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Equilibrium Solutions of Age-Specific Population Dynamics of Several Species

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Summary. A mathematical model describing the dynamics of a population consisting of several species is studied. The interactions in the population are assumed to be age-specific. Using an evolution equation approach, sufficient conditions for well-posedness in L^1 of the dynamics and for existence as well as for stability of equilibrium solutions are given.

Key words: Population dynamics – Age-dependent models – Equilibrium solutions – Stability – Evolution equations

0. Introduction

In this paper we study a mathematical model of a population consisting of n species with age-specific interactions. The dynamics of such a population is described by means of density functions $u_i(t, x)$, where t denotes time, x stands for age and i indicates the ith species. The governing equations for this model are

$$u_t^i(t,x) + u_x^i(t,x) + d_i(x)u^i(t,x) + f_i(x, u(t))u^i(t,x) = 0, \tag{1a}$$

$$u^i(t,0) = \int_0^\infty b_i(x)u^i(t,x)\,dx, \qquad t, x \geqslant 0, \tag{1b}$$

$$u^i(0,x) = u_0^i(x), \qquad i = 1, \ldots, n. \tag{1c}$$

The functions $b^i(x)$ and $d^i(x)$ denote the age-dependent "natural" vital (birth and death) rates of the ith species, where "natural" means that no interactions in the population occur. The function $f_i(x, u)$ describes the increase of death rate of the ith species resulting from interactions in the standing population u. Hence all quantities $b_i(x)$, $d_i(x)$, $f_i(x, u)$ are nonnegative and $f_i(x, 0) \equiv 0$ for all i. Since $u^i(t, x)$ represents a density, $u^i(t, x)$ should be nonnegative for all x, t. Furthermore, since $n^i(t) = \int_0^\infty u^i(t, x)\,dx$ is the total number of individuals of the ith species in the population, we should have $u^i(t, \cdot) \in L^1(\mathbb{R}_+)$ for all t, i.

The nonlinearity $f(x, u)$ has the general form

$$(F) \qquad f(x,u) = g\left(x, \int_0^\infty k(x,y)h(y,u(y))\,dy\right)$$

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where h: $\mathbb{R}_+^{n+1} \to \mathbb{R}_+^m$, k: $\mathbb{R}_+^2 \to \mathbb{R}_+^{m_1 m}$, g: $\mathbb{R}_+^{m_1+1} \to \mathbb{R}_+^n$; see section 2 for the hypotheses imposed on h, k, g. (F) allows for a reasonable biological interpretation: there are m_1 independent factors $w_j(x)$ which control the death rates: $g_i(x, w(x))$. The values of $w_j(x)$ in turn are determined by the standing population u according to

$$w_j(x) = \sum_{l=1}^{m} \int_0^\infty k_{jl}(x, y) h_l(y, u_1(y), \ldots, u_n(y))\, dy.$$

If $w_j(x) \equiv w_j$ for all j, the interactions are said to be *separable*. In the simplest case one would have $m_1 = n$, $w_j = \int_0^\infty u_j(y)\, dy$, the factors being now just the total sizes of the single species, but certainly such an assumption and even the separability hypothesis (cp. [13]) is too restrictive. It will become clear in section 3 that, as far as existence of equilibrium solutions is concerned, dispensing with separability means a transition from finite to infinite dimensional problems.

Note that we suppose the birth rates $b_i(x)$ to be independent of the standing population u, which perhaps is the most severe restriction in our present approach although it seems to be reasonable in many situations. In a forthcoming paper we shall dispense with this assumption.

The model described above was first proposed by von Foerster [5]; see also the derivation in [6]. For $n = 1$ a detailed analysis may be found in Gurtin and MacCamy [7] who admit $b = b(x, u)$ but assume separability. See also Sowunmi [14]. Coffman and Coleman [2] studied (1) for $n = 1$ under the hypotheses of a specific reproductive age x_f. Di Blasio [1] proved well-posedness of (1) for $n = 1$ with diffusion. For further biological background we refer to Rotenberg [13].

Our approach relies on the theory of semilinear evolution equations and so we consider (1) as an ordinary differential equation in an appropriate Banach space:

$$(P_1) \qquad u' = Au + F(u), \qquad u(0) = u_0.$$

Since $u^i(t, \cdot) \in L^1(\mathbb{R}_+)$ should hold, it is natural to consider $X = (L^1(\mathbb{R}_+))^n$, to choose $(Au)_i(x) = -u_x^i - d_i(x)u^i$, the domain of which will be specified later, and to put $F(u)_i = -f_i(x, u)u^i$. Clearly, A is a linear but unbounded operator in X. Finally, we shall study (P_1) in the standard cone $K \subset X$ since only nonnegative solutions are biological significant.

The linear part A of problem (1) will be studied in section 1. By means of abstract results concerning the initial value problem (P_1) we shall prove well-posedness of (1) in section 2 under mild assumptions on the structural functions d_i, b_i, f_i. In section 3 we shall take up the existence problem for equilibrium solutions of (1), i.e. solutions independent of t. Again, using some abstract invariant set techniques for (P_1), we shall prove a very general existence theorem. Finally, in section 4 we also give some stability results for equilibrium solutions.

Some notations used throughout all of this paper are listed below:

$\mathbb{R}_+^n = \{x \in \mathbb{R}^n: x_i \geqslant 0,\ i = 1, \ldots, n\}$ denotes the standard cone in $\mathbb{R}^n$. For $p \in [1, \infty]$ we let $L^p(a, b)$ be the usual spaces of p-summable functions defined on the interval (a, b), let $L^p = L^p(\mathbb{R}_+)$ for short, and let L_{loc}^p be the set of all measurable functions which are p-summable on compact subsets of $\mathbb{R}_+$. $u \in W^{1,p}(a, b)$ means $u \in L^p(a, b)$ is absolutely continuous with $u' \in L^p(a, b)$, and $W_{\text{loc}}^{1,p}$ is defined similarly as L^p_{loc}. $C[a,b]$ denotes the space of continuous functions defined on $[a,b]$ with values in $\mathbb{R}$ or $\mathbb{C}$. If X is some Banach space, we put $B_R(u) = \{v \in X\colon |u - v| \leqslant R\}$, and $\beta(B)$ denotes the ball-measure of non-compactness of the bounded subset $B \subset X$, i.e.

$$\beta(B) = \inf\{r > 0\colon B \text{ admits a finite covering by } r\text{-balls}\},$$

and for any bounded linear operator $T\colon X \to X$ we put

$$\beta(T) = \beta(TB_1(0)).$$

By $(\cdot, \cdot)_\pm$ we denote the semi-inner products on X given by

$$(u, v)_\pm = \begin{matrix}\max\\ \min\end{matrix}\{(u, v^*)\colon v^* \in X^*,\ |v^*| = |v|,\ (v, v^*) = |v|^2\},$$

where X^* stands for the normed dual of X and $(\cdot, \cdot)$ indicates the natural pairing between X and X^*.

1. The Linear Problem

This preliminary section is devoted to the study of the one-dimensional free problem, i.e.

$$\begin{aligned} &u_t + u_x + d_0(x)u = 0, \\ &u(t,0) = \int_0^\infty b_0(x)u(t,x)\,dx, \qquad x, t \geqslant 0, \\ &u(0,x) = u_0(x). \end{aligned} \tag{2}$$

Let the following assumptions hold:

(A_0) $\qquad b_0 \in L^\infty \cap L^1, \qquad b_0 \geqslant 0$ a.e., $\qquad d_0 \in L^\infty_{\mathrm{loc}}, \qquad d_0 \geqslant 0$ a.e.

We define $Y = L^1$, $K_0 = \{u \in Y\colon u \geqslant 0 \text{ a.e.}\}$ and

$$(A_0u)(x) = -(u' + d_0(x)u) \qquad \text{for} \qquad u \in D(A_0),$$

$$D(A_0) = \left\{u \in Y\colon u \in W^{1,1}_{\mathrm{loc}},\ A_0u \in Y,\ u(0) = \int_0^\infty b_0(x)u(x)\,dx\right\}. \tag{3}$$

It is easy to verify that A_0 is a closed densely defined linear operator in Y. In the following we shall consider several properties of A_0.

