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Stability of Spatial Steady State Solutions for Hypercycles Replication System

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Abstract

The system of semilinear parabolic equations which described the mechanism and dynamics organizing of complicated macromolecules in the process of prebyology evolution is considered [Eigen, Schuster, 1979]. The aim of investigation is searching and analyzing stability of spatial non uniform steady state solutions (SNSS solutions) of the system. It is proved that if the diffusion coefficients are sufficiently small then there exist SNSS solutions of the system in the form of over fall's waves or cycling wave with the m-th humps. This solution is not stable in usual sense. It is proved exclusion principal in case of a spatial dynamics of replication macromolecules by auto- catalyzing reaction. SNSS solutions of the system are stable in sense of mean integral values in case of replication dynamics macromolecules by hypercycles process. For open models of hypercycles replication reaction the analogous results was proved too. With help of the Galerkin method numerical solutions for various cases of realization SNSS solutions was obtained.

Key words

Hypercycles replication system, stability, spatial state solutions

1. Statement of the problem

Let D be a restricted domain $D \subset R^m$, $m = 1,2,3$ with smooth boundary γ then a spatial dynamics of replication macromolecules by auto-catalyzing reaction described with the help of following system of partial differential equations [Bratus', Posviansky, 2006] $(p > 0)$:

$$\frac{\partial v_i(x,t)}{\partial t} = v_i(k_i v_i^p - f_1(t)) + d_i \Delta v_i(x,t),$$
$$t > s \quad v_i(x,s) = \phi_i(x), \quad i = 1,2,\dots,n,$$
$$v_0(x,t) = v_n(x,t), \quad \Delta = \sum_{i=1}^{m} \frac{\partial^2}{\partial x_i^2}. \tag{1.1}$$

In case of replication dynamics macromolecules by hypercycles process we have the following system:

$$\frac{\partial v_i(x,t)}{\partial t} = v_i(k_i v_{i-1}^p - f_2(t)) + d_i \Delta v_i(x,t),$$
$$t>s, \quad v_i(x,s)=\varphi_i(x) \tag{1.2}$$

The nonnegative functions $v_i(x), \quad i = 1,2,...n$ define the concentration of i-th type of macromolecule, k_i, d_i and p are positive constants. The functions $f_1(t)$ and $f_2(t)$ will determine further.

Suppose that the systems are closed. Thus, in both cases we have the following boundary value problem

$$\left(\frac{\partial v_i}{\partial n}\right)_\gamma = 0 \tag{1.3}$$

Here n is a normal vector to the boundary γ.

We shall suppose that total number of integral mean of molecule's concentration doesn't change during the all time period. It means that there is the following integral invariant:

$$\sum_{i=1}^{n} \iint_D v_i(x,t)dx = 1 \tag{1.4}$$

This condition is analog condition on total number of elements in finite dimension case [Guckenheimer, Holmes, 1997]. From boundary value conditions (1.3) and equality (1.4) it follows the following expressions for the functions $f_1(t)$, $f_2(t)$:

$$f_1(t) = \sum_{i=1}^{n} \iint_D k_i v_i^{p+1}(x,t)dx \tag{1.5}$$

$$f_2(t) = \sum_{i=1}^{n} \iint_D k_i v_i v_{i-1}^p(x,t)dx \tag{1.6}$$

Finally, we obtain the mixed boundary value problem for system of semilinear parabolic equations with integral invariant (1.4) and functionals (1.5), (1.6).

We shall seek the solution of these problems on the set of the vector functions

$$v(x,t)=(v_1(x,t),v_2(x,t),\ldots,v_n(x,t)).$$

Suppose that for any fixed $x\in D$ each function $v_i(x,t)$ is differentiable with respect of variable t and belongs to space $H^1_{p+1}(D)$ as the function of variable x for any fixed $t>0$.

Here $H^1_{p+1}(D)$ is the space of functions with norm

$$\|u(x)\|_{H^1_{p+1}}=\left(\iint_D |u|^{p+1}\right)^{\frac{1}{p+1}}+\left(\iint_D \sum_{i=1}^{n}\left|\frac{\partial u}{\partial x_i}\right|^2 dx\right)^{\frac{1}{2}}$$

Note that if $p\ge 1$ then the space $H^1_{p+1}(D)\subseteq H^1_2(D)$. Here $H^1_2(D)$ is Sobolev space of quadratic summable functions along with its first partial derivatives.

Without loss of generality we shall assume further that volume of the domain D is equal to unity: $|D|=1$.

Our purpose is investigation existence and stability of steady state solution $u(x)=(u_1(x),u_2(x),\ldots,u_n(x))$ of the systems (1.2) and (1.3) respectively:

$$d_i\Delta u_i(x)+u_i(x)(k_iu_i^p(x)-\bar f_1)=0$$
$$i=1,2,\ldots n,\quad x\in D, \tag{1.7}$$

$$d_i\Delta u_i(x)+u_i(x)(k_iu_{i-1}^p(x)-\bar f_2)=0,$$
$$i=1,2,\ldots n,\quad u_0(x)=u_n(x),\quad x\in D, \tag{1.8}$$

$$\left(\frac{\partial u_i}{\partial n}\right)_\gamma=0.$$

Here $u_i(x)\in H^1_{p+1}(D)$.

