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STABILITY ANALYSIS OF A DISTRIBUTED PARAMETER MODEL FOR THE GROWTH OF MICRO-ORGANISMS

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Abstract—A distributed parameter system for the growth of micro-organisms in a chemostat is considered. The growth rate depends on the internal concentration in the cells of one essential nutritient and a partial differential equation describing the situation where different cells have different growth rates is studied.

1. INTRODUCTION

Consider a microbial population in a chemostat where the growth of the cells is limited by the availability of one essential nutritient. Even if the chemostat is well stirred it is reasonable to assume that different cells may have different growth rates due to varying internal concentrations of the limiting nutritient. The purpose of this paper is to study under what conditions the solutions of a mathematical model describing this distributed parameter system approaches the solutions of a corresponding model where the assumption is made that all cells are identical. The asymptotic behaviour of these solutions as $t \to \infty$ will also be studied.

It will be assumed that the age structure of the cells does not affect the growth rate and that the cells reproduce through division so that this part of the growth process will not appear explicitly in the model if it is formulated in terms of cell mass, and not numbers of cells. The chemostat is well stirred and the concentration of the nutritient in the medium being pumped into the chemostat at time t is $C(t)$. If $\sigma(t)$ is the total amount of nutritient, (in one form or another), in the chemostat and $s(t)$ is the total amount of nutritient inside the cells, then the concentration of nutritient in the medium in the chemostat is proportional to $\sigma(t) - s(t)$. The rate of uptake of nutritient from the medium into a cell with internal concentration q, (nutritient per cell mass), is assumed to be $f(q, \sigma(t) - s(t))$ and the differential growth rate, (of cell mass), of such a cell is $\mu(q)$. Now it is not assumed that distribution of cell mass with respect to the internal concentration q at time t is given by a density function but more generally through a measure $m(t, \cdot)$, i.e. $m(t, E) = \int_E \mathrm{d}m(t, q) =$ total mass of cells at time t with internal nutritient concentration in the set E. (If m is absolutely continuous, it is identified with its density function.) Using standard arguments one derives the following equation for m, (that in general only holds in the distribution sense):

$$\partial/\partial t\, m + \partial/\partial q(g(q, \sigma(t) - s(t))m) = (\mu(q) - D(t))m, \quad m(0, \cdot) = m_0, \tag{1.1}$$

$$s(t) = \int_{\mathbf{R}^+} q\, \mathrm{d}m(t, q),$$

where m_0 is a given nonnegative measure,

$$g(q, x) = -\mu(q)q + f(q, x), \tag{1.2}$$

($\mathbf{R}^+ = [0, \infty)$), $D(t)$ is the given fractional dilution rate and σ satisfies the equation

$$\sigma'(t) = D(t)(C(t)V - \sigma(t)), \tag{1.3}$$

where "$'$" $= \mathrm{d}/\mathrm{d}t$ and V is the (constant) volume of the chemostat.

If all the cells were identical, then one would get a system of differential equations consisting of (1.3) and the equations

$$X'(t) = (\mu(Q(t)) - D(t))X(t),$$
$$Q'(t) = -\mu(Q(t))Q(t) + f(Q(t), \sigma(t) - Q(t)X(t)). \tag{1.4}$$

Here X is the total cell mass and Q is the internal nutritient concentration.

Models of the form (1.3), (1.4) have been studied in e.g. [2–6, 9] and the references mentioned there. The main feature of these models is that the growth rate depends on the internal nutritient concentration and the most serious weakness seems to be that there is no time delay between the uptake of nutritient and its effects on the growth rate [1, 4, 5].

A certain kind of time delay will automatically be introduced in the second model to be considered. Here it is assumed that the nutritient is taken up in the (e.g. inorganic) form I and then transformed into the (e.g. organic) form II at the rate c_1q_1 and back again into form I at the rate c_2q_2 where q_1 and q_2 are the concentrations of the nutritient in the forms I and II respectively. Finally it is assumed that the growth rate is a function of q_2 only and that the rate of uptake of nutritient from the medium is independent of q_1 and q_2. If now the measure $M(t, \cdot)$ defined on $\mathbf{R}^+ \times \mathbf{R}^+$ denotes the distribution of cell mass with respect to q_1 and q_2, then one obtains the following equation corresponding to (1.1):

$$\partial/\partial tM + \partial/\partial q_1(g_1(q_1, q_2, \sigma(t) - s(t))M) + \partial/\partial q_2(g_2(q_1, q_2)M) = (\mu(q_2) - D(t))M, \quad M(0, \cdot) = M_0, \tag{1.5}$$

$$s(t) = \int_{\mathbf{R}^+\times\mathbf{R}^+} (q_1 + q_2)\,\mathrm{d}M(t, q_1, q_2),$$

where

$$g_1(q_1, q_2, x) = -(c_1 + \mu(q_2))q_1 + c_2q_2 + F(x), \tag{1.6}$$

$$g_2(q_1, q_2) = c_1q_1 - (c_2 + \mu(q_2))q_2, \tag{1.7}$$

and the function σ is defined to be the solution of equation (1.3).

If all the cells are identical, then one gets a system of equations consisting of (1.3) and the equations

$$X'(t) = (\mu(Q_2(t)) - D(t))X(t),$$
$$Q_1'(t) = -(c_1 + \mu(Q_2(t)))Q_1(t) + c_2Q_2(t) + F(\sigma(t) - (Q_1(t) + Q_2(t))X(t)),$$
$$Q_2'(t) = c_1Q_1(t) - (c_2 + \mu(Q_2(t)))Q_2(t). \tag{1.8}$$

This second model is related to similar ones that have been studied in, e.g. Refs. [7, 10]. It should be observed that here the reactions transforming nutritient in forms I and II into each other proceed at linear rates and this is a very strong assumption, but it is needed in the arguments to be used below.

2. STATEMENT OF RESULTS

The first result concerns equations (1.1), (1.2) and their relationship to the system (1.4).