(i) First we study the spectrum $\sigma(A_0)$ of A_0. Therefore, we solve

$$v' + d_0(x)v + \lambda v = f, \tag{4a}$$

$$v(0) = \int_0^\infty b_0(x)v(x)\,dx \tag{4b}$$

where $f \in Y$ and $\lambda \in \mathbb{C}$. The solutions of (4a) are given by

$$u(x) = \exp(-\varphi^0_\lambda(x))\left(v(0) + \int_0^x f(y)\exp(\varphi^0_\lambda(y))\,dy\right) \tag{5}$$

where

$$\varphi_\lambda^0(x) = \lambda x + \int_0^x d_0(\tau)\,d\tau.$$

Inserting into (4b) we find

$$v(0)\left(1 - \int_0^\infty b_0(x)\exp(-\varphi_\lambda^0(x))\,dx\right)$$
$$= \int_0^\infty b_0(x)\exp(-\varphi_\lambda^0(x)) \int_0^x f(y)\exp(\varphi_\lambda^0(y))\,dy\,dx. \tag{5'}$$

From (5) and (5′) it is easy to see that the essential spectrum $\sigma_e(A_0)$ of A_0 is contained in the half-space

$$\sigma_e(A_0) \subset \{\lambda \in \mathbb{C}\colon \operatorname{Re}\lambda \leqslant -d_\infty^0 = -\operatorname*{ess\,lim\,inf}_{x\to\infty} d_0(x)\}$$

and

$$\sigma(A_0) \subset \{\lambda \in \mathbb{C}\colon \operatorname{Re}\lambda \leqslant b_\infty^0 = \operatorname*{ess\,sup}_x (b_0(x) - d_0(x))\}.$$

Moreover, within the strip $-d_\infty^0 < \operatorname{Re}\lambda \leqslant b_\infty^0$ only isolated eigenvalues of A_0 may be found. These are exactly the solutions of

$$\int_0^\infty b_0(x)\exp\left(-\lambda x - \int_0^x d_0(\tau)\,d\tau\right)dx = 1. \tag{6}$$

There is exactly one real solution λ_0^0, possibly $\lambda_0^0 \leqslant -d_\infty^0$, and $\operatorname{Re}\lambda < \lambda_0^0$ holds for any other eigenvalue λ of A_0. Note that the eigenspace corresponding to λ_0^0 is one-dimensional and is generated by the positive function $\exp(-\varphi_{\lambda_0^0}^0(x))$. Therefore, by a direct calculation it is easy to verify that $(A_0 - \lambda_0^0)^2 u = 0$ implies $A_0 u = \lambda_0^0 u$, hence λ_0^0 is a simple eigenvalue.

(ii) Let us recall the Hille-Yosida Theorem on generation of C_0-semigroups [8].

Theorem A. *Let A be a closed, densely defined, linear operator in a Banach space X. Then, a necessary and sufficient condition for A to generate a C_0-semigroup $U(t) = e^{At}$ in X is*

"there are constants $M > 0$, $\omega \in \mathbb{R}$ such that

$|(\lambda I - A)^{-n}| \leqslant M(\lambda - \omega)^{-n}$ holds for all $\lambda > \omega$, $n \in \mathbb{N}$."

In this case, $U(t)$ is of type (M, ω), i.e. $|U(t)| \leqslant M \cdot e^{\omega t}$ for $t \in \mathbb{R}_+$, and $U(t)u = \lim_{n\to\infty}(I - (t/n)A)^{-n}u$ holds for all $u \in X$, $t \in \mathbb{R}_+$.

Now, equalities (5) and (5′) easily imply the estimate

$$|(\lambda I - A_0)^{-1}| \leqslant 1/(\lambda - b_\infty^0) \qquad \text{for} \qquad \lambda > b_\infty^0, \tag{7}$$

hence A_0 generates a C_0-semigroup $U_0(t)$ of type $(1, b_\infty^0)$ in Y, by Theorem A. Moreover, (5) and (5′) also imply $(\lambda I - A_0)^{-1}K_0 \subset K_0$ for $\lambda > b_\infty^0$, thus from the exponential formula easily follows invariance of K_0 under $U_0(t)$, i.e. $U_0(t)K_0 \subset K_0$

for all $t \in \mathbb{R}_+$. The semigroup $U_0(t)$ admits the representation

$$(U_0(t)u)(x) = \begin{cases} u(x-t)\exp\left(-\int_{x-t}^{x} d_0(\tau)\,d\tau\right), & x \geqslant t, \\ v(t-x)\exp\left(-\int_{0}^{x} d_0(\tau)\,d\tau\right), & x < t \end{cases} \tag{8}$$

where $v(x)$ denotes the solution of the integral equation

$$v(x) = \int_0^x b_0^1(x-y)v(y)\,dy + \int_0^\infty b_0^2(x,y)u(y)\,dy \tag{9}$$

and

$$b_0^1(x) = b_0(x)\exp\left(-\int_0^x d_0(\tau)\,d\tau\right),$$

$$b_0^2(x,y) = b_0(x+y)\exp\left(-\int_y^{x+y} d_0(\tau)\,d\tau\right).$$

(iii) In section 3 we shall need some sharp estimates of the ball-measure of noncompactness $\beta(U_0(t))$ of $U_0(t)$ in Y. To obtain such estimates, fix $t > 0$ and note that by (8) $U_0(t)$ decomposes in a natural manner: $U_0(t) = U_1^0(t) + U_2^0(t)$ where

$$U_1^0(t)u = \begin{cases} (U_0(t)u)(x), & x \geqslant t, \\ 0, & x < t, \end{cases} \qquad U_2^0(t)u = \begin{cases} 0, & x \geqslant t, \\ (U_0(t)u)(x), & x < t. \end{cases}$$

Put

$$T_1 \colon L^1(0,t) \to L^1(0,t), \qquad T_1 u = \int_0^x b_0^1(x-y)u(y)\,dy,$$

and

$$T_2 \colon L^1 \to L^1(0,t), \qquad T_2 u = \int_0^\infty b_0^2(x,y)u(y)\,dy;$$

then by (A_0) it is not hard to verify that T_2 is compact and T_1 is bounded with spectral radius zero. Thus, by (9) we get

$$(U_2^0(t)u)(x) = \begin{cases} 0, & x \geqslant t, \\ ((I-T_1)^{-1}T_2 u)(t-x)\exp\left(-\int_0^x d_0(\tau)\,d\tau\right), & x < t, \end{cases}$$

hence $U_2^0(t)$ is a compact linear operator for t fixed. Thus, we obtain

$$\beta(U_0(t)) = \beta(U_1^0(t)) \leqslant |U_1^0(t)| \leqslant e^{-d_0^0 t}, \tag{10}$$

where $d_0^0(x) = \operatorname{ess\,inf} d_0(x)$.

2. Existence for the Nonlinear Problem

As indicated in section 0, we want to put problem (1) into the framework of evolution equations in Banach spaces. In order to get an idea how this can be carried out we have to prepare some basic facts from that theory.

Let X be a Banach space, $D \subset X$ closed, A a generator of a C_0-semigroup $U(t)$ in X and F: $D \to X$ be locally Lipschitz and bounded ($F(B)$ is bounded for each $B \subset D$).

We are interested in the following abstract initial value problem

$$(P_1) \qquad u' = Au + F(u), \qquad u(0) = u_0 \in D.$$

A function u of class C^1 with values in $D \cap D(A)$ satisfying (P_1) is called a *strict solution* of (P_1). It is convenient to consider also

$$(P_2) \qquad u(t) = U(t)u_0 + \int_0^t U(t-s)F(u(s))\,ds.$$

Continuous solutions of (P_2) are called *mild solutions* of (P_1). By "variation of constant" each strict solution of (P_1) is a mild solution, but the converse need not be true.

