Quasi-Stable Solutions of the Genetic Networks Models

S D Glyzin\textsuperscript{1,2}, A Yu Kolesov\textsuperscript{1} and N Kh Rozov\textsuperscript{3}

\textsuperscript{1} P.G. Demidov Yaroslavl State University, Sovetskaya str., 14, Yaroslavl, 150000, Russia
\textsuperscript{2} Scientific Center in Chernogolovka RAS, Lesnaya str., 9, Chernogolovka, Moscow region, 142432, Russia
\textsuperscript{3} Lomonosov Moscow State University, Leninskiye Gory, Main Building, Moscow, 119991, Russia
E-mail: glyzin@uniyar.ac.ru; kolesov@uniyar.ac.ru; fpo.mgu@mail.ru

Abstract.
We consider dynamic properties of solutions of the simplest genetic network called repressilator. This network contains three elements unidirectionally coupled into ring. More specifically, the first of them inhibits the synthesis of the second, the second inhibits the synthesis of the third, and the third, which closes the cycle, inhibits the synthesis of the first one. The interaction of the protein concentrations and of mRNA (message RNA) concentration is surprisingly similar to the interaction of six ecological populations – three predators and three preys. This new mathematical model is represented by a system of unidirectionally coupled ordinary differential equations. The existence and stability of special periodic motions (traveling waves) for this system are studied. It is shown that, with a suitable choice of parameters and an increasing number $m$ of equations in the system, the number of coexisting traveling waves increases indefinitely, but all of them (except for a single stable periodic solution for odd $m$) are quasi-stable. The quasi-stability of a cycle means that some of its multipliers are asymptotically close to the unit, while the other multipliers (except for a simple unit one) are less than unity in absolute value.

1. Introduction
Consider the model system of ordinary differential equations
\begin{equation}
\dot{p}_j = -p_j + \frac{\alpha}{1 + u_{j-1}^\gamma} + \alpha_0, \quad \dot{u}_j = \beta(p_j - u_j), \quad j = 1, 2, 3, \quad u_0 = u_3,
\end{equation}
describing the simplest genetic network (see [1]). Here $m_j$ and $p_j$, $j = 1, 2, 3$ are concentrations of matrix ribonucleic acid (mRNA) and protein of the genetic oscillator, $\alpha$, $\alpha_0$, $\gamma$, $\beta$ are positive parameters.

Suppose that in (1) the parameters $\beta$ and $\alpha_0$ are small. Then, replacing $\beta t \to t$ and discarding the parameter $\alpha_0$, one obtains a singularly perturbed system, to which the well-known Tikhonov reduction principle [2] is applied. After reduction procedure we have the following system:
\begin{equation}
\dot{u}_j = -u_j + \frac{\alpha}{1 + u_{j-1}^\gamma}, \quad j = 1, 2, 3, \quad u_0 = u_3.
\end{equation}
The problem of self-excited oscillations in (2) and similar systems arising in the modeling of gene networks has been extensively investigated (see, e.g., [3, 4, 5, 6, 7, 8, 9, 10]). It is known that, for \( \gamma > 2 \) and a suitable increase of \( \alpha \), the model (2) has a stable cycle that is self-symmetric (i.e., invariant under cyclic permutations of the coordinates). The self-symmetry property implies that this cycle can be represented in the form

\[
(u_1, u_2, u_3) = (u(t), u(t + \Delta), u(t + 2\Delta)),
\]  

where \( \Delta > 0 \) is the phase shift. Here \( u(t) \) is a 3\( \Delta \)-periodic function.

Phenomenological model of genetic oscillator can be derived also from population dynamics systems. The interaction of the concentrations \( u_j \) and \( p_j \), described above is similar to the interaction of six ecological populations – three predators and three preys. Indeed, suppose that \( u_j, j = 1, 2, 3 \) and \( p_j, j = 1, 2, 3 \) are the population densities of the predators and preys, respectively. The gene network can be modeled using Yu. S. Kolesov’s approach [11]. In the case of an arbitrary number of elements this approach yields the system

\[
\dot{p}_j = \frac{r_1}{1 + a} [1 + a(1 - u_{j-1}) - p_j]p_j + \alpha, \quad \dot{u}_j = r_2[p_j - u_j]u_j, \quad j = 1, 2, \ldots, m, \quad u_0 = u_m, \tag{4}
\]

where \( r_1, r_2, a, \) and \( \alpha \) are positive constants.

