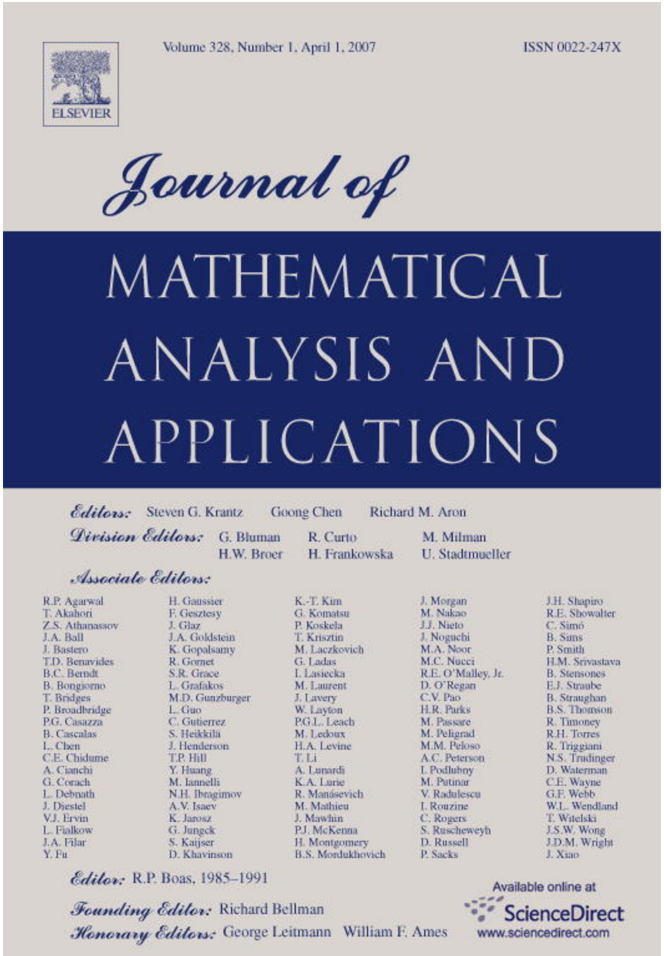
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Stability and regularity results for a size-structured population model

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Abstract

In the present paper a nonlinear size-structured population dynamical model with size and density dependent vital rate functions is considered. The linearization about stationary solutions is analyzed by semigroup and spectral methods. In particular, the spectrally determined growth property of the linearized semigroup is derived from its long-term regularity. These analytical results make it possible to derive linear stability and instability results under biologically meaningful conditions on the vital rates. The principal stability criteria are given in terms of a modified net reproduction rate.

Keywords: Population dynamics; Size-structured; Stability theory; Spectral analysis

1. Introduction

The dynamics of a size-structured population living in a closed territory can be described by the model equation

$$p_t(a,t) + \big(\gamma\big(a, P(t)\big)p(a,t)\big)_a = -\mu\big(a, P(t)\big)p(a,t), \quad 0 \leqslant a \leqslant m < \infty, \tag{1.1}$$

subject to the boundary condition

$$p(0,t) = \int_0^m \beta\big(a, P(t)\big)p(a,t)\,da, \quad t > 0, \tag{1.2}$$

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and an initial condition of the form

$$p(a,0)=p_0(a). \tag{1.3}$$

Here, the function $p=p(a,t)$ denotes the density of individuals of size $a\in[0,m]$ at time $t\in[0,\infty)$ where $m>0$ denotes the (finite) maximum size of any individual in the population. The model equation involves the vital rates $\mu=\mu(a,P)$—mortality, $\beta=\beta(a,P)$—fertility and $\gamma=\gamma(a,P)$—growth rate, which depend on the size a and on the total population quantity P, given by

$$P(t)=\int_0^m p(a,t)\,da \tag{1.4}$$

at time t. Consequently, Eq. (1.1) is nonlinear. Note that for simplicity we have normalized the size of any newborn individual to 0.

We make the following general assumptions on the vital rate functions:

$$\mu,\beta\in C^1\big([0,m]\times[0,\infty)\big),\qquad \beta\geqslant 0, \tag{1.5}$$

$$\gamma\in C^2\big([0,m]\times[0,\infty)\big),\qquad \gamma>0. \tag{1.6}$$

These assumptions will suffice (and could actually be relaxed) to make the analysis of the linearized problem work. They are, however, generally not strong enough to prove global existence results for the nonlinear problem. In addition, for practical purposes several other biologically relevant assumptions (such as $\mu>0$) will have to be imposed on these functions.