The condition (1.4) transfer to the following equality

$$\sum_{i=1}^{n}\iint_D u_i(x)dx=1 \tag{1.9}$$

The values $\bar f_1$ and $\bar f_2$ are constants:

$$\bar f_1=\sum_{i=1}^{n}\iint_D u_i^{p+1}(x)dx \tag{1.10}$$

$$\bar f_2=\sum_{i=1}^{n}\iint_D u_i(x)u_{i-1}^p(x)dx,$$
$$u_0(x)=u_n(x). \tag{1.11}$$

Suppose that $d_1=d_2=\ldots=d_n=0$. Then the critical points of correspondent dynamical systems (1.1) and (1.2) will steady state solutions of the system (1.7) and (1.8). This is so-called space-uniform steady state solutions (SUSS solution). Inverse assumption is correctly too. The all SUSS solution of the systems (1.7) and (1.8) are critical points of the dynamical system (1.1) and (1.2) respectively when $d_1=d_2=\ldots=d_n=0$.

Denote by $\beta_i=(k_i)^{-1/p}$ and consider the sum $\beta=\sum_{i=1}^{n}\beta_i$. Then all SUSS solutions of the system (1.7) are follows:

$$P=\frac{1}{\beta}(\beta_1,\beta_2,\ldots,\beta_n)$$

$$Q_j=\frac{1}{\beta}(\beta_1,\ldots,\beta_{j-1},0,\beta_{j+1},\ldots,\beta_n)$$

$$Q_{sj}=\frac{1}{\beta}(\beta_1,\ldots,\beta_{j-1},0,\beta_{j+1},\ldots,\beta_{s-1},0,\beta_{s+1},\ldots,\beta_n)$$

and go on to including the all apexes $R_i=(0,0,\ldots,0,1,0,\ldots,0)$ (unit on the i-th place) of simplex $\sum_{i=1}^{n}u_i=1,\quad u_i\ge 0$.

The SUSS solutions of the system (1.8) contains only one point: $P_0=\frac{1}{\beta}(\beta_2,\beta_3,\ldots,\beta_n,\beta_1)$.

2. Stability of SUSS solutions.

Theorem 2.1

For $p\ge 1$ all SUSS solutions of the system (1.1) are unstable with respect to any perturbations from the set H_δ if

$$0<\frac{d_i}{k_i}<\frac{p}{\lambda_1},\quad i=1,2,\ldots,n. \tag{2.4}$$

Solutions $R_i=(0,0,\ldots 0,1,0\ldots 0),\quad i=1,2,\ldots n$ (unit on the *i*-th place) becomes stable when

$$\frac{d_i}{k_i}>\frac{p}{\lambda_1},\quad i=1,2,\ldots,n. \tag{2.5}$$

Here λ_1 is the first nonzero eigenvalue of the problem

$$\Delta\psi(x)+\lambda\psi(x)=0, \quad x\in D, \quad \left(\frac{\partial\psi}{\partial n}\right)_\gamma=0 \qquad (2.2)$$

The system of the eigenfunctions of this problem $\psi_0(x)=1, \{\psi_i(x)\}_{i=1}^{\infty}$ formed a complete system in Sobolev space $H_1^1(D)$ so that

$$(\psi_s,\psi_m)=\iint_D \psi_s(x)\psi_m(x)dx=\delta_{sm} .$$

Here δ_{sm} is Kronecker symbol.

Proof. Let $W(x,t)=(W_1(x,t),W_2(x,t),...,W_n(x,t))$ be the vector function so that $W_i(x,t)\in H_\delta$ for any fixed moment *t*. Taking into account the equalities (2.1) and (2.3) we can seek the solution of the problem (1.1) in the form

$$v_i(x,t)=u_i^0+W_i(x,t)$$

$$W_i(x,t)=\sum_{s=0}^{n} c_i^s(t)\psi_s(x) \qquad (2.6)$$

Substituting (2.6) in to the equations (1.1) and separating only linear terms with respect to the functions W_i we obtain the following equations

$$\frac{\partial W_i}{\partial t}=(p+1)k_i\left(\overset{o}{u}_i\right)^p W_i-\bar{f}_1W_i+d_i\frac{\partial^2 W_i}{\partial x^2}$$

$$W_i(x,0)=\varphi_i(x)\in H_\delta$$

$$\left(\frac{\partial W_i}{\partial n}\right)_\gamma=0 \qquad (2.7)$$

Direct calculation shows that $\bar{f}_1=\beta^{-p}$ as $u^0=P$.

Multiplying the equation (2.7) sequentially on the functions $\psi_s(x)$ and integrating in $x\in D$ we obtain the following system of ordinary differential equation with respect to the functions $c_s^i(t)$:

$$\frac{dc_i^s(t)}{dt}=c_i^s(t)\left(\frac{p}{\beta^p}-d_i\lambda_s\right) \qquad (2.8)$$

$$i=1,2,...n, \quad s=0,1,2,...$$

For $s=0$ we have:

$$c_i^0(t)=c_i^0(0)\exp\left(\frac{p}{\beta^p}t\right) .$$

Therefore, $c_0^i(t)\to\infty$ as $t\to\infty$.

Note that from the condition (1.8) it follows that

$$\sum_{i=1}^{n} c_i^0(t)=0 \qquad (2.9)$$

Suppose now that $u^0=Q_j$ then

$$\bar{f}_1=\gamma_j^{-p}, \quad \gamma_j=\sum_{i=1,\ i\neq j}^{n}\beta_i .$$

Using the same way as in the case of equation (2.8) we obtain the following system of ordinary differential equations:

$$\frac{dc_j^s(t)}{dt}=-c_j^s(t)\left(\frac{1}{\gamma_j^p}+d_j\lambda_s\right)$$

$$\frac{dc_i^s(t)}{dt}=c_i^s(t)\left(\frac{1}{\gamma_j^p}-d_i\lambda_s\right), \quad i\neq j$$

$$i=1,2,..n, \quad s=0,1,2,...$$

Thus $c_i^0(t)\to\infty$ as $t\to\infty$, $i\neq j$.

