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Quasi-Stable Structures in Circular Gene Networks

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Abstract—A new mathematical model is proposed for a circular gene network representing a system of unidirectionally coupled ordinary differential equations. The existence and stability of special periodic motions (traveling waves) for this system is 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 circle, while the other multipliers (except for a simple unit one) are less than unity in absolute value.

Keywords: mathematical model, circular gene network, repressilator, traveling wave, asymptotics, quasi-stability, quasi-buffer phenomenon, system of ordinary differential equations, periodic solutions.

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1. FORMULATION OF THE PROBLEM

The study of artificial genetic oscillators is motivated by the circumstance that they are simplified models of key biological processes, such as cell cycle and circadian rhythms. The simplest genetic oscillator, known as a repressilator, was proposed in [1]. It consists of three elements A_j, $j = 1,2,3$, each unidirectionally inhibiting its neighbor. More specifically, A_1 inhibits the synthesis of A_2, A_2 inhibits the synthesis of A_3, and A_3, which closes the cycle, inhibits the synthesis of A_1.

The mathematical model of this gene network has the form

$$\dot{p}_j = -p_j + \frac{\alpha}{1 + u_{j-1}^{\gamma}} + \alpha_0, \quad \dot{u}_j = \beta(p_j - u_j), \quad j = 1,2,3, \tag{1.1}$$

where $u_0 = u_3$. Following [1], we assume that each element A_j is a set of mRNA (message RNA) of concentration p_j and protein of concentration u_j. Furthermore, the time variation in p_j is assumed to be characterized by synthesis and degradation. The former of these processes is described by the function $\alpha/(1 + u_{j-1}^{\gamma})$, where u_{j-1} is the concentration of the repressor protein for the jth mRNA, $\gamma = \text{const} > 0$ is the cooperativity coefficient, and $\alpha = \text{const} > 0$ is the transcription rate in the absence of the repressor. The latter process is described by the linear term $-p_j$. Finally, the additive term $\alpha_0 > 0$ in the equation for p_j describes the leakiness of the promoter.

In the case of protein concentrations u_j, the situation is simpler. Namely, we assume that their dynamics are characterized by linear synthesis (the term βp_j in the equation for u_j in system (1.1)) and by linear degradation (the term $-\beta u_j$ in the same equation). Here, $\beta = \text{const} > 0$ is the ratio of the protein degradation rate to the mRNA degradation rate.

As a rule, model (1.1) is studied assuming that β and α_0 are small. In this case, making the substitution $\beta t \to t$ and dropping the addition α_0 yields a singularly perturbed system, to which the Tikhonov well-known reduction principle is applied [2]. As a result, we obtain the system

$$\dot{u}_j = -u_j + \frac{\alpha}{1 + u_{j-1}^{\gamma}}, \quad j = 1,2,3, \quad u_0 = u_3. \tag{1.2}$$

The problem of self-excited oscillations in (1.2) and similar systems arising in the modeling of gene networks has been extensively investigated (see, e.g., [3–10]). Available analytical and numerical results suggest that, for $\gamma > 2$ and a suitable increase in α, model (1.2) 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

$$(u_1, u_2, u_3) = (u(t), u(t + \Delta), u(t + 2\Delta)), \tag{1.3}$$

where $\Delta > 0$ is the phase shift. Note that the period of cycle (1.3) is 3Δ.

The interaction of the concentrations u_j and p_j described above is surprisingly 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. Then, by virtue of (1.1), each predator u_j feeds on only one prey p_j (for $p_j \equiv 0$, u_j decays exponentially) and, at the same time, exerts pressure only on the prey p_{j+1}. The last means that the growth rate of p_{j+1} decreases with increasing u_j. Additionally, if the repressor predator is absent ($u_{j-1} \equiv 0$), then p_j tends to the threshold value $p_j = \alpha + \alpha_0$ as $t \to +\infty$.

In view of this ecological interpretation, the gene network can be modeled using Yu.S. Kolesov's approach [11]. In the case of an arbitrary number of elements A_j, $j = 1,2,\ldots,m$, interacting according to the circular principle, this approach yields the system

$$\begin{gathered}\dot{p}_j = \frac{r_1}{1+a}[1 + a(1 - u_{j-1}) - p_j]p_j + \alpha, \quad \dot{u}_j = r_2[p_j - u_j]u_j, \\ j = 1,2,\ldots,m, \quad u_0 = u_m,\end{gathered} \tag{1.4}$$

where r_1, r_2, a, and α are positive constants. It should be emphasized that the term $+\alpha$, which is similar to the addition α_0 in (1.1), was intentionally added to the equation for p_j, thereby violating its Volterra structure. As will be shown below, the condition $\alpha > 0$ cannot be omitted in our case, in contrast to system (1.1), where we can set $\alpha_0 = 0$.

As system (1.1), the new mathematical model of repressilator (1.4) can be simplified. Specifically, assume first that $r_2 \gg 1$ and $r_1 = r \sim 1$. Then, according to the reduction principle [2], as $r_2 \to +\infty$, 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 making the normalizations $u_j/(1+a) \to u_j$ and $\alpha/(1+a) \to \alpha$, becomes

$$\dot{u}_j = r[1 - u_j - au_{j-1}]u_j + \alpha, \quad j = 1,2,\ldots,m, \quad u_0 = u_m. \tag{1.5}$$

By *traveling waves* of system (1.5), we mean special periodic solutions that can be represented in the form

$$u_j = u(t + (j-1)\Delta), \quad j = 1,2,\ldots,m, \quad \Delta = \text{const} > 0. \tag{1.6}$$

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 on the order of unity. More precisely, we assume throughout that

$$a = \text{const} > 1, \quad \alpha = r\exp(-br), \quad r \gg 1, \quad b = \text{const} > 0. \tag{1.7}$$

It will be shown later that, under conditions (1.7), the number of coexisting periodic solutions (1.6) to system (1.5) 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.

2. GENERAL SCHEME FOR THE STUDY

To simplify the subsequent analysis, in system (1.5), we make the exponential changes of variables $u_j = \exp(x_j/\varepsilon)$, $j = 1,2,\dots,m$, where $\varepsilon = 1/r \ll 1$. As a result, in view of relations (1.7), the system becomes

$$\dot{x}_j = 1 - \exp\left(\frac{x_j}{\varepsilon}\right) - a\exp\left(\frac{x_{j-1}}{\varepsilon}\right) + \exp\left(-\frac{b + x_j}{\varepsilon}\right), \quad j = 1,2,\dots,m, \tag{2.1}$$

where $x_0 = x_m$. According to (1.6), we are interested in periodic solutions of system (2.1) that can be represented in the form

$$x_j = x(t + (j-1)\Delta, \varepsilon), \quad j = 1,2,\dots,m, \tag{2.2}$$

where $\Delta > 0$ and $x(t,\varepsilon)$ is a T-periodic solution of the auxiliary delay equation

$$\dot{x} = 1 - \exp\left(\frac{x}{\varepsilon}\right) - a\exp\left(\frac{x(t-\Delta)}{\varepsilon}\right) + \exp\left(-\frac{b + x}{\varepsilon}\right). \tag{2.3}$$

Direct verification shows that components (2.2) satisfy system (2.1) if and only if $T = m\Delta/k$, $k \in \mathbb{N}$.

Given a positive integer k, assume that Eq. (2.3) has the required periodic solution $x(t,\varepsilon)$ of period $T = m\Delta/k$. Then the stability analysis of the corresponding cycle (2.2) is reduced to analyzing the location of multipliers of the linear system

$$\dot{g}_j = A(t + (j-1)\Delta, \varepsilon)g_j + B(t + (j-1)\Delta, \varepsilon)g_{j-1}, \quad j = 1,2,\dots,m, \tag{2.4}$$

where $g_0 = g_m$ and the coefficients $A(t,\varepsilon)$ and $B(t,\varepsilon)$ are given by

$$A(t,\varepsilon) = -\frac{1}{\varepsilon}\left(\exp\left(\frac{x(t,\varepsilon)}{\varepsilon}\right) + \exp\left(-\frac{b + x(t,\varepsilon)}{\varepsilon}\right)\right), \quad B(t,\varepsilon) - \frac{a}{\varepsilon}\exp\left(\frac{x(t-\Delta,\varepsilon)}{\varepsilon}\right). \tag{2.5}$$

Along with (2.4), in what follows, we will need the auxiliary linear delay equation

$$\dot{g} = A(t,\varepsilon)g + æB(t,\varepsilon)g(t-\Delta), \tag{2.6}$$

where $g(t)$ is a scalar complex-valued function and æ is an arbitrary complex parameter. More precisely, we will be interested in its multipliers $\nu_l(æ)$, $l = 1,2,\dots$, arranged in decreasing order of moduli.

Let us explain the meaning of a multiplier as applied to Eq. (2.6). 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 $-\Delta - \sigma_0 \le t \le -\sigma_0$ with the norm

$$\|g\|_E = \max_{-\Delta-\sigma_0 \le t \le -\sigma_0} |g(t)|.$$

The *monodromy operator* of Eq. (2.6) is a bounded linear operator $V : E \to E$ acting on an arbitrary function $g_0(t) \in E$ according to the rule

$$Vg_0 = g(t + m\Delta/k, æ, \varepsilon), \quad -\Delta - \sigma_0 \le t \le -\sigma_0, \tag{2.7}$$

where $g(t,æ,\varepsilon)$ is the solution of Eq. (2.6) on the time interval $-\sigma_0 \le t \le m\Delta/k - \sigma_0$ with an initial function $g_0(t)$, $-\Delta - \sigma_0 \le t \le -\sigma_0$. Note that 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. (2.6), by analogy with ordinary differential equations, we mean the eigenvalues of operator (2.7).

To study the relation between the multipliers of system (2.4) and Eq. (2.6), the so-called *tuning method* with respect to the parameter æ was proposed in [12]. According to this method, we consider the family of equations

$$[\nu_l(æ)]^k = æ^m, \quad l \in \mathbb{N}. \tag{2.8}$$

It turns out that there is a correspondence between the nonzero roots of these equations and the multipliers of system (2.4). More precisely, the following assertion holds (see [12–14]).

Lemma 2.1. *For each multiplier* ν *of system* (2.4), *there is a positive integer* l_0 *that such*

$$\nu = \nu_{l_0}(æ_0), \tag{2.9}$$

where $æ_0$ *is a root of Eq.* (2.8) *at* $l = l_0$. *Conversely, given some* $l = l_0$, *if Eq.* (2.8) *has a nonzero root* $æ = æ_0$, *then the original system* (2.4) *has a multiplier of form* (2.9).