Suppose, to each $u_0 \in D$ there exists a local mild solution of (P_1) in D. Then, it is easy to see that

$$(S) \qquad \lim_{h \to 0+} h^{-1} d(U(h)u + hF(u), D) = 0 \qquad \text{for all} \qquad u \in D$$

holds true, where $d(\cdot, D)$ denotes distance to D. Usually, (5) is called "boundary" or "subtangential condition" w.r. to (P_1). The following well-posedness result for (P_1) holds (cp. [9] or [11]):

Theorem B. *Let X, D, A, F be like above and suppose (S) holds. Then,*

(i) *to each initial value $u_0 \in D$ there is exactly one local mild solution $u(t)$ to (P_1) with values in D; it depends continuously on u_0;*

(ii) *if F is C^1 in D (i.e. F is the restriction of a C^1-function F defined on some neighborhood of D), solutions $u(t)$ with $u(0) \in D(A)$ are strict solutions of (P_1);*

(iii) *if there are some $\kappa_0, \omega_0 \in \mathbb{R}$ such that*

$$(Av, v)_- \leqslant \omega_0 |v|^2 \qquad \text{for all} \qquad v \in D(A),$$

$$(F(u), u)_- \leqslant \kappa_0 |u|^2 \qquad \text{for all} \qquad u \in D$$

hold, each solution $u(t)$ extends to $\mathbb{R}_+$ and has growth

$$|u(t)| \leqslant |u(0)| e^{(\omega_0 + \kappa_0)t} \qquad \text{for all} \qquad t \in \mathbb{R}_+.$$

Conditions sufficient for (S) are given in

Lemma C. (i) *If $(I - \lambda A)^{-1} D \subset D$ for all $\lambda \in (0, \lambda_1)$ holds for some $\lambda_1 > 0$, then $U(t)$ is leaving D invariant.*

(ii) *Suppose U leaves D invariant and (S_0): $\lim_{h \to 0+} h^{-1} d(u + hF(u), D) = 0$ for all $u \in D$. Then (S) holds.*

(iii) *Suppose $D \cap D(A)$ is dense in the closed set $D \subset X$ and* (ii) *holds. If $(Au + Fu, u)_- \leqslant 0$ for all $u \in D \cap D(A)$, $|u| \geqslant R$, then (S) holds w.r. to $D \cap B_R(0)$.*

(iv) *Suppose $D \subset X$ is closed convex and (S) holds w.r. to D. If $u^* \in D(A^*)$, $H = \{u \in X\colon\ (u, u^*) \geqslant c\}$, $\mathring{H} \cap D \neq \emptyset$, and $(u, A^*u^*) + (Fu, u^*) \geqslant 0$ for all $u \in D \cap \partial H$, then (S) holds w.r. to $D \cap H$.*

Part (i) of Lemma C follows directly from the exponential formula in Theorem A and (ii) also is easily verified. On the other hand, (iii) and (iv) require some more arguments from semigroup theory, a proof is given in the appendix.

Now, let us turn to problem (1). As already indicated in section 0, it is natural to choose $X = Y^n = L^1(\mathbb{R}_+, \mathbb{R}^n)$ normed by $|u| = \max\{|u_i|,\ i = 1, \ldots, n\}$ and to consider as closed subset $D = K = \{u \in X\colon u_i \geq 0 \text{ a.e.}, i = 1, \ldots, n\}$ the standard cone in X. We suppose

(A) for each $i = 1, \ldots, n$: $b_i \in L^\infty \cap L^1$, $d_i \in L^\infty_{\text{loc}}$, $d_i, b_i \geq 0$ a.e.,

and define $A = \operatorname{diag}(A_1, \ldots, A_n)$ where A_i denote the operators described in (3), section 1, where index "0" is replaced by "i". Then, by section 1, A generates a C_0-semigroup $U(t)$ given by $U(t) = \operatorname{diag}(U_1(t), \ldots, U_n(t))$ which is leaving K invariant.

Moreover, if we put $d_0 = \min_i d_0^i$, $d_\infty = \min_i d_\infty^i$, $b_\infty = \max_i b_\infty^i$ where d_0^i, d_∞^i, b_∞^i are defined like d_0^0, d_∞^0, b_∞^0, respectively, we have

$$|U(t)| \leq e^{b_\infty t}, \qquad \beta(U(t)) \leq e^{-d_0 t} \qquad \text{for} \qquad t \in \mathbb{R}_+. \tag{13}$$

Concerning the nonlinearities f_i we will suppose

$$(F) \qquad f(x, u) = g\left(x, \int_0^\infty k(x, y) h(y, u(y))\, dy\right)$$

where

(F_1) $h\colon \mathbb{R}_+ \times \mathbb{R}^n_+ \to \mathbb{R}^m_+$ is continuous, $h(y, 0) \equiv 0$ and $|h(y, \xi) - h(y, \bar{\xi})| \leq L|\xi - \bar{\xi}|$ holds for all y, ξ.

(F_2) $k\colon \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}^{m_1 m}_+$ is measurable and bounded, and $\{k(\cdot, y)\colon y \in \mathbb{R}_+\}$ is equicontinuous.

(F_3) $g\colon \mathbb{R}_+ \times \mathbb{R}^{m_1}_+ \to \mathbb{R}^n_+$ is continuous, $g(x, 0) \equiv 0$ and $|g_i(x, \eta) - g_i(x, \bar{\eta})| \leq M(\rho)|\eta - \bar{\eta}|$ for all i and $|\eta|, |\bar{\eta}| \leq \rho$, $x \in \mathbb{R}_+$, where $M(\rho)$ is continuous and increasing.

Now, it is easy to verify that $F\colon K \to X$ defined by

$$(F(u)(x))_i = -f_i(x, u) u_i(x) \tag{14}$$

is locally Lipschitz, bounded and, moreover, since $f_i \geq 0$,

$$\lim_{h \to 0+} h^{-1} d(u + hF(u), K) = 0 \qquad \text{holds for all } u \in K.$$

Thus, applying Lemma C and Theorem B we obtain

Theorem 1. *Let (A), (F) as well as $(F_1) \sim (F_3)$ hold and let $u_0 \in K$. Then, there is exactly one mild solution $u(t)$ of (12) defined for all $t \geq 0$ in K. It depends continuously on u_0 and has growth*

$$|u(t)| \leq |u(0)| e^{b_\infty t}, \qquad t \geq 0.$$

Moreover, if $h(x, \xi) \equiv \xi$ and $g(x, \eta)$ is C^1 w.r. to η, solutions $u(t)$ satisfying $u(0) \in D(A) \cap K$ are strict solutions.

Note that growth estimate follows from

$$u_i(t) = U_i(t)u_{0i} + \int_0^t U_i(t-s)F_i(u(s))\,ds \leqslant U_i(t)u_{0i} \tag{14a}$$

and that the last assertion holds true since in that case F is differentiable.

3. Existence of Equilibrium Solutions

Now, we turn our attention to the question of existence of equilibrium solutions to (1)

$$\Phi_i' + d_i(x)\Phi_i(x) + f_i(x,\Phi)\Phi_i(x) = 0, \tag{15a}$$

$$\Phi_i(0) = \int_0^\infty b_i(x)\Phi_i(x)\,dx. \tag{15b}$$

Of course, we are interested in solutions $\Phi \in D(A) \cap K$ only. Recall the definition of λ_0^i as the real solution to

$$\int_0^\infty b_i(x)\exp\left(-\lambda x - \int_0^x d_i(\tau)\,d\tau\right)dx = 1, \tag{16}$$

and put $\lambda_0 = \max_i \lambda_0^i$. These quantities will play an important role in the sequel.

First, we note that the trivial solution $\Phi_0 \equiv 0$ always satisfies (15). If $\lambda_0^i < 0$ for some i, by (14a) we obtain $u_i(t) \to 0$ in L^1 as $t \to \infty$, for any solution $u(t)$ of (1) with $u(0) \in K$, since $|U_i(t)|$ is exponential decreasing; cp. also the introductory remarks of section 4. Hence, if $\lambda_0 < 0$ holds, $\Phi_0 \equiv 0$ is the only equilibrium solution of (1). Thus, a necessary condition for existence of nontrivial equilibrium solutions of (1) is $\lambda_0 \geqslant 0$ and each equilibrium Φ will satisfy $\Phi_i(x) \equiv 0$ for each i with $\lambda_0^i < 0$. This means that the ith species will die out if it cannot sufficiently reproduce. Moreover, each nontrivial solution of (15) admits the representation

$$\Phi_i(x) = \Phi_i(0)\exp\left(-\int_0^x d_i(\tau)\,d\tau - \int_0^x f_i(\tau,\Phi)\,d\tau\right), \qquad i = 1,\dots,n, \tag{17}$$

hence, if $\lambda_0^i > 0$ but $\sup\{f_i(\tau,u) \colon \tau \in \mathbb{R}_+, u \in K\} < \lambda_0^i$ holds, we obtain $\Phi_i(x) \equiv 0$ by (15b). Therefore, necessary for $\Phi_i(x)$ to be nontrivial in case $\lambda_0^i > 0$ is

$$\sup\{f_i(\tau,u) \colon \tau \in \mathbb{R}^+,\ u \in K\} \geqslant \lambda_0^i.$$

In the separable case $k(x,y) \equiv k(y)$ equations (15) reduce, after integration, to the finite-dimensional problem

$$\int_0^\infty b_i(x)q_i(x,P)\,dx = 1, \qquad i = 1,\dots,n,$$

$$P_i = \sum_{j=1}^n \int_0^\infty k_{ij}(y)h_j(y, c_1q_1(y,P),\dots,c_nq_n(y,P))\,dy, \qquad i = 1,\dots,k$$

where

$$q_i(y, P) = \exp\left(-\int_0^y d_i(\tau)\,d\tau - \int_0^y g_i(\tau, P)\,d\tau\right).$$

If P, c is a solution, the corresponding equilibrium is given by $\Phi_i(x) = c_i q_i(x, P)$, $i = 1, \ldots, n$.

