) = L_0(\alpha,\kappa)$ are complex and have the representation $\lambda_1(\alpha) = \lambda(\alpha) = \overline{\lambda_2(\alpha)}$, where $\lambda(\alpha) := \frac{1}{2}\sigma(\alpha) + i\omega(\alpha)$, $\sigma(\alpha_0^{\pm}) = 0$ and $\omega(\alpha_0^{\pm}) > 0$. Excluding the case $\kappa = 1/8$, we have two different critical values, $\alpha = \alpha_0^+$ and $\alpha = \alpha_0^-$ (see figure 1). So, in the strip $(0,1/8) \times \mathbb{R}_+$ we have three different regions determined by the parabola $\sigma(\alpha,\kappa) = 0$.

Therefore, for each $\kappa \in (0,1/8)$ we have exactly two positive values $\alpha_0^{\pm} > 0$ of α at which the unique steady state may shows a Hopf bifurcation. The corresponding Jacobian matrix at the equilibria

$$E_0^{\pm} = E_0(\alpha_0^{\pm};\kappa) \tag{3.8}$$

has the eigenvalues $\lambda_{1,2}(\alpha_0^+) = \pm i\omega(\alpha_0^+)$ and $\lambda_{1,2}(\alpha_0^-) = \pm i\omega(\alpha_0^-)$ respectively.

Let us analyse the stability of the equilibrium $E_0(\alpha;\kappa)$ for $(\alpha,\kappa) \in \mathbb{R}_+ \times (0,1/8]$. For a fixed κ in the open interval $(0,1/8)$ and from (3.4) we can check that $\sigma(\alpha) < 0$ for $\alpha \in (0,\alpha_0^-) \bigcup (\alpha_0^+,+\infty)$ and $\sigma(\alpha) > 0$ for $\alpha \in (\alpha_0^-,\alpha_0^+)$. That is to say, the equilibrium E_0 is locally asymptotically stable if $0 < \alpha < \alpha_0^-$, it is done unstable when $\alpha_0^- < \alpha < \alpha_0^+$, and finally it goes back to be locally asymptotically stable when $\alpha > \alpha_0^+$. In figure 1 the shaded regions are regions of stability and the

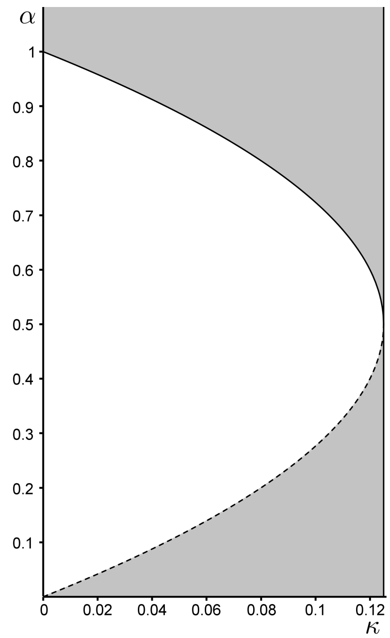

Figure 1: Bifurcation curve in the parameter space: κ vs α_0^+ (solid line); κ vs α_0^- (dashed line).

white region is the region of instability of the stationary state. Therefore $\alpha = \alpha_0^-(\kappa)$ and $\alpha = \alpha_0^+(\kappa)$ from (3.6) are two Hopf bifurcation curves for the stationary state E_0 of system (1.5) with $\kappa \in (0, 1/8)$. Notice that, at $\kappa = 1/8$ the bifurcation will not take place.

In figure 2(a) we can see the zero-isoclines of system (1.5) for $\kappa = 1/10$ and the corresponding values of α_0 according to the equality (3.6), i.e. $\alpha_0^\pm = (5 \pm \sqrt{5})/10$. In the same way, we consider the values $\kappa = 1/8$, $\alpha_0 = 1/2$ for figure 2(b).

