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Eventual stability properties in a non-autonomous model of population dynamics

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ABSTRACT

We prove that $(\lambda^*, C/\lambda^*)$ is an eventually uniform-asymptotically stable point in the large of the system

$$\dot{L} = C - LG,$$
$$\dot{G} = (L - \lambda(t))G.$$

on the quadrant $\{(L, G) : L \geq 0, G > 0\}$. Here function $\lambda(t)$ is positive and $\lambda(t) \to \lambda^* > 0$ as $t \to \infty$. The study was inspired by observations of distributions of peculiar carnivore and herbivore fish species in Lake Tanganyika.

1. The model

This study is inspired by observations of distributions of peculiar fish species in Lake Tanganyika [1]. In this lake, extraordinarily in the world, the carnivore fishes have asymmetric faces. Actually they can be divided into two groups: those with mouths turned to left and right, respectively. The members of the first group (with "left mouth") attack their prey mainly from the left while the other group prefers to attack from the right. One has observed that the prey, actually herbivore fish, try to adapt to the distribution of left and right attacks against them. Their strategy seems to be rather rigid: a given individual herbivore does not change his preference of paying more attention to against attacks from the left or from the right during his life.

The above situation suggests several mathematical models concerning the development of population numbers or total weights of the groups of left or right mouth carnivores and the groups of herbivores with various strategies against them.

Throughout this work let $\mathcal{I}$ and $\mathcal{K}$ be two (finite) index sets representing the groups of herbivores and carnivores, respectively. In the case described above we simply have two elements in both $\mathcal{I}$ and $\mathcal{K}$; namely, the groups of herbivores with right and left attention preference in $\mathcal{I}$, and the groups of carnivores with right and left distorted mouths in $\mathcal{K}$. However, for technical reasons we may not restrict the numbers of the subspecies. In the sequel we shall write $n_i = n_i(t)$ for the number of the herbivores at time t in group $i \in \mathcal{I}$. Similarly, $m_k = m_k(t)$ will denote the number of the carnivores at time t in group $k \in \mathcal{K}$. Our basic idea for constructing differential equations for these function is the following.

The whole system of the nutrition chain consisting of plants, herbivores and carnivores is supported by the energy flow provided by the Sun. We assume that the intensity of this flow is constant, and furthermore we assume that the growth

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of the total mass of the plants due to the constant solar energy flow is C per time unit. Plants will be eaten by herbivores: we assume that an individual with weight w consumes the percentage $\alpha(w)$ from the total mass of plants during a time unit. Here we make a crucial additional assumption: each group $i \in \mathcal{I}$ consists of individuals with the same weight $w_i(t)$ at the time t. Similarly we assume that each carnivore group $k \in \mathcal{K}$ consists of individuals with weight $u_k = u_k(t)$. By writing $K = K(t)$ for the total mass of plants at time t, our hypothesis concerning plants and herbivores can be formulated as follows:

$$\dot{K} = C - \sum_i n_i \alpha(w_i) K.$$

In this note we are only concerned with one period (actually one year) development without mating. We assume that carnivores do not die during this time, thus their numbers $m_k(t)$ are constant in time. On the other hand, the number of herbivores will be decreased by the carnivores. We assume that the various groups are homogeneously located in the lake and the number of attacks is proportional to their density. That is, with some constant ρ, in a time unit we have $\rho n_i m_k$ attacks by carnivores of type k against herbivores of type i. Concerning the outcome of such an attack, we assume that a herbivore from the group i with weight w will be eaten by a carnivore from the group k of weight u with a probability $\beta^{(i,k)}(w, u)$. Thus

$$\dot{n}_i = -\sum_k \rho \beta^{(i,k)}(w_i, u_k) n_i m_k.$$

Let $\gamma(e, w)$ denote the weight that a herbivore of weight w gains by eating e amount of plants. The weight that a carnivore loses without eating during a time unit is denoted by $\tilde{\gamma}(w)$. Thus

$$\dot{w}_i = \gamma(\alpha(w_i)K, w_i) - \tilde{\gamma}(w_i).$$

As we have assumed that during the period of development the carnivores do not die (they just lose weight), we have:

$$\dot{m}_k = 0.$$

Let $\delta(e, u)$ denote the weight that a carnivore of weight u gains by eating e amount of herbivores. The weight that a carnivore loses without eating during a time unit is denoted by $\tilde{\delta}(u)$. Thus

$$\dot{u}_k = \delta\left(\sum_i \rho \beta^{(i,k)}(w_i, u_k) w_i n_i m_k, u_k\right) - \tilde{\delta}(u_k).$$