As well as the system (1), the new mathematical model of repressilator (4) can be simplified. At first assume that \( r_2 \gg 1 \) and \( r_1 = r \sim 1 \). Then, according to the reduction principle [2], as \( r \to +\infty \), we have \( p_j = u_j, j = 1, 2, \ldots, m \). For the components \( u_j \), we obtain the system

\[
\dot{u}_j = \frac{r}{1 + a} [1 + a(1 - u_{j-1}) - u_j]u_j + \alpha, \quad j = 1, 2, \ldots, m, \quad u_0 = u_m,
\]

which, after the normalizations \( u_j/(1 + a) \to u_j \) and \( \alpha/(1 + a) \to \alpha \), becomes

\[
\dot{u}_j = r[1 - u_j - a u_{j-1}]u_j + \alpha, \quad j = 1, 2, \ldots, m, \quad u_0 = u_m. \tag{5}
\]

We consider special periodic solutions of the system (5) that can be represented in the form

\[
u_j = u(t + (j - 1)\Delta), \quad j = 1, 2, \ldots, m, \quad \Delta = \text{const} > 0.
\]  

This solution we call a traveling wave of (5).

Below, the existence and stability of such solutions are analyzed in the case where \( r \gg 1 \), \( \alpha \ll 1 \), and the parameter \( a \) is of the order of unity. More precisely, we assume throughout that

\[
a = \text{const} > 1, \quad \alpha = r \exp(-br), \quad r \gg 1, \quad b = \text{const} > 0. \tag{7}
\]

It will be shown that, under conditions (7), the number of coexisting periodic solutions (6) of the system (5) increases indefinitely as \( r \to +\infty \) and \( m \to +\infty \) consistently. However, all of them (except for a single stable solution for odd \( m \)) are quasi-stable. Namely, the stability spectrum of each of these periodic solutions contains a nonempty group of multipliers \( \nu \in \mathbb{C}, \nu \neq 1 \), lying at a distance of order \( \exp(-cr) \), \( c = \text{const} > 0 \) from the unit circle.

The quasi-stability phenomenon of solutions of the model of gene network is the main subject of the paper.
2. General research scheme
To simplify the subsequent analysis, in system (5), we make the exponential changes of variables
\[ u_j = \exp(x_j/\varepsilon), \ j = 1, 2, \ldots, m, \] where \( \varepsilon = 1/r \ll 1 \). As a result, in view of relations (7), the system becomes
\[ \dot{x}_j = 1 - \exp \left( \frac{x_j}{\varepsilon} \right) - a \exp \left( \frac{x_{j-1}}{\varepsilon} \right) + \exp \left( - \frac{b + x_j}{\varepsilon} \right), \quad j = 1, 2, \ldots, m, \] (8)
where \( x_0 = x_m \). According to (6), we are interested in periodic solutions of system (8) that can be represented in the form
\[ x_j = x(t + (j - 1)\Delta, \varepsilon), \quad j = 1, 2, \ldots, m, \] (9)
where \( \Delta > 0 \) and \( x(t, \varepsilon) \) is a \( T \)-periodic solution of the auxiliary delay equation
\[ \dot{x} = 1 - \exp \left( \frac{x}{\varepsilon} \right) - a \exp \left( \frac{x(t - \Delta)}{\varepsilon} \right) + \exp \left( - \frac{b + x}{\varepsilon} \right). \] (10)
Direct verification shows that components (9) satisfy system (8) if and only if \( T = m\Delta/k \), \( k \in \mathbb{N} \).

Given a positive integer \( k \), assume that Eq. (10) has the required periodic solution \( x(t, \varepsilon) \) of period \( T = m\Delta/k \). Then the stability analysis of the corresponding cycle (9) is reduced to analyzing the location of multipliers of the linear system
\[ \dot{y}_j = A(t + (j - 1)\Delta, \varepsilon) y_j + B(t + (j - 1)\Delta, \varepsilon) y_{j-1}, \quad j = 1, 2, \ldots, m, \] (11)
where \( y_0 = y_m \), and the coefficients \( A(t, \varepsilon) \) and \( B(t, \varepsilon) \) are given by
\[ A(t, \varepsilon) = -\frac{1}{\varepsilon} \left( \exp \left( \frac{x(t, \varepsilon)}{\varepsilon} \right) + \exp \left( - \frac{b + x(t, \varepsilon)}{\varepsilon} \right) \right), \quad B(t, \varepsilon) = -\frac{a}{\varepsilon} \exp \left( \frac{x(t - \Delta, \varepsilon)}{\varepsilon} \right). \] (12)
With (11), in what follows, we will need the auxiliary linear delay equation
\[ \dot{y} = A(t, \varepsilon) y + \kappa B(t, \varepsilon) y(t - \Delta), \] (13)
where \( g(t) \) is a scalar complex-valued function and \( \kappa \) is an arbitrary complex parameter. More precisely, we will be interested in its multipliers \( \nu_l(\kappa), l = 1, 2, \ldots \), arranged in decreasing order of moduli.