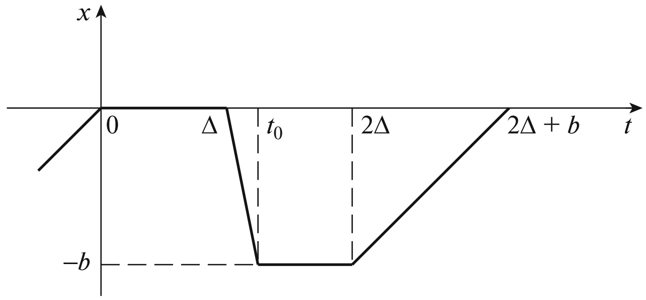

Fig. 1.

Thus, the analysis of the existence of cycles (2.2) in system (2.1) is reduced to the search for periodic solutions of the auxiliary scalar equation (2.3) with periods $T = m\Delta/k$. The stability of traveling waves is analyzed separately and, by Lemma 2.1, is reduced to the asymptotic computation of the roots of Eqs. (2.8). Below, both these issues are studied for positive integer m and k satisfying the conditions

$$m \geq 3, \quad 2 < \frac{m}{k} < a + 1. \tag{2.10}$$

3. ANALYSIS OF THE AUXILIARY NONLINEAR EQUATION

Our nearest goal is to show that, for any fixed values of the parameters a, b, Δ satisfying the inequalities

$$a > 1, \quad b > 0, \quad \Delta > \frac{b}{a-1}, \tag{3.1}$$

and for all $0 < \varepsilon \ll 1$, the auxiliary equation (2.3) has a nontrivial periodic solution.

For a formulation of corresponding result we consider periodic function

$$x_0(t) = \begin{cases} 0, \quad 0 \leq t \leq \Delta, \\ -(a-1)(t-\Delta), \quad \Delta \leq t \leq t_0, \\ -b, \quad t_0 \leq t \leq 2\Delta, \\ t - 2\Delta - b, \quad 2\Delta \leq t \leq T_0, \quad x_0(t+T_0) \equiv x_0(t), \end{cases} \tag{3.2}$$

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

Lemma 3.1. *Under conditions* (3.1), *for all sufficiently small* $\varepsilon > 0$, *Eq.* (2.3) *has a cycle* $x = x_*(t,\varepsilon)$ *of period* $T_*(\varepsilon)$ *that satisfies, as* $\varepsilon \to 0$, *the asymptotic equalities*

$$\max_{0 \leq t \leq T_*(\varepsilon)} \left| x_*(t,\varepsilon) - x_0(t) \right| = O(\varepsilon), \quad T_*(\varepsilon) = T_0 + O(\varepsilon). \tag{3.3}$$

First, we describe the general scheme for proving this lemma. Let σ_0 be a fixed constant satisfying the conditions

$$0 < \sigma_0 < \min\left(\frac{b}{2}, \frac{\Delta}{2}, \frac{b}{2(a-1)}, \frac{1}{2}\left(\Delta - \frac{b}{a-1}\right), \frac{\Delta}{a-1} \right). \tag{3.4}$$

The set $S \subset C[-\Delta - \sigma_0, -\sigma_0]$ of initial functions $\varphi(t)$ is defined as

$$S = \{\varphi(t)\colon -q_1 \leq \varphi(t) \leq -q_2 \text{ for } -\Delta - \sigma_0 \leq t \leq -\sigma_0,\ \varphi(-\sigma_0) = -\sigma_0\}, \tag{3.5}$$

where $q_1 > q_2 > 0$ are universal (independent of t, ε, φ) constants, which will be specified later. Below, we are interested in the solution $x = x_\varphi(t,\varepsilon)$, $t \geq -\sigma_0$, of Eq. (2.3) 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

$$x_\varphi(t - \sigma_0, \varepsilon) = -\sigma_0 \tag{3.6}$$

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

$$\Pi(\varphi)=x_\varphi(t+T_\varphi(\varepsilon),\varepsilon),\quad -\Delta-\sigma_0\le t\le-\sigma_0. \tag{3.7}$$

As will be shown later, with a suitable choice of the parameters q_1, q_2, operator (3.7) is defined on set (3.5) 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 Π is compact by virtue of the inequality $T_\varphi(\varepsilon)>\Delta$, the Schauder principle implies that Π has at least one fixed point $\varphi=\tilde\varphi(t,\varepsilon)$ in S. It is also clear that the solution $x_*(t,\varepsilon)=x_\varphi|_{\varphi=\tilde\varphi}$ of Eq. (2.3) is periodic with period $T_*(\varepsilon)=T_\varphi|_{\varphi=\tilde\varphi}$. This solution is the desired one, since it possesses asymptotic properties (3.3) (which will be shown later).

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. First, we consider the time interval

$$-\sigma_0\le t\le\sigma_0. \tag{3.8}$$

By virtue of the conditions imposed on σ_0 (see (3.4)), for t from interval (3.8), we have $x_\varphi(t-\Delta,\varepsilon)=\varphi(t-\Delta)$. Combining this relation with (3.5) yields

$$\exp\left(\frac{x_\varphi(t-\Delta,\varepsilon)}{\varepsilon}\right)=O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),\quad \varepsilon\to0, \tag{3.9}$$

here and below, the same letter q is used to denote different universal (independent of t, ε, φ) positive constants, whose exact values are of no matter. Assume that the following a priori estimate holds on interval (3.8):

$$b+x_\varphi(t,\varepsilon)\ge M,\quad M=\text{const}>0. \tag{3.10}$$

By analogy with the letter q in (3.9), the symbol const will denote different constants independent of t, ε, φ.

Combining relations (3.9) and (3.10), we conclude that, for t from interval (3.8), the solution $x_\varphi(t,\varepsilon)$ is determined by the Cauchy problem

$$\dot x=1-\exp\left(\frac{x}{\varepsilon}\right)+O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),\quad x|_{t=-\sigma_0}=-\sigma_0. \tag{3.11}$$

A simple analysis of (3.11) yields the asymptotic representation (uniform in $t\in[-\sigma_0,\sigma_0]$, $\varphi\in S$)

$$x=\varepsilon u_0(\tau)|_{\tau=t/\varepsilon}+O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),\quad \varepsilon\to0, \tag{3.12}$$

where $u_0(\tau)=\tau-\ln(1+\exp\tau)$. By virtue of (3.12), the a priori estimate (3.10) holds with any constant $M\in(0,b-\sigma_0)$.

At the second stage, we consider the interval

$$\sigma_0\le t\le\Delta-\sigma_0. \tag{3.13}$$

It is easy to see that, as before, $x_\varphi(t-\Delta,\varepsilon)=\varphi(t-\Delta)$ and, hence, asymptotic equality (3.9) is valid. Moreover, condition (3.10) is assumed to hold on interval (3.13). From (3.10) and (3.12), it follows that $x_\varphi(t,\varepsilon)$ can be found from a Cauchy problem similar to (3.11), namely,

$$\dot x=1-\exp\left(\frac{x}{\varepsilon}\right)+O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),\quad x|_{t=\sigma_0}=O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.14}$$

Problem (3.14) is easy to analyze: direct verification shows that the function $x\equiv0$ satisfies it up to $O(\exp(-q/\varepsilon))$ with respect to the discrepancy. From this, it is easy to conclude that, as $\varepsilon\to0$ uniformly in t from interval (3.13), $\varphi\in S$,

$$x_\varphi(t,\varepsilon)=O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.15}$$

It remains to be added that, by virtue of (3.15), the required a priori estimate (3.10) holds at this stage with any constant $M\in(0,b)$.

At the third stage, we consider t from the interval

$$\Delta - \sigma_0 \le t \le \Delta + \sigma_0. \tag{3.16}$$

In this case, by virtue of the first stage (see (3.12)), we have

$$x_\varphi(t-\Delta,\varepsilon) = \varepsilon u_0(\tau)\big|_{\tau=(t-\Delta)/\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{3.17}$$

Making the substitutions $x = \varepsilon v(\tau)$ and $\tau = (t-\Delta)/\varepsilon$ in Eq. (2.3) and taking into account relation (3.17) in its right-hand side, we assume that the a priori estimate (3.10) is valid as before. As a result, in view of (3.15), for finding the function $v = v_\varphi(\tau,\varepsilon) \overset{\text{def}}{=} (x_\varphi(t,\varepsilon)/\varepsilon)\big|_{t=\Delta+\varepsilon\tau}$, we obtain the Cauchy problem

$$\frac{dv}{d\tau} = 1 - \exp v - a\frac{\exp\tau}{1+\exp\tau} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad v\big|_{\tau=-\sigma_0/\varepsilon} = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.18}$$

First, consider the simplified equation

$$\frac{dv}{d\tau} = 1 - \exp v - a\frac{\exp\tau}{1+\exp\tau}.$$

Note that it has the solution

$$v_0(\tau) = -\ln\left\{\frac{1}{a-1}\frac{\exp\tau+1}{\exp\tau}[(\exp\tau+1)^{a-1}-1]\right\} \tag{3.19}$$

with asymptotics

$$\begin{gathered} v_0(\tau) = O(\exp\tau), \quad \tau \to -\infty, \\ v_0(\tau) = \ln(a-1) - (a-1)\tau + O(\exp(-\min(1,a-1)\tau)), \quad \tau \to +\infty. \end{gathered} \tag{3.20}$$

Setting $v_\varphi(\tau,\varepsilon) = v_0(\tau) + \omega_\varphi$ in (3.18), in the first approximation, we derive the following Cauchy linear problem for the remainder ω_φ:

$$\frac{d\omega_\varphi}{d\tau} = -\exp(v_0(\tau))\omega_\varphi + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \omega_\varphi\big|_{\tau=-\sigma_0/\varepsilon} = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.21}$$

An analysis of this problem is based on the obvious estimate

$$\max_{-\sigma_0/\varepsilon\le\tau\le\sigma_0/\varepsilon}\left|\int_{-\sigma_0/\varepsilon}^{\tau}\exp\left(-\int_s^\tau \exp(v_0(\sigma))d\sigma\right)f(s)ds\right| \le \frac{2\sigma_0}{\varepsilon}\max_{-\sigma_0/\varepsilon\le\tau\le\sigma_0/\varepsilon}|f(\tau)| \quad \forall f(\tau)\in C[-\sigma_0/\varepsilon,\sigma_0/\varepsilon]. \tag{3.22}$$

Indeed, writing the solution of problem (3.21) in explicit form and using inequality (3.22), we see that, uniformly in $\varphi \in S$,

$$\max_{-\sigma_0/\varepsilon\le\tau\le\sigma_0/\varepsilon}|\omega_\varphi| = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0.$$

Therefore, on interval (3.16), we have the asymptotic representation (uniform in t, φ)

$$x_\varphi(t,\varepsilon) = \varepsilon v_0(\tau)\big|_{\tau=(t-\Delta)/\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{3.23}$$

Note that, by virtue of (3.20) and (3.23), estimate (3.10) holds with any constant $M \in (0, b-(a-1)\sigma_0)$.