2. Simplification of the model

We assume that some functions in the model are linear: $\alpha(w) = \alpha w$, $\gamma(e, w) = \gamma e$, $\delta(e, u) = \delta e$, $\beta^{(i,k)}(w, u) \equiv \beta^{(i,k)}$, $\tilde{\gamma}(w) = \tilde{\gamma} w$ and $\tilde{\delta}(u) = \tilde{\delta} u$. Under these assumptions we have the equations

$$\begin{aligned}
\dot{K} &= C - \sum_i n_i \alpha w_i K, \\
\dot{n}_i &= -\sum_k \beta^{(i,k)} n_i m_k \rho, \\
\dot{w}_i &= \gamma \alpha w_i K - \tilde{\gamma} w_i, \\
\dot{u}_k &= \delta \rho \sum_i \beta^{(i,k)} w_i n_i m_k - \tilde{\delta} u_k.
\end{aligned}$$

We introduce the new variables $x_i := n_i w_i$ and $y_k := m_k u_k$ for the total weight of the herbivores and the carnivores, respectively. For the new variables we have

$$\begin{aligned}
\dot{x}_i &= \dot{n}_i w_i + n_i \dot{w}_i \\
&= -\sum_k \beta^{(i,k)} n_i m_k \rho w_i + n_i \gamma \alpha w_i K - n_i \gamma w_i \\
&= \left[\alpha \gamma K - \tilde{\gamma} - \rho \sum_k \beta^{(i,k)} m_k\right] x_i
\end{aligned}$$

and

$$\begin{aligned}
\dot{y}_k &= m_k \dot{u}_k \\
&= m_k^2 \delta \rho \sum_i \beta^{(i,k)} w_i n_i - m_k \tilde{\delta} u_k \\
&= m_k^2 \delta \rho \sum_i \beta^{(i,k)} x_i - \tilde{\delta} y_k.
\end{aligned}$$

Further on we will only deal with the development of the plants and the herbivores. Introducing the new notation $\tilde{\beta}^i = \sum_k \rho \beta^{(i,k)} m_k$ we have the system

$$\dot{K} = C - \alpha \left(\sum_i x_i \right) K,$$
$$\dot{x}_i = [\alpha \gamma K - (\tilde{\gamma} + \tilde{\beta}^i)] x_i.$$

From the second equation we obtain

$$x_i(t) = x_i(0) \exp\left(-\left(\tilde{\gamma} + \tilde{\beta}^i \right) t \right) \exp\left(\alpha\gamma \int_0^t K \right) \tag{2.1}$$

and

$$\dot{K} = C - \alpha \left(\sum_i x_i(0) \exp\left(-\left(\tilde{\gamma} + \tilde{\beta}^i \right) t \right) \right) K \exp\left(\alpha\gamma \int_0^t K \right).$$

Introducing the new variable

$$E := \exp\left(\alpha\gamma \int_0^t K \right)$$

we get

$$\dot{E} = \exp\left(\alpha\gamma \int_0^t K \right) \alpha\gamma K = \alpha\gamma E K$$

and

$$\dot{K} = C - \alpha \left(\sum_i x_i(0) \exp\left(-(\tilde{\gamma} + \tilde{\beta}^i) t \right) \right) E K.$$

Then with the new function

$$A(t) := \alpha \sum_i x_i(0) \exp\left(-\left(\tilde{\gamma} + \tilde{\beta}^i \right) t \right)$$

our system can be written as

$$\dot{K} = C - A(t) E K,$$
$$\dot{E} = \alpha\gamma E K.$$

We eliminate the constant $\alpha\gamma$ by the aid of the new time variable $\hat{t}$ such that

$$t = \hat{\lambda}\hat{t}, \quad L(\hat{t}) := K(\hat{\lambda}\hat{t}), \qquad F(\hat{t}) := E(\hat{\lambda}\hat{t}). \tag{2.2}$$

We choose $\hat{\lambda} := 1/\alpha\gamma$ to get

$$\frac{\mathrm{d}}{\mathrm{d}\hat{t}} L = \hat{C} - \hat{A}(\hat{t}) F(\hat{t}) L(\hat{t}),$$
$$\frac{\mathrm{d}}{\mathrm{d}\hat{t}} F = F(\hat{t}) L(\hat{t}),$$

where

$$\hat{C} = \frac{C}{\alpha\gamma}, \qquad \hat{A}(\hat{t}) = \frac{1}{\gamma} \sum_i x_i(0) \exp\left(-\frac{\tilde{\gamma} + \tilde{\beta}^i}{\alpha\gamma} \hat{t} \right) = \sum_i \mu_i \exp(-\lambda_i t),$$
$$\mu_i := \frac{x_i(0)}{\gamma}, \qquad \lambda_i := \frac{\tilde{\gamma} + \tilde{\beta}^i}{\alpha\gamma}.$$

Omitting the hats in the previous equations we get

$$\dot{L} = C - AFL,$$
$$\dot{F} = FL.$$

With the notation $G(t) = A(t)F(t)$ we have

$$\dot{G}(t) = \dot{A}(t)F(t) + A(t)\dot{F}(t) = \frac{\dot{A}(t)}{A(t)} A(t)F(t) + A(t)F(t).$$

If we introduce

$$\lambda(t) := -\frac{\dot{A}(t)}{A(t)}, \tag{2.3}$$

we get the system

$$\begin{aligned} \dot{L} &= C - LG, \\ \dot{G} &= (L - \lambda(t))G. \end{aligned} \tag{2.4}$$

on the quadrant

$$Q := \{(L, G) : L \geq 0, G > 0\}.$$

It is easy to see that Q is invariant with respect to (2.4).