Let us explain the meaning of a multiplier as applied to Eq. (13). For a fixed number \( \sigma_0 > 0 \), consider the space \( E = C[-\Delta - \sigma_0, -\sigma_0] \) of continuous complex-valued functions \( g(t) \) for \( -\Delta - \sigma_0 \leq t \leq -\sigma_0 \) with the norm \( ||g||_E = \max_{-\Delta - \sigma_0 \leq t \leq -\sigma_0} |g(t)| \). The monodromy operator of Eq. (13) is a bounded linear operator \( V : E \to E \) acting on an arbitrary function \( y_0(t) \in E \) according to the rule
\[ V y_0 = g(t + m\Delta/k, \kappa, \varepsilon), \quad -\Delta - \sigma_0 \leq t \leq -\sigma_0, \] (14)
where \( g(t, \kappa, \varepsilon) \) is the solution of Eq. (13) on the time interval \( -\sigma_0 \leq t \leq m\Delta/k - \sigma_0 \) with an initial function \( g_0(t) \), \( -\Delta - \sigma_0 \leq t \leq -\sigma_0 \). The spectrum of this operator is always discrete, since some power of \( V \) is compact (for \( m/k > 1 \), \( V \) is compact itself). By the multipliers of Eq. (13), by analogy with ordinary differential equations, we mean the eigenvalues of operator (14).

To study the relation between the multipliers of system (11) and Eq. (13), the so-called tuning method with respect to the parameter \( \kappa \) was proposed in [12]. According to this method, we consider the family of equations
\[ [\nu_l(\kappa)]^k = \kappa^m, \quad l \in \mathbb{N}. \] (15)
It turns out that there is a correspondence between the nonzero roots of these equations and
the multipliers of system (11). More precisely, the following assertion holds (see [12, 13, 14]).

**Lemma 1.** For each multiplier \( \nu \) of system (11), there is a positive integer \( l_0 \) such that

\[
\nu = \nu_0(\kappa_0),
\]

where \( \kappa_0 \) is a root of Eq. (15) at \( l = l_0 \). Conversely, given some \( l = l_0 \), if Eq. (15) has a nonzero root \( \kappa = \kappa_0 \), then the original system (11) has a multiplier of form (16).

Thus, the analysis of the existence of cycles (9) in system (8) is reduced to the search for
periodic solutions of the auxiliary scalar equation (10) with periods \( T = m\Delta/k \). The stability
of traveling waves is analyzed separately and, by Lemma 1, is reduced to the asymptotic
computation of the roots of Eqs. (15). Below, both these issues are studied for positive integer
\( m \) and \( k \) satisfying the conditions

\[
m \geq 3, \quad 2 < m/k < a + 1.
\]

3. **Analysis of the auxiliary nonlinear equation**

Our nearest goal is to show that, for any fixed values of the parameters \( a, b, \Delta \) satisfying the
inequalities

\[
a > 1, \quad b > 0, \quad \Delta(a - 1) > b,
\]

and for all \( 0 < \varepsilon \ll 1 \), the auxiliary equation (10) has a nontrivial periodic solution.

For a formulation of corresponding result we consider periodic function

\[
x_0(t) = \begin{cases} 
0 & 0 \leq t < \Delta, \\
-(a - 1)(t - \Delta) & \Delta \leq t \leq t_0, \\
-b & t_0 \leq t \leq 2\Delta, \\
\Delta \leq t \leq t_0, \\
t - 2\Delta - b & 2\Delta \leq t \leq T_0,
\end{cases}
\]

where \( t_0 = \Delta + b/(a - 1) \) and \( T_0 = 2\Delta + b \) (this function is plotted in Fig. 1).

**Lemma 2.** Under conditions (18), for all sufficiently small \( \varepsilon > 0 \), Eq. (10) has a cycle
\( x = x_*(t, \varepsilon) \) of period \( T_*(\varepsilon) \) that satisfies, as \( \varepsilon \to 0 \), the asymptotic equalities

\[
\max_{0 \leq t \leq T_*(\varepsilon)} |x_*(t, \varepsilon) - x_0(t)| = O(\varepsilon), \quad T_*(\varepsilon) = T_0 + O(\varepsilon).
\]