The population model treated here is equivalent to the one usually considered in the literature (see [1,2] and references therein) when the boundary condition (1.2) is replaced by

$$\gamma\big(0,P(t)\big)p(0,t)=\int_0^m \beta\big(a,P(t)\big)p(a,t)\,da,\qquad t>0, \tag{1.7}$$

and no population inflow from an external source takes place. Condition (1.2) incorporates the γ-term on the left of Eq. (1.7) in the birth rate β on the right. We prefer working with the boundary condition in the form of Eq. (1.2) to simplify the following developments. Local and global existence and uniqueness of solutions to this nonlinear problem have been analyzed in [2]. The model considered here reduces to the Gurtin–MacCamy (or McKendrick) nonlinear age-structured model if $\gamma\equiv 1$ (see [13]) and is a generalization of the simple problem treated in [10]. Similar physiologically structured population models have been studied intensively in the literature. Let us just mention the well-known works [20,22,25] for reference here.

The main purpose of the present work is to investigate the linear stability of stationary solutions of the system (1.1)–(1.3) using semigroup techniques and spectral methods based on the characteristic equation. Linear semigroup methods were successfully developed to study the linear stability and regularity of solutions of linearized fluid flow problems where the underlying dynamics is driven by a one-dimensional mass transport equation (see [14,18,19]). The model equations treated in this work are similar in nature. Sophisticated semigroup methods have recently been used to obtain sharp regularity results for one-dimensional hyperbolic–elliptic fluid flow problems (see [15,17]) and to explain the phenomenon that the roots of the underlying characteristic equations (eigenvalues) are lined up along certain curves (see [16]). Earlier, quite deep semigroup results for an n-dimensional age-structured model with constant growth rate can be found in [24]. Our results will extend these earlier results in one dimension to the size-structured case with nonconstant growth rate.

Any stationary solution $p_* = p_*(a)$ of the system (1.1)–(1.2) satisfies the equations

$$\big(\gamma(a, P_*)p_*(a)\big)_a = -\mu(a, P_*)p_*(a) \tag{1.8}$$

and

$$p_*(0) = \int_0^m \beta(a, P_*)p_*(a)\,da, \tag{1.9}$$

where $P_* = \int_0^m p_*(a)\,da$ denotes the total population of the stationary solution p_*. The general solution of Eq. (1.8) is found as

$$p_*(a) = p_*(0)\exp\left\{-\int_0^a \frac{\mu(s, P_*) + \gamma_a(s, P_*)}{\gamma(s, P_*)}\,ds\right\}. \tag{1.10}$$

Hence in case $p_*(0) \neq 0$, Eq. (1.9) gives the relation

$$1 = \int_0^m \beta(a, P_*)\exp\left\{-\int_0^a \frac{\mu(s, P_*) + \gamma_a(s, P_*)}{\gamma(s, P_*)}\,ds\right\}da. \tag{1.11}$$

Next we observe that

$$\exp\left\{-\int_0^a \frac{\gamma_a(s, P_*)}{\gamma(s, P_*)}\,ds\right\} = \frac{\gamma(0, P_*)}{\gamma(a, P_*)}. \tag{1.12}$$

Hence Eq. (1.11) can be cast in the form

$$1 = \int_0^m \gamma(0, P_*)\frac{\beta(a, P_*)}{\gamma(a, P_*)}\exp\left\{-\int_0^a \frac{\mu(s, P_*)}{\gamma(s, P_*)}\,ds\right\}da \tag{1.13}$$

if $p_*(0) \neq 0$. It is worthwhile to compare this size-structured case with the well-known age-structured case. In the age-structured model one introduces the net reproduction function

$$R(P) = \int_0^m \beta(a, P)\exp\left\{-\int_0^a \mu(s, P)\,ds\right\}da \quad (P \geqslant 0) \tag{1.14}$$

which is the expected number of newborns of an individual. This function was found to play a crucial role in the stability analysis of stationary solutions in the age-structured case, see [9,10].

In the model equation of interest here the right-hand side of Eq. (1.13) gives a modified version of the net reproduction function. Hence for $P \geqslant 0$ let us define the relative net reproduction rate

$$\tilde{R}(P) \stackrel{\text{def}}{=} \int_0^m \tilde{\beta}(a, P)\exp\left\{-\int_0^a \tilde{\mu}(s, P)\,ds\right\}da \tag{1.15}$$

with the normalized fertility and mortality rates

$$\tilde{\beta}(a, P) = \gamma(0, P)\frac{\beta(a, P)}{\gamma(a, P)} \quad \text{and} \quad \tilde{\mu}(a, P) = \frac{\mu(a, P)}{\gamma(a, P)}. \tag{1.16}$$

Note that $\tilde{R}(P_*) = 1$ for the total population P_* of a nonzero stationary solution p_*. We can express a stationary solution p_* by means of the total population quantity P_*. Specifically, we have

$$P_* = \int_0^m p_*(a)\,da = p_*(0) \int_0^m \exp\left\{ -\int_0^a \tilde{\mu}(s, P)\,ds \right\} \frac{\gamma(0, P_*)}{\gamma(a, P_*)}\,da. \tag{1.17}$$

Hence solving for $p_*(0)$ we obtain the stationary solution in terms of the vital rate functions and the total population

$$p_*(a) = \frac{P_* \exp\left\{-\int_0^a \frac{\mu(s,P_*)}{\gamma(s,P_*)}\,ds\right\}}{\int_0^m \exp\left\{-\int_0^\alpha \frac{\mu(s,P_*)}{\gamma(s,P_*)}\,ds\right\} \frac{\gamma(a,P_*)}{\gamma(\alpha,P_*)}\,d\alpha}. \tag{1.18}$$

We have shown the following result (in analogy to the age-structured model, see [13]).