But if there is no separability, (15) becomes a proper infinite-dimensional problem which even in case $m = m_1 = n = 1$ is by no means as simple. Our main result on existence for (15) is

Theorem 2. *Let* (*A*), (*F*), $(F_1) \sim (F_3)$ *hold, let* $d_0 > 0$ *and* $\lambda_0 > 0$. *Suppose, for each* i *with* $\lambda_0^i > 0$ *there is* $0 < N_i \leqslant \infty$ *such that* $0 < \mu_i \leqslant d_i(x) - b_i(x)$ *for* $x \geqslant N_i$, *and* $R_i > 0$ *such that*

$$b_i(x) \leqslant d_i(x) + \inf\left\{f_i(x, u) \colon u \in K \colon \int_0^{N_i} u_i(x)\,dx \geqslant R_i\right\} \qquad \text{for} \qquad x \leqslant N_i.$$

Then, (1) *has at least one nontrivial equilibrium solution.*

Roughly speaking, the main assumption of Theorem 2 states that for the species with a positive net reproduction rate (i.e. $\lambda_0^i > 0$) the birth rate $b_i(x)$ is bounded by the death rate if their frequency in young ages is large enough: $\int_0^{N_i} u_i(x)\,dx \geqslant R_i$, no matter what age distributions the other species are. Such an assumption seems to be natural in competition models. As a more concrete example for a situation when Theorem 2 applies consider $m = n$ and $h(y, \xi) \equiv \xi$ as well as $m_1 = 1$ and $g_i(x, \rho) \to \infty$ as $\rho \to \infty$ uniformly for x finite, and i with $\lambda_0^i > 0$. Then, if also $\inf_{x,y \leqslant N_i} k_i(x, y) > 0$ holds for all such i, the assumptions of Theorem 2 are fulfilled, hence there is a nontrivial equilibrium solution of (1).

The proof of Theorem 2 is an application of a general result on equilibrium solutions of the abstract problem (P_1):

$$(P_3) \qquad A\Phi + F(\Phi) = 0, \qquad \Phi \in D(A) \cap D.$$

This result is a slight generalization of Theorem 7.2 in [11] or Theorem 8 in [12], a short proof is given in the appendix at the end of these notes.

Theorem D. *Let* D *be a closed convex bounded subset of a Banach space* X, A *be a generator of a* C_0*-semigroup of type* $(1, \omega_0)$ *in* X, $F \colon D \to X$ *be locally Lipschitz and bounded such that*

$$(S) \qquad \lim_{h \to 0+} h^{-1} d(U(h)u + hF(u), D) = 0 \qquad \text{for all} \qquad u \in D,$$

$$(C) \quad \beta(F(B)) \leqslant \kappa_1 \beta(B) \text{ for } B \subset D,\ \beta(U(t)) \leqslant e^{\omega_1 t} \text{ for } t \in \mathbb{R}_+,\ \omega_1 + \kappa_1 < 0$$

are satisfied.

Then, problem (P_3) *admits at least one solution* $\Phi \in D(A) \cap D$.

For the application of Theorem D we use X, A, F like in section 2. Thus, we have to construct $D \subset K$ bounded with $0 \notin D$ and such that D remains invariant w.r. to (P_1) (i.e. (S) holds) and such that (C) is satisfied.

Proof of Theorem 2. We may assume $\lambda_0^i > 0$ for $i = 1, \dots, r$ and $\lambda_0^i \leqslant 0$ for $i = r+1, \dots, n$. We shall construct some closed convex bounded $D \subset K \backslash \{0\}$ such that (S) holds w.r. to D. This will be done in three steps using Lemma C.

i) First, consider

$$D_R = \{u \in K: |u| \leqslant R,\ u_{r+1} = \cdots = u_n = 0\};$$

D_R is closed, convex and bounded. To obtain invariance of D_R w.r. to (P_1), by Lemma C iii) it suffices to prove

$$(Au + Fu, u)_- \leqslant 0 \quad \text{for} \quad u \in D(A) \cap K, \quad |u| \geqslant R. \tag{18}$$

To verify (18) we have to compute $(\cdot, \cdot)_-$ in X, this is done in the following Lemma. Since the proof is very simple and uninteresting for the sequel we omit it here.

Lemma. (i) *Let* $u, v \in Y$; *then*

$$(u, v)_-^Y = |v| \left[\int_{v(x) \neq 0} u(x) \operatorname{sgn} v(x)\, dx - \int_{v(x) = 0} |u(x)|\, dx \right].$$

(ii) *Let* $u, v \in X = Y^n$; *then*

$$(u, v)_-^X = \min\{(u_i, v_i)_-^Y : i \text{ with } |v_i|_Y = |v|_X\}.$$

Hence, we obtain

$$(u, v)_-^X \leqslant |v| \min \left\{ \int_0^\infty u_i(x) \operatorname{sgn} v_i(x)\, dx \colon i \text{ with } \int_0^\infty |v_i(x)|\, dx = |v| \right\}.$$

Now, for $u \in D(A) \cap K$, $|u_i| = R$ we get

$$\begin{aligned}
(Au + F(u), u)_- &\leqslant |u| \int_0^\infty (-u_i' - d_i(x) u_i - f_i(x, u) u_i)\, dx \\
&= |u| \int_0^\infty (b_i(x) - d_i(x) - f_i(x, u)) u_i(x)\, dx \\
&= |u| \left[\int_0^{N_i} (\cdots)\, dx + \int_{N_i}^\infty (\cdots)\, dx \right] \\
&\leqslant |u| \left[\operatorname*{ess\,sup}_{x \leqslant N_i} (b_i(x) - d_i(x)) R_i - \mu_i (R - R_i) \right]
\end{aligned}$$

in case $\int_0^{N_i} u_i(x)\, dx < R_i$, and $(Au + F(u), u)_- \leqslant 0$ if $\int_0^{N_i} u_i(x)\, dx \geqslant R_i$ by the hypotheses of the Theorem. Therefore, (18) holds, provided R is chosen such that

$$\max_{i = 1, \dots, r} \left(R_i + \operatorname*{ess\,sup}_{x \leqslant N_i} (b_i(x) - d_i(x)) \frac{R_i}{\mu_i} \right) \leqslant R. \tag{18'}$$

ii) For technical reasons which will become clear later, we want to restrict D_R in order to control the decay of functions $u \in D$ at infinity. For this purpose we let

$$\varphi_i(x) = \exp\left(\int_0^x d_i(\tau)\, d\tau - d_\infty \cdot x/2 \right)$$

and consider

$$D_\varphi = \left\{ u \in D_R : \int_0^\infty u_i(x)\varphi_i(x)\,dx \leqslant \sigma,\ i = 1, \ldots, r \right\}$$

where $\sigma > 0$ will be fixed later. Although $\varphi_i(x) \to \infty$ as $x \to \infty$, D_φ is closed convex and bounded. We shall verify (S) w.r. to D_φ directly. So let $u_0 \in D_\varphi$ and $i \in \{1, \ldots, r\}$ be fixed. Then

$$\left| \left(I - \frac{t}{n} A_i \right)^{-n} u_0^i \right| \leqslant \left| \left(I - \frac{t}{n} A_i \right)^{-1} \right|^n |u_0^i| \leqslant \left(1 - b_\infty \frac{t}{n} \right)^{-n} R$$

$$\leqslant R + 1 \qquad \text{for all} \qquad n \in \mathbb{N}, \tag{19}$$

provided $t > 0$ is sufficiently small. Now, $v_i = (I - \lambda A_i)^{-1} u_0^i$ satisfies $(\lambda > 0)$