THEOREM 1

Assume that V > 0, $\sigma_0 > 0$ *and that*

C *and* D *are continuous, nonnegative and bounded functions on* $\mathbf{R}^+$, (2.1) f *is a continuously differentiable function on* $\mathbf{R}^+ \times \mathbf{R}^+$, *nonincreasing in its first and nondecreasing in its second variable and nonnegative on* $\{0\} \times \mathbf{R}^+$ *and nonpositive on* $\mathbf{R}^+ \times \{0\}$, (2.2)

μ *is a continuously differentiable, nondecreasing function on* $\mathbf{R}^+$, $\mu(0) = 0$ *and* $\mu \not\equiv 0$, (2.3)

m_0 *is a finite, nonnegative Borel measure with compact support in* $\mathbf{R}^+$, $m_0(\mathbf{R}^+) > 0$ *and* $\int_{\mathbf{R}^+} q \, dm_0(q) \leqq \sigma_0$. (2.4)

Then there exists a unique solution m *of the system* (1.1)–(1.3) *when* $t \geqq 0$, $q \geqq 0$ *and* $\sigma(0) = \sigma_0$, ((1.1) *holds in the distribution sense*), *such that for each* $t, m(t, \cdot)$ *is a finite, nonnegative Borel measure on* $\mathbf{R}^+$ *with support in a compact set independent of* t *and for each continuous function* ψ *the function* $\int_{\mathbf{R}^+} \psi(q) \, dm(t, q)$ *is continuous. If moreover*

$$\liminf_{t\to\infty} C(t) > 0 \text{ and } \liminf_{t\to\infty} D(t) > 0 \tag{2.5}$$

then $m(t, \mathbf{R}^+)$ *is bounded on* $\mathbf{R}^+$ *and there exist positive numbers* T, σ_T, X_T, Q_T *and nonnegative continuous functions* C_* *and* D_* *on* $[T, \infty)$ *such that*

$$\lim_{t\to\infty} (|C_*(t) - C(t)| + |D_*(t) - D(t)|) = 0 \tag{2.6}$$

and such that the solution of the system (1.3), (1.4) *on* $t \geqq T$ *with* $\sigma(T) = \sigma_T$, $X(T) = X_T$, $Q(T) = Q_T$ *and* C *and* D *replaced by* C_* *and* D_* *satisfies*

$$\lim_{t\to\infty} \left(\left| X(t) - m(t, \mathbf{R}^+) \right| + \left| Q(t)X(t) - \int_{\mathbf{R}^+} q \, dm(t, q) \right| \right) = 0. \tag{2.7}$$

Moreover, either $\lim_{t\to\infty} m(t, \mathbf{R}^+) = 0$ *or* $\lim_{t\to\infty} \operatorname{diam} (\operatorname{supp}(m(t, \cdot))) = 0$.

Here $\operatorname{diam}(E) = \sup \{|x - y| \mid x, y \in E\}$ and $\operatorname{supp}(m(t, \cdot))$ is the support of $m(t, \cdot)$.

The conclusion (2.7) implies that one can at least from a practical point of view, just as well use the simpler system (1.3), (1.4) instead of the more complicated equations (1.1)–(1.3). In the next theorem the asymptotic behaviour of the system (1.3), (1.4) and thus by Theorem 1 also that of (1.1)–(1.3), is studied.

THEOREM 2

Assume that $V > 0$, $\sigma_0 > 0$, $X_0 > 0$, $Q_0 \geqq 0$, $Q_0 X_0 \leqq \sigma_0$, $C_\infty > 0$, $D_\infty > 0$, (2.1)–(2.3) *hold and that*

$$\lim_{t\to\infty} (C(t), D(t)) = (C_\infty, D_\infty), \tag{2.8}$$

there exists a unique number $Q_\infty > 0$ *such that* $\mu(Q_\infty) = D_\infty$ *and a unique number* $X_\infty > 0$ *such that* $f(Q_\infty, C_\infty V - Q_\infty X_\infty) = D_\infty Q_\infty$. (2.9)

Then the solution of the system (1.3), (1.4) *on* $t \geqq 0$ *with* $X(0) = X_0$, $Q(0) = Q_0$ *and* $\sigma(0) = \sigma_0$ *satisfies*

$$\lim_{t\to\infty} (X(t), Q(t), \sigma(t)) = (X_\infty, Q_\infty, C_\infty V). \tag{2.10}$$

Observe that the assumptions made in Theorem 2 do not guarantee that the linearization of the system (1.3), (1.4) around the equilibrium point is asymptotically stable.

Next an analoque of Theorem 1 for the system (1.3), (1.5)–(1.7) will be established.

THEOREM 3

Assume that $V > 0$, $\sigma_0 > 0$, $c_1 > 0$, $c_2 \geqq 0$ (2.1) *and* (2.3) *hold and that*

F *is a continuously differentiable, nondecreasing function on* $\mathbf{R}^+$ *and* $F(0) = 0$ (2.11)

M_0 *is a finite, nonnegative Borel measure with compact support in* $\mathbf{R}^+\times\mathbf{R}^+$, $M_0(\mathbf{R}^+\times\mathbf{R}^+) > 0$ *and* $\int_{\mathbf{R}^+\times\mathbf{R}^+}(q_1+q_2)\,dM_0(q_1,q_2)\leqq\sigma_0$. (2.12)

Then there exists a unique solution M *of the system* (1.3), (1.5)–(1.7) *when* $t\geqq 0$, $q_1\geqq 0$, $q_2\geqq 0$ *and* $\sigma(0)=\sigma_0$, ((1.5) *holds in the distribution sense*), *such that for each* t, $M(t,\cdot)$ *is a finite, nonnegative Borel measure on* $\mathbf{R}^+\times\mathbf{R}^+$ *with support in a compact set independent of* t *and for each continuous function* ψ *the function* $\int_{\mathbf{R}^+\times\mathbf{R}^+}\psi(q_1,q_2)\,dM(t,q_1,q_2)$ *is continuous. Moreover, if* (2.5) *holds, then* $M(t,\mathbf{R}^+\times\mathbf{R}^+)$ *is bounded on* $\mathbf{R}^+$ *and if also*

$$c_1>\sup\{(c_2(q\mu'(q)+\mu(q))+\mu(q)(2q\mu'(q)))/(2c_2+3\mu(q)+\mu'(q)q)\mid 0\leqq\mu(q)q \leqq F(V\limsup_{t\to\infty}C(t))\} \tag{2.13}$$

then there exist positive numbers T, σ_T, X_T, Q_{1T}, Q_{2T} *and nonnegative continuous functions* C_* *and* D_* *on* $[T,\infty)$, *such that* (2.6) *holds and such that the solution of the system* (1.3), (1.8) *on* $t\geqq T$ *with* $\sigma(T)=\sigma_T$, $X(T)=X_T$, $Q_1(T)=Q_{1T}$, $Q_2(T)=Q_{2T}$ *and* C *and* D *replaced by* C_* *and* D_* *satisfies*

$$\lim_{t\to\infty}\Big(|X(t)-M(t,\mathbf{R}^+)|+\Big|Q_1(t)X(t)-\int_{\mathbf{R}^+\times\mathbf{R}^+}q_1\,dM(t,q_1q_2)\Big| +\Big|Q_2(t)X(t)-\int_{\mathbf{R}^+\times\mathbf{R}^+}q_2\,dM(t,q_1q_2)\Big|\Big)=0. \tag{2.14}$$