Proposition 1.1. *For given vital rates μ, β, γ, the function p_* is a positive stationary solution of problem* (1.1)–(1.2) *if and only if p_* is determined by Eq.* (1.18) *with the positive total population quantity P_* satisfying Eq.* (1.11) *or equivalently $\tilde{R}(P_*) = 1$.*

2. The linear semigroup

Given a stationary solution p_* of the system (1.1)–(1.2), we introduce the perturbation $u = u(a,t)$ of p by making the ansatz $p = u + p_*$. Hence u has to satisfy the equations

$$u_t(a,t) + \big(\gamma(a,P)u(a,t)\big)_a + \mu(a,P)u(a,t) = -\big(\gamma(a,P)p_*(a)\big)_a - \mu(a,P)p_*(a), \tag{2.1}$$

$$u(0,t) = \int_0^m \beta(a,P)\big(u(a,t) + p_*(a)\big)\,da - p_*(0), \tag{2.2}$$

where $P(t) = \int_0^m u(a,t)\,da + P_*$. Now we linearize the vital rates. To this end we note that the functional dependence of the vital rates on P rather than on p requires the linearization about P_*. Specifically, when using the approximations

$$\mu(a,P) = \mu(a,P_*) + \mu_P(a,P_*)(P - P_*) + \text{higher order terms},$$
$$\beta(a,P) = \beta(a,P_*) + \beta_P(a,P_*)(P - P_*) + \text{higher order terms},$$
$$\gamma(a,P) = \gamma(a,P_*) + \gamma_P(a,P_*)(P - P_*) + \text{higher order terms}$$

in Eqs. (2.1)–(2.2) and dropping all nonlinear terms, we arrive at the linearized problem

$$\begin{aligned} &u_t(a,t) + \gamma(a,P_*)u_a(a,t) + \big(\gamma_a(a,P_*) + \mu(a,P_*)\big)u(a,t) \\ &\quad + \big(\gamma_{aP}(a,P_*)p_*(a) + \mu_P(a,P_*)p_*(a) + \gamma_P(a,P_*)p_*'(a)\big)\bar{U}(t) = 0, \end{aligned} \tag{2.3}$$

$$u(0,t) = \int_0^m \left(\beta(a,P_*) + \int_0^m \beta_P(\alpha,P_*)p_*(\alpha)\,d\alpha\right) u(a,t)\,da, \tag{2.4}$$

where we have set

$$\bar{U}(t) \stackrel{\text{def}}{=} \int_0^m u(a,t)\,da. \tag{2.5}$$

Equations (2.3)–(2.4) are accompanied by the initial condition

$$u(a,0) = u_0(a). \tag{2.6}$$

Let $\mathcal{X}$ be the Lebesgue space $L^1(0,m)$, endowed with the usual L^1-norm, denoted by $\|\cdot\|$. When we introduce the bounded linear functional Φ on $\mathcal{X}$ by

$$\Phi(u) = \int_0^m \left(\beta(a, P_*) + \int_0^m \beta_P(\alpha, P_*)p_*(\alpha)\,d\alpha\right)u(a)\,da \tag{2.7}$$

and the operators

$$\mathcal{A}u = -\gamma(\cdot, P_*)u_a \quad \text{with domain } \operatorname{Dom}(\mathcal{A}) = \{u \in W^{1,1}(0,m) \mid u(0) = \Phi(u)\}, \tag{2.8}$$

$$\mathcal{B}u = -\big(\gamma_a(\cdot, P_*) + \mu(\cdot, P_*)\big)u \quad \text{on } \mathcal{X}, \tag{2.9}$$

$$\mathcal{C}u = -\big(\gamma_{aP}(\cdot, P_*)p_* + \mu_P(\cdot, P_*)p_* + \gamma_P(\cdot, P_*)p'_*\big)\int_0^m u(a)\,da \quad \text{on } \mathcal{X}, \tag{2.10}$$

then the linearized system (2.3)–(2.4) can be cast in the form of an abstract ordinary differential equation on $\mathcal{X}$

$$\frac{d}{dt}u = (\mathcal{A} + \mathcal{B} + \mathcal{C})u \tag{2.11}$$

with the initial condition

$$u(0) = u_0. \tag{2.12}$$

To obtain the semigroup property for solutions of the abstract initial value problem (2.11)–(2.12), we proceed similarly to the developments in [8] for a simple transport problem subject to "boundary perturbation."