Continuing this process we at last obtain the corresponding equations for case of points $R_i=(0,0,...0,1,0...0)$, $i=1,2,...,n$ (unit on the *i*-th place).

$$\frac{dc_j^s(t)}{dt}=-c_j^s(t)(k_s+d_j\lambda_s), \quad j\neq i$$

$$\frac{dc_i^s(t)}{dt}=c_i^s(t)(k_i-d_i\lambda_s),$$

$$i=1,2,...n, \quad s=0,1,2,...$$

Therefore, if $j\neq i$ then $c_j^0(t)\to 0$ as $t\to\infty$.

Taking into account condition (2.9) we obtain that $c_i^0(t)\to 0$.

Consider evolution of the rest functions $c_s^i(t)$, $s=1,2,...$. Suppose that the inequality (2.4) is fulfilled then it follows that $c_i^s(t)\to\infty$, $s=1,2,...$ as $t\to\infty$. In opposite case all functions $c_i^s(t)$, $s=1,2,...$ tend to zero as $t\to\infty$.

Theorem 2.2.

If $p \ge 1$ then SUSS solution $P_0 = \frac{1}{\beta}(\beta_2, \beta_3, ..., \beta_n, \beta_1)$ of the system (1.2) is unstable with respect to any perturbations from the set H_δ when

$$\prod_{i=1}^{n} d_i < \left(\frac{p}{\beta^p \pi^2} \right)^n$$

Proof. As a before we will seek the solution of the system (1.2) in the form (2.6). Substituting the expression (2.6) in to the equations (1.2) and separating only linear terms with respect to the functions W_i we obtain the following equations

$$\frac{\partial W_i}{\partial t} = pk_i \left(u_{i-1}^0 \right)^{p-1} u_i^0 W_{i-1} + k_i \left(u_{i-1}^0 \right)^p W_i -$$
$$- \bar{f}_2 W_i + d_i \frac{\partial^2 W_i}{\partial x^2}, \quad W_i(x,0) = \varphi_i(x) \in H_\delta \tag{2.11}$$

Multiplying the equation (2.11) sequentially on the eigenfunctions $\psi_s(x)$ of the problem (2.2) and integrating in $x \in D$ we obtain the following system of ordinary differential equation:

$$\frac{dc_i^s(t)}{dt} = \frac{p}{\beta^p} \left(\frac{k_i}{k_{i+1}} \right) c_{i-1}^s(t) - d_i \lambda_s c_i^s(t)$$
$$i = 1,2,...,n \quad s = 1,2,... \tag{2.12}$$

Note that in this case $f_2 = \beta^{-p}$.

Applying the Routh-Hurwitz criterion we obtain that the system (2.12) is unstable when the condition (2.11) is fulfilled for n=2,3,4. General result can be obtained with the help of induction method.

3. Existence of 1D non-uniform steady state solutions for systems of auto-catalyzing and hypercycles replication.

Consider one dimensional case of the systems (1.1), (1.2): $D = (0,l)$, $\Delta = \frac{\partial^2}{\partial x^2}$. The corresponding boundary value problem has a form

$$\frac{\partial v_i(0,t)}{\partial x} = \frac{\partial v_i(0,t)}{\partial x} = 0$$

Without loss of generality we shall assume further that $l = 1$.

Theorem 3.1

For $0 < p \le 2$ there exist of spatial non-uniform steady state solutions of the system (1.1) when the following inequality takes place

$$\sum_{i=1}^{n} \left(\frac{d_i}{k_i} \right)^{\frac{1}{p}} < \left(\frac{p}{\pi^2} \right)^{\frac{1}{p}} \tag{3.1}$$

Theorem 3.2

Suppose that inequality (3.1) is fulfilled. If a coefficients of the system (1.2) can be presented as result of the following one parametric perturbation

$$d_i = d_0 + \varepsilon l_i, \quad k_i = k_0 + \varepsilon m_i$$
$$l_i, m_i = const, \quad \varepsilon > 0.$$

(here ε is a small parameter) then there exist of spatial non-uniform steady state solutions of the system (1.2).

The proving consists of two steps. In the first one we consider the problem of existence solution for boundary value problem of the following system

$$d_i u_i'' + u_i (k_i u_i^p - \bar{f}_1) = 0, \quad i = 1,2,...,n,$$
$$u_i'(0) = u_i'(1) = 0. \tag{3.2}$$

Here

$$\bar{f}_1 = \sum_{i=1}^{n} \int_0^1 u_i^{p+1}(x) dx.$$

As a before in this case we have

$$\sum_{i=1}^{n} \int_0^1 u_i(x) dx = 1. \tag{3.3}$$

Each equation of the system (3.2) can be written in the form of Hamiltonian system (see Fig. 1)

$$\frac{du_i}{dx} = \frac{\partial H_i}{\partial p_i}, \quad \frac{dp_i}{dx} = -\frac{\partial H_i}{\partial u_i}. \tag{3.4}$$

Here $H_i = \frac{v_i^2}{2} + \frac{1}{d_i} \left(\frac{k_i}{p+2} u_i^{p+2} - \frac{\bar{f}_1}{2} u_i^2 \right)$.

It is proved that if the inequality (3.1) takes place then Hamiltonian systems (3.4) have the solutions which satisfy to the boundary value conditions and integral invariant (3.3).

In the second step we consider the initial boundary value problem (1.8) for the 1D case as a perturbation of the problem (3.2). Using the results of perturbation for Hamiltonian system on the plane [Guckenheimer, Holmes, 1997] we obtain the result of theorem 3.2.