At the fourth stage, we consider the time interval

$$\Delta + \sigma_0 \le t \le t_0 - \sigma_0. \tag{3.24}$$

By virtue of (3.4), its length is positive and does not exceed the delay Δ. According to the estimate for Δ in (3.1), we have $t - \Delta \in [\sigma_0, t_0 - \Delta - \sigma_0] \subset [\sigma_0, \Delta - \sigma_0]$; therefore, it follows from (3.15) that the function $x_\varphi(t-\Delta,\varepsilon)$ is exponentially small, i.e., uniformly in t, φ,

$$x_\varphi(t-\Delta,\varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{3.25}$$

Assume also that, the following a priori conditions are valid on interval (3.24):

$$x_\varphi(t,\varepsilon) \le -M_1, \quad b + x_\varphi(t,\varepsilon) \ge M_2, \tag{3.26}$$

where $M_1, M_2 = \text{const} > 0$.

Combining the above information, we conclude that, at this stage, Eq. (2.3) becomes

$$\dot{x} = -(a-1) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right).$$

According to asymptotic representations (3.20) and (3.23), it has to be supplemented by the initial condition

$$x\big|_{t=\Delta+\sigma_0} = -(a-1)\sigma_0 + \varepsilon\ln(a-1) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right).$$

From this, we easily obtain the asymptotic equality (uniform in $t \in [\Delta+\sigma_0, t_0-\sigma_0]$, $\varphi \in S$)

$$x_\varphi(t,\varepsilon) = -(a-1)(t-\Delta) + \varepsilon\ln(a-1) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{3.27}$$

Now we check the a priori assumptions (3.26). It follows from (3.27) that the required estimates are valid with constants $M_1, M_2 \in (0,(a-1)\sigma_0)$.

At the fifth stage, we consider t from the interval

$$t_0 - \sigma_0 \le t \le t_0 + \sigma_0. \tag{3.28}$$

In this case, by virtue of (3.4), $t-\Delta \in [b/(a-1)-\sigma_0, b/(a-1)+\sigma_0] \subset [\sigma_0, \Delta-\sigma_0]$ and, according to formula (3.15), $x_\varphi(t-\Delta,\varepsilon)$ satisfies (3.25). Substituting (3.25) into the right-hand side of Eq. (2.3) and making the substitution $x = -b + \varepsilon w(\tau)$ and $\tau = (t-t_0)/\varepsilon$, we obtain the following equation for finding $w_\varphi(\tau,\varepsilon)(x_\varphi(t,\varepsilon)+b)/\varepsilon\big|_{t=t_0+\varepsilon\tau}$:

$$\frac{dw}{d\tau} = 1 - a + \exp(-w) - \exp\left(-\frac{b}{\varepsilon} + w\right) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.29}$$

According to (3.27), it has to be supplemented by the initial condition

$$w\big|_{\tau=-\sigma_0/\varepsilon} = \frac{(a-1)\sigma_0}{\varepsilon} + \ln(a-1) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.30}$$

The analysis of Cauchy problem (3.29), (3.30) is similar to that of problem (3.18). As before, from (3.29), we first pass to the simplified equation

$$dw/d\tau = 1 - a + \exp(-w),$$

which has the solution

$$w_0(\tau) = \ln\left(\frac{1}{a-1} + (a-1)\exp(-(a-1)\tau)\right) \tag{3.31}$$

with properties

$$\begin{aligned} w_0(\tau) &= \ln(a-1) - (a-1)\tau + O(\exp(a-1)\tau), \quad \tau \to -\infty,\\ w_0(\tau) &= -\ln(a-1) + O(\exp(-(a-1)\tau)), \quad \tau \to +\infty. \end{aligned} \tag{3.32}$$

Next, setting $w_\varphi(\tau,\varepsilon) = w_0(\tau) + \omega_\varphi$ in (3.29) and (3.30) and using representations (3.32), in the first approximation, we obtain a linear Cauchy problem for ω_φ similar to (3.21), namely,

$$\frac{d\omega_\varphi}{d\tau} = -\exp(-w_0(\tau))\omega_\varphi + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \omega_\varphi\big|_{\tau=-\sigma_0/\varepsilon} = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right).$$

The analysis of this problem is easy to do and is based on an estimate similar to (3.22), i.e.,

$$\max_{-\sigma_0/\varepsilon\le\tau\le\sigma_0/\varepsilon}\left|\int_{-\sigma_0/\varepsilon}^{\tau}\exp\left(-\int_s^\tau \exp(-w_0(\sigma))d\sigma\right)f(s)ds\right| \le \frac{2\sigma_0}{\varepsilon}\max_{-\sigma_0/\varepsilon\le\tau\le\sigma_0/\varepsilon}|f(\tau)| \quad \forall f(\tau) \in C[-\sigma_0/\varepsilon, \sigma_0/\varepsilon],$$

As a result, we conclude that the remainder ω_φ is exponentially small. Thus, we have the following asymptotic representation, which is uniform in t from interval (3.28) and $\varphi \in S$:

$$x_\varphi(t,\varepsilon) = -b + \varepsilon w_0(\tau)\big|_{\tau=(t-t_0)/\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{3.33}$$

At the sixth stage, we consider the time interval

$$t_0 + \sigma_0 \le t \le 2\Delta - \sigma_0. \tag{3.34}$$

In this case, $t - \Delta \in [b/(a-1) + \sigma_0, \Delta - \sigma_0] \subset [\sigma_0, \Delta - \sigma_0]$, and, hence, the asymptotic equality (3.25) holds as before. Assume that the a priori condition

$$x_\varphi(t,\varepsilon) \le -M, \quad M = \text{const} > 0, \tag{3.35}$$

is fulfilled on interval (3.34). Then it is easy to see that the solution $x_\varphi(t,\varepsilon)$ satisfies the equation

$$\dot{x} = 1 - a + \exp\left(-\frac{x+b}{\varepsilon}\right) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.36}$$

According to asymptotic representations (3.32) and (3.33), it has to be supplemented by the initial condition

$$x\big|_{t=t_0+\sigma_0} = -b - \varepsilon\ln(a-1) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.37}$$

The resulting Cauchy problem (3.36), (3.37) is similar to (3.14). Direct verification shows that, up to $O(\exp(-q/\varepsilon))$, its solution is the function $x = -b - \varepsilon\ln(a-1)$. From this, we easily derive the asymptotic representation (uniform in $t \in [t_0 + \sigma_0, 2\Delta - \sigma_0]$, $\varphi \in S$)

$$x_\varphi(t,\varepsilon) = -b - \varepsilon\ln(a-1) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{3.38}$$

It should also be noted that, by virtue of (3.38), the a priori condition (3.35) holds on interval (3.34) with any constant $M \in (0,b)$.

At the seventh stage, we consider t from the interval

$$2\Delta - \sigma_0 \le t \le 2\Delta + \sigma_0. \tag{3.39}$$

In this case, by virtue of (3.23),

$$x_\varphi(t-\Delta,\varepsilon) = \varepsilon v_0(\tau)\big|_{\tau=(t-2\Delta)/\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.40}$$

Moreover, we assume that the a priori estimate (3.35) remains valid on interval (3.39). Taking into account these relations and making the substitutions $x = -b + \varepsilon z(\tau)$ and $\tau = (t-2\Delta)/\varepsilon$ in Eq. (2.3), for the function $z_\varphi(\tau,\varepsilon) = (x_\varphi(t,\varepsilon) + b)/\varepsilon\big|_{t=2\Delta+\varepsilon\tau}$, we derive the equation

$$dz/d\tau = 1 - a\exp(v_0(\tau)) + \exp(-z) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.41}$$

According to the preceding stage (see (3.38)), it has to be supplemented with the initial condition

$$z\big|_{\tau=-\sigma_0/\varepsilon} = -\ln(a-1) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{3.42}$$

To analyze the Cauchy problem (3.41), (3.42), we need the function

$$z_0(\tau) = \ln\left(\int_{-\infty}^{\tau} \frac{K(\tau)}{K(s)}\,ds\right), \tag{3.43}$$

where

$$K(\tau) = \frac{(1+\exp\tau)^{a(a-1)}\exp\tau}{[(1+\exp\tau)^{a-1} - 1]^a}. \tag{3.44}$$

Formulas (3.43) and (3.44) imply that

$$z_0(\tau) = -\ln(a-1) + O(\exp\tau), \quad \tau \to -\infty,$$
$$z_0(\tau) = \tau + \ln c_* + O(\exp(-\min(1, a-1)\tau)), \quad c_* = \int_{-\infty}^{+\infty} \frac{ds}{K(s)}, \quad \tau \to +\infty. \tag{3.45}$$

Furthermore, it follows from (3.43)–(3.45) that $z = z_0(\tau)$ satisfies Cauchy problem (3.41), (3.42) up to $O(\exp(-q/\varepsilon))$ with respect to the discrepancy. From this, we conclude that (see similar arguments in the analysis of problems (3.18) and (3.29), (3.30))

$$x_\varphi(t,\varepsilon) = -b + \varepsilon z_0(\tau)\big|_{\tau=(t-2\Delta)/\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \tag{3.46}$$

uniformly in $t \in [2\Delta - \sigma_0, 2\Delta + \sigma_0]$, $\varphi \in S$. It is remains to note that, according to (3.45) and (3.46), the a priori estimate (3.35) is satisfied on interval (3.39) with any constant $M \in (0, b - \sigma_0)$.

Finally, at the eighth stage, we consider the time interval

$$2\Delta + \sigma_0 \le t \le 2\Delta + b - \sigma_0/2. \tag{3.47}$$

In this case, under the a priori assumptions

$$x_\varphi(t-\Delta,\varepsilon) \le -M_1, \quad x_\varphi(t,\varepsilon) \le -M_2, \quad b + x_\varphi(t,\varepsilon) \ge M_3, \tag{3.48}$$

where $M_1, M_2, M_3 = \mathrm{const} > 0$, we follow the method of steps, i.e., divide interval (3.47) into subintervals of length at most Δ, which are considered sequentially.