We describe the general scheme for proving this lemma. Let \( \sigma_0 \) be a fixed constant satisfying
the conditions

\[
0 < \sigma_0 < \min \left( \frac{b}{2}, \frac{\Delta}{2}, \frac{b}{2(a - 1)}, \frac{1}{2} \left( \frac{\Delta}{a - 1} \right), \frac{\Delta}{a - 1} \right).
\]
The set \( S \subset C[-\Delta - \sigma_0, -\sigma_0] \) of initial functions \( \varphi(t) \) is defined as

\[
S = \{ \varphi(t) : -q_1 \leq \varphi(t) \leq -q_2 \quad -\Delta - \sigma_0 \leq t \leq -\sigma_0, \quad \varphi(-\sigma_0) = -\sigma_0 \},
\]

where \( q_1 > q_2 > 0 \) are universal (independent of \( t, \varepsilon, \varphi \)) constants, which will be specified later. Below, we are interested in the solution where \( \phi \) principle implies that \( \Pi \) has at least one fixed point convex and the operator \( \Pi \) is compact by virtue of the inequality \( T \in S \) and, moreover, \( \Pi(\varphi(t, \varepsilon), t \geq -\sigma_0) \) of Eq. (10) with an arbitrary initial value \( \varphi(t) \in S, \ t \in [-\Delta - \sigma_0, -\sigma_0] \).

For each function \( \varphi(t) \in S \), let \( t = T_\varphi(\varepsilon) \) denote the second positive root of the equation

\[
x_\varphi(t - \sigma_0, \varepsilon) = -\sigma_0
\]

(if it exists). The operator \( \Pi \) from \( S \) to \( C[-\Delta - \sigma_0, -\sigma_0] \) is defined as

\[
\Pi(\varphi) = x_\varphi(t + T_\varphi(\varepsilon), \varepsilon), \quad -\Delta - \sigma_0 \leq t \leq -\sigma_0.
\]

We proof that for a suitable choice of the parameters \( q_1, q_2 \) operator (24) is defined on set (22) and, moreover, \( \Pi(S) \subset S, \ T_\varphi(\varepsilon) > \Delta \forall \varphi \in S \). Furthermore, since \( S \) is closed, bounded, and convex and the operator \( \Pi \) is compact by virtue of the inequality \( T_\varphi(\varepsilon) > \Delta \), the Schauder principle implies that \( \Pi \) has at least one fixed point \( \varphi = \tilde{\varphi}(t, \varepsilon) \) in \( S \). It is also clear that the solution of Eq. (10) is periodic with period \( T_\varepsilon(\varepsilon) = T_\varphi|_{\varphi=\tilde{\varphi}} \). This solution is the desired one, since it possesses asymptotic properties (20).

To implement the above-described scheme, we need to know a uniform (with respect to \( \varphi \in S \)) asymptotic representation of the solution \( x_\varphi(t, \varepsilon) \) on various intervals of \( t \). The corresponding constructions are divided into eight stages. The proof of Lemma 2 due to the bulkiness is not given (see [15]).

4. Analysis of the auxiliary linear equation

In this section, we study the asymptotic behavior of multipliers of a linear equation similar to (13), namely,

\[
\dot{g} = A_s(t, \varepsilon)g + \varkappa B_s(t, \varepsilon)g(t - \Delta),
\]

with coefficients given by (12) at \( x(t, \varepsilon) = x_\ast(t, \varepsilon) \).

Consider the set of initial functions

\[
B_0 = \{ g_0(t) \in E : g_0(-\sigma_0) = 0, \ ||g_0|| \leq 2 \},
\]

where, as in Section 2, \( E \) is the space \( C[-\Delta - \sigma_0, -\sigma_0] \) over the field of complex numbers and \( ||*|| \) is the norm in \( E \) (defined in a usual manner). Let \( g_1(t, g_0, \varkappa, \varepsilon) \) denote the solution of Eq. (25) with an arbitrary initial function \( g_0(t) \) from set (26), and let \( g_2(t, \varkappa, \varepsilon) \) be the solution of this equation with the initial function \( g_2 \equiv 1, \ t \in [-\Delta - \sigma_0, -\sigma_0] \). Integrating Eq. (25) by the method of steps, we see that, on the interval \( t \in [-\sigma_0, T_\varepsilon(\varepsilon) - \sigma_0] \), the functions are power functions of \( \varkappa \), i.e.,

\[
g_1(t, g_0, \varkappa, \varepsilon) = \sum_{n=1}^{n_0} g_{1,n}(t, g_0, \varepsilon)\varkappa^n, \quad g_2(t, \varkappa, \varepsilon) = \sum_{n=0}^{n_0} g_{2,n}(t, \varepsilon)\varkappa^n,
\]

where

\[
n_0 = \begin{cases} T_\varepsilon(\varepsilon)/\Delta & \text{if } T_\varepsilon(\varepsilon)/\Delta \text{ is an integer,} \\ \lfloor T_\varepsilon(\varepsilon)/\Delta \rfloor + 1 & \text{otherwise,} \end{cases}
\]

and \( \lfloor * \rfloor \) is the integer part. Note also that

\[
g_{1,n}(t, g_0, \varepsilon) \equiv g_{2,n}(t, \varepsilon) \equiv 0 \quad t \in [-\sigma_0, (n - 1)\Delta - \sigma_0], \ n \geq 2.
\]