3.1. PDE model

Now we consider the spatially homogeneous equilibrium $E_0 = (\delta/\alpha, \delta)$ with respect to the reaction-diffusion PDE model (1.1). Next, we linearize the steady state system (1.3) around the equilibrium E_0, defining the new variables $\phi := u - \delta/\alpha$, $\psi := v - \delta$ and we consider the corresponding eigenvalue problem

$$D_u \Delta_x \phi - \alpha\phi + A(\alpha)\psi \;=\; \mu\phi, \qquad x \in \Omega, \tag{3.9a}$$

$$D_v \Delta_x \psi + \alpha\phi + B(\alpha)\psi \;=\; \mu\psi, \qquad x \in \Omega, \tag{3.9b}$$

$$\partial_\nu \phi = \partial_\nu \psi \;=\; 0, \qquad x \in \partial\Omega, \tag{3.9c}$$

where

$$A(\alpha) := \frac{2(\kappa - \alpha)}{\alpha}, \qquad B(\alpha) := \frac{\alpha - 2\kappa}{\alpha}. \tag{3.10}$$

We can write the system (3.9) in the form

$$L(\alpha)\Phi = \mu\Phi, \qquad \partial_\nu \Phi = 0,$$

where

$$L(\alpha) := \begin{pmatrix} D_u\Delta_x - \alpha & A(\alpha) \\ \alpha & D_v\Delta_x + B(\alpha) \end{pmatrix} \qquad \text{and} \qquad \Phi := \begin{pmatrix} \phi \\ \psi \end{pmatrix},$$

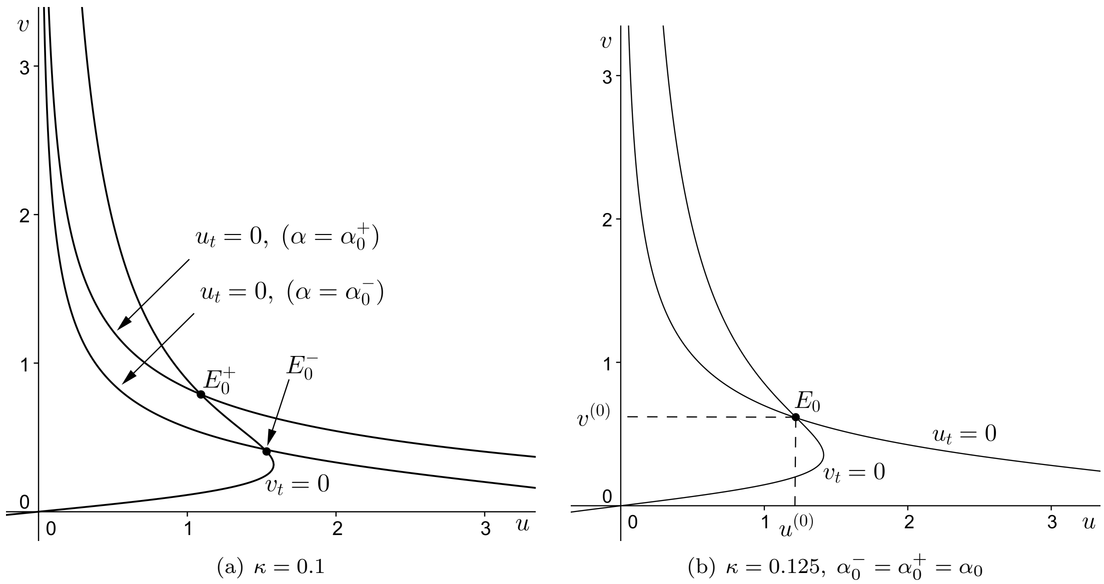

Figure 2: Zero-isoclines at the Hopf bifurcation ($\alpha = \alpha_0$)

Denoting by $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \cdots \leq \mu_n \leq \cdots$, the eigenvalues of the operator $-\Delta_x$ with homogeneous Neumann boundary condition in Ω, we can define for each $n \in \mathbb{N} \setminus \{0\}$ the matrix

$$L_n(\alpha) := \begin{pmatrix} -D_u\mu_n - \alpha & A(\alpha) \\ \alpha & -D_v\mu_n + B(\alpha) \end{pmatrix}.$$

In this moment we only consider the eigenvalue $\mu_0 = 0$ in the above matrix and we have the Jacobian matrix (3.3). The next section is dedicated to the existence proof of the limit cycle as a product of Hopf bifurcations for system (1.5).