Theorem 2.1. *The operator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ generates a strongly continuous semigroup $\{\mathcal{T}(t)\}_{t\geqslant 0}$ of bounded linear operators on $\mathcal{X}$.*

Proof. Since the operator $\mathcal{B} + \mathcal{C}$ is bounded on $\mathcal{X}$, it suffices to prove that $\mathcal{A}$ generates a semigroup. To this end, we introduce the modified operator

$$\tilde{\mathcal{A}}u = -\gamma(\cdot, P_*)u_a \quad \text{with domain } \operatorname{Dom}(\tilde{\mathcal{A}}) = \{u \in W^{1,1}(0,m) \mid u(0) = 0\}.$$

Since γ is positive, it is obvious that $\tilde{\mathcal{A}}$ generates a nilpotent semigroup $\{\mathcal{S}(t)\}_{t\geqslant 0}$ on $\mathcal{X}$, given by

$$\big(\mathcal{S}(t)u\big)(a) = \begin{cases} u(\Gamma^{-1}(\Gamma(a) - t)) & \text{if } \Gamma(a) \geqslant t, \\ 0 & \text{otherwise,} \end{cases} \tag{2.13}$$

where

$$\Gamma(a) = \int_0^a \frac{1}{\gamma(\alpha, P_*)}\, d\alpha. \tag{2.14}$$

In addition, we readily obtain that $\tilde{\mathcal{A}}$ is invertible. Now let $\mathcal{X}_{-1}$ be the completion of $\mathcal{X}$ in the norm $\|\cdot\|_{-1} \stackrel{\text{def}}{=} \|\tilde{\mathcal{A}}^{-1}\cdot\|$. We define the extended semigroup $\{\mathcal{S}_{-1}(t)\}_{t\geqslant 0}$ on $\mathcal{X}_{-1}$ by

$$\mathcal{S}_{-1}(t) = \tilde{\mathcal{A}}^{-1}\mathcal{S}(t)\tilde{\mathcal{A}} \tag{2.15}$$

and denote its generator by $\tilde{\mathcal{A}}_{-1}$. Then $\tilde{\mathcal{A}}_{-1}$ is an extension of $\tilde{\mathcal{A}}$ with domain $\operatorname{Dom}(\tilde{\mathcal{A}}_{-1}) = \mathcal{X}$ and range in $\mathcal{X}_{-1}$. Finally we define the perturbing operator $\mathcal{P} \in L(\mathcal{X}, \mathcal{X}_{-1})$ by

$$\mathcal{P}u \stackrel{\text{def}}{=} -\Phi(u)\tilde{\mathcal{A}}_{-1}1, \tag{2.16}$$

where $\tilde{\mathcal{A}}_{-1}1$ denotes the action of $\tilde{\mathcal{A}}_{-1}$ on the constant function $1(\cdot) = 1$ in $\mathcal{X}$. Then the operator $\mathcal{A}$ is just the part of the operator $\tilde{\mathcal{A}}_{-1} + \mathcal{P}$ in $\mathcal{X}$

$$\mathcal{A} = (\tilde{\mathcal{A}}_{-1} + \mathcal{P})|_{\mathcal{X}}. \tag{2.17}$$

The claim of the theorem follows from a version of the Desch–Schappacher perturbation theorem (see [8] and also [12] for related developments) if for some $t_0 > 0$, $1 \leqslant q < \infty$ the condition

$$\int_0^{t_0} \mathcal{S}_{-1}(t_0 - s)\mathcal{P}f(s)\, ds \in \mathcal{X} \tag{2.18}$$

holds true for all $f \in L^q([0, t_0]; \mathcal{X})$. This condition is equivalent to the condition

$$\int_0^{t_0} \Phi\big(f(s)\big)\mathcal{S}(t_0 - s)1(\cdot)\, ds \in \operatorname{Dom}(\tilde{\mathcal{A}}). \tag{2.19}$$

With $t_0 = m$ and q arbitrary we obtain

$$\int_0^m \Phi\big(f(s)\big)\mathcal{S}(m - s)1(\cdot)\, ds = \int_{m-\Gamma(\cdot)}^m \Phi\big(f(s)\big)\, ds \stackrel{\text{def}}{=} F(\cdot). \tag{2.20}$$

Since for any $f \in L^q([0, t_0]; \mathcal{X})$ we have $F \in W^{1,1}(0, m)$ and $F(0) = 0$, the claim is proven. □

Theorem 2.1 has the following immediate consequence.

Corollary 2.2. *For initial data $u_0 \in L^1(0, m)$ the linear boundary-initial value problem* (2.3)–(2.6) *has a unique solution u in $C([0, \infty); L^1(0, m))$, given by*

$$u(t, a) = \big(\mathcal{T}(t)u_0\big)(a). \tag{2.21}$$

3. Regularity properties of the semigroup

In this section we will prove two regularity results. The first result will imply that the spectrally determined growth property holds true and that the linear stability of the steady-state solution is governed by the location of the leading eigenvalue, while the second result will establish that under certain assumptions on the vital rates the leading eigenvalue will be real rather than complex. Analogous developments in the context of one-dimensional fluid flow problems are given in [14,15,17–19].