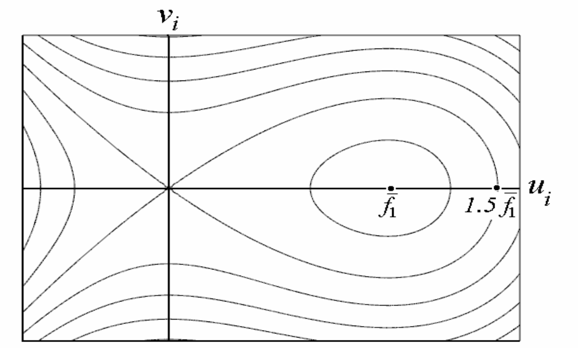

Fig. 1

4. Limit behavior of spatial autocatalyzing and hypercycling replication systems.

Consider the dynamical system of autocatalyzing replication (1.1) without taking account a spatial distribution
($d_i = 0, \quad i = 1,2,...,n$).

$$\frac{dw_i(t)}{dt} = w_i(t)(k_i w_i^p(t) - f_0(t))$$

$$f_0(t) = \sum_{j=1}^{n} w_j^{p+1}(t), \quad t > s, \qquad (4.1)$$

$$w_i(s) = \xi_i, \quad i = 1,2,...,n, \quad \sum_{i=1}^{n} w_i(t) = 1$$

The solutions of this system can be presented in the following forms

$$w_i(t) = \left(\frac{\xi_i \exp(-pF_0(t,s))}{1 - k_i \xi_i I_0(t,s)} \right)^{\frac{1}{p}}$$

Here and further

$$F_0(t,s) = \int_s^t f_0(\tau) d\tau$$

$$I_0(t,s) = \int_s^t \exp(-pF_0(s,\tau)) d\tau$$

Now we introduce the following definition.

Definition 4.1

We shall say that initial conditions for system (1.1) and the system (4.1) are coordinated if

$$\xi_i = \overline{\varphi}_i = \iint_D \varphi_i(x) dx$$

Suppose that initial conditions for systems (1.1), (4.1) are coordinated then integrating the system (1.1) in x and using the equality

$$\iint_D \Delta v(x) dx = \int_\gamma \frac{\partial v}{\partial n} ds = 0$$

we obtain

$$\frac{d\bar{v}_i(t)}{dt} = k_i \iint_D v_i^{p+1}(x) dx - \bar{v}_i(t) f_1(t)$$

$$t > s, \quad \bar{v}_i(s) = \overline{\varphi}_i = \xi_i, \quad i = 1,2,...,n.$$

Here and further

$$\bar{v}_i(t) = \iint_D v_i(x,t) dx .$$

Since the volume of domain D is equal unity ($|D| = 1$) we have

$$\iint_D v_i^{p+1}(x,t) dx \geq \left(\iint_D v_i(x,t) dx \right)^{p+1} = \bar{v}_i^{p+1}(t)$$

Using this inequality we obtain the following differential inequality for functions $\bar{v}_i(t) \geq 0$

$$\frac{d\bar{v}_i(t)}{dt} \geq \bar{v}_i^{p+1}(t) - \bar{v}_i(t) f_1(t)$$

$$t > s, \quad \bar{v}_i(s) = \overline{\varphi}_i = \xi_i, \quad i = 1,2,...,n.$$

From theorem on differential inequality it follows

$$\bar{v}_i(t) \geq \left(\frac{\varphi_i \exp(-pF_1(t,s))}{1 - k_i \varphi_i I_1(t,s)} \right)^{\frac{1}{p}} \qquad (4.2)$$

Here and further

$$F_1(t,s) = \int_s^t f_1(\tau) d\tau,$$

$$I_1(t,s) = \int_s^t \exp(-pF_1(s,\tau)) d\tau.$$

Lemma 4.1

Let us initial conditions for systems (1.1), (4.1) are coordinated then necessary and sufficient to be an inequality

$$\beta^{-p} \leq f_0(t) \leq f_1(t) \qquad (4.3)$$

Here $\beta = \sum_{i=1}^{n} \beta_i, \ \beta_i = (k_i)^{-1/p}$.

Proof. Let us prove at first the left side of inequality (4.3). Using the condition (1.4) and Heidel's inequality we obtain

$$1=\left(\sum_{i=1}^{n} w_i(t)\right)^{p+1} \le$$

$$\le \left(\sum_{i=1}^{n} \frac{1}{k_i^{1/p}}\right)^p \left(\sum_{i=1}^{n} k_i w_i^{p+1}\right) = \beta^p f_1(t)$$

Under the condition (1.4) we have $\sum_{i=1}^{n} \bar{v}_i(t) = 1$.

On the other hand we have $\sum_{i=1}^{n} w_i(t) = 1$.

Therefore from the inequality (4.2) it follows the following inequality

$$\sum_{i=1}^{n} \left(\frac{\overline{\varphi}_i \exp(-pF_1(t,s))}{1-k_i\overline{\varphi}_i I_1(t,s)}\right)^{\frac{1}{p}} \le \sum_{i=1}^{n} \left(\frac{\overline{\varphi}_i \exp(-pF_0(t,s))}{1-k_i\overline{\varphi}_i I_0(t,s)}\right)^{\frac{1}{p}} \tag{4.4}$$

Note that inequality (4.4) is fulfilled for any coordinated initial conditions $\overline{\varphi}_i$ and value $s \le t$.

It is easy to see that if the inequality (4.3) satisfied then inequality (4.4) takes place.