The first step corresponds to the time interval

$$2\Delta + \sigma_0 \le t \le \min(3\Delta + \sigma_0, 2\Delta + b - \sigma_0/2). \tag{3.49}$$

For these t, by virtue of (3.45), (3.46), and (3.48), we need to consider the Cauchy problem

$$\dot{x} = 1 + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad x\big|_{t=2\Delta+\sigma_0} = -b + \sigma_0 + \varepsilon\ln c_* + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right).$$

Thus, on interval (3.49), we have the asymptotic representation (uniform in t, φ)

$$x_\varphi(t,\varepsilon) = t - 2\Delta - b + \varepsilon\ln c_* + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{3.50}$$

At the subsequent steps, the argument is similar: by virtue of estimates (3.48), we again deal with the equation $\dot{x} = 1 + O(\exp(-q/\varepsilon))$. At the left endpoint of the interval, supplementing it with an initial condition known from the preceding step, we obtain asymptotic representation (3.50) at the current step.

Thus, under conditions (3.48), equality (3.50) will hold on the entire interval (3.47). Now let us show that conditions (3.48) are valid. Combining formula (3.50) with the asymptotic representations obtained at the fourth to seventh stages and taking into account condition (3.4) for σ_0, we see that estimates (3.48) are satisfied with constants $M_1 \in (0, (a-1)\sigma_0)$, $M_2 \in (0, \sigma_0/2)$, and $M_3 \in (0, \sigma_0)$.

Summarizing, the formulas for $x_\varphi(t,\varepsilon)$ obtained at the eight stage imply that the root $t = T_\varphi(\varepsilon)$ of Eq. (3.6) belongs to the time interval $2\Delta + 2\sigma_0 \le t \le 2\Delta + b + \sigma_0/2$, on which $x_\varphi(t - \sigma_0, \varepsilon)$ has the asymptotic representation (following from (3.50))

$$x_\varphi(t-\sigma_0,\varepsilon) = t - \sigma_0 - 2\Delta - b + \varepsilon\ln c_* + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0.$$

Combining this representation with the obvious equality $\dot{x}_\varphi(t,\varepsilon) = 1 + O(\exp(-q/\varepsilon))$, we see that the root $t = T_\varphi(\varepsilon)$ is simple and, as $\varepsilon \to 0$, has the asymptotic expansion (uniform in $\varphi \in S$)

$$T_\varphi(\varepsilon) = T_0 - \varepsilon\ln c_* + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \tag{3.51}$$

where, recall, $T_0 = 2\Delta + b$. Next, relying on the above asymptotic representations for the solution $x_\varphi(t,\varepsilon)$ (see (3.12), (3.15), (3.23), (3.27), (3.33), (3.38), (3.46), and (3.50)), we conclude that

$$\max_{-\sigma_0 \le t \le T_0 - \sigma_0/2} \left|x_\varphi(t,\varepsilon) - x_0(t)\right| = O(\varepsilon), \quad \varepsilon \to 0, \tag{3.52}$$

where $x_0(t)$ is function (3.2) and the remainder is uniform in $\varphi \in S$.

Formulas (3.51) and (3.52) imply that operator (3.7) is defined on the set S and, uniformly in φ,

$$\max_{-\Delta-\sigma_0\le t\le-\sigma_0}\left|x_\varphi(t+T_\varphi(\varepsilon),\varepsilon)-x_0(t)\right|=O(\varepsilon),\quad \varepsilon\to 0. \tag{3.53}$$

By virtue of (3.53), the required inclusion $\Pi(S)\subset S$ is satisfied for all sufficiently small $\varepsilon>0$ if

$$x_0(t)\in\widehat{S}, \tag{3.54}$$

where $\widehat{S}$ is the set of functions obtained from S by replacing the nonstrict inequalities in (3.5) by strict ones. Recall that the parameter σ_0 is assumed to satisfy constraints (3.4), which ensure that $x_0(-\sigma_0)=-\sigma_0$ and $x_0(t)<0$ for $-\Delta-\sigma_0\le t\le-\sigma_0$. Accordingly, the validity of inclusion (3.54) is achieved by using the parameters q_1, q_2, assuming that

$$q_1>-\min_{-\Delta-\sigma_0\le t\le-\sigma_0}x_0(t),\quad 0<q_2<-\max_{-\Delta-\sigma_0\le t\le-\sigma_0}x_0(t). \tag{3.55}$$

Thus, the operator Π, which is compact due to the obvious inequality $T_\varphi(\varepsilon)>\Delta$ (see (3.51)), under conditions (3.4) and (3.55) on the parameters σ_0, q_1, and q_2, transforms the closed bounded convex set S into itself. Thus, by the Schauder principle, Π has at least one fixed point $\varphi=\tilde{\varphi}(t,\varepsilon)$ in S and the corresponding solution $x_*(t,\varepsilon)=x_\varphi\big|_{\varphi=\tilde{\varphi}}$ of Eq. (2.3) is periodic with period $T_*(\varepsilon)=T_\varphi\big|_{\varphi=\tilde{\varphi}}$. The required asymptotic representations (3.3) follow formulas (3.51) and (3.52). Lemma 3.1 is proved.

4. ANALYSIS OF THE AUXILIARY LINEAR EQUATION

In this section, we study the asymptotic behavior of multipliers of a linear equation similar to (2.6), namely,

$$\dot{g}=A_*(t,\varepsilon)g+æB_*(t,\varepsilon)g(t-\Delta) \tag{4.1}$$

with coefficients given by (2.5) at $x(t,\varepsilon)=x_*(t,\varepsilon)$.

Consider the set of initial functions

$$B_0=\{g_0(t)\in E: g_0(-\sigma_0)=0,\|g_0\|\le 2\}, \tag{4.2}$$

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 $g_1(t,g_0,æ,\varepsilon)$ denote the solution of Eq. (4.1) with an arbitrary initial function $g_0(t)$ from set (4.2), and let $g_2(t,æ,\varepsilon)$ be the solution of this equation with the initial function $g_2\equiv 1$, $t\in[-\Delta-\sigma_0,-\sigma_0]$. Integrating Eq. (4.1) by the method of steps, we see that, on the interval $t\in[-\sigma_0,T_*(\varepsilon)-\sigma_0]$, the above-mentioned functions are power functions of $æ$, i.e.,

$$g_1(t,g_0,æ,\varepsilon)=\sum_{n=1}^{n_0}g_{1,n}(t,g_0,\varepsilon)æ^n,\quad g_2(t,æ,\varepsilon)=\sum_{n=0}^{n_0}g_{2,n}(t,\varepsilon)æ^n, \tag{4.3}$$

where

$$n_0=\begin{cases}T_*(\varepsilon)/\Delta & \text{if}\quad T_*(\varepsilon)/\Delta \text{ is an integer,}\\ \lfloor T_*(\varepsilon)/\Delta\rfloor+1 & \text{otherwise.}\end{cases} \tag{4.4}$$

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

$$g_{1,n}(t,g_0,\varepsilon)\equiv g_{2,n}(t,\varepsilon)\equiv 0\quad \text{for}\quad t\in[-\sigma_0,(n-1)\Delta-\sigma_0],\quad n\ge 2. \tag{4.5}$$

For an asymptotic analysis of the multipliers of Eq. (4.1), we need the following result.

Lemma 4.1. *There exists a sufficiently small* $\varepsilon_0>0$ *such that, for all* $0<\varepsilon\le\varepsilon_0$, $æ\in\Lambda_0\overset{\text{def}}{=}\{æ\in\mathbb{C}:|æ|\le 1\}$, $g_0\in B_0$ *on the interval* $-\sigma_0\le t\le T_*(\varepsilon)-\sigma_0$, *the estimates*

$$\sum_{n=0}^{n_0}\left|\frac{\partial^n g_1}{\partial æ^n}(t,g_0,æ,\varepsilon)\right|\le\exp\left(-\frac{q}{\varepsilon}\right),\quad \sum_{n=0}^{n_0}\left|\frac{\partial^n g_2}{\partial æ^n}(t,æ,\varepsilon)\right|\le M \tag{4.6}$$

hold with constants $q, M > 0$ independent of $t, \varepsilon, æ, g_0$. Moreover, as $\varepsilon \to 0$, the asymptotic representations

$$\frac{\partial^n}{\partial æ^n} g_2(T_*(\varepsilon) - \sigma_0, æ, \varepsilon) = [æ^2]^{(n)} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad n = 0, 1, \dots, n_0, \tag{4.7}$$

hold uniformly in æ (*here and below,* $[*]^{(n)}$ *denotes the nth derivative with respect to* æ).

Proof. The first inequality in (4.6) is proved by induction. For this purpose, the time interval $[-\sigma_0, T_*(\varepsilon) - \sigma_0]$ is divided into subintervals of the form $[(n-1)\Delta - \sigma_0, n\Delta - \sigma_0]$, $n = 1, 2, \dots, n_0 - 1$, and $[(n_0 - 1)\Delta - \sigma_0, T_*(\varepsilon) - \sigma_0]$, where n_0 is given by (4.4).

At the first step, i.e., for $-\sigma_0 \le t \le \Delta - \sigma_0$, the solution $g_1(t, g_0, æ, \varepsilon)$ is given by the explicit formula

$$g_1(t, g_0, æ, \varepsilon) = æ \int_{-\sigma_0}^{t} \exp\left(\int_s^t A_*(\sigma, \varepsilon) d\sigma\right) B_*(s, \varepsilon) g_0(s - \Delta) ds. \tag{4.8}$$

Furthermore, combining (4.8) with the estimates

$$\exp\left(\int_s^t A_*(\sigma, \varepsilon) d\sigma\right) \le 1 \quad \text{for} \quad t \ge s, \quad \max_{-\sigma_0 \le t \le \Delta - \sigma_0} \left|B_*(t, \varepsilon)\right| \le \exp\left(-\frac{q}{\varepsilon}\right), \tag{4.9}$$

which follow from (2.5) and the well-known properties of $x_*(t, \varepsilon)$ (see (3.3)), we see that

$$\max_{-\sigma_0 \le t \le \Delta - \sigma_0} \left(|g_1| + \left|\frac{\partial g_1}{\partial æ}\right|\right) \le \exp\left(-\frac{q}{\varepsilon}\right). \tag{4.10}$$

At the $(n-1)$th step, according to (4.3)–(4.5), the function g_1 is a polynomial in æ of degree $n - 1$. Assume that it satisfies an estimate similar to (4.10), namely,

$$\max_{(n-2)\Delta - \sigma_0 \le t \le (n-1)\Delta - \sigma_0} \sum_{k=0}^{n-1} \left|\frac{\partial^k g_1}{\partial æ^k}\right| \le \exp\left(-\frac{q}{\varepsilon}\right). \tag{4.11}$$

By analogy with (4.8), we have

$$\begin{aligned} g_1(t, g_0, æ, \varepsilon) &= g_1((n-1)\Delta - \sigma_0, g_0, æ, \varepsilon) \exp\left(\int_{(n-1)\Delta - \sigma_0}^{t} A_*(\sigma, \varepsilon) d\sigma\right) \\ &+ æ \int_{(n-1)\Delta - \sigma_0}^{t} \exp\left(\int_s^t A_*(\sigma, \varepsilon) d\sigma\right) B_*(s, \varepsilon) g_1(s - \Delta, g_0, æ, \varepsilon) ds \end{aligned} \tag{4.12}$$

on the nth interval $[(n-1)\Delta - \sigma_0,\ n\Delta - \sigma_0]$. Combining inequalities (4.9) and (4.11) with the estimate

$$\max_{\Delta - \sigma_0 \le t \le T_*(\varepsilon) - \sigma_0} \left|B_*(t, \varepsilon)\right| \le \frac{M}{\varepsilon}, \quad M = \text{const} > 0,$$

which follows from (3.3), we derive from (4.12) an estimate of form (4.11) at the nth step. Thus, after n_0 steps, we obtain the first inequality from (4.6).