4. NON DEGENERACY: PROOF OF THE THEOREM 2..1

To apply the normal form theorem (see [8]) to the Hopf bifurcation analysis in each of the critical values α_0^+ and α_0^-, we must verify when the genericity conditions of the theorem (th. 3.3, [8]) are satisfied. We start with the transversality condition (B.2), that is,

$$\frac{\partial \sigma}{\partial \alpha}(\alpha_0^{\pm}) \neq 0.$$

In this section we always consider $\delta > 0$ and $0 < \kappa < 1/8$.
The derivative of (3.4) with respect to α is

$$\frac{\partial \sigma}{\partial \alpha} = -1 + \frac{2\kappa}{\alpha^2}.$$

from where we can verify the transversality condition for $\alpha = \alpha_0^- = \frac{1}{2}(1 - \sqrt{1 - 8\kappa})$, i.e.

$$\frac{\partial \sigma}{\partial \alpha}(\alpha_0^-) = \frac{1}{4}(1 - 8\kappa + \sqrt{1 - 8\kappa}) > 0.$$

To analyse the case of $\alpha = \alpha_0^+ = \frac{1}{2}(1 + \sqrt{1 - 8\kappa})$, we first consider a new parameter β by the change $\alpha = 1 - \beta$. We substitute this change of parameter in (3.3) and (3.4) to obtain the new jacobian matrix

$L_{0,\beta}(\beta,\kappa)$ and the new trace $\sigma_\beta(\beta,\kappa)$, wish becomes zero for $\beta_0^+ = 1-\alpha_0^+$. For the new determinant we have

$$\omega_\beta^2(\beta_0^+) = \det L_{0,\beta}(\beta_0^+,\kappa) = 1-\beta_0^+ = \frac{1}{2}(1-\sqrt{1+8\kappa}) > 0. \tag{4.1}$$

In this case the derivative of $\sigma_\beta := \sigma(1-\beta,\kappa)$ with respect to β is also positive for $\beta=\beta_0^+$, in fact

$$\frac{\partial\sigma_\beta}{\partial\beta}(\beta_0^+) = -\frac{\partial\sigma}{\partial\alpha}(\alpha_0^+) = -\frac{1}{4}(1-8\kappa-\sqrt{1-8\kappa}) > 0.$$

Then the transversality condition holds too. Hereinafter, occasionally to abbreviate we will write α_0 instead of α_0^- and β_0 instead of β_0^+.

Now, we will verify if the non degeneracy condition (B.1) is satisfied. That is, we have to compute the Lyapunov's first coefficient and to check if this number is different to zero on the bifurcation curves. To do this, we will fix the parameter α in its critical value α_0. The following computations are valid if we change α_0 by $1-\beta_0$.
For $\alpha=\alpha_0$ the equilibria E_0 has the coordinates

$$u^{(0)} = \frac{\delta_0}{\alpha_0}, \qquad v^{(0)} = \delta_0,$$

where $\delta_0^2 = \delta_0^2(\kappa) = \frac{1}{2}(1-2\kappa\pm\sqrt{1-8\kappa})$ and $\alpha_0 = \alpha_0(\kappa) = \delta_0^2(\kappa)+\kappa$.
Translate the origin of the coordinates by the change of variables

$$\begin{aligned} u &= u^{(0)}+\xi_1,\\ v &= v^{(0)}+\xi_2. \end{aligned}$$

This transform the ODE system

$$\begin{aligned} \dot{u} &= f(u,v),\\ \dot{v} &= g(u,v), \end{aligned}$$

where $f(u,v)$ and $g(u,v)$ are the functions in (3.2), in

$$\begin{aligned} \dot{\xi_1} &= -\alpha_0\xi_1 - \frac{2(\kappa-\alpha_0)}{\alpha_0}\xi_2 - 2\delta_0\xi_1\xi_2 - \frac{\delta_0}{\alpha_0}\xi_2^2 - \xi_1\xi_2^2 =: F_1(\xi_1,\xi_2),\\ \dot{\xi_2} &= \alpha_0\xi_1 + \frac{\alpha_0-2\kappa}{\alpha_0}\xi_2 + 2\delta_0\xi_1\xi_2 + \frac{\delta_0}{\alpha_0}\xi_2^2 + \xi_1\xi_2^2 =: F_2(\xi_1,\xi_2). \end{aligned}$$

This system can be represented as

$$\dot{\xi} = \mathbf{A}\xi + \frac{1}{2}\mathbf{B}(\xi,\xi) + \frac{1}{6}\mathbf{C}(\xi,\xi,\xi),$$

where $\mathbf{A} = L_0(\alpha_0,\kappa)$ (see (3.3)) and the multilineal functions $\mathbf{B}$ and $\mathbf{C}$ take on the planar vectors $\xi=(\xi_1,\xi_2)$, $\eta=(\eta_1,\eta_2)$ and $\zeta=(\zeta_1,\zeta_2)$ the values

$$\mathbf{B}(\xi,\eta) = \left[2\delta_0(\xi_1\eta_2+\xi_2\eta_1) + \frac{2\delta_0}{\alpha_0}\xi_2\eta_2\right]\begin{pmatrix} -1\\ 1\end{pmatrix}$$

and

$$\mathbf{C}(\xi,\eta,\zeta) = 6(\xi_1\eta_2\zeta_2+\xi_2\eta_1\zeta_2+\xi_2\eta_2\zeta_1)\begin{pmatrix} -1\\ 1\end{pmatrix}.$$