Suppose now that there exist such moment t^* that $f_0(t^*) > f_1(t^*)$. Consider the following coordinated initial conditions: $\varphi_i(s) = 0$, $i \ne j$, $\varphi_j(s) \ne 0$, $s = t^* - \varepsilon$. From (4.4) it follows

$$\left(\frac{\overline{\varphi}_j \exp(-pF_1(t,s))}{1-k_j\overline{\varphi}_j I_1(t,s)}\right) \le \left(\frac{\overline{\varphi}_j \exp(-pF_0(t,s))}{1-k_j\overline{\varphi}_j I_0(t,s)}\right) \tag{4.5}$$

From continuity of the functions $f_1(t^*), f_0(t^*)$ it follows that $f_0(t) > f_1(t)$ for $t \in (s, t^* + \varepsilon)$ when $\varepsilon > 0$ is sufficient small value. Therefore in this neighborhood we obtain $F_0(t,s) > F_1(t,s)$, $I_1(t,s) > I_0(t,s)$. Thus the inequality (4.5) is not fulfilled. This contradiction completes the proof of Lemma 4.1.

Theorem 4.1 (Exclusive principal) Suppose that $p \ge 1$ then for almost all initial conditions $\varphi_i(x)$, $\sum_{i=1}^{n} \varphi_i(x) = 1$ of the problem (1.1) there is positive integer j, $1 \le j \le n$ (that depends on $\varphi_i(x)$) such that $v_i(x,t) \to 0$ for all $i \ne j$ and therefore $\bar{v}_j(t) \to 1$ as $t \to \infty$.

Proof. Since $p \ge 1$ then space $H^1_{p+1} \subseteq H^1_2$. Here H^1_2 is a Sobolev space of quadratic summable functions along with its first derivative. The eigenfunctions $\psi_s(x)$, $s = 0,1,2\ldots$ of the problem (2.2) formed the complete system in the space H^1_2.

Consider the following representation for functions $\varphi_i(x)$, $i = 1,2,\ldots,n$:

$$\varphi_i(x) = \bar{c}_i^0 + z_i(x), \quad z_i(x) = \sum_{s=1}^{\infty} \bar{c}_i^s \psi_s(x)$$

Let us $w_i(t)$, $i = 1,2,\ldots,n$ are the solutions of autocatalyzing replication system (4.1) without taking account a spatial distribution. Suppose also that initial conditions of system (4.1) and system (1.1) are coordinated. We can seek the solution of the problem (1.1) in the form

$$\begin{aligned} &v_i(x,t) = w_i(t) + z_i(x,t), \\ &z_i(x,t) = \sum_{s=1}^{\infty} c_1^s(t)\psi_s(x), \\ &w_i(0) = c_i^0, \quad c_i^m(0) = \bar{c}_i^m, \quad m = 1,2,\ldots \end{aligned} \tag{4.3}$$

It is possible since $f_0(t) \le f_1(t)$. Substituting representation (4.7) into the equations (1.1) we obtain the following equality

$$\frac{dw_i(t)}{dt} + \frac{\partial z_i(x,t)}{\partial t} = k_i v_i^{p+1}(x,t) - $$
$$- f_1(t)(w_i(t) + z_i(x,t)) + d_i \frac{\partial^2 z_i(x,t)}{\partial x^2}$$

Integrating last equality in x and using formula

$$\iint_D \psi_s(x)dx = 0, \quad s = 1,2,\ldots$$

and boundary condition (1.3) we obtain the following equations

$$\frac{dw_i(t)}{dt} = k_i \iint_D v_i^{p+1}(x,t)dx - f_1(t)w_i(t)$$

Since the functions $w_i(t)$ are solution of the system (4.1) then we get

$$k_i \iint_D v_i^{p+1}(x,t)dx = (f_0(t) - f_1(t))w_i(t) +$$
$$+ k_i w_i^{p+1}(t) \quad (4.6)$$

On the other hand a solution of the system (4.1) has a property of multystability [Hoffbauer, Zigmund, 1998]. It means that for almost all initial conditions ξ_i, $\sum_{i=1}^{n} \xi_i = 1$ of the problem (4.1) there is positive integer j, $1 \le j \le n$ (that depends on ξ_i) such that $w_i(t) \to 0$ for all $i \ne j$ and therefore $w_j(t) \to 1$ as $t \to \infty$. Thus from equality (4.6) we obtain that for all $i \ne j$

$$k_i \iint_D v_i^{p+1}(x,t)dx \to 0, \quad t \to \infty.$$

This concludes the proof.

Now consider the case of spatial hypercycles replication system (1.2)

After integrating equations (1.2) in variable $x \in D$ we obtain the following dynamical system

$$\frac{d\bar{v}_i(t)}{dt} = k_i(v_{i-1}^p, v_i) - f_2(t)\bar{v}_i(t)$$
$$s < t, \quad v_i(s) = \bar{\varphi}_i$$

Here $\bar{v}_i(t) = \iint_D v_i(x,t)dx$, $\bar{\varphi}_i = \iint_D \varphi_i(x)dx$ are integral mean values of the functions

$v_i(x,t)$ and $\varphi_i(x)$ in domain D correspondently, $(v_{i-1}^p, v_i) = \iint_D v_{i-1}^p(x,t)v_i(x,t)dx$ is a scalar product of the functions $v_i(x,t)$ and $v_{i-1}^p(x,t)$ in domain D.

Definition 4.2

We shall say that spatial steady state solution $U(x) = (u_1(x), u_2(x), ..., u_n(x))$ of the system (1.1) or (1.2) has property stability in sense of mean integral value if for any $\varepsilon > 0$ there is $\delta > 0$ such that for initial conditions satisfied to the inequalities

$$|\bar{\varphi}_i - \bar{u}_i| < \delta, \quad i = 1,2,...,n$$

it follows that

$$|\bar{v}_i(t) - \bar{u}_i| < \varepsilon, \quad i = 1,2,...,n$$

for any $t > 0$.