The second inequality from (4.6) and formulas (4.7) are established simultaneously by means of the asymptotic integration of Eq. (4.1) with the initial condition $g \equiv 1$ on the interval $t \in [-\Delta - \sigma_0, -\sigma_0]$. The corresponding analysis is divided into the same eight stages as in the case of Eq. (2.3). Omitting the technical details, we present the results.

At the first stage, i.e., for t from interval (3.8), the coefficient $B_*(t, \varepsilon)$ is exponentially small (see (4.9)), while the coefficient $A_*(t, \varepsilon)$, in view of (2.5), (3.9), and (3.12), has the representation

$$A_*(t, \varepsilon) = -\frac{1}{\varepsilon} \frac{\exp \tau}{1 + \exp \tau}\bigg|_{\tau = t/\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right).$$

In view of these results, for the function g_2, which is a polynomial in æ of the first degree for t under consideration, we obtain the formulas (uniform in t, æ)

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = \frac{\partial^n}{\partial æ^n}\left(\frac{1}{1+\exp\tau}\bigg|_{\tau=t/\varepsilon}\right) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0, 1. \tag{4.13}$$

At the second stage, the coefficients of Eq. (4.1) have the asymptotic representations

$$A_*(t, \varepsilon) = -\frac{1}{\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad B_*(t, \varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0.$$

Combining them with (4.13), we see that, as $\varepsilon \to 0$, uniformly in $t \in [\sigma_0, \Delta - \sigma_0]$, $æ \in \Lambda_0$,

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad n = 0, 1. \tag{4.14}$$

At the third stage, for $A_*(t, \varepsilon)$ and $B_*(t, \varepsilon)$, we have

$$A_*(t, \varepsilon) = -\frac{1}{\varepsilon}\exp[v_0(\tau)|_{\tau=(t-\Delta)/\varepsilon}] + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),$$
$$B_*(t, \varepsilon) = -\frac{a}{\varepsilon}\frac{\exp\tau}{1+\exp\tau}\bigg|_{\tau=(t-\Delta)/\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0,$$

where $v_0(\tau)$ is function (3.19) and, by virtue of (4.13), $g_2(t-\Delta, æ, \varepsilon)$ satisfies

$$\frac{\partial^n}{\partial æ^n} g_2(t-\Delta, æ, \varepsilon) = \frac{\partial^n}{\partial æ^n}\left(\frac{1}{1+\exp\tau}\bigg|_{\tau=(t-\Delta)/\varepsilon}\right) + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0, 1.$$

These formulas imply that the function g_2, which is now a second-degree polynomial in æ, satisfies the asymptotic representations (uniform in $t \in [\Delta - \sigma_0, \Delta + \sigma_0]$, $æ \in \Lambda_0$)

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = \frac{\partial^n}{\partial æ^n}[æ v_0'(\tau)|_{\tau=(t-\Delta)/\varepsilon}] + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0, 1, 2, \tag{4.15}$$

where the prime denotes differentiation with respect to τ.

At the fourth stage, the coefficients of Eq. (4.1) become

$$A_*(t, \varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad B_*(t, \varepsilon) = -\frac{a}{\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0,$$

while $g_2(t-\Delta, æ, \varepsilon)$, according to (4.14), satisfies the equation

$$\frac{\partial^n}{\partial æ^n} g_2(t-\Delta, æ, \varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0, 1. \tag{4.16}$$

Taking into account these results, we see that, uniformly in $t \in [\Delta + \sigma_0, t_0 - \sigma_0]$, $æ \in \Lambda_0$,

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = [-æ(a-1)]^{(n)} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0, 1, 2. \tag{4.17}$$

At the fifth stage, we consider t from interval (3.28). In this case,

$$A_*(t, \varepsilon) = -\frac{1}{\varepsilon}\exp[-w_0(\tau)|_{\tau=(t-t_0)/\varepsilon}] + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),$$
$$B_*(t, \varepsilon) = -\frac{a}{\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0,$$

where $w_0(\tau)$ is function (3.31). Moreover, by virtue of (4.14), formulas (4.16) hold for $g_2(t-\Delta, æ, \varepsilon)$ as before. Combining them with (4.17), we conclude that, uniformly in $t \in [t_0 - \sigma_0,\ t_0 + \sigma_0]$, $æ \in \Lambda_0$,

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = \frac{\partial^n}{\partial æ^n}[æ w_0'(\tau)|_{\tau=(t-t_0)/\varepsilon}] + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0, 1, 2. \tag{4.18}$$

The sixth stage is related to time interval (3.34), on which

$$A_*(t,\varepsilon) = -\frac{a-1}{\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad B_*(t,\varepsilon) = -\frac{a}{\varepsilon} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0,$$

and formulas (4.16) are again valid. Combining these relations with asymptotic representations (4.18), we conclude that, as $\varepsilon \to 0$, uniformly in $t \in [t_0 + \sigma_0, 2\Delta - \sigma_0]$, $æ \in \Lambda_0$,

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad n = 0,1,2. \tag{4.19}$$

The seventh stage, at which we deal with time interval (3.39), is the most complicated. Here, as $\varepsilon \to 0$, the coefficients (2.5) have the representations

$$A_*(t,\varepsilon) = -\frac{1}{\varepsilon}\exp[-z_0(\tau)|_{\tau=(t-2\Delta)/\varepsilon}] + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),$$
$$B_*(t,\varepsilon) = -\frac{a}{\varepsilon}\exp[v_0(\tau)|_{\tau=(t-2\Delta)/\varepsilon}] + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right),$$

where $z_0(\tau)$ is function (3.43) and $g_2(t-\Delta, æ, \varepsilon)$ is given by formulas (4.15) (in which t is replaced by $t-\Delta$). Combining these results with equalities (4.19) from the preceding stage, we conclude that, first, for t under consideration, the function g_2 is a third-degree polynomial in æ and, second, uniformly in t,

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = \frac{\partial^n}{\partial æ^n}[æ^2 z_0'(\tau)|_{\tau=(t-2\Delta)/\varepsilon}] + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0,1,2,3. \tag{4.20}$$

Finally, at the eighth stage, we consider time interval (3.47). In this case, the coefficients $A_*(t,\varepsilon)$ and $B_*(t,\varepsilon)$ are exponentially small and g_2 is a polynomial in æ of degree at most n_0 (see (4.4)). Based on these results and relations (4.20), we obtain the asymptotic representations (uniform in t, æ)

$$\frac{\partial^n}{\partial æ^n} g_2(t, æ, \varepsilon) = [æ^2]^{(n)} + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \quad n = 0,1,\ldots,n_0. \tag{4.21}$$

It remains to be noted that the second estimate in (4.6) and equalities (4.7) follow automatically from formulas (4.13)–(4.15) and (4.17)–(4.21). Lemma 4.1 is proved.

Now we pass to the asymptotic computation of the multipliers of Eq. (4.1). For this purpose, we consider the monodromy operator $V_*(æ,\varepsilon)$ of this equation acting on the space E according to the rule (similar to (2.7))

$$V_*(æ,\varepsilon)g_0 = g(t + T_*(\varepsilon), æ, \varepsilon), \quad -\Delta - \sigma_0 \le t \le -\sigma_0, \tag{4.22}$$

where $g(t, æ, \varepsilon)$, $-\sigma_0 \le t \le T_*(\varepsilon) - \sigma_0$, is the solution of Eq. (4.1) with an initial function $g_0(t) \in E$. Let $\nu_s(æ,\varepsilon)$, $s \in \mathbb{N}$, denote the eigenvalues of operator (4.22) arranged in decreasing order of moduli. The following assertion holds.

Lemma 4.2. *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* $0 < \varepsilon \le \varepsilon_0$, $æ \in \Lambda_{\delta,R} \stackrel{\text{def}}{=} \{æ \in \mathbb{C} : \exp(-\delta/\varepsilon) \le |æ| \le R\}$,

$$\sup_{s\ge 2}|\nu_s(æ,\varepsilon)| \le \exp\left(-\frac{q}{\varepsilon}\right). \tag{4.23}$$

The multiplier $\nu_1(æ,\varepsilon)$ *is simple, depends analytically on* $æ \in \Lambda_{\delta,R}$, *and, as* $\varepsilon \to 0$, *has the* æ *asymptotic representations* (*uniform in* æ)

$$\nu_1(æ,\varepsilon) = æ^2 + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \frac{\partial \nu_1}{\partial æ}(æ,\varepsilon) = 2æ + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right). \tag{4.24}$$

Proof. We fix an arbitrary $R > 0$ and assume that the parameter æ from (4.1) belongs to the set $\Lambda_{\delta,R}$ for some $\delta > 0$ (δ will be specified later). Assuming that $\|g_0\| \le 1$, operator (4.22) can be represented in the form

$$V_*(æ,\varepsilon)g_0 = g_1(t + T_*(\varepsilon), \tilde{g}_0, æ, \varepsilon) + g_0(-\sigma_0)g_2(t + T_*(\varepsilon), æ, \varepsilon), \quad -\Delta - \sigma_0 \le t \le -\sigma_0, \tag{4.25}$$

where $\tilde{g}_0(t) = g_0(t) - g_0(-\sigma_0) \in B_0$ (see (4.2)) and g_1, g_2 are the above-investigated solutions of Eq. (4.1). Representation (4.25) implies that $V_*(æ,\varepsilon) = V_1(æ,n) + V_2(æ,\varepsilon)$, where the operators V_1, V_2 are given by

$$V_1(æ,\varepsilon)g_0 = g_1(t + T_*(\varepsilon), \tilde{g}_0, æ, \varepsilon), \quad V_2(æ,\varepsilon)g_0 = g_0(-\sigma_0)g_2(t + T_*(\varepsilon), æ, \varepsilon) \tag{4.26}$$

and, by virtue of (4.6), satisfy the estimates

$$\begin{gathered} \|V_1(æ,\varepsilon)\|_{E\to E} + \left\|\frac{\partial V_1}{\partial æ}(æ,\varepsilon)\right\|_{E\to E} \le \exp\left(-\frac{q}{\varepsilon}\right), \\ \|V_2(æ,\varepsilon)\|_{E\to E} + \left\|\frac{\partial V_2}{\partial æ}(æ,\varepsilon)\right\|_{E\to E} \le M, \quad M = \text{const} > 0. \end{gathered} \tag{4.27}$$