In our model the dynamics of the total weights $x_i(t)$ of herbivores and the mass $L(t)$ of plants (see (2.2)) are described by (2.1) and (2.4). As general in population dynamics, one is interested in long-time behavior of these variables. The first step is to determine stability properties of system (2.4) with respect to L, which can be used to study x_i by the aid of (2.1). We will show that $L(t)$ tends uniformly to λ^* as $t \to \infty$, where $\lambda^* := \lim_{t\to\infty} \lambda(t)$.

3. The main result

To formulate our main theorem we need some definitions from stability theory [2] (see also [3]). Consider a system of differential equations

$$\dot{x} = f(t, x) \tag{3.1}$$

with $f : \mathbb{R}^+ \times \Omega \to \mathbb{R}^n$, where $\mathbb{R}^+ = [0, \infty)$ and Ω is an open subset of $\mathbb{R}^n$; $0 \in \Omega$. Let $\|\cdot\|$ denote any norm in $\mathbb{R}^n$. Suppose that for every $t_0 \geq 0$ and $x_0 \in \Omega$ there exists a unique solution $x(t) = x(t; t_0, x_0)$ of Eq. (3.1) for $t \geq t_0$ satisfying the initial condition $x(t_0; t_0, x_0) = x_0$.

Definition 3.1. $x = 0$ is an *eventually stable point* of (3.1) if for every $\varepsilon > 0$ and for every $t_0 \geq 0$ there exist $S(\varepsilon) \geq 0$ and $\delta(\varepsilon, t_0) > 0$ such that $t_0 \geq S(\varepsilon)$ and $\|x_0\| < \delta(\varepsilon, t_0)$ imply $\|x(t; t_0, x_0)\| < \varepsilon$ for all $t \geq t_0$. If $\delta = \delta(\varepsilon) > 0$ can be independent of t_0, then the eventual stability is *uniform*.

Definition 3.2. $x = 0$ is an *eventually asymptotically stable point of* (3.1) *in the large* if it is eventually stable point and every solution tends to zero, as $t \to \infty$.

Definition 3.3. $x = 0$ is an *eventually quasi-uniform-asymptotically stable point of* (3.1) *in the large* if for every compact set $\Gamma \subset \Omega$ and for every $\gamma > 0$ there are $S(\Gamma, \gamma)$ and $T(\Gamma, \gamma) > 0$ such that $x_0 \in \Gamma$, $t_0 \geq S(\Gamma, \gamma)$ and $t \geq t_0 + T(\Gamma, \gamma)$ imply $\|x(t; t_0, x_0)\| < \gamma$.

Definition 3.4. $x = 0$ is an *eventually uniform-asymptotically stable point of* (3.1) *in the large* if it is eventually uniform-stable and quasi-uniform-asymptotically stable in the large.

Let $\lambda^* := \min\{\lambda_i : i \in \mathcal{I}\}$. It will be shown in Lemma 4.3 that

$$\lim_{t\to\infty} \lambda(t) = \lambda^*.$$

Now we can formulate our theorem:

Theorem 3.5. $(\lambda^*, C/\lambda^*)$ *is an eventually uniform-asymptotically stable point in the large of* (2.4).

The proof of this theorem will use some notions and a basic fact of the theory of limiting equations.

A point $x^* \in \overline{\Omega}$ is said to be a *positive limit point* of a solution x of (3.1) if there exists a sequence $\{t_j\}$ such that $t_j \to \infty$ and $x(t_j) \to x^*$ as $j \to \infty$. The set of all positive limit points of x is called the *positive limit set* of x and is denoted by $\Lambda^+(x)$.

The *translate* of a function $f : \mathbb{R}^+ \times \Omega \to \mathbb{R}^n$ by $a > 0$ is defined as $f_a(t, x) := f(t + a, x)$. The function f is called *asymptotically autonomous* if there exists a function $f^* : \Omega \to \mathbb{R}^n$ such that $f_a(t, x) \to f^*(x)$ as $a \to \infty$ uniformly on every compact subset of $\mathbb{R}^+ \times \Omega$. f^* and $\dot{x} = f^*(x)$ will be called the *limit function* and the *limit equation*, respectively.