Here and further $v_i(x,t)$, $i = 1,2,...,n$ are the solutions of system (1.1) or (1.2).

$$\iint_D v_i(x,t)dx = \bar{v}_i(t), \quad \bar{\varphi}_i = \iint_D \varphi_i(x,s)dx,$$
$$\bar{u}_i = \iint_D u_i(x)dx, \quad i = 1,2,...,n.$$

It is clear that property of mean integral value stability is much weaker then stability in usual sense (Lyapunov's stability).

Theorem 4.2

Let us $U(x) = (u_1(x), u_2(x), ..., u_n(x))$ be a spatial non uniform steady state (SNSS) solution of the system (1.2) such that

$$\bar{U}(x) = (\bar{u}_1(x), \bar{u}_2(x), ..., \bar{u}_n(x)) =$$
$$= \frac{1}{\beta}(\beta_2, \beta_3, ..., \beta_n, \beta_1)$$

Here $P_0 = \frac{1}{\beta}(\beta_2, \beta_3, ...\beta_n, \beta_1)$ is unique SUSS solutions of the system (1.2).

Then $\bar{U}(x)$ is a stable solution of the system (1.2) in sense of mean integral value.

Let us introduce the new functions

$$v_i(x,t) = w_i(x,t)k_i^{-1/p}R$$
$$i = 1,2,...n, \quad R = \iint_D \sum_{j=0}^{n-1} k_j^{1/p} v_j(x,t)dx$$

It is easy to verify that

$$\sum_{j=0}^{n-1} \iint_D w_i(x,t)dx = 1.$$

Note that new variable transfer the point $P_0 = \frac{1}{\beta}(\beta_2, \beta_3, ..., \beta_n, \beta_1)$ in to the point $\bar{P} = \left(\frac{1}{n}, \frac{1}{n}, ..., \frac{1}{n}\right)$. The initial system transfer to the topological equivalent system

$$\frac{d\bar{w}_i(t)}{dt} = R^p(t)((w_{i-1}^p, w_i) - f(t)\bar{w}_i(t)),$$
$$f(t) = \sum_{j=0}^{n-1} \iint_D w_i(x,t)w_j^p(x,t)dx.$$

Let us introduce the following Lyapunov's function

$$V(\bar{w}_1, \bar{w}_2, ..., \bar{w}_n) = -ln(\bar{w}_1\bar{w}_2, ..., \bar{w}_n) - n\ln n$$

It is easy to see that $V(\bar{P}) = 0$ and $V(\bar{w}_1, \bar{w}_2, ..., \bar{w}_n) > 0$ in neighborhood Z_δ of the point $\bar{P}$.

$$Z_\delta = \left\{ \begin{array}{l} \bar{w}_i, \quad i = 1,2,\dots,n,: \\ \sum\limits_{j=1}^{n} \bar{w}_i = 1, \quad \sum\limits_{i=1}^{n} \left| \bar{w}_i - \frac{1}{n} \right| \le \delta \end{array} \right\}.$$

Here δ is sufficient small value.

$$\dot{V} = -\sum_{i=1}^{n} \frac{\dot{\bar{w}}_i}{\bar{w}_i} = -R^p \sum_{i=1}^{n} \left(\frac{(w_i, w_{i-1}^p)}{\bar{w}_i} - f \right) =$$

$$= -R^p \left(\sum_{i=1}^{n} \frac{(w_i, w_{i-1}^p)}{\bar{w}_i} - nf \right) =$$

$$= -R^p \sum_{i=1}^{n} (w_i, w_{i-1}^p)\left(\frac{1}{\bar{w}_i} - n\right)$$

Denote by μ the following value:

$$\mu = \min_{1 \le i \le n} \left\{ \inf_t \left((w_i, w_{i-1}^p) \right) \right\}.$$

Thus the functions $w_i(x,t)$, $i = 1,2,\dots,n$ are nonnegative then $\mu \ge 0$. Therefore we have

$$\dot{V} \le -R^p \mu \left(\sum_{i=1}^{n} \left(\frac{1}{\bar{w}_i}\right) - n^2 \right).$$

On the other hand using inequality between arithmetic and geometric means we get

$$\sum_{i=1}^{n} \frac{1}{\bar{w}_i} \ge \frac{n}{\sqrt[n]{\prod\limits_{i=1}^{n} \bar{w}_i}}$$

Since $\sum\limits_{i=1}^{n} \bar{w}_i = 1$, $\bar{w}_i \ge 0$ then the function $\prod\limits_{i=1}^{n} \bar{w}_i$ reached its maximal value at the point $\bar{P} = \left(\frac{1}{n}, \frac{1}{n}, \dots, \frac{1}{n} \right)$. Therefore we have the following inequality

$$\frac{n}{\sqrt[n]{\prod\limits_{i=1}^{n} \bar{w}_i}} \ge n^2.$$

Finally we obtain that $\dot{V}(\bar{w}_1, \bar{w}_2, \dots, \bar{w}_n) \le 0$. This completes the proof of theorem 4.2.