At the next stage, we examine the spectral properties of $V_2(æ,\varepsilon)$. According to the second equality in (4.26), this operator is finite-dimensional and its spectrum consists of two points: the simple eigenvalue $\nu = \nu_*(æ,\varepsilon)$, where $\nu_*(æ,\varepsilon) = g_2(T_*(\varepsilon) - \sigma_0, æ, \varepsilon)$, and the eigenvalue $\nu = 0$ of infinite multiplicity. It follows from (4.7) that the eigenvalue $\nu_*(æ,\varepsilon)$ has the asymptotic representations (uniform in $æ \in \Lambda_{\delta,R}$)

$$\nu_*(æ,\varepsilon) = æ^2 + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \frac{\partial \nu_*}{\partial æ}(æ,\varepsilon) = 2æ + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{4.28}$$

Returning to the original operator $V_*(æ,\varepsilon)$, we note that, by virtue of the relations

$$V_* = V_1 + V_2, \quad (\nu I - V_*)^{-1} = (I - (\nu I - V_2)^{-1}V_1)^{-1}(\nu I - V_2)^{-1},$$

where I is the identity operator, any value $\nu \in \mathbb{C}$ satisfying

$$\left\|(\nu I - V_2(æ,\varepsilon))^{-1}V_1(æ,\varepsilon)\right\|_{E\to E} < 1, \tag{4.29}$$

belongs to the resolvent set of $V_*(æ,\varepsilon)$. Recall that the operator V_1 satisfies the first estimate in (4.27). For the operator $(\nu I - V_2)^{-1}$, using its explicit form

$$(\nu I - V_2)^{-1}g_0 = \frac{g_0(t)}{\nu} + \frac{g_0(-\sigma_0)}{\nu(\nu - \nu_*(æ,\varepsilon))}g_2(t + T_*(\varepsilon), æ, \varepsilon), \quad -\Delta - \sigma_0 \le t \le -\sigma_0,$$

and the second estimate from (4.6), we obtain the inequality

$$\left\|(\nu I - V_2(æ,\varepsilon))^{-1}\right\|_{E\to E} \le \frac{M(1 + |\nu|)}{|\nu| \cdot |\nu - \nu_*(æ,\varepsilon)|} \quad \forall \nu \in \mathbb{C}, \quad \nu \ne 0, \nu_*(æ,\varepsilon), \tag{4.30}$$

where $M = \text{const} > 0$.

At the final stage of the proof of Lemma 4.2, combining estimates (4.27) and (4.30) with asymptotic representations (4.28), we see that condition (4.29) is satisfied for any $æ \in \Lambda_{\delta,R}$, $\nu \in \mathbb{C}\backslash\{O_1 \cup O_2\}$, where

$$O_1 = \{\nu : |\nu| < \exp(-\delta_1/\varepsilon)\}, \quad O_2 = \{\nu : |\nu - \nu_*(æ,\varepsilon)| < \exp(-\delta_2/\varepsilon)\}, \tag{4.31}$$

and $\delta, \delta_1, \delta_2 > 0$ by are suitably small constants. Thus, the spectrum of operator (4.22) belongs to balls (4.31), which implies inequality (4.23).

Relations (4.24) are proved as follows. When the operator $V_2(,\varepsilon)$ is perturbed by an addition $V_1(æ,\varepsilon)$ of order $O(\exp(-q/\varepsilon))$ that is analytic in æ, the eigenvalue $\nu = \nu_*(æ,\varepsilon)$ passes into a simple eigenvalue $\nu = \nu_1(æ,\varepsilon)$ depending analytically on $æ \in \Lambda_{\delta,R}$; moreover,

$$\nu_1(æ,\varepsilon) - \nu_*(æ,\varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0 \tag{4.32}$$

(in the C^1 metric with respect to æ). Combining (4.28) with (4.32), we conclude that, for $æ \in \Lambda_{\delta,R}$, the multiplier $\nu_1(æ,\varepsilon)$ has all the required properties. Lemma 4.2 is proved.

5. FINAL RESULTS

Recall that the analysis of the existence of traveling waves (2.2) for system (2.1) is reduced to the search for periodic solutions of the auxiliary equation (2.3) 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. (2.3) provided by Lemma 3.1 and its period are denoted by $x_*(t,\varepsilon,\Delta)$ and $T_*(\varepsilon,\Delta)$, respectively, in order to emphasize that these functions depend on Δ.

Let m and k be fixed positive integers related by inequalities (2.10). These inequalities imply that the quantity $\widehat{\Delta}_{(k)} = b/(m/k - 2)$ satisfies the condition $\widehat{\Delta}_{(k)} > b/(a-1)$. In what follows, we assume that the parameter Δ in (2.3) ranges over some interval $K \subset (b/(a-1), +\infty)$ for which $\Delta = \widehat{\Delta}_{(k)}(\varepsilon)$ is an interior point. Then, according to (3.51), we have the asymptotic representation (uniform in $\Delta \in K$)

$$T_*(\varepsilon,\Delta) = 2\Delta + b + O(\varepsilon), \quad \varepsilon \to 0. \tag{5.1}$$

In view of formula (5.1), it is easy to see that the equation

$$T_*(\varepsilon,\Delta) = \frac{m}{k}\Delta \tag{5.2}$$

has at least one root $\Delta = \widehat{\Delta}_{(k)}(\varepsilon)$ such that

$$\widehat{\Delta}_{(k)}(\varepsilon) = \widehat{\Delta}_{(k)} + O(\varepsilon), \quad \varepsilon \to 0. \tag{5.3}$$

Therefore, the following assertion holds.

Theorem 5.1. *Let* $a > 1$, $b > 0$, *and* m, k *be positive integers related by inequalities* (2.10). *Then there is a sufficiently small* $\varepsilon_0 > 0$ *such that, for all* $0 < \varepsilon \le \varepsilon_0$, *system* (2.1) *has a cycle* (*traveling wave*)

$$C_k: \quad x_j = \widehat{\Delta}_{(k)}(t + (j-1)\widehat{\Delta}_{(k)}(\varepsilon), \varepsilon), \quad j = 1, 2, \dots, m, \tag{5.4}$$

where $\widehat{\Delta}_{(k)}(t,\varepsilon) = x_*(t,\varepsilon,\Delta)\Big|_{\Delta=\widehat{\Delta}_{(k)}(\varepsilon)}$ *and* $\widehat{\Delta}_{(k)}(\varepsilon)$ *is root* (5.3) *of Eq.* (5.2).

Let us analyze the stability of cycle (5.4).

Theorem 5.2. *Cycle* (5.4) *is exponentially orbitally stable if* $k = (m-1)/2$ *and quasi-stable otherwise*.

Proof sketch. For cycle (5.4), we consider a variational system similar to (2.4), namely,

$$\dot{g}_j = \widehat{A}_*(t + (j-1)\Delta, \varepsilon)g_j + \widehat{B}_*(t + (j-1)\Delta, \varepsilon)g_{j-1}, \quad j = 1, 2, \dots, m, \quad g_0 = g_m, \tag{5.5}$$

where $\Delta = \widehat{\Delta}_{(k)}(\varepsilon)$ and $\widehat{A}_*(t,\varepsilon)$, $\widehat{B}_*(t,\varepsilon)$ are coefficients (2.5) with $x(t,\varepsilon) = \hat{x}_{(k)}(t,\varepsilon)$ and $\Delta = \widehat{\Delta}_{(k)}(\varepsilon)$. Let $V(\varepsilon)$ 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 (5.4) can be determined via the asymptotic computation of the spectrum of $V(\varepsilon)$. The corresponding analysis is based on Lemma 2.1, according to which any eigenvalue ν of this operator is given by the equality $\nu = \hat{\nu}_{l_0}(æ_0, \varepsilon)$, where $\hat{\nu}_l(æ,\varepsilon)$, $l \ge 1$, are the multipliers of the auxiliary equation (4.1) for $\Delta = \widehat{\Delta}_{(k)}(\varepsilon)$ and $æ_0$ is a nonzero root of the equation

$$[\hat{\nu}_l(æ,\varepsilon)]^k = æ^m, \quad l \in \mathbb{N}, \tag{5.6}$$

for $l = l_0$. Thus, the proof of Theorem 5.2 is reduced to analyzing the location of the roots of Eqs. (5.6).

First, we determine the values of æ for which it Eqs. (5.6) make sense. Specifically, we show that these equations have no roots in the set

$$\{æ \in \mathbb{C} : |æ| > R\} \tag{5.7}$$

for sufficiently large fixed $R > 0$. For this purpose, we need the following result.

Lemma 5.1. *It is true that*

$$\|\mathcal{V}(\varepsilon)\|_{\mathbb{R}^m \to \mathbb{R}^m} \le \frac{M}{\varepsilon^{n_0(m-1)}}, \quad M = \mathrm{const} > 0, \tag{5.8}$$

where n_0 is a positive integer given by the equality (*similar to* (4.4))

$$n_0 = \begin{cases} m/k, & \text{if } m/k \text{ is an integer}, \\ \lfloor m/k \rfloor + 1 & \text{otherwise.} \end{cases} \tag{5.9}$$

Proof. To prove inequality (5.8), the original time interval $-\sigma_0 \le t \le m\Delta/k - \sigma_0$ is divided into the subintervals

$$[(n-1)\Delta - \sigma_0, n\Delta - \sigma_0], \quad n = 1, 2, \dots, n_0 - 1, \quad [(n_0 - 1)\Delta - \sigma_0, m\Delta/k - \sigma_0],$$

where n_0 is given by (5.9). Consider the resulting intervals sequentially.