Let $f(t, x)$ be asymptotically autonomous. A set $F \subset \Omega$ is said to be *semi-invariant* with respect to Eq. (3.1) if for every $(t_0, x_0) \in \mathbb{R}^+ \times F$ there is at least one non-continuable solution $x^* : (\alpha, \omega) \to \mathbb{R}^n$ of the limit equation $\dot{x} = f^*(x)$ with $x^*(t_0) = x_0$ such that $x^*(t) \in F$ for every $t \in (\alpha, \omega)$.

Theorem A ([4]). *Suppose that f is asymptotically autonomous. Then for every solution x of Eq.* (3.1) *the limit set $\Lambda^+(x) \cap \Omega$ is semi-invariant.*

The steps of the proof of Theorem 3.5 are the following:

1. We prove that the equilibrium point $(\lambda^*, C/\lambda^*)$ of the limit equation
$$\begin{aligned} \dot{L} &= C - LG, \\ \dot{G} &= (L-\lambda^*)G \end{aligned} \tag{3.2}$$
is asymptotically stable in the large. To this end, at first we linearize the system to prove the (local) asymptotic stability. Then we construct a Lyapunov function and, by the mean of LaSalle's invariance principle, we prove that the equilibrium is asymptotically stable in the large.
2. We prove that $(\lambda^*, C/\lambda^*)$ is an eventually uniform-stable point of the original non-autonomous equation (2.4).
3. Using the eventual uniform stability and the semi-invariance theorem, we prove that $(\lambda^*, C/\lambda^*)$ is an eventually asymptotically stable point of (2.4) in the large.
4. Using the eventual uniform stability and the structure of the derivative of the Lyapunov function we prove the eventual quasi-uniform-asymptotic stability in the large.

As is known, the exponential stability is very important in applications (e.g., in control theory). For linear systems the exponential stability is equivalent to the uniform asymptotic stability, so the latter can be considered as the generalization of the exponential stability to nonlinear systems. For this reason, we have formulated our main theorem on *uniform* asymptotic stability. Those readers interested only in (non-uniform) asymptotic stability may omit the rather sophisticated step 4 of the proof about the uniformity.

4. Preliminary lemmas

Lemma 4.1. *The equilibrium point* $(\lambda^*, C/\lambda^*)$ *of the limit equation* (3.2) *is asymptotically stable.*

Proof. To place the equilibrium in the origin we use the transformation $\ell = L - \lambda^*$, $g = G - C\lambda^*$. We get the system
$$\begin{aligned} \dot{\ell} &= -\frac{C}{\lambda^*}\ell - \lambda^* g - \ell g \\ \dot{g} &= \frac{C}{\lambda^*}\ell + \ell g. \end{aligned} \tag{4.1}$$

The Jacobian of the linearized equation has the eigenvalues
$$-\frac{C}{2\lambda^*} \pm \sqrt{\left(\frac{C}{2\lambda^*}\right) - C}.$$

Since $C > 0$, the equilibrium point $(0, 0)$ is asymptotically stable. In the case of $\lambda^* > \sqrt{C}/2$, the solutions oscillate; if $\lambda^* < \sqrt{C}/2$, the solutions do not oscillate. $\square$

Lemma 4.2. *The equilibrium point* $(\lambda^*, C/\lambda^*)$ *of the limit equation* (3.2) *is asymptotically stable in the large on quadrant* Q.

Proof. Let us define the Lyapunov function
$$V(L, G) = \frac{1}{2}(L-\lambda^*)^2 - C\ln G + \lambda^* G - C + C\ln\frac{C}{\lambda^*} \tag{4.2}$$
on the set $R := \{(L, G) : L \in \mathbb{R}, G > 0\}$. In order to show that V is positive definite, let us represent it in the form
$$V(L, G) = \frac{1}{2}(L-\lambda^*)^2 + \lambda^* \left\{\left(G - \frac{C}{\lambda^*}\right) - \frac{C}{\lambda^*}\left[\ln G - \ln\frac{C}{\lambda^*}\right]\right\}$$
and define the function
$$h(x) := (x-a) - a[\ln x - \ln a] \quad (a > 0;\ x > 0).$$
Since
$$h(a) = 0, \qquad h'(a) = \left[1 - \frac{a}{x}\right]_{x=a} = 0, \qquad h''(a) = \frac{1}{a} > 0,$$
and $h'(x) \neq 0$ $(x \neq a)$, function h is positive definite around $x = a$ for $x > 0$. Consequently, V is positive definite around $(\lambda^*, C/\lambda^*)$ on R. For the derivative $\dot{V}_{(3.2)}$ we have

$$\begin{aligned}\dot{V}(L,G) &= (L-\lambda^*)\dot{L} - C\frac{\dot{G}}{G} + \lambda^*\dot{G}\\ &= (L-\lambda^*)(C-LG) - \left(\frac{C}{G}-\lambda^*\right)(L-\lambda^*)G\\ &= (L-\lambda^*)\left[C-LG-C+\lambda^*G\right]\\ &= -(L-\lambda^*)^2G \le 0.\end{aligned}$$