$$\lambda(v_i' + d_i v_i) + v_i = u_0^i, \qquad v_i(0) = \int_0^\infty b_i(x) v_i(x)\,dx$$

hence by integration

$$\sigma \geqslant \int_0^\infty u_0^i \varphi_i\,dx \geqslant \int_0^N v_i \varphi_i\,dx + \lambda \int_0^N (v_i' + d_i v_i)\varphi_i\,dx$$

$$= \int_0^N v_i \varphi_i\,dx + \lambda \left[\frac{d_\infty}{2} \int_0^N v_i \varphi_i\,dx + v_i(N)\varphi_i(N) - \int_0^\infty b_i(x) v_i(x)\,dx \right]$$

and $N \to \infty$ yields

$$\sigma \geqslant \int_0^\infty v_i \varphi_i\,dx + \lambda \left[\frac{d_\infty}{2} \int_0^\infty v_i \varphi_i\,dx - b_\infty(R + 1) \right]$$

which in turn implies $\int_0^\infty v_i(x)\varphi_i(x)\,dx \leqslant \sigma$, provided $\sigma > 2b_\infty(R + 1)/d_\infty$. By induction it is easy to see that

$$\int_0^\infty \left(I - \frac{t}{n} A_i \right)^{-n} u_0^i \varphi_i\,dx \leqslant \sigma \qquad \text{holds for all} \qquad n \in \mathbb{N},$$

provided $t > 0$ is small enough, hence by exponential formula (Theorem A)

$$\int_0^\infty U_i(h) u_0^i \varphi_i\,dx \leqslant \sigma \qquad \text{if } h > 0 \text{ is sufficiently small.} \tag{19'}$$

Now, let $u(h)$ be the solution of (P_1) with initial value u_0. We already know $u(h) \in D_R$ for all $h > 0$ and $|U(h)u_0 + hF(u_0) - u(h)| = 0(h)$ as $h \to 0+$, but also $u(h) \in D_\varphi$ for $h > 0$ small and so (S) holds w.r. to D_φ. In fact, considering the ith component $u_i(h)$ again, by (19′) we obtain

$$\int_0^\infty u_i(h)\varphi_i\,dx = \int_0^\infty U_i(h) u_0^i \varphi_i\,dx + \int_0^\infty \int_0^h U_i(h - s) F_i(u(s))\,ds\,\varphi_i\,dx \leqslant \sigma$$

since $F_i(u(s)) \leqslant 0$ and $U_i(t)$ preserves inequalities.

iii) Finally, we want to exclude 0 from D_φ and for this purpose we consider the intersection of D_φ with some appropriate half-space H. For to construct H, from the hypotheses of Theorem 2 recall that $\lambda_0 > 0$, a fact we did not use up to now. For $i = 1, \ldots, r$ we consider the eigenfunctions $\psi_i(x)$ of the problem adjoint to "$A_i v = \lambda_0^i v$", i.e.

$$\psi_i' = -b_i + d_i\psi_i + \lambda_0^i\psi, \qquad \psi_i(0) = 1. \tag{20}$$

It is easy to verify that $\psi_i(x) > 0$ for all $x \in \mathbb{R}_+$ and $\psi_i(x) \to 0$ as $x \to \infty$, and that $\psi_i \in D(A_i^*)$ for all i. Put $\psi = (\psi_1, \ldots, \psi_r, 0, \ldots, 0) \in D(A^*)$,

$$H = \left\{ u \in X\colon (u, \psi) = \sum_1^r \int_0^\infty \psi_i u_i \, dx \geqslant \rho > 0 \right\},$$

where $\rho > 0$ will be fixed below, and define $D = D_\varphi \cap H$. Obviously, $D \subset K \backslash \{0\}$ is closed convex bounded. To prove that (S) holds w.r. to D we will use Lemma C (iv). Since $f_i(x, 0) \equiv 0$ for each i, there is $r_0 > 0$ such that $f_i(x, u) \leqslant \lambda_0^i$ holds for $i = 1, \ldots, r$ if $|u| \leqslant r_0$. Now, let $u \in D_\varphi \cap \partial H$; then $\int_0^\infty \psi_i u_i \, dx \leqslant \rho$ for $i = 1, \ldots, r$, hence

$$|u_i| = \int_0^\infty u_i \, dx \leqslant \left(\min_{x \leqslant N} \psi_i(x) \right)^{-1} \rho + \left(\min_{x \geqslant N} \varphi_i(x) \right)^{-1} \sigma \leqslant r_0$$

choosing N large enough first and then $\rho > 0$ small enough. This observation and (20) yield

$$\begin{aligned} (u, A^*u) + (Fu, u^*) &= \sum_1^r \int_0^\infty u_i[\psi_i' + b_i - d_i\psi_i - f_i(x, u)\psi_i] \, dx \\ &= \sum_1^r \int_0^\infty u_i\psi_i[\lambda_0^i - f_i(x, u)] \, dx \geqslant 0 \end{aligned}$$

hence, by Lemma C (iv), (S) holds w.r. to D.

iv) We are going to prove that condition (C) of Theorem D holds. For this purpose we put $V(t) = U(t)e^{-\gamma t}$ and $G(u) = \gamma u + F(u)$; the pair $V(t)$, G also corresponds to (P_1) since (P_1) may be written as $u' = Au - \gamma u + \gamma u + F(u)$ and $A - \gamma$ generates the semigroup $V(t)$.

From estimate (10), section 1, we obtain

$$\beta(V(t)) = \beta(U(t)e^{-\gamma t}) \leqslant e^{-(d_0 + \gamma)t} \qquad \text{for} \qquad t \in \mathbb{R}_+. \tag{21}$$

On the other hand, we also have

$$\beta(G(B)) \leqslant \gamma\beta(B) \qquad \text{for} \qquad B \subset D \tag{22}$$

provided $\gamma > 0$ is chosen such that

$$\gamma \geqslant \sup\{f_i(x, u)\colon x \in \mathbb{R}_+,\ i = 1, \ldots, r,\ u \in D\},$$

which is possible by $(F_1) \sim (F_3)$. In fact, let $\varepsilon > 0$ and $B \subset D$ be given and choose $\{v^j\}_1^l \subset X$ such that $B \subset \bigcup_1^l B_\alpha(v^j)$, where $\alpha \leqslant \beta(B) + \varepsilon/4\gamma$. Moreover, choose $N > 0$ large enough that $\int_N^\infty |v_i^j(x)| \, dx \leqslant \varepsilon/8\gamma$ holds for all i, j. Since $\{f_i(x, u)\colon u \in D\}$ is bounded and equicontinuous in $x \in [0, N]$ by $(F_1) \sim (F_3)$, Arzela-Ascoli's theorem implies the existence of functions $w_i^\nu \in C[0, N]$, $\nu = 1, \ldots, s_i$ such that

$$|\gamma - f_i(x, u) - w_i^\nu(x)| \leqslant \varepsilon/4 \cdot \max|v^j|$$

holds in $[0, N]$ for all $u \in D$ and suitable $\nu = \nu(u)$. Defining $w_i^\nu(x) = w_i^\nu(N)$ for $x \geqslant N$ extends w_i^ν to all of $\mathbb{R}_+$. Now, put $z_i^{\nu j}(x) = w_i^\nu(x) v_i^j(x)$ to obtain

$$\begin{aligned}
|(\gamma - f_i(\cdot, u))u_i - z_i^{\nu j}| &\leqslant |(\gamma - f_i(\cdot, u))(u_i - v_i^j)| + |(\gamma - f_i(\cdot, u) - w_i^\nu) v_i^j| \\
&\leqslant \gamma\alpha + \sup_{x \leqslant N} |\gamma - f_i(x, u) - w_i^\nu(x)|\, |v_i^j| \\
&\quad + \sup_{x \geqslant N} |\gamma - f_i(x, u) - w_i^\nu(x)| \int_N^\infty |v_i^j|\, dx \\
&\leqslant \gamma\beta(B) + \varepsilon/4 + \varepsilon/4 \cdot \frac{|v_i^j|}{\max|v^j|} + (\gamma + |w_i^\nu(N)|) \int_N^\infty |v_i^j| dx \\
&\leqslant \gamma\beta(B) + \varepsilon,
\end{aligned}$$

hence $|G(u) - z^{\nu j}| \leqslant \gamma\beta(B) + \varepsilon$. Therefore, $G(B) \subset \bigcup_{\nu, j} B_\alpha, (z^{\nu j})$ i.e. (22) holds since $\varepsilon > 0$ may be chosen arbitrarily small. By assumption $d_0 > 0$ and so all hypotheses of Theorem D are satisfied and therefore the proof of Theorem 2 is complete.

q.e.d.