For an asymptotic analysis of the multipliers of Eq. (25), we need the following result.
Lemma 3. There exists a sufficiently small $\varepsilon_0 > 0$ such that, for all $0 < \varepsilon \leq \varepsilon_0$, $\varepsilon \in \Lambda_0 \equiv \{ \varepsilon \in \mathbb{C}: |\varepsilon| \leq 1 \}$, $g_0 \in B_0$ on the interval $-\sigma_0 \leq t \leq T_*(\varepsilon) - \sigma_0$, the estimates
\[
\sum_{n=0}^{\infty} \left| \frac{\partial^n g_1(t, g_0, \varepsilon)}{\partial \varepsilon^n} \right| \leq \exp(-q/\varepsilon), \quad \sum_{n=0}^{\infty} \left| \frac{\partial^n g_2(t, \varepsilon)}{\partial \varepsilon^n} \right| \leq M \tag{30}
\]
hold with constants $q, M > 0$ independent of $t, \varepsilon, g_0$. Moreover, as $\varepsilon \to 0$, the asymptotic representations
\[
\frac{\partial^n}{\partial \varepsilon^n} g_2(T_*(\varepsilon) - \sigma_0, \varepsilon) = \varepsilon^2 + O(\exp(-q/\varepsilon)), \quad n = 0, 1, \ldots, n_0 \tag{31}
\]
hold uniformly in $\varepsilon$ (here and below, $[\varepsilon]^{(n)}$ denotes the $n$th derivative with respect to $\varepsilon$).

Proof. The first inequality in (30) is proved by induction. For this purpose, the time interval $[-\sigma_0, T_*(\varepsilon) - \sigma_0]$ is divided into subintervals $[n-1)\Delta - \sigma_0, n\Delta - \sigma_0]$, $n = 1, 2, \ldots, n_0 - 1$, and $[(n_0-1)\Delta - \sigma_0, T_*(\varepsilon) - \sigma_0]$, where $n_0$ is given by (28). The proof of Lemma 3, like Lemma 2, is divided into 8 stages. This technical result is not given here (see [15]).

Now we pass to the asymptotic computation of the multipliers of Eq. (25). For this purpose, we consider the monodromy operator $V_*(\varepsilon, \varepsilon)$ of this equation acting on the space $E$ according to the rule (similar to (14))
\[
V_*(\varepsilon, \varepsilon)g_0 = g(t + T_*(\varepsilon), \varepsilon, \varepsilon), \quad -\Delta - \sigma_0 \leq t \leq -\sigma_0, \tag{32}
\]
where $g(t, \varepsilon, \varepsilon), -\sigma_0 \leq t \leq T_*(\varepsilon) - \sigma_0$, is the solution of Eq. (25) with an initial function $g_0(t) \in E$. Let $\nu_s(\varepsilon, \varepsilon), s \in \mathbb{N}$, denote the eigenvalues of operator (32) arranged in decreasing order of moduli. The following assertion holds.

Lemma 4. For any $R > 0$, there are $\varepsilon_0 = \varepsilon_0(R) > 0$, $q = q(R) > 0$, and $\delta = \delta(R) > 0$ such that, for all $0 < \varepsilon \leq \varepsilon_0$, $\varepsilon \in \Lambda_{\delta, R} \equiv \{ \varepsilon \in \mathbb{C}: \exp(-\delta/\varepsilon) \leq |\varepsilon| \leq R \}$
\[
\sup_{s \geq 2} |\nu_s(\varepsilon, \varepsilon)| \leq \exp(-q/\varepsilon). \tag{33}
\]
The multiplier $\nu_1(\varepsilon, \varepsilon)$ is simple, depends analytically on $\varepsilon \in \Lambda_{\delta, R}$, and, as $\varepsilon \to 0$, has the asymptotic representations (uniform in $\varepsilon$)
\[
\nu_1(\varepsilon, \varepsilon) = \varepsilon^2 + O(\exp(-q/\varepsilon)), \quad \frac{\partial \nu_1}{\partial \varepsilon}(\varepsilon, \varepsilon) = 2\varepsilon + O(\exp(-q/\varepsilon)) \tag{34}
\]