For an arbitrary point $(L(0), G(0)) \in Q$ there exists a $\mu > 0$ such that the point $(L(0), G(0))$ is inside the level set $V(L, G) \le \mu$ because

$$\lim_{G-\ln G\to\infty,\,|L|\to\infty} V(L,G) = \infty.$$

As the derivative of the Lyapunov function along the trajectories of (3.2) is less than or equal to zero, the solution started from the point $(L(0), G(0))$ will remain inside the level set $V(L, G) \le \mu$ for all $t > 0$. From LaSalle's invariance principle we know that the limit set of the solution is a subset of the set $\dot{V}_{(3.2)} = 0$, i. e., in our case, of the line $L = \lambda^*$. Except for the equilibrium point $(\lambda^*, C/\lambda^*)$, the solutions of (3.2) move from the line $L = \lambda^*$, so it follows that the limit set is the singleton $\{(\lambda^*, C/\lambda^*)\}$. □

To prove that the point $(\lambda^*, C/\lambda^*)$ is eventually stable with respect to the original non-autonomous system (2.4), we need the following property of the function λ defined in (2.3):

Lemma 4.3. *The function λ defined in (2.3) is decreasing and tends to λ^*, as $t \to \infty$.*

Proof. Obviously,

$$\lambda(t) = -\frac{\dot{A}(t)}{A(t)} = \frac{\sum_{i=1}^{3}\lambda_i\mu_i e^{-\lambda_i t}}{\sum_{i=1}^{3}\mu_i e^{-\lambda_i t}} = \frac{\sum_{i=1}^{3}\lambda_i\mu_i e^{-(\lambda_i-\lambda^*)t}}{\sum_{i=1}^{3}\mu_i e^{-(\lambda_i-\lambda^*)t}} \to \lambda^*.$$

Let $f := -\dot{A}$ and $g := A$, so $\lambda = f/g$, where f and g are two decreasing positive functions. By differentiation we obtain

$$\dot{\lambda} = \left(\dot{\frac{f}{g}}\right) = \frac{\dot{f}g - f\dot{g}}{g^2}.$$

Let us check the sign of the numerator:

$$\dot{f}(t)g(t) = -\sum_{i,j=1}^{3}\lambda_i^2\mu_i\mu_j e^{-(\lambda_i+\lambda_j)t}, \qquad f(t)\dot{g}(t) = -\sum_{i,j=1}^{3}\lambda_i\lambda_j\mu_i\mu_j e^{-(\lambda_i+\lambda_j)t},$$

$$\begin{aligned}\dot{f}(t)g(t) - f(t)\dot{g}(t) &= -\sum_{i,j=1}^{3}\left(\lambda_i^2-\lambda_i\lambda_j\right)\mu_i\mu_j e^{-(\lambda_i+\lambda_j)t}\\ &= -\frac{1}{2}\sum_{i,j=1}^{3}\left(\lambda_i-\lambda_j\right)^2\mu_i\mu_j e^{-(\lambda_i+\lambda_j)t} \le 0,\end{aligned}$$

which completes the proof. □

We will see that the derivative of function (4.2) does not keep its sign along solutions of the non-autonomous system (2.4), so (4.2) is not a Lyapunov function to this system. However, as the next assertion shows, it can be used as a "pseudo" Lyapunov function to this system.

Lemma 4.4. *There is a constant M such that*

$$V(L(t), G(t)) \le V(L(0), G(0)) + M \quad (t \ge 0) \tag{4.3}$$

holds for all solutions of (2.4). Moreover, for every $\varepsilon > 0$ there exists a $\tau(\varepsilon) \ge 0$ such that if $t_0 \ge \tau(\varepsilon)$ then every solution of (2.4) satisfies the inequality

$$V(L(t), G(t)) \le V(L(t_0), G(t_0)) + \varepsilon \quad (t \ge t_0). \tag{4.4}$$

Proof. The derivative of (4.2) with respect to the non-autonomous system (2.4) is

$$\begin{aligned}\dot{V}(L,G)_{(2.4)} &= (L-\lambda^*)\dot{L} - \dot{G}/G + \lambda^*\dot{G}\\ &= (L-\lambda^*)(C-GL) - C(L-\lambda(t)) + \lambda^*(L-\lambda(t))G\\ &= (L-\lambda^*)[C-GL-C] + C(\lambda(t)-\lambda^*) + \lambda^*[(L-\lambda^*)-(\lambda(t)-\lambda^*)]\\ &= (L-\lambda^*)(-GL+\lambda^*G) + C(\lambda(t)-\lambda^*) - \lambda^*(\lambda(t)-\lambda^*)G\\ &= -(L-\lambda^*)^2G + (\lambda(t)-\lambda^*)(C-\lambda^*G)\\ &\le -(L-\lambda^*)^2G + (\lambda(t)-\lambda^*)C. \end{aligned} \tag{4.5}$$