Theorem 3.1. *The semigroup $\{\mathcal{T}(t)\}_{t\geqslant 0}$ generated by the operator $\mathcal{A}+\mathcal{B}+\mathcal{C}$ is eventually compact. Specifically, the semigroup operator $\mathcal{T}(t)$ is compact if $t>2\Gamma(m)$.*

Proof. Since the operator $\mathcal{C}$ is compact on $\mathcal{X}=L^1(0,m)$, it suffices to establish the claim for the operator $\mathcal{A}+\mathcal{B}$. To this end, we note that the abstract differential equation

$$\frac{d}{dt}u=(\mathcal{A}+\mathcal{B})u \tag{3.1}$$

corresponds to the partial differential equation

$$u_t(a,t)+\gamma(a,P_*)u_a(a,t)+\big(\gamma_a(a,P_*)+\mu(a,P_*)\big)u(a,t)=0, \tag{3.2}$$

subject to the boundary condition (2.4). For $t_0>0$ let us introduce

$$v(a)=u\big(a,t(a)\big), \tag{3.3}$$

where

$$t(a)=t_0+\Gamma(a) \tag{3.4}$$

with Γ defined in (2.14). Then v satisfies the equation

$$v_a(a)+\frac{\gamma_a(a,P_*)+\mu(a,P_*)}{\gamma(a,P_*)}v(a)=0, \tag{3.5}$$

hence

$$v(a)=\Phi\big(u(\cdot,t_0)\big)\exp\left\{-\int_0^a\frac{\gamma_a(\alpha,P_*)+\mu(\alpha,P_*)}{\gamma(\alpha,P_*)}\,d\alpha\right\}. \tag{3.6}$$

However, for $t-\Gamma(a)>0$ this implies

$$\begin{aligned}u(a,t)={}&\int_0^m\left(\beta(\alpha,P_*)+\int_0^m\beta_P(\kappa,P_*)p_*(\kappa)\,d\kappa\right)u\big(\alpha,t-\Gamma(a)\big)\,d\alpha\\&\times\exp\left\{-\int_0^a\frac{\gamma_a(\alpha,P_*)+\mu(\alpha,P_*)}{\gamma(\alpha,P_*)}\,d\alpha\right\}.\end{aligned} \tag{3.7}$$

Therefore, if $t>\Gamma(m)=\max_{0\leqslant a\leqslant m}\Gamma(a)$, u is continuous in a and t. Consequently, Eq. (3.2) implies that u is continuously differentiable if $t>2\Gamma(m)$. Hence the semigroup generated by $\mathcal{A}+\mathcal{B}$ is differentiable for $t>2\Gamma(m)$. Since $W^{1,1}(0,m)$ is compactly imbedded in $L^1(0,m)$, the claim follows. □

See [17] for a similar regularity result. The semigroup generated by $\mathcal{A}+\mathcal{B}+\mathcal{C}$ can actually be shown to be differentiable for all times $t>2\Gamma(m)$.

Theorem 3.1 has the following immediate, though noteworthy consequences (see [8,23]).

Corollary 3.2. *The spectrum of the semigroup generator $\mathcal{A}+\mathcal{B}+\mathcal{C}$ consists of isolated eigenvalues of finite multiplicity only. Moreover, the Spectral Mapping Theorem holds true, i.e.,*

$$\sigma\big(\mathcal{T}(t)\big) = \{0\} \cup \exp\big\{\sigma(\mathcal{A}+\mathcal{B}+\mathcal{C})t\big\}, \quad t > 0. \tag{3.8}$$

Because of Corollary 3.2 the linear stability of the steady-state solution is spectrally determined (see [8,23]). Hence in the following it suffices to investigate the location of the leading eigenvalue of the semigroup generator. This analysis would be much simpler if it was known that the eigenvalue with largest real part was real. The following result allows us to draw this conclusion in certain circumstances.

Theorem 3.3. *Suppose that*

$$\gamma_{aP}(\cdot, P_*)p_* + \mu_P(\cdot, P_*)p_* + \gamma_P(\cdot, P_*)p_*' \leqslant 0, \tag{3.9}$$

$$\beta(\cdot, P_*) + \int_0^m \beta_P(\alpha, P_*)p_*(\alpha)\, d\alpha \geqslant 0. \tag{3.10}$$

Then the semigroup $\{\mathcal{T}(t)\}_{t\geqslant 0}$ generated by the operator $\mathcal{A}+\mathcal{B}+\mathcal{C}$ is positive.