Fix an arbitrary initial vector $g_0 = (g_{1,0}, g_{2,0}, \dots, g_{m,0}) \in \mathbb{R}^m$ with $\|g_0\|_{\mathbb{R}^m} = 1$ (here, $\|*\|_{\mathbb{R}^m}$ is the Euclidean norm) and denote by

$$g(t,\varepsilon) = (g_1(t,\varepsilon), g_2(t,\varepsilon), \dots, g_m(t,\varepsilon)), \quad -\sigma_0 \le t \le m\Delta/k - \sigma_0, \tag{5.10}$$

the solution of system (5.5) with the initial condition $g|_{t=-\sigma_0} = g_0$. The components $g_j(t,\varepsilon)$, $j = 1, 2, \dots, m$, of solution (5.10) will be estimated using the formulas

$$\begin{gathered} g_j(t,\varepsilon) = g_j(t_0,\varepsilon)\exp\left(\int_{t_0}^{t} \widehat{A}_*(s + (j-1)\Delta, \varepsilon)ds\right) + \int_{t_0}^{t} \exp\left(\int_{s}^{t} \widehat{A}_*(\sigma + (j-1)\Delta, \varepsilon)d\sigma\right) \\ \times \widehat{B}_*(s + (j-1)\Delta, \varepsilon) g_{j-1}(s,\varepsilon)ds, \quad j = 1, 2, \dots, m \end{gathered} \tag{5.11}$$

and the following properties of the coefficients of system (5.5):

$$\begin{gathered} \exp\left(\int_{s}^{t} \widehat{A}_*(\sigma + (j-1)\Delta, \varepsilon)d\sigma\right) \le 1 \quad \text{for} \quad t \ge s, \quad \max_{-\sigma_0 \le t \le m\Delta/k - \sigma_0} \left|\widehat{B}_*(t,\varepsilon)\right| \le \frac{M}{\varepsilon}, \\ \max_{-\sigma_0 \le t \le \Delta - \sigma_0} \left|\widehat{B}_*(t,\varepsilon)\right| \le \exp\left(-\frac{q}{\varepsilon}\right), \quad M = \text{const} > 0. \end{gathered} \tag{5.12}$$

First, we consider the interval $-\sigma_0 \le t \le \Delta - \sigma_0$. Applying formula (5.11) at $t_0 = -\sigma_0$ and estimate (5.12), for the indicated t, we obtain a series of inequalities of the form

$$\max_t |g_j(t,\varepsilon)| \le \frac{M_{j,1}}{\varepsilon^{j-1}} + \frac{M_{j,2}}{\varepsilon^{j-1}} \exp\left(-\frac{q}{\varepsilon}\right) \max_t |g_m(t,\varepsilon)|, \quad j = 1, 2, \dots, m, \tag{5.13}$$

where $M_{j,1}$, $M_{j,2} = \text{const} > 0$ for $j = 1, 2, \dots, m$. In turn, it follows from (5.13) that

$$\max_{-\sigma_0 \le t \le \Delta - \sigma_0} |g_j(t,\varepsilon)| \le \frac{M}{\varepsilon^{j-1}}, \quad j = 1, 2, \dots, m, \quad M = \text{const} > 0. \tag{5.14}$$

At the next stage, we consider the interval $\Delta - \sigma_0 \le t \le 2\Delta - \sigma_0$. According to the equality $m\Delta = kT$, where T is the period of the function $\hat{x}_{(k)}(t,\varepsilon)$, we have $\widehat{B}_*(t + (m-1)\Delta, \varepsilon) = \widehat{B}_*(t - \Delta, \varepsilon)$. Since $t - \Delta \in [-\sigma_0, \Delta - \sigma_0]$, it follows from (5.12) that

$$\widehat{B}_*(t + (m-1)\Delta, \varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0. \tag{5.15}$$

The subsequent argument is standard: writing formulas (5.11) for the initial time $t_0 = \Delta - \sigma_0$ and combining (5.14) with properties (5.12) and (5.15), we obtain estimates similar to (5.13), namely,

$$\begin{gathered} \max_t |g_j(t,\varepsilon)| \le \frac{M_{j,1}}{\varepsilon^{j-1}} + \frac{M_{j,2}}{\varepsilon^{j}} \max_t |g_m(t,\varepsilon)|, \quad j = 1, 2, \dots, m-1, \\ \max_t |g_m(t,\varepsilon)| \le \frac{M_{m,1}}{\varepsilon^{m-1}} + \frac{M_{m,2}}{\varepsilon^{m-1}} \exp\left(-\frac{q}{\varepsilon}\right) \max_t |g_m(t,\varepsilon)|, \end{gathered} \tag{5.16}$$

where $M_{j,1}, M_{j,2} = \text{const} > 0,\ j = 1,2,\dots,m$. From these relations, it is easy to derive that

$$\begin{aligned} &\max_{\Delta-\sigma_0\le t\le 2\Delta-\sigma_0} |g_j(t,\varepsilon)| \le \frac{M}{\varepsilon^{m+j-1}}, \quad j = 1,2,\dots,m-1, \\ &\max_{\Delta-\sigma_0\le t\le 2\Delta-\sigma_0} |g_m(t,\varepsilon)| \le \frac{M}{\varepsilon^{m-1}}, \quad M = \text{const} > 0. \end{aligned} \tag{5.17}$$

Assume that, at the $(n-1)$th step, i.e., for t from the time interval $(n-2)\Delta - \sigma_0 \le t \le (n-1)\Delta - \sigma_0$, $n \ge 2$, we have a series of estimates similar to (5.17), namely,

$$\begin{aligned} &\max_t |g_j(t,\varepsilon)| \le \frac{M}{\varepsilon^{(n-2)m+j-1}}, \quad j = 1,2,\dots,m-(n-2), \\ &\max_t |g_{m-j}(t,\varepsilon)| \le \frac{M}{\varepsilon^{(n-2)(m-1)+n-3-j}}, \quad j = 0,1,\dots,n-3, \end{aligned} \tag{5.18}$$

where $M = \text{const} > 0$. Let us show that estimates (5.18) with n replaced by $n+1$ then hold on the interval $(n-1)\Delta - \sigma_0 \le t \le n\Delta - \sigma_0$.

A characteristic feature of the nth step is that

$$\widehat{B}_*(t + (m-n+1)\Delta, \varepsilon) = O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \varepsilon \to 0, \tag{5.19}$$

whose validity can be shown in the same way as in the case $n = 2$ (see (5.15)). Combining relation (5.19) with formulas (5.11) at $t_0 = (n-1)\Delta - \sigma_0$ and properties (5.12), we derive estimates similar to (5.16):

$$\begin{gathered} \max_t |g_j(t,\varepsilon)| \le \frac{M_{j,1}}{\varepsilon^{(n-2)m+j-1}} + \frac{M_{j,2}}{\varepsilon^{j}} \max_t |g_m(t,\varepsilon)|, \quad j = 1,2,\dots,m-(n-1), \\ \max_t |g_{m-j}(t,\varepsilon)| \le \frac{M_{j,3}}{\varepsilon^{(n-1)(m-1)+n-2-j}} + \frac{M_{j,4}}{\varepsilon^{m-j-1}} \exp\left(-\frac{q}{\varepsilon}\right) \max_t |g_m(t,\varepsilon)|, \\ j = 0,1,\dots,n-2, \end{gathered}$$

where $M_{j,s} = \text{const} > 0,\ s = 1,2,3,4$. These inequalities, in turn, yield the required estimates

$$\begin{aligned} &\max_t |g_j(t,\varepsilon)| \le \frac{M}{\varepsilon^{(n-1)m+j-1}}, \quad j = 1,2,\dots,m-(n-1), \\ &\max_t |g_{m-j}(t,\varepsilon)| \le \frac{M}{\varepsilon^{(n-1)(m-1)+n-2-j}}, \quad j = 0,1,\dots,n-2, \quad M = \text{const} > 0, \end{aligned} \tag{5.20}$$

on the interval $(n-1)\Delta - \sigma_0 \le t \le n\Delta - \sigma_0$.

Summarizing, we note that the entire collection of inequalities (5.20) for $n = 1,2,\dots,n_0$ implies that

$$\|\mathcal{V}(\varepsilon)\|_{\mathbb{R}^m\to\mathbb{R}^m} \le M/\varepsilon^{\alpha},$$

where $\alpha = \max(n_0(m-1), (n_0-1)(m-1) + n_0 - 2) = n_0(m-1)$. Lemma 5.1 is proved.

The values of the parameter æ can be tentatively localized by applying this lemma. Specifically, combining estimate (5.8) with relations (2.8) and (2.9), which hold for any multiplier ν of system (5.5), we conclude that

$$|\nu| = |\hat{\nu}_{l_0}(æ_0,\varepsilon)| = |æ_0|^{m/k} \le \|\mathcal{V}(\varepsilon)\|_{\mathbb{R}^m\to\mathbb{R}^m} \le M/\varepsilon^{n_0(m-1)}.$$

Thus, all possible roots $æ_0$ of Eqs. (5.6) lies to the disk

$$\left\{ æ \in \mathbb{C} : |æ| \le \frac{M^{k/m}}{\varepsilon^{\alpha_0}} \right\}, \tag{5.21}$$

where $\alpha_0 = n_0(m-1)k/m$ and M is the constant from (5.8).

To reduce the set (5.21) of admissible values of æ, we consider the operator $\widehat{V}_*(æ,\varepsilon)$ obtained from (4.22) at $\Delta = \widehat{\Delta}_{(k)}(\varepsilon)$. Note that relations (4.3)–(4.5), (4.25), estimates (4.6), and formulas (4.13)–(4.15) and (4.17)–(4.21) imply the representation

$$\widehat{V}_*(æ,\varepsilon) = \sum_{n=0}^{n_0} \widehat{V}_{*,n}(\varepsilon)æ^n, \tag{5.22}$$

where $\widehat{V}_{*,n}(\varepsilon) : E \to E$ are bounded linear operators satisfying the estimates

$$\begin{gathered}\left\|\widehat{V}_{*,n}(\varepsilon)\right\|_{E\to E} \le M_n, \quad M_n = \text{const} > 0, \quad n = 0,1,2,\\ \left\|\widehat{V}_{*,n}(\varepsilon)\right\|_{E\to E} \le \exp\left(-\frac{q}{\varepsilon}\right), \quad n = 3,\dots,n_0.\end{gathered} \tag{5.23}$$

It follows from (5.22) and (5.23) that

$$\sup_{l\ge1}\left|\hat{\nu}_l(æ,\varepsilon)\right| \le \sum_{n=0}^{n_0}|æ|^n \left\|\widehat{V}_{*,n}(\varepsilon)\right\|_{E\to E} \le M_0 + M_1|æ| + M_2|æ|^2 + \exp\left(-\frac{q}{\varepsilon}\right)\sum_{n=3}^{n_0}|æ|^n. \tag{5.24}$$

Finally, it should be noted that the inequality

$$M_0 + M_1|æ| + M_2|æ|^2 + \exp\left(-\frac{q}{\varepsilon}\right)\sum_{n=3}^{n_0}|æ|^n < |æ|^{m/k} \tag{5.25}$$

holds on the subset $\{æ \in \mathbb{C} : R \le |æ| \le M^{k/m}/\varepsilon^{\alpha_0}\}$ of set (5.21) for sufficiently large fixed $R > 0$ by virtue of the condition $m/k > 2$ (see (2.10)).