Using another simple trick weakens the assumption that $d_0 > 0$:

Corollary 1. *Let all of the hypotheses of Theorem 2 hold except that "$d_0 > 0$" is now replaced by "$d_\infty > 0$". Then, the conclusion of Theorem 2 also holds.*

Indication of Proof. We only have to alter step (iv) in the proof of Theorem 2, and this will be done by means of a new norm on X defined in the following manner: For $u \in Y$ put

$$\|u\|^i = \sup_{t \geqslant 0} |U_1^i(t) e^{\alpha t} u|_Y, \qquad \text{where} \qquad \alpha = d_\infty/2.$$

$\|\cdot\|^i$ is equivalent to $|\cdot|_Y$ and we have $\|U_1^i(t)\|^i \leqslant e^{-\alpha t}$ for $t \in \mathbb{R}_+$. Then, for $u \in X$ define $\|u\| = \max_i \|u_i\|^i$. With respect to this norm, similar to (21), we obtain

$$\beta_{\|\cdot\|}(V(t)) \leqslant e^{-(\alpha + \gamma)t} \qquad \text{for} \qquad t \in \mathbb{R}^+, \tag{21'}$$

where $\beta_{\|\cdot\|}$ denotes β-measure w.r. to $\|\cdot\|$. Now, surprisingly the analog to (22) also holds:

$$\beta_{\|\cdot\|}(G(B)) \leqslant \gamma \beta_{\|\cdot\|}(B) \qquad \text{for} \qquad B \subset D. \tag{22'}$$

This can be seen by passing through the proof of (22) taking the new norm into account. Thus, Theorem D may be applied in this case, too. q.e.d.

4. Stability Analysis for Equilibrium Solutions

We start recalling some definitions from stability theory. Again, let X be a Banach space, A be a generator of a C_0-semigroup in X, F: $B_R(\Phi) \to X$ Lipschitz and differentiable at Φ, and let Φ be an equilibrium solution of

$$(P_3) \qquad A\Phi + F(\Phi) = 0.$$

Definition. (i) Φ is *stable* (w.r. to (P_1)) if to each $\varepsilon > 0$ there is $\delta > 0$ such that $|\Phi - u_0| < \delta$ implies that the mild solution $u(t, u_0)$ of (P_1) exists on all of $\mathbb{R}^+$ and satisfies $|\Phi - u(t, u_0)| < \varepsilon$ on $\mathbb{R}_+$.

(ii) Φ is *asymptotically stable* if it is stable and there is $\delta_0 > 0$ such that $\lim_{t\to\infty} u(t, u_0) = \Phi$ holds for all $|\Phi - u_0| \leqslant \delta_0$.

(iii) Φ is *unstable* if it is not stable.

One method to study stability of (P_1) is to consider the linearization of (P_1)

$$(P_4) \qquad w' = Aw + F'(\Phi)w = A_\phi w.$$

It is possible to characterize stability of Φ w.r. to (P_1) almost completely by means of spectral properties of the operator A_Φ. To state this result we need some further preparation concerning C_0-semigroups; see Hille/Phillips [8]. If A generates a C_0-semigroup $U(t) = e^{At}$ in X, we put

$$\omega_0(A) = \lim_{t\to\infty} t^{-1} \log|U(t)|, \qquad \omega_1(A) = \lim_{t\to\infty} t^{-1} \log \beta(U(t)). \tag{23}$$

It is a standard argument in semigroup theory to show that both limits exist and of course we have $\omega_1(A) \leqslant \omega_0(A)$. Moreover, $e^{\omega_0 t}$ and $e^{\omega_1 t}$ are precisely the radii of the spectrum of $U(t)$ and of the essential spectrum of $U(t)$, respectively. Since

$$e^{\sigma(A)t} \subset \sigma(e^{At}) \qquad \text{and} \qquad e^{\sigma_p(A)t} = \sigma_p(e^{At})\backslash\{0\}$$

holds, where σ_p denotes point spectrum, we also have

$$\omega_0 \geqslant \sup\{\operatorname{Re}\lambda\colon \lambda \in \sigma(A)\}, \qquad \omega_1 \geqslant \sup\{\operatorname{Re}\lambda\colon \lambda \in \sigma_e(A)\}, \tag{24}$$

but, in contrary to the case of bounded A, strict inequalities may occur. On the other hand, if $\omega_0 > \omega_1$ holds, the first inequality in (24) becomes an equality, hence to each $\varepsilon > 0$ there is $M_\varepsilon \geqslant 1$ such that

$$|U(t)| \leqslant M_\varepsilon \exp((\sup \operatorname{Re}\sigma(A) + \varepsilon)t) \qquad \text{for} \qquad t \in \mathbb{R}_+. \tag{24a}$$

Moreover, if all eigenvalues λ of A with $\operatorname{Re}\lambda = \sup \operatorname{Re}(A)$ are simple, in this case we even obtain

$$|U(t)| \leqslant M \exp(\sup \operatorname{Re}\sigma(A)t) \qquad \text{for} \qquad t \in \mathbb{R}_+. \tag{24b}$$

Theorem E. *Let A be a generator of a C_0-semigroup in Banach space X, $F\colon B_R(\Phi) \to X$ be Lipschitz and differentiable at Φ, let Φ satisfy (P_3) and put $A_\Phi = A + F'(\Phi)$. Then, we have:*

(i) $\omega_0(A_\Phi) < 0$ *implies asymptotic stability of* Φ.

(ii) $\omega_0(A_\Phi) > 0$ *and* $\omega_1(A_\Phi) \leqslant 0$ *imply instability of* Φ.

This result is proved in Dalecki/Krein [4] for the case of bounded A but their proof extends to our setting almost directly. Note that in case $\omega_0(A_\Phi) = 0$ linearization yields no information and as known from ordinary differential equations in $\mathbb{R}^n$ both stability and instability may then occur. Let us also mention that in case e^{At} is a compact operator for $t \geqslant t_0 \geqslant 0$, there results $\omega_1(A) = -\infty$ and equalities hold in (24). Hence, if X is finite-dimensional, Theorem E reduces to the classical result of Ljapunov for ordinary differential equations.

We want to apply Theorem E to problem (1). So let X, A, F be as described in section 2. First, consider the trivial equilibrium $\Phi_0 \equiv 0$. Since $F'(\Phi_0) = 0$ we obtain a rather complete description of the stability behaviour of $\Phi_0 \equiv 0$:

Theorem 3. *Let (A), (F) as well as $(F_1)\sim(F_3)$ hold.*

(i) *If $\lambda_0 < 0$, $\Phi_0 \equiv 0$ is asymptotically stable and $u(t) \to 0$ as $t \to \infty$ holds for any solution $u(t)$ with $u(0) \in K$.*

(ii) *If $\lambda_0 = 0$, $\Phi_0 \equiv 0$ is stable in K.*

(iii) *If $\lambda_0 > 0$, $\Phi_0 \equiv 0$ is unstable.*

For a proof note that (i) and (iii) are directly implied by Theorem E, whereas (ii) follows from (14a), (24b) and simplicity of λ_0.

Next, we consider some fixed nonnegative nontrivial equilibrium solution Φ of (1). Thus, we may assume $\Phi_i \not\equiv 0$ for $i = 1, \ldots, r$, $\Phi_i \equiv 0$ for $i = r+1, \ldots, n$ and $r \in \{1, \ldots, n\}$. Since differentiability of F at Φ is crucial for Theorem E, we have to assume

(F_4) $\qquad m = n, \quad h(x, \xi) \equiv \xi, \quad g(x, \eta)$ is of class C^1 w.r. to η.