Since $\lambda(t) \searrow \lambda^*$ as $t \to \infty$ exponentially, integrating the previous estimate along a solution over the intervals $[0, t]$ and $[t_0, t]$ one gets the assertions of the lemma. $\square$

Lemma 4.5. *$(\lambda^*, C/\lambda^*)$ is an eventually uniformly stable point of the non-autonomous system (2.4).*

Proof. For $\rho > 0$, let $C(\rho)$ and $D(\rho)$ denote the circle and the open disc, respectively, with center at $(\lambda^*, C/\lambda^*)$ and radius ρ. We have to prove that for every $\varepsilon > 0$ and for every $t_0 \ge 0$ there exist $S(\varepsilon) \ge 0$ and $\delta(\varepsilon) > 0$ such that $t_0 \ge S(\varepsilon)$ and $(L, G) \in D(\delta(\varepsilon))$ imply $(L(t), G(t)) \in D(\varepsilon)$ for all $t \ge t_0$.

Let $\varepsilon > 0$ be given. Since function (4.2) is positive definite around $(\lambda^*, C/\lambda^*)$, we have

$$m(\varepsilon) := \min\{V(L,G) : (L,G) \in C(\varepsilon)\} > 0,$$

and there is a $\delta(\varepsilon) > 0$ such that $V(L, G) < m(\varepsilon)/2$, provided that $(L, G) \in D(\delta(\varepsilon))$. By Lemma 4.4, if $t_0 \ge \tau(m(\varepsilon)/2)$ and $(L(t_0), G(t_0)) \in D(\delta(\varepsilon))$, then

$$V(L(t), G(t)) \le V(L(t_0), G(t_0)) + \frac{m(\varepsilon)}{2} < m(\varepsilon),$$

whence $(L(t), G(t)) \in D(\varepsilon)$ for $t \ge t_0$. This means that the definition of the eventual uniform stability is satisfied with $S(\varepsilon) := \tau(m(\varepsilon)/2)$ and $\delta(\varepsilon)$. $\square$

Lemma 4.6. *$(\lambda^*, C/\lambda^*)$ is an eventually asymptotically stable point of the original non-autonomous system (2.4) in the large.*

Proof. We have to prove that every solution of (2.4) tends to $(\lambda^*, C/\lambda^*)$ as $t \to \infty$. Let us consider an arbitrary solution (L, G) of (2.4). It is precompact because of the first assertion of Lemma 4.4, so its positive limit set Λ^+ is not empty. We show that $\Lambda^+ = \{(\lambda^*, C/\lambda^*)\}$.

Suppose the contrary, i.e. there exists a point $(L_0, G_0) \in \Lambda^+$ different from $(\lambda^*, C/\lambda^*)$. By Theorem A the set Λ^+ is semi-invariant with respect to the limit equation (3.2). But $(\lambda^*, C/\lambda^*)$ is a globally asymptotically stable equilibrium of (3.2), and Λ^+ is compact, so $(\lambda^*, C/\lambda^*) \in \Lambda^+$. Now let $\varepsilon_0 > 0$ satisfy $(L_0, G_0) \notin D(\varepsilon_0)$ and take the numbers $S(\varepsilon_0/2) \ge 0$, $\delta(\varepsilon_0/2) > 0$ belonging to $\varepsilon_0/2$ in the sense of Definition 3.1 of the eventual uniform stability of $(\lambda^*, C/\lambda^*)$. Since $(\lambda^*, C/\lambda^*) \in \Lambda^+$, the point $(L(t_*), G(t_*))$ has to be in $D(\delta(\varepsilon_0/2))$ for some $t_* > S(\varepsilon_0/2)$, and, therefore, $(L(t), G(t))$ remains in $D(\varepsilon_0/2)$ for all $t \ge t_*$. At the same time, $(L(t), G(t))$ goes arbitrarily near to (L_0, G_0) for large values of t, which is a contradiction. $\square$

5. Proof of Theorem 3.5

Let us introduce the notation

$$d(L,G) := \sqrt{(L-\lambda^*)^2 + \left(G - \frac{C}{\lambda^*}\right)^2}.$$

We have to prove eventual quasi-uniform-asymptotic stability in the large, namely that for every $K > 0$ and $\gamma > 0$ there exist $S(K, \gamma) \ge 0$ and $T(K, \gamma) > 0$ such that $t_0 \ge S(K, \gamma)$ and $(1 + |\ln G_0|)\, d(L_0, G_0) \le K$ imply

$$d\left((L(t; t_0, L_0, G_0), G(t; t_0, L_0, G_0))\right) < \gamma \tag{5.1}$$

for all $t \ge t_0 + T(K, \gamma)$. Due to the eventual uniform stability, instead of (5.1) it is enough to prove the existence of a $T_* = T_*(K, \gamma) > 0$ with

$$d\left((L(t_0+T_*; t_0, L_0, G_0), G(t_0+T_*; t_0, L_0, G_0))\right) < \delta(\gamma), \tag{5.2}$$

where $\delta(\gamma)$ belongs to γ in the sense of the eventual uniform stability (see Definition 3.1).