5. Main results
Recall that the analysis of the existence of traveling waves (9) for system (8) is reduced to the search for periodic solutions of the auxiliary equation (10) with the periods $T$ given by the equalities $T = m\Delta/k$, $k \in \mathbb{N}$. In this context, in what follows, the periodic solution of Eq. (10) provided by Lemma 2 and its period are denoted by $x_s(t, \varepsilon, \Delta)$ and $T_*(\varepsilon, \Delta)$, respectively, in order to emphasize that these functions depend on $\Delta$. Let $m$ and $k$ be fixed positive integers related by inequalities (17). These inequalities imply that the quantity $\Delta_{(k)} = b/(m/k - 2)$ satisfies the condition $\Delta_{(k)} > b/(a - 1)$. In what follows, we assume that the parameter $\Delta$ in (10) ranges over some interval $K \subset (b/(a - 1), +\infty)$ for which $\Delta = \Delta_{(k)}$ is an interior point. Then we have the asymptotic representation (uniform in $\Delta \in K$)
\[
T_*(\varepsilon, \Delta) = 2\Delta + b + O(\varepsilon), \quad \varepsilon \to 0. \tag{35}
\]
In view of formula (35), it is easy to see that the equation
\[
T_*(\varepsilon, \Delta) = m\Delta/k \tag{36}
\]
has at least one root \( \Delta = \hat{\Delta}((\varepsilon)) \) such that
\[
\hat{\Delta}((\varepsilon)) = \hat{\Delta} + O(\varepsilon), \quad \varepsilon \to 0.
\] (37)

Therefore, the following assertion holds.

**Theorem 1.** Let \( a > 1, b > 0, \) and \( m, k \) be positive integers related by inequalities (17). Then there is a sufficiently small \( \varepsilon_0 > 0 \) such that, for all \( 0 < \varepsilon \leq \varepsilon_0 \), system (8) has a cycle (traveling wave)
\[
C_k : \quad x_j = \hat{x}(t_j) + \hat{A}_k(t_j) + B_x(t_j) + O(\varepsilon), \quad j = 1, 2, \ldots, m,
\] (38)
where \( \hat{x}(t_j) = x_*(t, \varepsilon) |_{\Delta = \hat{\Delta}((\varepsilon))} \) and \( \hat{\Delta}((\varepsilon)) \) is root (37) of Eq. (36).

Let us analyze the stability of cycle (38).

**Theorem 2.** Cycle (38) is exponentially orbitally stable if \( k = (m - 1)/2 \) and quasi-stable otherwise.

**Proof sketch.** For cycle (38), we consider a variational system similar to (11), namely,
\[
\dot{g}_j = \hat{A}_k(t_j) + \hat{B}_x(t_j) + O(\varepsilon), \quad j = 1, 2, \ldots, m, \quad g_0 = g_m, \quad g_m = 0,
\] (39)
where \( \Delta = \hat{\Delta}((\varepsilon)) \) and \( \hat{A}_k(t_j), \hat{B}_x(t_j) \) are coefficients (12) with \( x(t, \varepsilon) = \hat{x}(t_j) \) and \( \Delta = \hat{\Delta}((\varepsilon)) \). Let \( \mathcal{V}(\varepsilon) \) denote the shift operator along the solutions of this system over the time from \( t = -\sigma_0 \) to \( t = m\Delta/k - \sigma_0 \). Obviously, the stability properties of cycle (38) can be determined via the asymptotic computation of the spectrum of \( \mathcal{V}(\varepsilon) \). The corresponding analysis is based on Lemma 1, according to which any eigenvalue \( \nu \) of this operator is given by the equality \( \nu = \hat{\nu}_l(x_0, \varepsilon) \), where \( \hat{\nu}(x, \varepsilon) \) are the multipliers of the auxiliary equation (25) for \( \Delta = \hat{\Delta}((\varepsilon)) \) and \( x_0 \) is a nonzero root of the equation
\[
[\hat{\nu}(x, \varepsilon)]^k = x^m, \quad l \in \mathbb{N}
\] (40)
for \( l = l_0 \). Thus, the proof of Theorem 2 is reduced to analyzing of the roots of Eqs. (40).

First, we determine the values of \( \nu \) for which it Eqs. (40) make sense. Specifically, we show that these equations have no roots in the set
\[
\{x \in \mathbb{C} : \ |x| > R\}
\] (41)
for sufficiently large fixed \( R > 0 \). For this purpose, we need the following result.