Moreover, either $\lim_{t\to\infty}M(t,\mathbf{R}^+\times\mathbf{R}^+)=0$ *or* $\lim_{t\to\infty}\operatorname{diam}(\operatorname{supp}(M(t,\cdot)))=0$.

It is not at all clear whether the assumption (2.13), (or something similar to it) is really essential for the assertion of Theorem 3 to hold. But observe that this condition is not needed in the next result where the asymptotic behaviour of the system (1.3), (1.8) is studied.

THEOREM 4

Assume that $V>0$, $\sigma_0>0$, $c_1>0$, $c_2\geqq 0$, $X_0>0$, $Q_{10}\geqq 0$, $Q_{20}\geqq 0$, $(Q_{10}+Q_{20})X_0\leqq\sigma_0$, $D_\infty>0$, $C_\infty>0$, (2.1), (2.3), (2.8) *and* (2.11) *hold and that*

there exists a unique number $Q_{2\infty}$ *such that* $\mu(Q_{2\infty})=D_\infty$ *and a unique number* X_∞ *such that* $(F(C_\infty V-(Q_{1\infty}+Q_{2\infty})X_\infty)=D_\infty(Q_{1\infty}+Q_{2\infty})$ *where* $C_1Q_{1\infty}=(C_2+D_\infty)Q_{2\infty}$. (2.15)

Then the solution of the system (1.3), (1.8) *on* $t\geqq 0$ *with* $X(0)=X_0$, $Q_1(0)=Q_{10}$, $Q_2(0)=Q_{20}$ *and* $\sigma(0)=\sigma(0)$ *satisfies*

$$\lim_{t\to\infty}(X(t),Q_1(t),Q_2(t),\sigma(t))=(X_\infty,Q_{1\infty},Q_{2\infty},C_\infty V). \tag{2.16}$$

3. PROOF OF THEOREM 1

From eqn (1.3) we see that if $\sigma(0)=\sigma_0$, then

$$\sigma(t)=\exp\Big(-\int_0^t D(s)\,ds\Big)\sigma_0+V\int_0^t\exp\Big(-\int_s^t D(\tau)\,d\tau\Big)D(s)C(s)\,ds,\quad t\geqq 0. \tag{3.1}$$

It follows from (2.1) and (3.1), as $\sigma_0>0$, that

$$0<\sigma(t)\leqq\max\{\sigma_0,\sup_{t\geqq 0}C(t)V\}\overset{\text{def}}{=}\sigma_m<\infty. \tag{3.2}$$

By (2.2)–(2.4) there exists a number α such that

$$\operatorname{supp}(m_0)\subset[0,\alpha],\quad q\mu(q)>f(q,\sigma_m),\quad q\geqq\alpha. \tag{3.3}$$

We are going to solve eqn (1.1) using the method of characteristics and therefore we consider the following system of equations:

$$y'(t,\lambda) = (\mu(p(t,\lambda)) - D(t))y(t,\lambda), \quad y(0,\lambda)=1$$

$$p'(t,\lambda) = -\mu(p(t,\lambda))p(t,\lambda) + f(p(t,\lambda), \tag{3.4}$$

$$\sigma(t) - z(t)), \quad p(0,\lambda) = \lambda$$

$$z(t) = \int_{[0,\alpha]} p(t,\lambda)y(t,\lambda)\,\mathrm{d}m_0(\lambda), \quad \lambda \in [0,\alpha], \quad t \geqq 0.$$

If we extend the functions μ and f in a suitable manner to $\mathbf{R}$ and $\mathbf{R}\times\mathbf{R}$, then it follows from standard results that this system has at least a local, continuously differentiable, unique solution that depends continuously on the parameter λ. If we can prove that

$$0 \leqq p(t,\lambda) \leqq \alpha, \quad 0 \leqq z(t) \leqq \sigma(t), \tag{3.5}$$

as long as the solution exists, then we get a global solution. To establish (2.5) we first observe that by (1.3) and (3.4) we have

$$\sigma'(t) - z'(t) = D(t)C(t)V - D(t)(\sigma(t) - z(t))$$

$$-\int_{\mathbf{R}^+} f(p(t,\lambda), \sigma(t) - z(t))y(t,\lambda)\,\mathrm{d}m_0(\lambda), \quad t \geqq 0.$$

From this equation we conclude with the aid of (2.1), (2.2), (2.4) and the fact that $y(t,\lambda) > 0$ that $\sigma(t) - z(t) \geqq 0$. If we moreover note that $z(t) \geqq 0$ provided that $p(t,\lambda) \geqq 0$ for all λ, then we can derive the remaining assertion of (3.5) from (2.1)–(2.3) using the standard argument that at the boundary the derivative points into the region claimed to be invariant. Thus the existence of a unique global solution of (3.4) satisfying (3.5) has been established.