5. Numerical solution.

Figures 2-7 show the results of numerical calculations for gypercycle steady state solutions of the system (1.2) in the case $n = 3$ when $p = 1$,

$$k_1 = k_2 = k_3 = 1, \qquad d_1 = 1 \cdot 10^{-3},$$
$$d_2 = 2 \cdot 10^{-3}, \qquad d_3 = 3 \cdot 10^{-3}.$$

Notice that each solutions $u_i(x)$ correspond solutions $u_i(1-x)$. The condition (3.1) is fulfilled since

$$\sum_{i=1}^{3} d_i = 6 \cdot 10^{-3} < \pi^{-2}.$$

Corresponding value of the functional f (see (1.6)) is indicated below of the pictures. With help of Galerkin method and the following expansion

$$u_i(x,t) = u_{i,0} + \sum_{j=1}^{m} u_{i,j} \cos(\pi j x)$$

the initial problem reduced to the system of algebraic equation with respect to magnitudes $u_{i,j}$ and parameter f.

In fig. 9-11 the surface $u_i(x,t)$ for the same values of parameters is presented with initial conditions

$$\phi_1(x) = 0.1, \quad \phi_2(x) = 0.0536 \cdot 5^{2x},$$
$$\phi_3(x) = 1.6765 \cdot 5^{-2x}.$$

In the fig.8 shows the corresponding graph for function $f(t)$.