**Lemma 5.** It is true that
\[
||\mathcal{V}(\varepsilon)||_{\mathbb{R}^m \rightarrow \mathbb{R}^m} \leq M\varepsilon^{-n_0(m-1)}, \quad M = \text{const} > 0
\] (42)
where \( n_0 \) is a positive integer given by the equality (similar to (28))
\[
n_0 = \begin{cases} \frac{m}{k} & \text{if } m/k \text{ is an integer,} \\ \left\lceil \frac{m}{k} \right\rceil + 1 & \text{otherwise.} \end{cases}
\] (43)

The proof of Lemma 5 is carried out similarly to Lemma 2.

The values of the parameter \( \nu \) can be tentatively localized by applying this lemma. Specifically, combining estimate (42) with relations (15) and (16), which hold for any multiplier of system (39), we conclude that
\[
|\nu| = |\hat{\nu}_l(x_0, \varepsilon)| = |x_0|^{m/k} \leq ||\mathcal{V}(\varepsilon)||_{\mathbb{R}^m \rightarrow \mathbb{R}^m} \leq M\varepsilon^{-n_0(m-1)}.
\]
Thus, all possible roots \( \varkappa_0 \) of Eqs. (40) lies to the disk
\[
\left\{ \varkappa \in \mathbb{C} : |\varkappa| \leq M^{k/m} r_0^{-\alpha_0} \right\},
\]
where \( \alpha_0 = n_0 (m - 1) k/m \) and \( M \) is the constant from (42).

To reduce the set (44) of admissible values of \( \varkappa \), we consider the operator obtained from (32) at \( \Delta = \tilde{\Delta}_\kappa (\varepsilon) \). Note that relations (27) – (29) and estimates (30) imply the representation
\[
\hat{V}_s (\varkappa, \varepsilon) = \sum_{n=0}^{n_0} \hat{V}_{s,n} (\varepsilon) \varkappa^n,
\]
where \( \hat{V}_{s,n} (\varepsilon) : E \to E \) are bounded linear operators satisfying the estimates
\[
||\hat{V}_{s,n} (\varepsilon)||_{E \to E} \leq M_n, \quad M_n = \text{const} > 0, \quad n = 0, 1, 2, \quad ||\hat{V}_{s,n} (\varepsilon)||_{E \to E} \leq \exp (-q/\varepsilon), \quad n = 3, \ldots, n_0.
\]

It follows from (45) and (46) that
\[
\sup_{t \geq 1} |\hat{v}_t (\varkappa, \varepsilon)| \leq \sum_{n=0}^{n_0} |\varkappa|^n ||\hat{V}_{s,n} (\varepsilon)||_{E \to E} \leq M_0 + M_1 |\varkappa| + M_2 |\varkappa|^2 + \exp (-q/\varepsilon) \sum_{n=3}^{n_0} |\varkappa|^n.
\]

Finally, it should be noted that the inequality
\[
M_0 + M_1 |\varkappa| + M_2 |\varkappa|^2 + \exp \left(-\frac{q}{\varepsilon}\right) \sum_{n=3}^{n_0} |\varkappa|^n < |\varkappa|^{m/k}.
\]
holds on the subset \( \{ \varkappa \in \mathbb{C} : R \leq |\varkappa| \leq M^{k/m} r_0^{-\alpha_0} \} \) of set (44) for sufficiently large fixed \( R > 0 \) by virtue of the condition \( m/k > 2 \) (see (2.10)).

Estimates (47) and (48) imply that, with a suitable choice of \( R > 0 \), Eqs. (40) have no roots in set (41). In what follows, we assume that the constant \( R \) is suitably chosen.

The above analysis implies that the consideration of Eqs. (40) can be restricted to the values of \( \varkappa \) from the set \( \Delta_{3,R} \), where the constant \( \delta \) is determined by \( R \) according to Lemma 4 at \( \Delta = \tilde{\Delta}_\kappa (\varepsilon) \). Note also that, by virtue of (34), Eq. (40) with \( l = 1 \) has exactly \( m - 2k \) simple roots in the indicated set. These roots include the unit one, since, for \( \varkappa = 1 \) and \( \Delta = \tilde{\Delta}_\kappa (\varepsilon) \), Eq. (25) is the linearization of Eq. (10) around the cycle \( x = \tilde{x}_\kappa (\varepsilon, t) \) and, hence, admits a unit multiplier. The other \( m - 2k - 1 \) roots of the equation have, as \( \varepsilon \to 0 \), the asymptotic representation
\[
\varkappa_s = \theta_s + O (\exp (-q/\varepsilon)), \quad \theta_s = \exp \left(i2\pi s (m-2k)^{-1}\right), \quad s = 1, 2, \ldots, m - 2k - 1.
\]