We define the measure $m(t,\cdot)$ as follows: $m(t,E) = \int_{E_t} y(t,\lambda)\,\mathrm{d}m_0(\lambda)$, where $E_t = \{\lambda \in [0,\alpha] \mid p(t,\lambda) \in E\}$. We see that $m(t,\cdot)$ is a finite, nonnegative Borel measure on $\mathbf{R}$ with support contained in $[0,\alpha]$. If ψ is a continuous function on $\mathbf{R}^+$, then it follows from our definition that $\int_{\mathbf{R}^+} \psi(q)\,\mathrm{d}m(t,q) = \int_{[0,\alpha]} \psi(p(t,\lambda))y(t,\lambda)\,\mathrm{d}m_0(\lambda)$. Denote this function by v. If ψ is continuously differentiable, this is true for v too and a calculation involving (1.2) and (3.4) shows that

$$v'(t) = \int_{\mathbf{R}^+} (\psi'(q)g(q,\sigma(t) - z(t)) + \psi(q)(\mu(q) - D(t)))\times\,\mathrm{d}m(t,q).$$

Multiply this equation by $\varphi(t)$, where φ is an arbitrary continuously differentiable function with compact support on $\mathbf{R}$, and integrate over $\mathbf{R}^+$. This yields after an intergation by parts

$$-\int_{\mathbf{R}^+}\int_{\mathbf{R}^+} \varphi'(t)\psi(q)\,\mathrm{d}m(t,q)\,\mathrm{d}t - \int_{\mathbf{R}^+} \varphi(0)\psi(q)\,\mathrm{d}m_0(t,q)$$

$$-\int_{\mathbf{R}^+}\int_{\mathbf{R}^+} \varphi(t)\psi'(q)g(q,\sigma(t) - z(t))\,\mathrm{d}m(t,q)\,\mathrm{d}t$$

$$= \int_{\mathbf{R}^+}\int_{\mathbf{R}^+} \varphi(t)\psi(q)(\mu(q) - D(t))\,\mathrm{d}m(t,q)\,\mathrm{d}t.$$

Using this result we are able to see that eqn (1.1) holds in the distribution sense because smooth functions of two variables can be approximated by sums of functions of the form $\varphi(t)\psi(q)$ and it follows from the definitions that $z(t) = s(t)$.

To establish the uniqueness we proceed as follows. Suppose that the measure $m(t, \cdot)$ is a solution of the system (1.1)–(1.3). Let $y(t, \lambda)$ and $p(t, \lambda)$ be the solutions of the first two equations in (3.4) with $z(t) = \int_{\mathbf{R}^+} q \, dm(t, q)$. Now we define the measure $m_1(t, \cdot)$ by

$$\int_{[0, \alpha]} \psi(p(t, \lambda))y(t, \lambda) \, dm_1(t, \lambda) = \int_{\mathbf{R}^+} \psi(q) \, dm(t, q).$$

A calculation shows that if Ψ is a smooth function with compact support in $\mathbf{R} \times \mathbf{R}$, then

$$\begin{aligned}\int_{\mathbf{R}^+} \int_{[0, \alpha]} \frac{d}{dt} (\Psi(t, p(t, \lambda))y(t, \lambda)) \, dm_1(t, \lambda) \, dt \\ = -\int_{[0, \alpha]} \Psi(0, p(0, \lambda))y(0, \lambda) \, dm_1(0, \lambda) \, dt \\ = -\int_{[0, \alpha]} \Psi(0, q) \, dm_0(q).\end{aligned}$$

Since $y(t, \lambda) > 0$ we can choose Ψ such that $\Psi(t, p(t, \lambda))y(t, \lambda) = \varphi(t)\psi(\lambda)$ for some functions φ and ψ and hence

$$\int_{\mathbf{R}^+} \varphi'(t) \int_{[0, \alpha]} \psi(\lambda) \, dm_1(t, \lambda) \, dt = -\varphi(0) \int_{[0, \alpha]} \psi(q) \, dm_0(q).$$

It follows that $m_1(t, \cdot) = m_0$ and then the assertion concerning uniqueness follows from the uniqueness of the solutions of equation (2.4) and the fact that $z(t) = s(t)$.

From now on we assume that (2.5) holds and next we will show that $\limsup_{t \to \infty} m(t, \mathbf{R}^+) < \infty$. Choose a number τ so large that there exists a positive number d such that $D(t) \geqq d$, $t \geqq \tau$. Let $q_0 = \sup \{q \mid \mu(q) \leqq d/2\}$. Now we claim that

$$m(t, \mathbf{R}^+) \leqq \max \{2(\mu(\alpha) - d/2)\sigma_m/(dq_0), m(\tau, \mathbf{R}^+)\}, \; t \geqq \tau. \tag{3.6}$$

It follows from the definition of the measure $m(t, \cdot)$ and (3.4) that

$$d/dt \, m(t, \mathbf{R}^+) = \int_{[0, \alpha]} (\mu(p(t, \lambda)) - D(t))y(t, \lambda) \, dm_0(\lambda), \quad t \geqq 0. \tag{3.7}$$

By (3.2), (3.4) and (3.5) it follows that

$$\int_{A_t} y(t, \lambda) \, dm_0(\lambda) \leqq \sigma/q_0$$

where (3.8)

$$A_t = \{\lambda \mid p(t, \lambda) \geqq q_0\}.$$

Since $D(t) \geqq d$, $t \geqq \tau$ and $\mu(p(t, \lambda)) \leqq \mu(\alpha)$, it follows from (3.7), (3.8) and the definition of q_0 that if (3.6) is not satisfied for some $t > \tau$ then $d/dt \, m(t, \mathbf{R}^+) < 0$ and we get a contradiction. Thus we have established (3.6).

Next we observe that it follows from (2.2), (2.3), (3.4) and (3.5) that $p(t, \lambda)$ is a nondecreasing function of λ. Moreover if $w(t) = p(t, \alpha) - p(t, 0)$, then $w'(t) \leqq -\mu(p(t, \alpha))w(t)$. Thus we see that if $w(t)$ does not converge to zero, then $\int_0^\infty \mu(p(t, \alpha)) \, dt < \infty$ and then it follows from (3.4) that $\lim_{t \to \infty} y(t, \lambda) \to 0$ uniformly in λ because $\int_0^\infty D(t) \, dt = +\infty$ by (2.5) and $\mu(p(t, \lambda)) \leqq \mu(p(t, \alpha))$. But then $\lim_{t \to \infty} m(t, \mathbf{R}^+) = 0$ and we get the last assertion of Theorem 1 because $\operatorname{supp}(m(t, \cdot)) \subset [p(t, 0), p(t, \alpha)]$.