Write the matrix $\mathbf{A}$ in the form

$$\mathbf{A} = \begin{pmatrix} -\omega^2 & -(\omega^2+1) \\ \\ \omega^2 & \omega^2 \end{pmatrix},$$

where ω^2 is given by formulas (3.7) or (4.1)[1]. Now it is easy to check that complex vectors

$$q \sim \begin{pmatrix} \omega^2+1 \\ -\omega(\omega+i) \end{pmatrix}, \qquad p \sim \begin{pmatrix} \omega \\ \omega - i \end{pmatrix},$$

are proper eigenvectors, that is to say

$$\mathbf{A}q = i\omega q, \qquad \mathbf{A}^{\mathrm{T}}p = -i\omega p.$$

To achieve the necessary normalization $\langle p, q\rangle = 1$, where $\langle \cdot, \cdot \rangle$ means the standard scalar product in $\mathbb{C}$, $\langle p, q\rangle = \bar{p}_1 q_1 + \bar{p}_2 q_2$, we can take, for example,

$$q = \frac{1}{2\omega}\begin{pmatrix} 1+i\omega \\ -i\omega \end{pmatrix}, \qquad p = \begin{pmatrix} \omega \\ \omega - i \end{pmatrix}.$$

The hardest part of the job is done, and now we can simply calculate[2]

$$g_{20} = \langle p, \mathbf{B}(q,q)\rangle = \frac{\delta_0}{2\omega^2}(2\omega + i(2\omega^2-1)), \qquad g_{11} = \langle p, \mathbf{B}(q,\bar{q})\rangle = \frac{\delta_0(1-2\omega^2)}{2\omega^2} i,$$

$$g_{21} = \langle p, \mathbf{C}(q,q,\bar{q})\rangle = \frac{3}{4\omega}(-3\omega + i),$$

and compute the first Lyapunov coefficent by formula

$$l_1(\alpha_0) = \frac{1}{2\omega^2}\mathrm{Re}(ig_{20}g_{11} + \omega g_{21}) = \frac{2\omega^4 - 2\omega^2 - 1}{8\omega^3},$$

where (see (3.7))

$$\omega = \omega^{\pm} = \frac{1}{\sqrt{2}}\left(1 \pm \sqrt{1-8\kappa}\right)^{1/2}. \tag{4.3}$$

We must analyze if $l_1(\alpha_0) \neq 0$. From (4.3) we can see that $0 < \omega^{\pm} < 1$, then we easily verify that

$$l_1(\alpha_0^-) < 0, \qquad \text{and} \qquad l_{1,\beta}(\beta_0^+) = l_1(1-\beta_0^+) < 0. \tag{4.4}$$

Now we consider that the parameters α, in the first case, and $\beta = 1-\alpha$, in the second one, vary in increasing sense. Therefore, on the one hand, the equilibrium E_0 shows a supercritical Hopf bifurcation when the parameter α passes across α_0^- for all $\kappa \in (0, 1/8)$. In this case, a unique and stable limit cycle appears for $\alpha > \alpha_0^-$ (see figure 3)).

On the other hand, when β overpass β_0^+, the equilibrium E_0 shows a Hopf bifurcation for all $\kappa \in (0, 1/8)$ and the limit cycle appears for $\beta > \beta_0^+$. The parameters β and $\alpha = 1-\beta$ grow in opposed directions, then we conclude that the limit cycle that emerges for $\alpha > \alpha_0^-$, remains for $\alpha \in (\alpha_0^-, \alpha_0^+)$ and disappears for $\alpha > \alpha_0^+ = 1 - \beta_0^+$. Thus, the second Hopf bifurcation of E_0 for the original bifurcation parameter α is subcritical (see figure 3). $\square$