Proof. Condition (3.9) ensures that the operator $\mathcal{C}$ is positive. Hence we can restrict ourselves to the operator $\mathcal{A}+\mathcal{B}$ and the associated differential equation (3.2) subject to the boundary condition (2.4). Suppose u is any solution of Eq. (3.2) such that (2.4) holds true. Then the function w defined by

$$w(a,t) = u(a,t)\exp\left\{\int_0^a \frac{\gamma_a(\alpha, P_*) + \mu(\alpha, P_*)}{\gamma(\alpha, P_*)}\, d\alpha\right\} \tag{3.11}$$

satisfies

$$w_t(a,t) + \gamma(a, P_*)w_a(a,t) = 0, \tag{3.12}$$

$$w(0,t) = \Phi\left(w(\cdot,t)\exp\left\{-\int_0^{\cdot} \frac{\gamma_a(\alpha, P_*) + \mu(\alpha, P_*)}{\gamma(\alpha, P_*)}\, d\alpha\right\}\right) \stackrel{\text{def}}{=} \Psi\big(w(\cdot,t)\big). \tag{3.13}$$

This system corresponds to the modified semigroup generator

$$\mathcal{A}_m w = -\gamma(\cdot, P_*)w_a \quad \text{with domain } \operatorname{dom}(\mathcal{A}_m) = \big\{w \in W^{1,1}(0,m) \bigm| w(0) = \Psi(w)\big\}. \tag{3.14}$$

It suffices to show that the semigroup generated by $\mathcal{A}_m$ is nonnegative. To this end, we note that for $\lambda \geqslant 0$ sufficiently large and $g \in L^1(0,m)$ the resolvent equation

$$\lambda w - \mathcal{A}_m w = g \tag{3.15}$$

has the implicitly given solution

$$w(a) = e^{-\lambda\Gamma(a)}\Psi(w) + \int_0^a e^{\lambda(\Gamma(\alpha)-\Gamma(a))}\frac{g(\alpha)}{\gamma(\alpha, P_*)}\, d\alpha. \tag{3.16}$$

Applying Ψ we obtain

$$\Psi(w) = \left(1 - \Psi\left(e^{-\lambda \Gamma(\cdot)}\right)\right)^{-1} \Psi\left(\int_0^{\cdot} e^{\lambda(\Gamma(\alpha) - \Gamma(\cdot))} \frac{g(\alpha)}{\gamma(\alpha, P_*)}\, d\alpha \right). \tag{3.17}$$

Now we derive from the definition of Ψ and condition (3.10) that the solution w, given by Eq. (3.16) is nonnegative if g is nonnegative a.e. and λ is sufficiently large. Hence for such λ the resolvent operator of $\mathcal{A}_m$ is positive. However, this result implies the claim. □

Remark 3.4. It is possible to relax the positivity conditions (3.9), (3.10) by a slightly more general (though more complicated) condition which can be easily derived from analyzing the whole operator $\mathcal{A} + \mathcal{B} + \mathcal{C}$. While such a condition might be desirable in certain circumstances, we shall restrict ourselves to conditions (3.9), (3.10) above for their simplicity. It can also easily be seen that Eqs. (3.9), (3.10) are direct generalizations of the equivalent positivity conditions in the age-structured case, given in [24].

The positivity and eventual compactness of the semigroup allows us to draw the following important conclusion (see [8]).

Corollary 3.5. *Suppose that conditions* (3.9)–(3.10) *hold true. Then the spectral bound* $s(\mathcal{A} + \mathcal{B} + \mathcal{C}) = \sup\{\operatorname{Re} \lambda \mid \lambda \in \sigma(\mathcal{A} + \mathcal{B} + \mathcal{C})\}$ *belongs to the spectrum* $\sigma(\mathcal{A} + \mathcal{B} + \mathcal{C})$*. Specifically, the spectral bound* $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$ *is a dominant eigenvalue, and any other point* λ *in the spectrum has real part less than* $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$*.*

4. The characteristic equation

In the light of Corollary 3.2 the linear stability of stationary solutions of the system (1.1)–(1.3) is entirely determined by the eigenvalues of the semigroup generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$. Hence in this section we will derive a characterization of the eigenvalues in the form of zeros of a characteristic equation.

Theorem 4.1. $\lambda \in \mathbb{C}$ *is an eigenvalue of the operator* $\mathcal{A} + \mathcal{B} + \mathcal{C}$ *if and only if* λ *is a solution of the characteristic equation*

$$K(\lambda) - 1 = \begin{vmatrix} A_{11}(\lambda) & A_{12}(\lambda) - 1 \\ A_{21}(\lambda) - 1 & A_{22}(\lambda) \end{vmatrix} = 0, \tag{4.1}$$

where we define

$$A_{11}(\lambda) \stackrel{\text{def}}{=} \int_0^m F(\lambda, \mu, \gamma, a)\, da, \tag{4.2}$$

$$A_{12}(\lambda) \stackrel{\text{def}}{=} \int_0^m \beta(a, P_*) F(\lambda, \mu, \gamma, a)\, da, \tag{4.3}$$