By the results above we have either $\lim_{t \to \infty} w(t) = 0$ or $\int_0^\infty \mu(p(t, \alpha)) \, dt < \infty$ so that in both cases it follows that $\lim_{t \to \infty} (\mu(p(t, 0)) - \mu(p(t, \lambda))) = 0$ uniformly in λ, (because $p(t, \lambda)$ is a

Lipschitz continuous function of t). Thus, if T is sufficiently large, then the function D_* defined by

$$D_*(t) = D(t) + \int_{[0,\alpha]} (\mu(p(t,0)) - \mu(p(t,\lambda)))y(t,\lambda)\,dm_0(\lambda)/m(t,\mathbf{R}^+)$$

is nonnegative, continuous and bounded on $\mathbf{R}^+$ and moreover $\lim_{t\to\infty}(D_*(t) - D(t)) = 0$. Thus if we take $X_T = m(T,\mathbf{R}^+)$ then $X(t) = m(t,\mathbf{R}^+)$ satisfies the first equation in (1.4) when D is replaced by D_*. We take $Q_T = p(T,0)$ and then $Q(t) = p(t,0)$ satisfies the second equation provided that we choose C_* so that the corresponding solution σ_* of (3.1) satisfies $\sigma_*(t) - Q(t)X(t) = \sigma(t) - s(t)$. If T is sufficiently large we can choose such a nonnegative continuous and bounded function C_* on $[T,\infty)$ because it is straightforward to check that

$$\lim_{t\to\infty}(|Q(t)X(t) - s(t)| + |\,d/dt(Q(t)X(t) - s(t))|)$$

$$\leqq \lim_{t\to\infty}\Big(\int_{[0,\alpha]} |p(t,0) - p(t,\lambda)|y(t,\lambda)\,dm_0(\lambda)$$

$$+ \int_{[0,\alpha]} (|p'(t,0) - p'(t,\lambda)|$$

$$+ |p(t,0) - p(t,\lambda)||(p(t,\lambda)) - D(t)|)y(t,\lambda)\,dm_0(\lambda)\Big) = 0$$

either because $\lim_{t\to\infty} w(t) = 0$ or $\lim_{t\to\infty} m(t,\mathbf{R}^+) = 0$. This completes the proof of Theorem 1.

4. PROOF OF THEOREM 2

It follows from the proof of Theorem 1, that we can apply Theorem 1 to the system (1.3), (1.4) by taking m_0 to be a measure with total mass X_0 concentrated at Q_0. Thus we conclude that $Q(t)$ and $X(t)$ remain bounded an $\mathbf{R}^+$, but we must also show that

$$\liminf_{t\to\infty} X(t) > 0. \tag{4.1}$$

It follows from (3.1) and (2.8) that

$$\lim_{t\to\infty} \sigma(t) = C_\infty V. \tag{4.2}$$

By (2.2), (2.3) and (2.9) there exists a positive number δ such that

$$\mu(q)q \leqq f(q, C_\infty V - Q_\infty X_\infty/2) + \delta \text{ if } q \leqq Q_\infty + \delta. \tag{4.3}$$

From (2.8), (2.9) and (4.2) we see that we can choose τ to be so large that

$$\sigma(t) \geqq C_\infty V - Q_\infty X_\infty/4,\ D(t) < \mu(Q_\infty + \delta), \quad t \geqq \tau.$$

But then we conclude from (1.4), (2.2) and (4.3) that if $t \geqq \tau$, $X(t) \leqq X_\infty Q_\infty/(4(Q_\infty + \delta))$ and $Q(t) \leqq Q_\infty + \delta$, then $Q'(t) \geqq \delta$ and if $Q(t) \geqq Q_\infty + \delta$, then $X'(t) > 0$. If we combine this result with the fact that $X(t) \geqq X(s)\exp(-(t-s)\sup_{r\geqq 0} D(r))$, then we see that (4.1) holds.

Let

$$v(t) = X(t) - X_\infty, \quad u(t) = Q(t)X(t) - Q_\infty X_\infty.$$

From this definition, (1.4) and (2.9) we conclude that

$$\begin{aligned} v'(t) &= k_1(t)(u(t) - Q_\infty v(t)) + e_1(t) \\ u'(t) &= -(D_\infty + k_2(t))(u(t) - Q_\infty v(t)) - k_3(t)u(t) + e_2(t) \end{aligned} \tag{4.4}$$

where

$$k_1(t) = (\mu(Q(t)) - \mu(Q_\infty))/(Q(t) - Q_\infty),$$

$$k_2(t) = (f(Q_\infty, C_\infty V - Q(t)X(t))$$

$$- f(Q(t), C_\infty V - Q(t)X(t)))/(Q(t) - Q_\infty), \tag{4.5}$$

$$k_3(t) = (f(Q_\infty, C_\infty V - Q_\infty X_\infty) - f(Q_\infty, C_\infty V - Q(t)X(t)))X(t)/u(t),$$

$$e_1(t) = (D_\infty - D(t))X(t), \; e_2(t) = (f(Q(t), \sigma(t) - Q(t)X(t))$$

$$- f(Q(t), C_\infty V - Q(t)X(t)))X(t) + (D_\infty - D(t))Q(t)X(t).$$

It is clear that the functions k_j are continuous and bounded and moreover we deduce from (2.2), (2.3), (2.9), (4.1), (4.2) and (4.5) that

$$\lim_{t\to\infty} e_j(t) = 0 \quad j = 1, 2, \tag{4.6}$$

and

$k_2(t) \geqq 0$, $t \geqq 0$ and for each $\epsilon > 0$ there exists a number $\delta(\epsilon) > 0$ such that $k_1(t) \geqq \delta(\epsilon)$ if $|u(t) - Q_\infty v(t)| \geqq \epsilon$ and $k_3(t) \geq \delta(\epsilon)$ if $|u(t)| \geqq \epsilon$. (4.7)

Let $\epsilon > 0$ be arbitrary and choose

$$\epsilon_1 = \delta(\epsilon)/(2(D_\infty + \sup_{t\geq 0} k_2(t))). \tag{4.8}$$

Define $L(t) = \max\{|u(t)|, Q_\infty|v(t)|/(1+\epsilon_1)\}$. From (4.6) we see that if T is sufficiently large, then

$$|e_1(t)| \leqq \epsilon_1\epsilon\delta(\epsilon_1\epsilon)/2, \; |e_2(t)| \leqq \epsilon\delta(\epsilon)/4, \quad t \geqq T'. \tag{4.9}$$

Suppose that $t > T$ and $L(t) > \epsilon$. If $L(t) = Q_\infty|v(t)|/(1+\epsilon_1)$, then by (4.4), (4.7) and (4.9)

$$\mathrm{d}/\mathrm{d}t|v(t)| \leqq -\epsilon\epsilon_1\delta(\epsilon\epsilon_1)/2$$

and if $L(t) = |u(t)|$, then (4.4), (4.7), (4.8) and (4.9) imply that

$$\mathrm{d}/\mathrm{d}t|u(t)| \leqq -\epsilon\delta(\epsilon)/4.$$

Combining these two cases we see that if $L(t) > \epsilon$, then

$$L'(t) \leqq -\min\{Q_\infty\epsilon\epsilon_1\delta(\epsilon\epsilon_1)/2(1+\epsilon_1), \epsilon\delta(\epsilon)/4\}.$$

Therefore $\limsup_{t\to\infty} L(t) \leqq \epsilon$ and since ϵ was arbitrary and ϵ_1 remains bounded as $\epsilon \to 0$ we deduce from the definitions of L, v and u that the assertion of Theorem 2 holds.