Suppose the contrary, i.e., there exist $\overline{K} > 0$ and $\overline{\gamma}$ such that for every $S \ge 0$ and $T > 0$ there are $t_0 \ge S$ and (L_0, G_0) with $(1 + |\ln G_0|)\, d(L_0, G_0) \le \overline{K}$ such that

$$d\left((L(t; t_0, L_0, G_0), G(t; t_0, L_0, G_0))\right) \ge \delta(\overline{\gamma}) \quad \text{for all } t \in [t_0, t_0 + T]. \tag{5.3}$$

In what follows, by solutions we mean only solutions possessing this property.

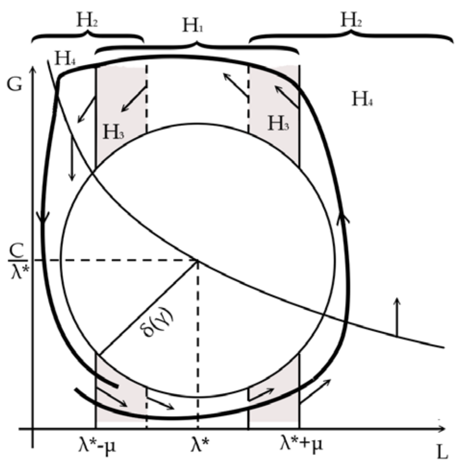

Fig. 1. The sets $H_1, \ldots, H_4$.

To get a contradiction we will use the Lyapunov function V defined in (4.2). It is easy to see that there are $a, b : [0, \infty) \to (0, \infty)$ strictly increasing functions vanishing at 0 and such that

$$a\left((1 + |\ln G|)\, d(L, G)\right) \le V(L, G) \le b\left((1 + |\ln G|)\, d(L, G)\right) \tag{5.4}$$

holds on the upper half-plane. For any solution of (2.4) we introduce the notation

$$v(t) = v(t; t_0, L_0, G_0) := V\left(L(t; t_0, L_0, G_0), G(t; t_0, L_0, G_0)\right).$$

By (5.4) and Lemma 4.4 we have

$$v(t) \le b(\overline{K}) + M \quad (t \ge t_0) \tag{5.5}$$

for any solution of (2.4).

The derivative (4.5) of V with respect to (2.4) is not negative definite, so we have to differ some subsets of Q where $\dot{V}$ is large or small. For $\mu > 0$, let

$$\begin{aligned} H_{\le}(\mu) := \{(L, G) \in Q : d(L, G) &\ge \delta(\overline{\gamma}),\ (1 + |\ln G|)\, d(L, G) \\ &\le a^{-1}\left(b(\overline{K}) + M\right),\ |L - \lambda^*| \le \mu\}, \\ H_{\ge}(\mu) := \{(L, G) \in Q : d(L, G) &\ge \delta(\overline{\gamma}),\ \ (1 + |\ln G|)\, d(L, G) \\ &\le a^{-1}\left(b(\overline{K}) + M\right),\ |L - \lambda^*| \ge \mu\}, \end{aligned}$$

and consider the sets

$$\begin{aligned} &H_1(\mu) := H_{\le}(\mu), \qquad H_2(\mu) := H_{\ge}\left(\frac{\mu}{2}\right), \\ &H_3(\mu) := H_{\le}(\mu) \cap H_{\ge}\left(\frac{\mu}{2}\right), \qquad H_4(\mu) := H_{\ge}(\mu); \end{aligned}$$

(see Fig. 1).

We will need the fact that a trajectory cannot remain in H_1 for a too long time. To this end we estimate $|\dot{L}|$ from below:

$$\begin{aligned} |\dot{L}| &= |C - GL| = \left|\lambda^*\left(\frac{C}{\lambda^*} - G\right) - G(L - \lambda^*)\right| \\ &\ge \lambda^*\left|\frac{C}{\lambda^*} - G\right| - |G(L - \lambda^*)| \\ &\ge \lambda^*\left|\frac{C}{\lambda^*} - G\right| - \left(\frac{C}{\lambda^*} + \delta(\overline{\gamma})\right)\mu > 0 \end{aligned}$$

for sufficiently small μ. Therefore, there exists a $\kappa_1 > 0$ such that

$$|\dot{L}| \ge \kappa_1 > 0 \qquad ((L, G) \in H_1). \tag{5.6}$$

While a trajectory of a solution is in H_2, the Lyapunov function decreases fast along the solution. In fact, by (5.4) we have

$$a^{-1}(b(\overline{K}) + M) \ge (1 + |\ln G|)\, d(L, G) \ge |\ln G|\delta(\overline{\gamma}),$$

so

$$G \geq \exp\left[-\frac{a^{-1}(b(\overline{K})+M)}{\delta(\overline{\gamma})}\right].$$