$$A_{21}(\lambda) \stackrel{\text{def}}{=} -p_*(0) \int_0^m F(\lambda, \mu, \gamma, a) \left(\int_0^a G(\mu, \gamma, s) \exp\left\{ \int_0^s \frac{\lambda}{\gamma(r, P_*)}\, dr \right\} ds \right) da, \tag{4.4}$$

$$A_{22}(\lambda) \stackrel{\text{def}}{=} p_*(0)\int_0^m \beta_P(a,P_*)F(\lambda,\mu,\gamma,a)\exp\left\{\int_0^a \frac{\lambda}{\gamma(s,P_*)}\,ds\right\}da$$
$$- p_*(0)\int_0^m \beta(a,P_*)F(\lambda,\mu,\gamma,a)$$
$$\times\left(\int_0^a G(\mu,\gamma,s)\exp\left\{\int_0^s \frac{\lambda}{\gamma(r,P_*)}\,dr\right\}ds\right)da \tag{4.5}$$

and

$$F(\lambda,\mu,\gamma,a) \stackrel{\text{def}}{=} \exp\left\{-\int_0^a \frac{\lambda+\gamma_a(s,P_*)+\mu(s,P_*)}{\gamma(s,P_*)}\,ds\right\}, \tag{4.6}$$

$$G(\mu,\gamma,a) \stackrel{\text{def}}{=} \frac{\gamma_{aP}(a,P_*)+\mu_P(a,P_*)}{\gamma(a,P_*)} - \frac{\gamma_P(a,P_*)(\mu(a,P_*)+\gamma_a(a,P_*))}{\gamma(a,P_*)^2}. \tag{4.7}$$

Proof. To determine the spectrum of the semigroup generator, we substitute $u(a,t)=e^{\lambda t}U(a)$ into the linearized system (2.3)–(2.4). This ansatz gives the equations

$$\lambda U(a)+\gamma(a,P_*)U'(a)+\big(\gamma_a(a,P_*)+\mu(a,P_*)\big)U(a)$$
$$+\big(\gamma_{aP}(a,P_*)p_*(a)+\mu_P(a,P_*)p_*(a)+\gamma_P(a,P_*)p_*'(a)\big)\bar{U}=0, \tag{4.8}$$

$$U(0)=\int_0^m\left(\beta(a,P_*)+\int_0^m \beta_P(\alpha,P_*)p_*(\alpha)\,d\alpha\right)U(a)\,da, \tag{4.9}$$

where we let $\bar{U}=\int_0^m U(a)\,da$. The general solution U of Eq. (4.8) takes the form

$$U(a)=F(\lambda,\mu,\gamma,a)\left(U(0)-\bar{U}\int_0^a \frac{1}{F(\lambda,\mu,\gamma,s)}\right.$$
$$\left.\times\frac{p_*(s)(\gamma_{aP}(s,P_*)+\mu_P(s,P_*))+p_*'(s)\gamma_P(s,P_*)}{\gamma(s,P_*)}\,ds\right). \tag{4.10}$$

Hence Eq. (4.9) requires that

$$\bar{U}=U(0)\int_0^m F(\lambda,\mu,\gamma,a)\,da-\bar{U}\int_0^m F(\lambda,\mu,\gamma,a)\int_0^a \frac{1}{F(\lambda,\mu,\gamma,s)}$$
$$\times\frac{p_*(s)(\gamma_{aP}(s,P_*)+\mu_P(s,P_*))+p_*'(s)\gamma_P(s,P_*)}{\gamma(s,P_*)}\,ds\,da. \tag{4.11}$$

When we use these relations in Eq. (4.9) and note that

$$p_*(a) = p_*(0)\exp\left\{-\int_0^a \frac{\mu(r,P_*)+\gamma_a(r,P_*)}{\gamma(r,P_*)}\,dr\right\}, \tag{4.12}$$

$$p_*'(a) = p_*(a)\left(\frac{-\mu(a,P_*)-\gamma_a(a,P_*)}{\gamma(a,P_*)}\right), \tag{4.13}$$

the result follows. □

5. Linear stability results

This section is devoted to prove asymptotic stability and instability of stationary solutions in some intuitively interpretable and biologically relevant cases. The relative net reproduction rate $\tilde{R}(P)$ introduced in Eq. (1.15) will be used to formulate the stability/instability conditions. Our first result addresses the stability of the trivial stationary solution $p_* \equiv 0$.