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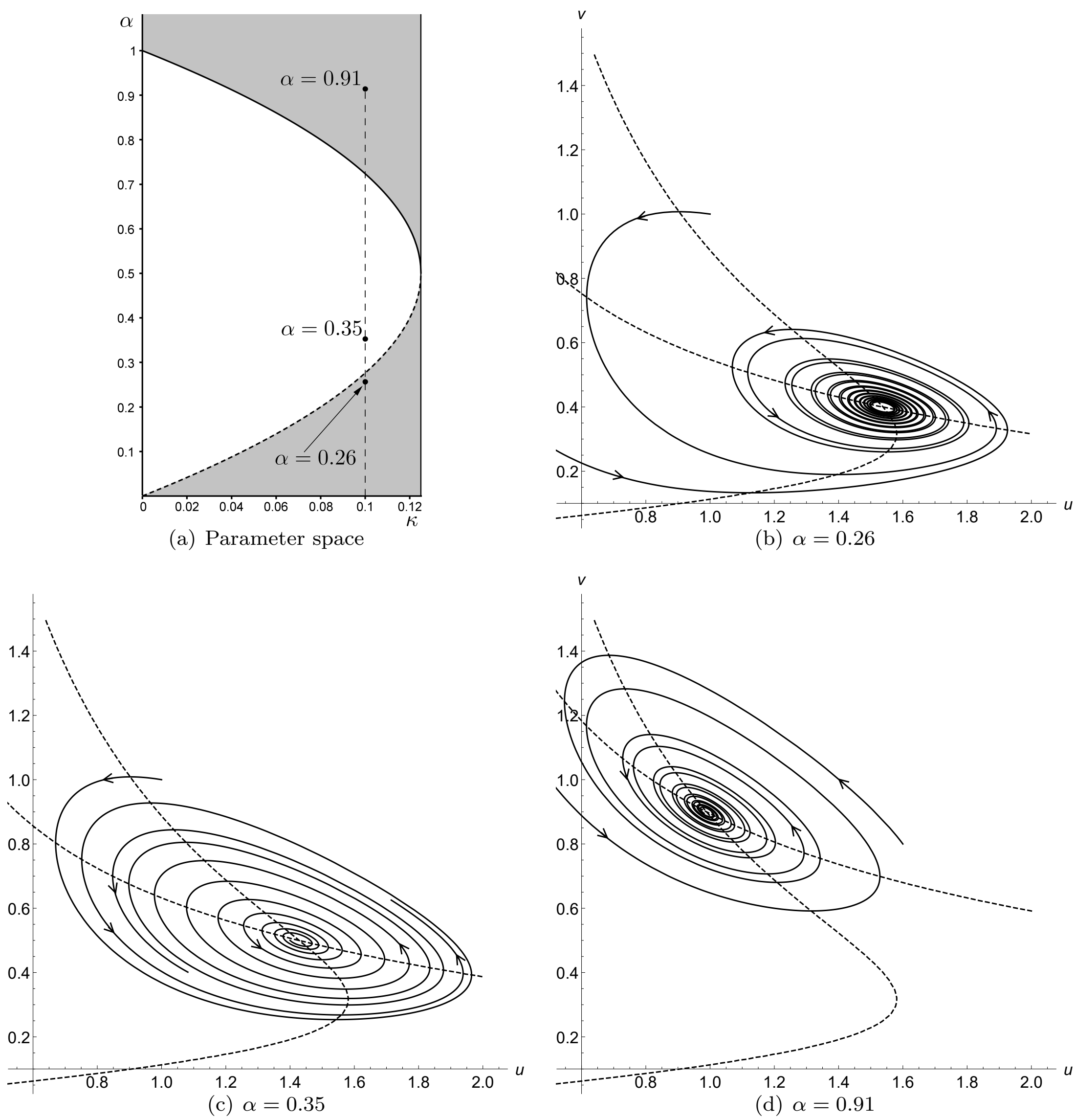
[1] It is always useful to express the Jacobian matrix using ω, since this simplifies the expressions for the eigenvectors.

[2] There exists another way to compute g_{20}, g_{11} and g_{21} (which may be simpler if we use a symbolic manipulation software). We can see it in [8, Ch. 3].



(a) Parameter space
(b) $\alpha = 0.26$
(c) $\alpha = 0.35$
(d) $\alpha = 0.91$

Figure 3: Hopf bifurcation in glycolysis model with $\kappa = 0.1$. The bifurcations points are the α-axes of the intersection of the bifurcation curves and line $\kappa = 0.1$ in graphic (a), i.e. $\alpha_0^- \approx 0.276$ and $\alpha_0^+ \approx 0.724$. The graphics (b) and (d) represents stable focuses in the meantime than we can observe an unstable focus in graphic (c), where the orbits approximate to a limit cycle.

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