5. PROOF OF THEOREM 3

We observe that (3.1) and (3.2) still hold and that we now can find numbers α_1 and α_2 such that

$$\begin{gathered} \operatorname{supp}(M_0) \subset [0, \alpha_1] \times [0, \alpha_2] \overset{\text{def}}{=} A \\ c_2\alpha_2 + F(\sigma_m) < c_1\alpha_1 < (c_2 + \mu(\alpha_2))\alpha_2. \end{gathered} \tag{5.1}$$

Again we use the method of characteristics to solve equation (1.5) and therefore we consider the following system of equations

$$\begin{aligned}
&y'(t,\Lambda) = (\mu(p_2(t,\Lambda)) - D(t))y(t,\Lambda), \quad y(0,\Lambda) = 1\\
&p_1'(t,\Lambda) = -(c_1 + \mu(p_2(t,\Lambda)))p_1(t,\Lambda) + c_2p_2(t,\Lambda)\\
&\qquad + F(\sigma(t) - z(t)), \quad p_1(0,\Lambda) = \lambda_1\\
&p_2'(t,\Lambda) = c_1p_1(t,\Lambda) - (c_2 + \mu(p_2(t,\Lambda)))p_2(t,\Lambda), \; p_2(0,\Lambda) = \lambda_2\\
&z(t) = \int_A (p_1(t,\Lambda) + p_2(t,\Lambda))y(t,\Lambda)\,\mathrm{d}M_0(\Lambda),\\
&t \geqq 0, \quad \Lambda = (\lambda_1,\lambda_2) \in A.
\end{aligned} \tag{5.2}$$

Using (1.3), (3.2), (5.1), (5.2) and arguments similar to the ones employed in the proof of Theorem 1, we see that the system (5.2) has a unique global solution on $\mathbf{R}^+$ such that

$$y(t,\Lambda) > 0, (p_1(t,\Lambda), p_2(t,\Lambda)) \in A, 0 \leqq z(t) \leqq \sigma(t), t \geqq 0. \tag{5.3}$$

We define the measure $M(t,\cdot)$ by $M(t,E) = \int_{E_t} y(t,\Lambda)\,\mathrm{d}M_0(\Lambda)$, $E \subset \mathbf{R}^+ \times \mathbf{R}^+$ where $E_t = \{\Lambda \in A | (p_1(t,\Lambda), p_2(t,\Lambda)) \in E\}$. Then we deduce that $M(t,\cdot)$ is a Borel measure on $\mathbf{R} \times \mathbf{R}$ with support in the compact set $A (= [0,\alpha_1] \times [0,\alpha_2])$, see (5.3). In the same way as in the proof of Theorem 1 we can show that we have thus found a solution of the system (1.3), (1.5)–(1.7) that has the desired continuity and uniqueness properties.

Next we assume that (2.5) holds and we can use almost the same proof as in Theorem 1 to show that $m(t,\mathbf{R}^+)$ remains bounded as $t \to \infty$.

Suppose now that (2.13) holds. It follows from (2.3), (5.2) and standard results that the functions $p_1(t,\Lambda)$ and $p_2(t,\Lambda)$ are continuously differentiable with respect to Λ. Let

$$\begin{aligned}
&w_1(t,\Lambda) = \partial p_1(t,\Lambda)/\partial\Lambda + c_1^{-1}\mu(p_2(t,\Lambda))\partial p_2(t,\Lambda)/\partial\Lambda\\
&w_2(t,\Lambda) = \partial p_2(t,\Lambda)/\partial\Lambda, \; w(t,\Lambda) = (w_1(t,\Lambda), w_2(t,\Lambda))
\end{aligned} \tag{5.4}$$

where the derivates in question are Frechet derivates. From (5.2) we deduce that w satisfies the equation

$$w'(t,\Lambda) = B(t,\Lambda)w(t,\Lambda) \tag{5.5}$$

where

$$\begin{aligned}
&B(t,\Lambda) = (b_{ij}(t,\Lambda)) \text{ with } b_{11}(t,\Lambda) = -c_1, \; b_{21}(t,\Lambda) = c_1\\
&b_{12}(t,\Lambda) = c_2(1 - (p_2(t,\Lambda)\mu'(p_2(t,\Lambda)) + \mu(p_2(t,\Lambda)))/c_1)\\
&\qquad + \mu(p_2(t,\Lambda))(1 - (2p_2(t,\Lambda)\mu'(p_2(t,\Lambda))\\
&\qquad + \mu(p_2(t,\Lambda)))/c_1),\\
&b_{22}(t,\Lambda) = -(c_2 + 2\mu(p_2(t,\Lambda)) + p_2(t,\Lambda)\mu'(p_2(t,\Lambda))).
\end{aligned} \tag{5.6}$$

Let $I(t,\Lambda) = \|w_1(t,\Lambda)\| + \|w_2(t,\Lambda)\|$; ($\|\ \|$ denotes some operator, i.e. matrix, norm on $\mathbf{R}^2$). Then we see that I is an absolutely continuous function and from (5.5) and (5.6) we have

$$I'(t,\Lambda) \leqq (b_{22}(t,\Lambda) + |b_{12}(t,\Lambda)|)\|w_2(t,\Lambda\|, \text{ a.e. } t \geqq 0. \tag{5.7}$$