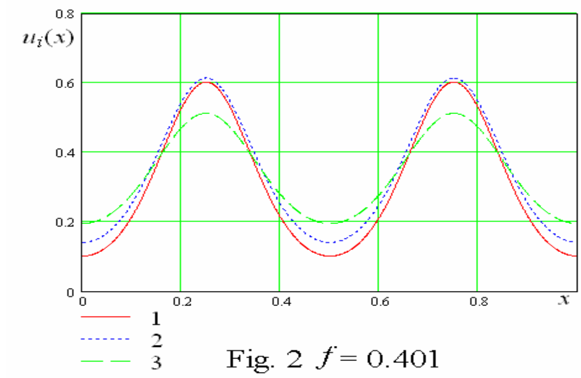

Fig. 2 $f = 0.401$

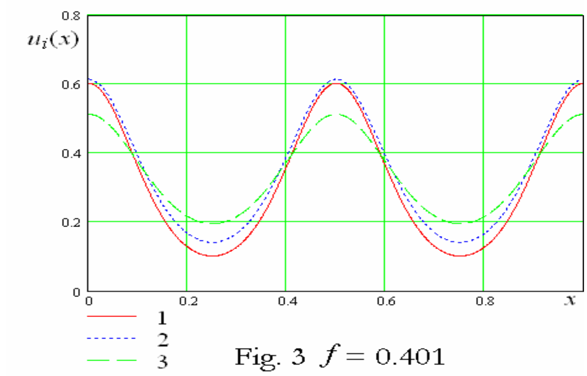

Fig. 3 $f = 0.401$

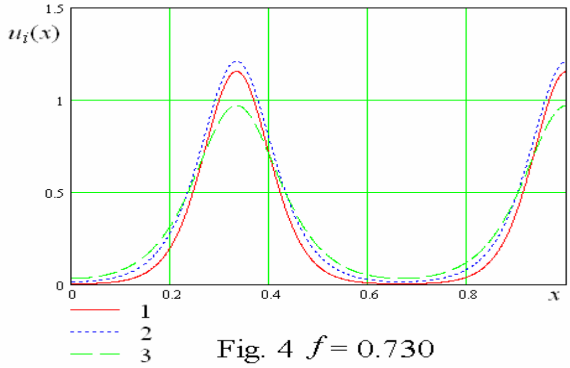

Fig. 4 $f = 0.730$

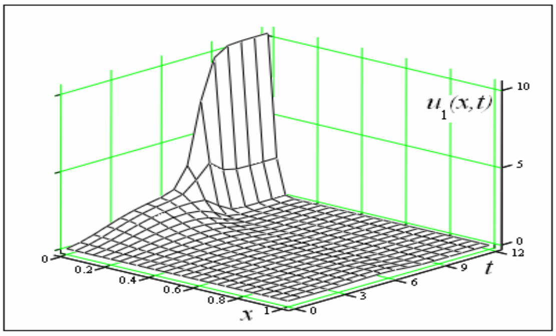

Fig. 9

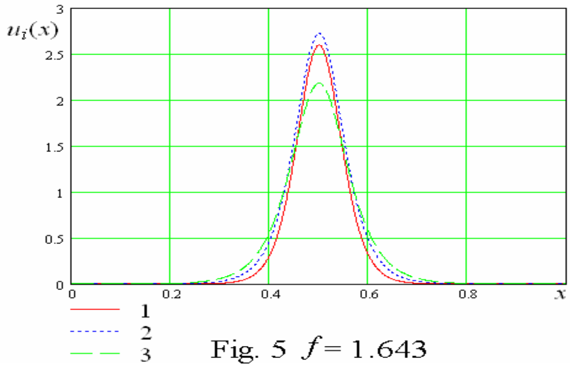

Fig. 5 $f = 1.643$

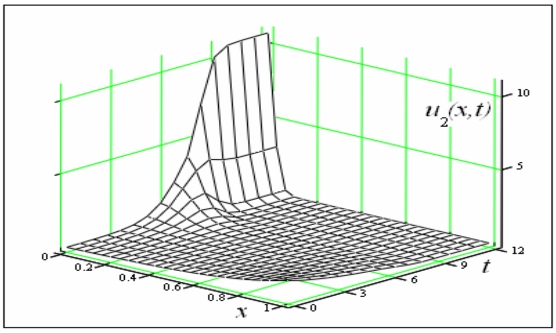

Fig. 10

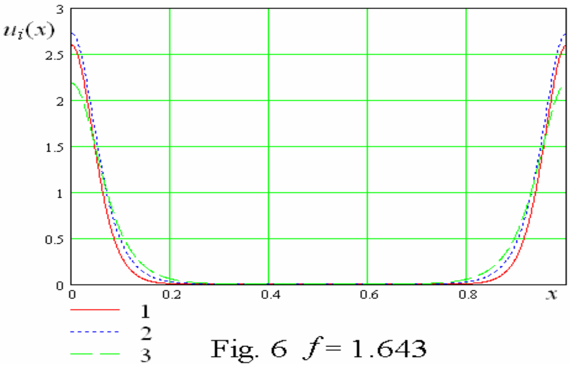

Fig. 6 $f = 1.643$

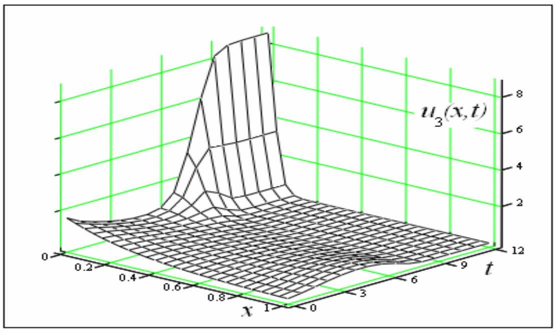

Fig. 11

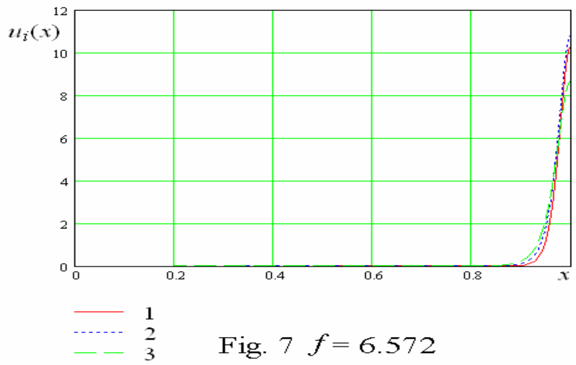

Fig. 7 $f = 6.572$

6. Open model of replication reaction for hypercycles.

The conditions of constancy for total number of macromolecule's concentration doesn't fulfilled in two models proposed in [Boerlijst, Hogeweg, 1991; Cronhjort, Nyberg, 1996]. In the first case we have the system

$$\frac{\partial v_i}{\partial t} = k_i v_i v_{i-1} e^{-f(t)} - g_i v_i + d_i \frac{\partial^2 v_i}{\partial x^2},$$

$$v_i(x,0) = \varphi_i(x), \quad i = 1,2,\dots,n.$$

In second case [6] the system has the form

$$\frac{\partial v_i}{\partial t} = -\delta_i v_i + (1 - f(t))(\rho_i + k_i v_{i-1}) v_i + d_i \frac{\partial^2 v_i}{\partial x^2},$$

$$v_i(x,0) = \varphi_i(x), \quad i = 1,2,\dots,n.$$

The functions $v_i(x,t)$ satisfy to the following boundary value conditions

$$\frac{\partial v_i}{\partial x}(0,t) = \frac{\partial v_i}{\partial x}(l,t) = 0$$

Here $v_i(x,t)$ is density of i-th type of macromolecule k_i, d_i and g_i are positive constants, $f(t)$ is the following function:

$$f(t) = \sum_{i=1}^{n} \int_0^1 v_i(x,t)\,dx\,.$$

As a before we investigate a steady state solution for the corresponding boundary value problems generated with the systems (11) and (12). Therefore in first case we have the following system of ordinary differential equations

$$\begin{aligned} &k_i u_i u_{i-1} e^{-\bar{f}} - g_i u_i + d_i u_i'' = 0, \\ &u_i'(0) = u_i'(1) = 0, \quad i = 1,2,\dots,n. \end{aligned} \tag{6.1}$$

In second case we obtain the system

$$\begin{aligned} &-\delta u_i + (1-\bar{f})(\rho_i + k_i u_{i-1})u_i + d_i u'' = 0, \\ &u_i'(0) = u_i'(1) = 0, \quad i = 1,2,\dots,n. \end{aligned} \tag{6.2}$$

Here $\bar{f}$ is the constant

$$\bar{f} = \sum_{i=1}^{n} \int_0^1 u_i(x)\,dx\,.$$

Theorem 6.1 (Existence of SNSS solution for open 1D hypercicle's system).
Suppose that the following inequalities take place for cases of the systems (6.1) and (6.2) correspondingly

$$\sum_{i=1}^{n} \frac{d_i}{k_i} \le \mu \frac{e^{-1}}{\pi^2}, \quad 0 < \mu < 1,$$

$$\sum_{i=1}^{n} \frac{d_i}{k_i} \le \frac{\mu}{4\pi^2}, \quad 0 < \mu < 1,$$

then there exist SNSS solution of this systems in the form of over fall's waves.
All result of this part can be extended on general class of the system, which described by the following equalities

$$\frac{\partial v_i(x,t)}{\partial t} = k_i v_i v_{i-1} G(f) - g_i v_i + d_i \frac{\partial^2 v_i(x,t)}{\partial x^2},$$

$$v_i(x,0) = \varphi_i(x), \quad i = 1,2,\dots,n,$$

$$\frac{\partial v_i}{\partial x}(0,t) = \frac{\partial v_i}{\partial x}(l,t) = 0,$$

$$f(t) = \sum_{i=1}^{n} \int_0^1 v_i(x,t)\,dx\,.$$

Here the differentiable function $G(f)$ satisfies to following conditions:

1. The function $G(f)$ tends to zero when f tends to some fixed value (it is possible variant when $f \to \infty$);
2. The function $f\,G(f)$ reach its unique maximal value when $f = f^*$, where $0 < f^* < \infty$.

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