From (4.5) we obtain the estimate

$$\dot{V}(L,G,t) \leq -\frac{\mu^2}{4}\exp\left[-\frac{a^{-1}(b(\overline{K})+M)}{\delta(\overline{\gamma})}\right] + C(\lambda(t)-\lambda^*) \quad ((L,G)\in H_2,\ t\geq 0),$$

which implies the existence of $\bar{t}$ and $\kappa_2 > 0$ such that

$$\dot{V}(L,G,t) \leq -\kappa_2 \quad (t \geq \bar{t},\ (L,G)\in H_2). \tag{5.7}$$

By (5.4) and Lemma 4.4 the trajectory of every solution is precompact, so there is a $\kappa_3 > 0$ such that

$$|\dot{L}(t)| \leq \kappa_3 \quad (t \geq t_0).$$

For given $T > 0$ and $t_0 \geq \bar{t}$, consider a solution $t \mapsto (L(t), G(t))$ with property (5.3). Then there exists a sequence

$$t_0 \leq s_1 < t_1 < s_2 < \cdots < t_{n-1} < s_n < t_n \leq t_0 + T$$

such that

$$\text{if } s_i < t < t_i,\ \text{then } (L(t),G(t))\in H_4 \quad (i=1,2,\ldots,n),$$

$$\text{if } t\in[t_0,t_0+T]\setminus\left(\cup_{i=1}^n[s_i,t_i]\right),\ \text{then } (L(t),G(t))\in H_1. \tag{5.8}$$

The main idea of the remaining part of the proof is that v decreases at least a constant during every time interval $[s_i, t_i]$, and $n = n(T) \to \infty$ as $T \to \infty$. Since v is of bounded total variation on $[t_0, \infty)$, this means that T cannot be arbitrarily large in contradiction to the existence of $\overline{K}, \overline{\gamma}$. To conclude the proof we set forth this idea in details.

Since $H_4 \subset H_2$, from (5.4), Lemma 4.4, and (5.7) we obtain

$$\sum_{i=1}^n (t_i - s_i) \leq \frac{b(\overline{K})+M}{\kappa_2} =: \overline{T}.$$

Furthermore, in virtue of (5.6) and (5.8), $s_i - t_{i-1} \leq 2\mu/\kappa_1$ for all $i = 2, 3, \ldots, n$. The last two estimates together imply that

$$n = n(T) \geq \frac{T-\overline{T}}{\frac{2\mu}{\kappa_1}} \to \infty \quad (T\to\infty). \tag{5.9}$$

On the other hand, using the notations

$$[x]_+ := \max\{x,0\}, \qquad [x]_- := \max\{-x,0\}, \qquad (x\in\mathbb{R}),$$

we have

$$-\int_{t_0}^{t_0+T}[\dot{v}(t)]_-\mathrm{d}t \leq -\sum_{i=2}^n\int_{t_{i-1}}^{s_i}[\dot{v}(t)]_-\mathrm{d}t \leq \int_{(L(t),G(t))\in H_3}\dot{v}(t)\mathrm{d}t$$
$$\leq -2(n-2)\kappa_2\frac{\mu}{2\kappa_3}.$$

Consequently,

$$-b(\overline{K}) - M \leq v(t_0+T) - v(t_0) = \int_{t_0}^{t_0+T}([\dot{v}(t)]_+ - [\dot{v}(t)]_-)\,\mathrm{d}t$$
$$\leq M - 2(n-2)\kappa_2\frac{\mu}{\kappa_3} \to -\infty \quad (T\to\infty).$$

This means that T cannot be arbitrarily large in contradiction to the existence of $\overline{K}, \overline{\gamma}$. This contradiction completes the proof of Theorem 3.5. □

Remark 5.1. Thieme [5] established a method yielding sufficient conditions for the large-time behaviour of solutions of asymptotically autonomous systems to be the same as the large-time behaviour of solutions of their limiting systems. Castillo-Chavez and Thieme formulated a corollary [6, Corollary 2.2] of this method which applies to our situation guaranteeing that every *bounded forward solution* of (2.4) converges towards an equilibrium of (3.2) as time tends to infinity. In other words, the assertion of Lemma 4.6 follows from Lemma 4.4 and this collorary. We included Lemma 4.6 to make our paper self-contained.

The main idea in the proof of Theorem 3.5 is to use a Lyapunov function of the limit equation (3.2) to prove stability properties for the original asymptotically autonomous equation (2.4). This method was introduced by Yoshizawa [7], LaSalle [8]; it was further developed by Artstein [9]. For example, from Lemma 4.4 and [9, Theorem 8.3] it follows that every solution of (2.4) tends to the line $\{L = \lambda^*\}$.

It should be emphasized, however, that these results cannot be applied to get eventual uniform stability properties for the point $(\lambda^*, C/\lambda^*)$.

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