In order to be able to use the assumption (2.13) we need some estimates on $p_2(t, \Lambda)$ for large t. It follows from (2.5) and (3.1) that

$$\limsup_{t\to\infty} \sigma(t) \leqq V \limsup_{t\to\infty} C(t).$$

This inequality combined with (2.3), (2.11) and (5.2) implies that for each $\delta_1 > 0$, there exists a number τ_1, independent of Λ, such that $c_1 p_1(t, \Lambda) - c_2 p_2(t, \Lambda) \leqq F(V \limsup_{t\to\infty} C(t)) + \delta_1$, $t \geqq \tau_1$, and therefore it follows from (2.3) and (5.2) that for each $\delta_2 > 0$, there exists a number τ_2, independent of Λ, such that

$$p_2(t, \Lambda)\mu(p_2(t, \Lambda)) \leqq F(V \limsup_{t\to\infty} C(t)) + \delta_2, \quad t \geqq \tau_2.$$

Thus we conclude from (2.3), (2.13), (5.6) and (5.7) by choosing δ_2 to be sufficiently small that there exists a number $\epsilon > 0$ such that

$$I'(t, \Lambda) \leqq -\epsilon\mu(p_2(t, \Lambda))\|w_2(t, \Lambda\|, \text{ a.e. } t \geqq \tau_2, \quad \Lambda \in A. \tag{5.8}$$

We can immediately conclude that $w(t, \Lambda)$ is uniformly bounded with respect to Λ as $t \to \infty$ and therefore $\mu(p_2(t, \Lambda))\|w_2(t, \Lambda)\|$ is a Lipschitz continuous function of t, see (5.2) and (5.5). Thus we see that if for some Λ_0, $\lim_{t\to\infty} I(t, \Lambda_0) = \delta > 0$, then $\lim_{t\to\infty} \mu(p_2(t, \Lambda_0))\|w_2(t, \Lambda_0)\| = 0$. From (5.5) and (5.6) we then have, because $I(t, \Lambda_0)$ is nonincreasing on (τ_2, ∞) that if $t \geqq \tau_2$ and $\|w_2(t, \Lambda_0)\| \leqq \delta \min\{1, c_1/\sup_{t>0}|b_{1\,2}(t, \Lambda_0)|\}/4$ then $\mathrm{d}/\mathrm{d}t\|w_1(t, \Lambda_0\| \leqq -c_1\delta/2$. Because $\|w_2(t, \Lambda_0)\|$ is Lipschitz continuous, we conclude that we cannot have $\liminf_{t\to\infty} \|w_2(t, \Lambda_0)\| = 0$. Therefore we have proved, recall the definitions of I and w, that

$$\begin{gathered}\text{either } \lim_{t\to\infty} \mu(p_2(t, \Lambda)) = 0 \text{ or} \\ \lim_{t\to\infty} \|\partial p_j(t, \Lambda)/\partial\Lambda\| = 0 \quad j = 1, 2.\end{gathered} \tag{5.9}$$

Assume next that $\limsup_{t\to\infty} M(t, \mathbf{R}^+ \times \mathbf{R}^+) > 0$. Then there must exist an index $\Lambda_1 \in A$ such that $\liminf_{T\to\infty} \int_0^T (\mu(p_2(t, \Lambda_1)) - D(t))\,\mathrm{d}t > -\infty$. But then it is in view of (2.3), (2.5) and (5.3) possible to find a constant $\delta > 0$ such that

$$\liminf_{T\to\infty} \int_0^T (\mu(p_2(t, \Lambda_1))(p_1(t, \Lambda_1) + p_2(t, \Lambda_1)) - \delta)\,\mathrm{d}t > -\infty. \tag{5.10}$$

If we define $p(t, \Lambda) = p_1(t, \Lambda) + p_2(t, \Lambda)$ then we have by (5.2) the equation

$$p'(t, \Lambda) = F(\sigma(t) - z(t)) - \mu(p_2(t, \Lambda)p(t, \Lambda), \ t \geqq 0. \tag{5.11}$$

Since $p(t, \Lambda_1)$ is bounded, see (5.3), it follows from (5.10) and (5.11), (with $\Lambda = \Lambda_1$), that

$$\liminf_{T\to\infty} \int_0^T (F(\sigma(t) - z(t)) - \delta)\,\mathrm{d}t > -\infty.$$

But this inequality combined with (5.3) and (5.11) implies that there is no $\Lambda \in A$ such that $\lim_{t\to\infty} \mu(p_2(t, \Lambda)) = 0$. Thus we deduce from (5.9) that either $\lim_{t\to\infty} M(t, \mathbf{R}^+ \times \mathbf{R}^+) = 0$ or $\lim_{t\to\infty} \|\partial p_j(t, \Lambda)/\partial\Lambda\| = 0$, $j = 1, 2$, $\Lambda \in A$. In the second case it follows that $\lim_{t\to\infty} \operatorname{diam}(\operatorname{supp}(M(t, \cdot))) = 0$ because $p_j(t, \Lambda)$ is Lipschitz continuous with respect to Λ, uniformly with respect to $t \in \mathbf{R}^+$. The remaining assertion of Theorem 3 can be established in the same way as the corresponding ones in Theorem 1. This completes the proof of Theorem 3.

6. PROOF OF THEOREM 4

In the same way as in the proof of Theorem 2 we observe that we can deduce from the results in the proof of Theorem 3 that

$$\begin{gathered} 0 \leqq Q_j(t) \leqq \alpha_j, \ 0 \leqq (Q_1(t) + Q_2(t))X(t) \leqq \sigma(t), \\ X(t) > 0, \ t \geqq 0 \text{ and } \sup_{t\geqq 0} X(t) < \infty. \end{gathered} \tag{6.1}$$

We proceed to show that (4.1) holds and therefore we study the following system of equations

$$\begin{aligned} y_1'(t) &= -(c_1+\mu(y_2))y_1 + c_2y_2 + F(VC_\infty) \\ y_2'(t) &= c_1y_1 - (c_2+\mu(y_2))y_2, \quad t \geqq 0. \end{aligned} \tag{6.2}$$