Note that $g'(x, \eta)$, the derivative of g w.r. to η is uniformly bounded in x, by (F_3). If (F_4) holds, F is of class C^1 and we get

$$(F'(\phi)w)_i(x) = -f_i(x, \Phi)w_i(x) - \Phi_i(x)g_i'(x, K\Phi)(Kw)(x), \tag{25}$$

where $(Kw)(x) = \int_0^\infty k(x, y)w(y)\,dy$ and g_i' denotes the ith row of g'. Put

$$p(x, y) = g'(x, K\Phi)k(x, y) \tag{26}$$

and define

$$(P_\Phi w)_i(x) = \Phi_i(x)\left(\int_0^\infty p(x, y)w(y)\,dy\right)_i,$$

$$(B_\Phi W)_i(x) = -w_i' - d_i(x)w_i - f_i(x, \Phi)w_i, \tag{27}$$

to obtain

$$A_\Phi w = B_\Phi w - P_\Phi w, \qquad D(A_\Phi) = D(B_\Phi) = D(A). \tag{28}$$

Since $P_\Phi\colon X \to X$ is a compact linear operator we have

$$\beta(e^{A_\Phi t}) = \beta(e^{B_\Phi t}) \leqslant M_\varepsilon e^{(\varepsilon - d_\infty)t} \qquad \text{for} \qquad t \in \mathbb{R}_+,$$

where the last inequality is obtained like (13). Therefore, if $d_\infty > 0$ we deduce $\omega_1(A_\Phi) \leqslant -d_\infty < 0$ and so the stability behavior of (1) at Φ is determined by the location of the eigenvalues of A_Φ alone. Thus, by Theorem E we get

Theorem 4. *Let (A), (F) as well as $(F_1)\sim(F_4)$ hold and let $d_\infty > 0$. Then, if $\operatorname{Re}\mu < 0$ holds for all eigenvalues of A_Φ, Φ is asymptotically stable. If $\operatorname{Re}\mu > 0$ for at least one eigenvalue of A_Φ, Φ is unstable.*

Although stability of nonnegative equilibrium solutions of (1) is almost completely characterized in Theorem 4, it may be very difficult to estimate the real parts of the eigenvalues of A_Φ or even to compute them. Before we consider some special cases we note some general facts concerning $\sigma_P(A_\Phi)$.

First, consider B_Φ; eigenvalue with largest real part of B_Φ is $\lambda = 0$, one eigenfunction being Φ itself. Thus, stability behaviour depends on how P_Φ alters $\sigma_P(B_\Phi)$ into $\sigma_P(A_\Phi)$.

Secondly, since $(P_\Phi w)_i \equiv 0$ for $i = r+1, \dots, n$, the point spectrum $\sigma_P(A_\Phi)$ decomposes into $n - r + 1$ parts: eigenvalues of the operators $(B_\Phi)_i$, $i = r+1, \dots, n$, i.e. the ith component of B_Φ, and eigenvalues of A^r_Φ, i.e. A_Φ restricted to the first r components. Since B_Φ is diagonal, it is an easy matter to estimate the former. In fact, their real parts are less than μ^i_0, where μ^i_0 is defined as the real solution of

$$\int_0^\infty e^{-\mu x} b_i(x) \exp\left(- \int_0^x d_i(\tau)\, d\tau - \int_0^x f_i(\tau, \Phi)\, d\tau \right) dx = 1; \tag{29}$$

cp. (6) in section 1. If $\mu^i_0 < 0$ for all $i = r+1, \dots, n$, only eigenvalues of A^r_Φ may have positive real parts, but on the other hand $\mu^i_0 > 0$ for some $i \in \{r+1, \dots, n\}$ implies instability of Φ. Note that it is possible to have $\lambda^i_0 > 0$ but $\mu^i_0 < 0$, i.e. the trivial state of the ith species may be stabilized by the presence of other species.

We are going to consider some

Special Cases. (i) Suppose g and k are independent of x, i.e. the death rate increase arising from population interactions is equal for all ages. Then

$$p(x, y) = p(y) = g'\left(\int_0^\infty k(y)\Phi(y)\, dy \right) k(y)$$

and the calculation of eigenvalues is considerably eased. In fact, suppose $0 \neq \mu \in \mathbb{C}$, $\operatorname{Re}\mu \geqslant 0$ is an eigenvalue of A_Φ with eigenfunction w, and let $\mu^i_0 < 0$ for $i = r+1, \dots, n$. Put $q = \int_0^\infty p(y) w(y)\, dy$ and let $i \in \{1, \dots, r\}$; then integration yields

$$w_i(x) = \Phi_i(x) e^{-\mu x}[w_i(0)/\Phi_i(0) + q_i/\mu] - \Phi_i(x) q_i/\mu,$$

and using boundary condition (4b) we obtain $w_i(0) = -\Phi_i(0) q_i/\mu$, hence

$$w_i(x) = -\Phi_i(x) q_i/\mu \qquad \text{for} \qquad x \in \mathbb{R}_+, \qquad i = 1, \dots, r.$$

Moreover, we have $w_i(x) \equiv 0$ for $i = r+1, \dots, n$ and so we obtain

$$q = \int_0^\infty p(y) w(y)\, dy = -\mu^{-1} \int_0^\infty p(y)(\Phi(y) q)\, dy,$$

i.e. $-\mu$ is an eigenvalue of the $r \times r$-matrix R whose entries are

$$R_{ij} = \int_0^\infty p_{ij}(y) \Phi_j(y)\, dy. \tag{30}$$

This latter claim also holds if $\mu = 0$, as can be seen by a similar consideration. Note also that $\mu^i_0 = \lambda^i_0 - f_i(\Phi)$ in this case. Summarizing we obtain

Corollary 2. *Let g, k be independent of x. Then:*

(i) *If $f_i(\Phi) < \lambda^i_0$ for some $i \in \{r+1, \dots, n\}$, Φ is unstable.*

(ii) *If $f_i(\Phi) > \lambda^i_0$ for $i = r+1, \dots, n$ and R defined by* (30) *admits some eigenvalue with negative real part, Φ is unstable.*

(iii) *If* $f_i(\Phi) > \lambda_0^i$ *for* $i = r+1, \ldots, n$ *and all eigenvalues of R have positive real parts,* Φ *is asymptotically stable.*

Note that in case of only one equation, i.e. $n = m_1 = r = 1$, (30) becomes trivial:

$$R = \int_0^\infty p(y)\Phi(y)\,dy = g'\left(\int_0^\infty k(y)\Phi(y)\,dy\right)\int_0^\infty k(y)\Phi(y)\,dy.$$

Since $k \geqslant 0$ we have instability if $f'(\Phi) < 0$ holds and asymptotic stability if $f'(\Phi) > 0$.

(ii) Suppose k is independent of x, i.e. we have separability. For $n = 1$ this case was studied in [6] and [13]. Then,

$$p(x,y) = g'(x, K\Phi)k(y) = p(x)k(y).$$

Again, let $\mu \in \mathbb{C}\backslash\{0\}$, $\operatorname{Re}\mu \geqslant 0$ be an eigenvalue of A_Φ with eigenfunction w and let $\mu_0^i < 0$ for $i = r+1, \ldots, n$. Put $q = \int_0^\infty k(y)w(y)\,dy$ and let $i \in \{1, \ldots, r\}$; as before integration yields

$$w_i(x) = \Phi_i(x)e^{-\mu x}\left[w_i(0)/\Phi_i(0) - \int_0^x e^{\mu y}p_i(y)\,dy\,q\right],$$

and by (4b) we obtain

$$\left(1 - \Phi_i(0)^{-1}\int_0^\infty b_i\Phi_i e^{-\mu x}\,dx\right)w_i(0) + \left(\int_0^\infty b_i(x)\Phi_i(x)\int_0^x e^{-\mu(x-y)}p_i(y)\,dy\right)q = 0$$

which we write as

$$D(\mu)w(0) + R(\mu)q = 0. \tag{31}$$

On the other hand,

$$q = \int_0^\infty k(y)w(y)\,dy = S(\mu)w(0) - T(\mu)q \tag{32}$$

where

$$T(\mu)_{ij} = \sum_{l=1}^r \int_0^\infty k_{i1}(y)\Phi_l(y)\int_0^y p_{lj}(\tau)e^{-\mu(y-\tau)}\,d\tau\,dy, \qquad 1 \leqslant i, \qquad j \leqslant m_1$$

and

$$S(\mu)_{ij} = \int_0^\infty k_{ij}(y)e^{-\mu y}\Phi_j(y)/\Phi_j(0)\,dy \quad \text{for} \quad 1 \leqslant i \leqslant m_1, \quad 1 \leqslant j \leqslant r.$$

Thus, the pair $(w(0), q)$ is a nontrivial solution of

$$\begin{pmatrix} D(\mu) & R(\mu) \\ -S(\mu) & I + T(\mu) \end{pmatrix}\begin{pmatrix} w(0) \\ q \end{pmatrix} = 0$$

which implies that μ is a zero of $\psi(\rho)$ defined by

$$\psi(\rho) = \det\begin{pmatrix} D(\rho) & R(\rho) \\ -S(\rho) & I + T(\rho) \end{pmatrix}. \tag{33}$$

Summarizing we get

Corollary 3. *Let k be independent of x. Then,*

(i) *If $\mu_0^i > 0$ for some $i \in \{r+1, \dots, n\}$ or $\psi(\rho)$ admits a zero of positive real part, ϕ is unstable.*

(ii) *If $\mu_0^i < 0$ for $i = r+1, \dots, n$ and $\psi(\rho) = 0$ has no solutions in $\mathbb{C}$ with nonnegative real part, Φ is asymptotically stable.*

In case $n = m_1 = r = 1$, $\psi(\rho)$ reduces to

$$\psi(\rho) = D(\rho)(1 + T(\rho)) + R(\rho)S(\rho)$$

where now D, T, R, S are complex-valued functions.