Summarizing, we note that all multipliers \( \nu \in \mathbb{C} \) of cycle (38), except for the simple unit one, are divided into two groups. Indeed, according to (15), (16), (34), and (49), there is a group of so-called critical multipliers that are exponentially close to the unit circle. More precisely, as \( \varepsilon \to 0 \), they satisfy the asymptotic equalities
\[
\nu_s = \theta_s^2 + O (\exp (-q/\varepsilon)), \quad s = 1, 2, \ldots, m - 2k - 1.
\]

The other \( 2k \) multipliers correspond to the roots of Eqs. (40) lying in the disk \( \{ \varkappa \in \mathbb{C} : |\varkappa| \leq \exp (-\delta_0/\varepsilon) \} \), where \( \delta_0 = \text{const} > 0 \). Moreover, since \( \nu = \varkappa^{m/k} \), these multipliers are exponentially small in absolute value.

It remains to note that, in the case \( k = (m - 1)/2 \), the group of critical multipliers (50) is empty; therefore, cycle (38) is exponentially orbitally stable. In the case \( k \neq (m - 1)/2 \), this cycle is quasi-stable. Theorem 5.2 is proved.
Note that, for fixed $a > 1$ as $m \to +\infty$, the number of indices $k$ satisfying conditions (17) increases indefinitely. From this and Theorems 1 and 2, it follows that the number of coexisting traveling waves (38) also increases indefinitely as $\varepsilon \to 0$ and $m \to +\infty$ consistently. However, all of them (except for a single stable periodic motion for $k = (m - 1)/2$) are quasi-stable. Thus, a quasi-buffer phenomenon occurs in this case. In contrast to the usual buffer phenomenon, which is associated with the unlimited accumulation of coexisting attractors, in this case, quasi-stable structures are accumulated unlimitedly with growing $m$.

6. Conclusions

First, we discuss the limits of the applicability of model (5). Note that, in contrast to system (1) we cannot set $\alpha = 0$. This is clear even for $m = 3$. Indeed, in the three-dimensional case, for $a > 2$ and $\alpha = 0$, system (5) has a stable homoclinic triangle formed by the saddles $O_1 = (1, 0, 0), O_2 = (0, 1, 0), O_3 = (0, 0, 1)$ and the corresponding separatrices (see Fig. 2, where this triangle is shown for $m = 3, r = 1, a = 10, \alpha = 0$). It is also clear that this steady state is not biologically reasonable, since it corresponds to the extinction of one of the genes. For $\alpha > 0$, the stable homoclinic triangle transforms into a stable cycle lying in the cone $\mathbb{R}^3_+ = \{(u_1, u_2, u_3) : u_j > 0, j = 1, 2, 3\}$. In other words, the self-excited oscillations are properly regularized. For $m = 3, r = 1, a = 10, \alpha = 0.01$, the above cycle has the form shown in Fig. 3. Thus, the case of (7) corresponds to the limit of applicability of model (5).

That is why it exhibits a quasi-buffer phenomenon. Due to this phenomenon, under conditions (7), the phase point of system (7) can stay in a neighborhood of the quasi-stable cycle (6) over a time interval on the order of $\exp(cr), c = \text{const} > 0$. Thus, we deal with an effect similar to the well-known Arnold diffusion.

It should be noted that, for $\alpha \sim 1$, quasi-stable structures collapse. A numerical analysis shows that, in this case for odd $m$, the only attractor of system (5) is a traveling-wave cycle, which is the continuation of cycle (38) with respect to the parameter $\alpha$ for $k = (m - 1)/2$.

For $m = 9, r = 1, a = 10, \alpha = 0.01$, the component $u = u_1(t)$ of this cycle in the plane $(t, u)$ is plotted in Fig. 4. In the case $m = 2m_0$, where $m_0 \geq 1$, system (5) represents a genetic
trigger [16]: for $a > 1$, and $\tilde{\alpha} < (a - 1)/4$, where $\tilde{\alpha} = \alpha/r$, it admits two stable equilibria

$$O_1 = (u_0^0, u_1^0, u_2^0, \ldots, u_1^0, u_2^0), \quad O_2 = (u_2^0, u_1^0, u_2^0, u_1^0, \ldots, u_2^0, u_1^0)$$

with components

$$u_1^0 = \frac{\tilde{\alpha}}{(a - 1)u_2^0}, \quad u_2^0 = \frac{1}{2} \left(1 + \sqrt{1 - \frac{4\tilde{\alpha}}{a - 1}}\right).$$

Figure 4. The component $u = u_1(t)$ of traveling-wave cycle for $m = 9$, $r = 1$, $a = 10$, $\alpha = 0.01$

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