Since $VC_\infty \leqq \sigma_m$ it follows from (2.3), (2.11) and (5.1) that $[0, \alpha_1] \times (0, \alpha_2]$ is an invariant set for (6.2). Moreover, by (2.3), (2.11) and (2.15) there exists a unique equilibrium point $(Y_1, Y_2) \in (0, \alpha_1) \times (0, \alpha_2)$ such that $Y_2 > Q_{2\infty}$. Using ([8], Lemma VI 3.1) we see that every nontrivial periodic solution of (6.2) in $[0, \alpha_1] \times [0, \alpha_2]$ is asymtotically orbitally stable. Since the equilibrium point is unique and asymptotically stable, because the eigenvalues of the linearized equation have negative real parts, it follows from the Poincaré-Bendixson theorem, see ([8], Chap. II), that the point (Y_1, Y_2) is globally attractive in $[0, \alpha_1] \times [0, \alpha_2]$. Now we are able to conclude, using the facts that the eigenvalues of the equation (6.2) linearized around the equilibrium point have strictly negative real parts and that the set $[0, \alpha_1] \times [0, \alpha_2]$ is compact that if $\epsilon > 0$ is given, then there exist numbers $\tau(\epsilon)$ and $\gamma(\epsilon)$ such that if

$$|\sigma(t) - Q(t)X(t) - VC_\infty| < \gamma(\epsilon),\ t \in [t_2, t_1],\ t_2 - t_1 > \tau(\epsilon) \tag{6.3}$$

then the solution $Q_1(t)$, $Q_2(t)$ of (1.8) satisfies

$$|Q_1(t) - Y_1| + |Q_2(t) - Y_2| < \epsilon,\ t \in [t_1 + \tau(\epsilon), t_2]. \tag{6.4}$$

Since (4.2) holds and $X(t) \geqq X(s)\exp(-(t-s)\sup_{r\geqq 0} D(r))$ we see that if $\liminf_{t\to\infty} X(t) = 0$, then we can for arbitrarily small $\epsilon > 0$ find an interval $[t_1, t_2]$ such that (6.3) holds and $X'(t_2) \leqq 0$. But since $Y_2 > Q_{2\infty}$ and (2.15) hold we see from (6.4) that if ϵ is sufficiently small, then $X'(t) > 0$ on $[t_1 + \tau(\epsilon), t_2]$ and we have a contradiction. Thus we see that (4.1) holds.

We proceed in the same manner as in the proof of Theorem 2 and we define

$$\begin{aligned} &Q(t) = Q_1(t) + Q_2(t), \quad Q_\infty = Q_{1\infty} + Q_{2\infty}, \quad v(t) = X(t) - X_\infty \\ &u(t) = Q(t)X(t) - Q_\infty X_\infty, \quad w(t) = Q_2(t)X(t) - Q_{2\infty}X_\infty. \end{aligned}$$

From (1.8), (2.15) and this definition we see that

$$\begin{aligned} v'(t) &= k_1(t)(w(t) - Q_{2\infty}v(t)) + e_1(t) \\ w'(t) &= c_1u(t) - (c_1 + c_2 + D_\infty)w(t) + e_2(t) \\ u'(t) &= -D_\infty(u(t) - Q_\infty v(t)) - k_2(t)u(t) + e_3(t) \end{aligned} \tag{6.5}$$

where

$$\begin{aligned} &k_1(t) = (\mu(Q_2(t)) - \mu(Q_{2\infty}))/(Q_2(t) - Q_{2\infty}) \\ &k_2(t) = (F(VC_\infty - Q_\infty X_\infty) - F(VC_\infty - Q(t)X(t)))X(t)/u(t) \\ &e_1(t) = (D_\infty - D(t))X(t),\ e_2(t) = (D_\infty - D(t))Q_2(t)X(t) \\ &e_3(t) = (F(\sigma(t) - Q(t)X(t)) - F(VC_\infty - Q(t)X(t)))X(t) + (D_\infty - D(t))Q(t)X(t). \end{aligned} \tag{6.6}$$

Again we observe that the functions k_j and e_j are bounded and continuous and from (2.3), (2.11), (2.15), (4.1), (4.2) and (6.6) we see that

$$\lim_{t\to\infty} e_j(t) = 0, \quad j = 1, 2, 3, \tag{6.7}$$

and

for each $\epsilon > 0$ there exists $\delta(\epsilon) > 0$ such that $k_1(t) \geqq \delta(\epsilon)$ if $|w(t) - Q_{2\infty}v(t)| \geqq \epsilon$ and $k_2(t) \geqq \delta(\epsilon)$ if $|u(t)| \geqq \epsilon$. (6.8)

Let $\epsilon > 0$ be arbitrary and choose $\epsilon_1 > 0$ so that

$$2\epsilon_1 + \epsilon_1^2 = \delta(\epsilon)/(2D_\infty). \tag{6.9}$$

Define

$$L(t) = \max\{|u(t)|, Q_\infty|w(t)|/(Q_{2\infty}(1+\epsilon_1)), Q_\infty|v(t)|/(1+\epsilon_1)^2\}. \tag{6.10}$$

By (6.7) we can choose T to be so large that

$$\begin{aligned} &|e_1(t)| \leqq \epsilon\epsilon_1(1+\epsilon_1)Q_{2\infty}\delta(\epsilon\epsilon_1(1+\epsilon_1)Q_{2\infty}/Q_\infty)/(2Q_\infty), \\ &|e_2(t)| \leqq c_1\epsilon\epsilon_1/2, |e_3(t)| \leqq \epsilon\delta(\epsilon)/4, \quad t \geqq T. \end{aligned} \tag{6.11}$$

If we proceed in almost exactly the same manner as in the proof of Theorem 2 and use the fact that $c_1Q_\infty = (c_1 + c_2 + D_\infty)Q_{2\infty}$, see (2.15), then we deduce from (6.5) and (6.8)–(6.11) that if $t > T$ and $L(t) > \epsilon$, then

$$L'(t) \leqq -\min\{\epsilon\epsilon_1(1+\epsilon_1)Q_{2\infty}\delta(\epsilon\epsilon_1(1+\epsilon_1)Q_{2\infty}/Q_\infty)/2, c_1\epsilon\epsilon_1Q_\infty/(2Q_{2\infty}(1+\epsilon_1)), \epsilon\delta(\epsilon)/4\}.$$

Therefore it follows that $\limsup_{t\to\infty} L(t) \leqq \epsilon$ and since ϵ was arbitrary and ϵ_1 remains bounded as $\epsilon \to 0$ we get the desired assertion from the definitions.

This completes the proof of Theorem 4.

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