If $p(x) = g'(x, K\Phi) < 0$ for all $x \in \mathbb{R}_+$, we obtain $\psi(0) < 0$ and since $\lim_{\rho \to \infty} \psi(\rho) = 1$ always holds, there is a positive zero of ψ, hence Φ is an unstable equilibrium solution, in analogy with the case when g is independent of x. On the other hand, if $p(x) > 0$ for all $x \in \mathbb{R}_+$, it is easy to see that $\psi(\rho) > 0$ for all $\rho \in \mathbb{R}_+$, but it may happen that $\psi(\rho)$ has conjugate complex zeros with positive real part.

Appendix

We are going to prove Lemma C, parts (iii) and (iv) as well as Theorem D.

Proof of Lemma C (iii). Let $v \in D$, $|v| > R$; we claim there is $\delta > 0$ such that $v(t) = U(t)v_0 \in D$ satisfies

$$|v(t)| \leqslant |v| \exp\left(-\int_0^t |v(s)|^{-2}(Fv(s), v(s))_- \, ds\right) \quad \text{for} \quad t \in [0, \delta]. \tag{34}$$

In fact, since $D \cap D(A)$ is dense in D, there is $(v_n) \subset D \cap D(A)$ such that $|v_n| > R$ and $v_n \to v$. $v_n(t) = U(t)v_n \in D \cap D(A)$ satisfies (D^-: left upper Dini-derivative)

$$D^-|v_n(t)|\,|v_n(t)| \leqslant (v_n', v_n)_- \leqslant (Av_n + Fv_n, v_n)_- - (Fv_n, v_n)_- \leqslant -(Fv_n, v_n)_-$$

for $t \in [0, \delta]$, where $\delta > 0$ is sufficiently small. Integration yields (34) with v replaced by v_n, and passing to the limit we arrive at (34) since $(\cdot, \cdot)_-$ is lower semicontinuous. It is also clear that $\delta = \delta(v) > 0$ can be chosen uniformly positive if v is also allowed to vary in some compact set $\subset D$ with $|v| \geqslant R + \varepsilon > R$.

Now, let $u(t)$ be any mild solution of (P_1) in D and suppose $|u(t)| > R$. If we let $v_h(s) = U(s)u(t-h)$ for $t > h > 0$, by (34) we obtain

$$\begin{aligned}
&(|u(t)| - |u(t-h)|)|u(t)| \\
&\quad \leqslant (u(t) - u(t-h), u(t))_- \\
&\quad \leqslant (U(h)u(t-h) - u(t-h), u(t))_+ + \left(\int_{t-h}^t U(t-s)F(u(s))\,ds, u(t)\right)_- \\
&\quad \leqslant |u(t-h)|\,|u(t)|\left(\exp\left(-\int_0^h |v_h(s)|^{-2}(Fv_h(s), v_h(s))_- \, ds\right) - 1\right) \\
&\qquad + h(Fu(t), u(t))_- + o(h),
\end{aligned}$$

provided $h > 0$ is sufficiently small. Division by $h > 0$ and passing to the limit $h \to 0+$ yields

$$D^-|u(t)|\,|u(t)| \leqslant |u(t)|^2(-\,|u(t)|^{-2}(Fu,u)_-) + (Fu,u)_- = 0,$$

where we used lower semicontinuity of $(\cdot,\cdot)_-$ again. Thus $D^-|u(t)| \leqslant 0$ holds for all $t > 0$ such that $|u(t)| > R$. This inequality in turn implies $|u(t)| \leqslant R$ in $\mathbb{R}_+$ provided $|u(0)| \leqslant R$, hence $D \cap B_R(0)$ remains invariant with respect to (P_1), and so (S) holds for $D \cap B_R(0)$. q.e.d.

Proof of Lemma C (iv). Let $x_0 \in \mathring{H} \cap D$, $\varepsilon > 0$ and consider the approximate problem

$$(P_1^\varepsilon) \qquad u' = Au + Fu - \varepsilon(u - x_0), \qquad u(0) = u_0.$$

Since D is convex it is easy to verify that (S) also holds for D with respect to (P_1^ε). Let $u_\varepsilon(t)$ be the mild solution of (P_1^ε). Put $\varphi(t) = (u_\varepsilon(t), u^*)$; then we have

$$\varphi(t+h) - \varphi(t) = (u_\varepsilon(t), U^*(h)u^* - u^*) + \left(\int_t^{t+h} U(t+h-s)(Fu_\varepsilon - \varepsilon(u_\varepsilon - x_0))\,ds, u^*\right).$$

Dividing by $h > 0$ and passing to the limit $h \to 0$ yields

$$\varphi'(t) = (u_\varepsilon(t), A^*u^*) + (Fu_\varepsilon(t), u^*) - \varepsilon\varphi(t) + \varepsilon(x_0, u^*),$$

since $u^* \in D(A^*)$ and $h^{-1}(U^*(h)u^* - u^*) \to A^*u^*$ with respect to the weak*-topology on X^*; cp. [8]. Hence, for $u_0 \in D \cap H$ we obtain $\varphi'(t) > 0$ for all t with $\varphi(t) = c$, and $\varphi(0) \geqslant c$, which in turn implies $\varphi(t) = (u_\varepsilon(t), u^*) \geqslant c$, i.e. $u_\varepsilon(t) \in D \cap H$. Passing to the limit as $\varepsilon \to 0+$ implies $u(t) \in D \cap H$ for all $t \geqslant 0$ provided $u_0 \in D \cap H$, hence $D \cap H$ is invariant with respect to $(P1)$. Therefore, the subtangential condition (S) also holds for $D \cap H$. q.e.d.

Proof of Theorem D. For simplicity let us assume that X is separable. The hypotheses of Theorem D imply that to each initial value u_0 there is exactly one global mild solution $u(t; u_0)$ in D and it depends continuously on u_0, by Theorem B. Thus, the solution operator for $(P1)$ $S(t)\colon D \to D$ defined by $S(t)u_0 = u(t; u_0)$ is continuous. But we also have

$$\beta(S(t)B) \leqslant k(t)\beta(B) \qquad \text{for all } B \subset D \text{ countable}, \tag{35}$$

where $k(t) = e^{(\omega_1 + \kappa_1)t} < 1$. In fact, since X is separable β commutes with integration (see Mönch and von Harten [10]), thus we obtain

$$\varphi(t) = \beta(S(t)B) \leqslant \beta(U(t)B) + \beta\left(\int_0^t U(t-s)FS(s)B\,ds\right)$$
$$\leqslant e^{\omega_1 t}\beta(B) + \int_0^t e^{\omega_1(t-s)}\kappa_1\varphi(s)\,ds$$

which in turn implies (35), by Gronwall's Lemma.

Now, by an extension of Darbo's Fixed Point Theorem due to Daher [3], $S(T)$ admits a fixed point, i.e. $(P1)$ has a T-periodic solution for each (small) $T > 0$. Finally, let $T_n = T_0 \cdot 2^{-n}$; then the corresponding T_n-periodic solutions $u_n(t)$ are T_0-periodic, hence from (35) we deduce $\beta(\{u_n(t)\}) \equiv 0$. So there is $\Phi(t)$ and a subsequence $u_{n_k}(t) \rightrightarrows \Phi(t)$, and $\Phi(t)$ is constant since it is T_n-periodic for each $n \in \mathbb{N}$. q.e.d.

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