Estimates (5.24) and (5.25) imply that, with a suitable choice of $R > 0$, Eqs. (5.6) have no roots in set (5.7). In what follows, we assume that the constant R is suitably chosen.

The above analysis implies that the consideration of Eqs. (5.6) can be restricted to the values of æ from the set $\Lambda_{\delta,R}$, where the constant δ is determined by R according to Lemma 4.2 at $\Delta = \hat{\Delta}_{(k)}(\varepsilon)$. Note also that, by virtue of (4.24), Eq. (5.6) with $l = 1$ has exactly $m - 2k$ simple roots in the indicated set. These roots include the unit one, since, for $æ = 1$ and $\Delta = \hat{\Delta}_{(k)}(\varepsilon)$, Eq. (4.1) is the linearization of Eq. (2.3) around the cycle $x = \hat{x}_{(k)}(t,\varepsilon)$ and, hence, admits a unit multiplier. The other $m - 2k - 1$ roots of the equation have, as $\varepsilon \to 0$, the asymptotic representation

$$æ_s = \theta_s + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad \theta_s = \exp\left(i\frac{2\pi s}{m-2k}\right), \quad s = 1,2,\dots,m-2k-1. \tag{5.26}$$

Summarizing, we note that all multipliers $\nu \in \mathbb{C}$ of cycle (5.4), except for the simple unit one, are divided into two groups. Indeed, according to (2.8), (2.9), (4.24), and (5.26), 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

$$\nu_s = \theta_s^2 + O\left(\exp\left(-\frac{q}{\varepsilon}\right)\right), \quad s = 1,2,\dots,m-2k-1. \tag{5.27}$$

The other $2k$ multipliers correspond to the roots of Eqs. (5.6) lying in the disk $\{æ \in \mathbb{C} : |æ| \le \exp(-\delta_0/\varepsilon)\}$, where $\delta_0 = \text{const} > 0$. Moreover, since $\nu = æ^{m/k}$, 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 (5.27) is empty; therefore, cycle (5.4) is exponentially orbitally stable. In the case $k \ne (m-1)/2$, 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 (2.10) increases indefinitely. From this and Theorems 5.1 and 5.2, it follows that the number of coexisting traveling waves (5.4) 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 accu-

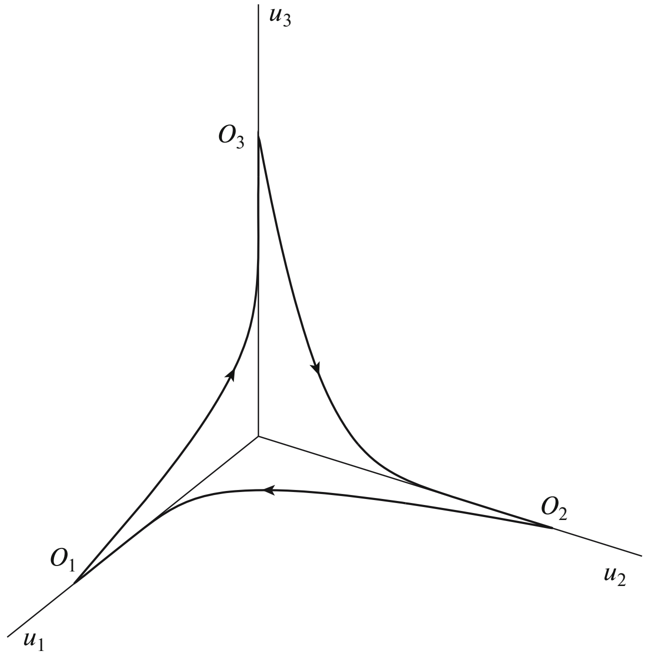

Fig. 2.

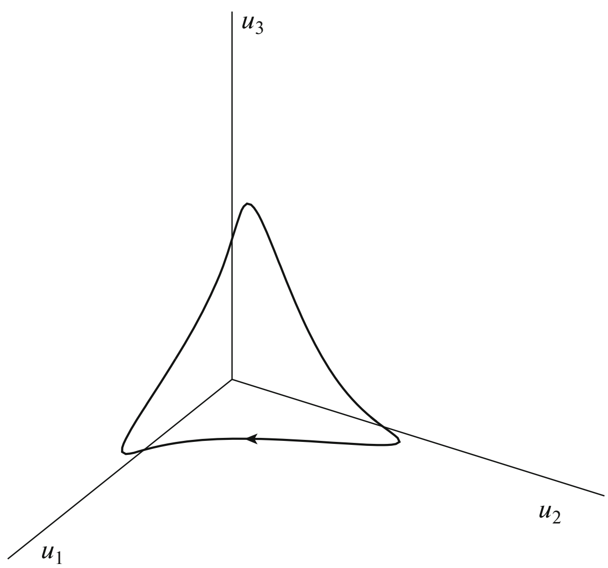

Fig. 3.

mulation 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 (1.5). Note that, in contrast to system (1.1), the leakiness of the promoter cannot be neglected in this case, i.e., we cannot set $\alpha = 0$. The causes of this are clear even for $m = 3$. Indeed, in the three-dimensional case, for $a > 2$ and $\alpha = 0$, system (1.5) 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

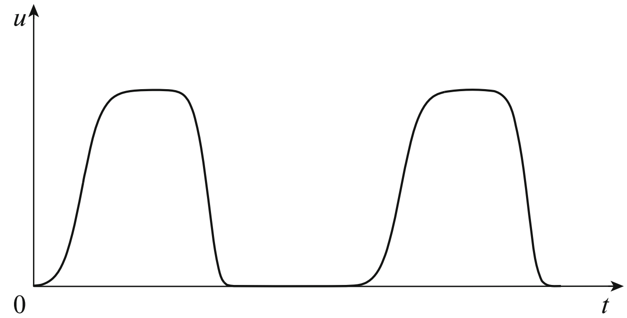

Fig. 4.

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. When the promoter leakiness is taken into account, i.e., for $\alpha > 0$, the stable homoclinic triangle passes 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 $m = 3$, $r = 1$, $a = 10$, and $\alpha = 0.01$, the above cycle has the form shown in Fig. 3.

Thus, the case of (1.7) corresponds to the limit of applicability of model (1.5). That is why it exhibits a quasi-buffer phenomenon. Due to this phenomenon, under conditions (1.7), the phase point of system (1.5) can stay in a neighborhood of the quasi-stable cycle (1.6) 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.

Note that quasi-stable regimes are biologically implementable for two reasons. First, although the time of their existence is finite, it can be comparable with the lifetime of the system. Second, from a biological point of view, it is the small values of α that are of greatest interest.

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 (1.5) is a traveling-wave cycle, which is the continuation of cycle (5.4) with respect to the parameter α for $k = (m-1)/2$. For $m = 9$, $r = 1$, $a = 10$, and $\alpha = 0.01$, the component $u = u_1(t)$ of this cycle in the (t, u) plane is plotted on a 1 : 20 scale in Fig. 4. In the case $m = 2m_0$, where $m_0 \geq 1$, system (1.5) represents a genetic trigger [15]: for $a > 1$ and $\tilde{\alpha} < (a-1)/4$, where $\tilde{\alpha} = \alpha/r$, it admits two stable equilibria

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

with components

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

To conclude, we add that similar dynamics is observed in the multidimensional case of system (1.2), i.e., for the model

$$\dot{u}_j = -u_j + \frac{\alpha}{1 + u_{j-1}^{\gamma}}, \quad j = 1, 2, \dots, m, \quad u_0 = u_m.$$

Specifically, this model has a unique stable cycle of form (1.6) for odd m (with a suitable choice of the parameters α, γ) and is a genetic trigger for even m.

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REFERENCES

1. M. B. Elowitz and S. Leibler, "A synthetic oscillatory network of transcriptional regulators," Nature **403**, 335–338 (2000).
2. A. N. Tikhonov, "Systems of differential equations containing small parameters in the derivatives," Mat. Sb. **31** (3), 575–586 (1952).
3. E. P. Volokitin, "On limit cycles in the simplest model of a hypothetical genetic network," Sib. Zh. Ind. Mat. **7** (3), 57–65 (2004).
4. O. Buse, A. Kuznetsov, and R. A. Peréz, "Existence of limit cycles in the repressilator equations," Int. J. Bifurcation Chaos **19** (12), 4097–4106 (2009).
5. O. Buse, A. Pérez, and A. Kuznetsov, "Dynamical properties of the repressilator model," Phys. Rev. E **81** (066206) 066206-1–066206-7 (2010).
6. V. A. Likhoshvai, Yu. G. Matushkin, and S. I. Fadeev, "Problems in the theory of the functioning genetic networks," Sib. Zh. Ind. Mat. **6** (2), 64–80 (2003).
7. V. A. Likhoshvai, G. V. Demidenko, S. I. Fadeev, Yu. G. Matushkin, and N. A. Kolchanov, "Mathematical simulation of regulatory circuits of gene networks," Comput. Math. Math. Phys. **44** (12), 2166–2183 (2004).
8. S. I. Fadeev and V. A. Likhoshvai, "On hypothetic genetic networks," Sib. Zh. Ind. Mat. **6** (3), 134–153 (2003).
9. A. Yu. Kolesov, N. Kh. Rozov, and V. A. Sadovnichii, "Periodic solutions of travelling-wave type in circular gene networks," Izv. Math. **80** (3), 523–548 (2016).
10. S. D. Glyzin, A. Yu. Kolesov, and N. Kh. Rozov, "Existence and stability of the relaxation cycle in a mathematical repressilator model," Math. Notes **101** (1), 71–86 (2017).
11. A. Yu. Kolesov and Yu. S. Kolesov, *Relaxation Oscillations in Mathematical Models of Ecology* (Am. Math. Soc., Providence, 1997).
12. S. D. Glyzin, A. Yu. Kolesov, and N. Kh. Rozov, "Relaxation self-oscillations in Hopfield networks with delay," Izv. Math. **77** (2), 271–312 (2013).
13. S. D. Glyzin, A. Yu. Kolesov, and N. Kh. Rozov, "Periodic traveling-wave-type solutions in circular chains of unidirectionally coupled equations," Theor. Math. Phys. **175** (1), 499–517 (2013).
14. S. D. Glyzin, A. Yu. Kolesov, and N. Kh. Rozov, "The buffer phenomenon in ring-like chains of unidirectionally connected generators," Izv. Math. **78** (4), 708–743 (2014).
15. Yu. M. Romanovskii, N. V. Stepanova, and D. S. Chernavskii, *Mathematical Modeling in Biophysics* (Inst. Komp'yut. Issled., Moscow, 2003) [in Russian].

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