Theorem 5.1. *The trivial steady-state solution $p_* \equiv 0$ is linearly asymptotically stable if $\tilde{R}(0) < 1$ and linearly unstable if $\tilde{R}(0) > 1$.*

Proof. For $p_* \equiv 0$ the characteristic equation (4.1) reduces to

$$K(\lambda) = A_{12}(\lambda) = \int_0^m \beta(a,0)\exp\left\{-\int_0^a \frac{\lambda+\gamma_a(s,0)+\mu(s,0)}{\gamma(s,0)}\,ds\right\}da = 1. \tag{5.1}$$

Since the conditions (3.9)–(3.10) of Theorem 3.3 are satisfied, we invoke Corollary 3.5 and restrict ourselves to $\lambda \in \mathbb{R}$ rather than $\lambda \in \mathbb{C}$. With

$$\Gamma_0(a) \stackrel{\text{def}}{=} \int_0^a \frac{1}{\gamma(s,0)}\,ds \tag{5.2}$$

we have

$$K(\lambda) = \int_0^m e^{-\lambda\Gamma_0(a)}\beta(a,0)\exp\left\{-\int_0^a \frac{\gamma_a(s,0)+\mu(s,0)}{\gamma(s,0)}\,ds\right\}da. \tag{5.3}$$

Observe that

$$\int_0^m \beta(a,0)\exp\left\{-\int_0^a \frac{\gamma_a(s,0)+\mu(s,0)}{\gamma(s,0)}\,ds\right\}da = \tilde{R}(0). \tag{5.4}$$

Therefore if $\tilde{R}(0) < 1$ holds, then by the Mean Value Theorem of Integral Calculus the characteristic function cannot have nonnegative roots. If, however, $\tilde{R}(0) > 1$ holds, then the Intermediate Value Theorem gives a positive root since $K(0) > 1$ and $\lim_{\lambda\to\infty} K(\lambda) = 0$. □

Remark 5.2. Recall that in the linear setting asymptotic stability is equivalent to uniform exponential stability.

Before addressing stability/instability of positive stationary solutions p_*, let us summarize some straightforward facts about the function K of the characteristic equation.

Lemma 5.3. *Let p_* be a nontrivial, stationary solution corresponding to the population quantity P_*. Then the function K defined in Eq.* (4.1) *has the following properties*

$$K(0) = P_* \tilde{R}'(P_*) + 1 \quad \text{and} \quad \lim_{\lambda\to\infty} K(\lambda) = 0, \tag{5.5}$$

the limit being taken in $\mathbb{R}$.

Proof. The definitions (4.2)–(4.3) of A_{11} and A_{12} give immediately that

$$\lim_{\lambda\to\infty} A_{11}(\lambda) = 0 = \lim_{\lambda\to\infty} A_{12}(\lambda). \tag{5.6}$$

For A_{21} defined in (4.4) we also obtain that

$$\lim_{\lambda\to\infty} A_{21}(\lambda) = 0 \tag{5.7}$$

by Lebesgue Dominated Convergence, since we have for $0 \leqslant s \leqslant a \leqslant m$ and $\lambda > 0$,

$$\left|\exp\left\{\lambda\left(\int_0^s \frac{1}{\gamma(r, P_*)}\,dr - \int_0^a \frac{1}{\gamma(r, P_*)}\,dr\right)\right\}\right| \leqslant 1 \tag{5.8}$$

and

$$\lim_{\lambda\to\infty} \exp\left\{\lambda\left(\int_0^s \frac{1}{\gamma(r, P_*)}\,dr - \int_0^a \frac{1}{\gamma(r, P_*)}\,dr\right)\right\} = 0. \tag{5.9}$$

The same argument applies to the second term of A_{22} given in (4.5), while the first term is easily seen to be independent of λ. Hence we have

$$\lim_{\lambda\to\infty} A_{22}(\lambda) = C \tag{5.10}$$

for some constant C. However, these limits establish that $\lim_{\lambda\to\infty} K(\lambda) = 0$.

By Eq. (1.11) we have

$$A_{12}(0) = 1. \tag{5.11}$$

Moreover, we obtain from Eq. (1.10) that

$$\begin{aligned} A_{11}(0) &= \int_0^m \exp\left\{-\int_0^a \frac{\gamma_a(s, P_*) + \mu(s, P_*)}{\gamma(s, P_*)}\,ds\right\} da \\ &= \frac{1}{p_*(0)} \int_0^m p_*(a)\,da = \frac{P_*}{p_*(0)}, \end{aligned} \tag{5.12}$$

i.e.,

$$K(0) = \frac{P_*}{p_*(0)} A_{22}(0) + 1. \tag{5.13}$$

Next a standard calculation using the definition (1.15) yields that

$$
\begin{aligned}
A_{22}(0) &= p_*(0) \int_0^m F(0, \mu, \gamma, a)\beta_P(a, P_*)\, da \\
&\quad - p_*(0) \int_0^m F(0, \mu, \gamma, a)\beta(a, P_*) \int_0^a G(\mu, \gamma, s)\, ds\, da \\
&= p_*(0)\tilde{R}'(P_*).
\end{aligned}
\tag{5.14}
$$

This result proves the claim. □

The preceding lemma has the following important consequence.

Theorem 5.4. *The nontrivial, stationary solution p_* with corresponding population quantity P_* is linearly unstable if $\tilde{R}'(P_*) > 0$.*

Proof. It suffices to show that there exists a positive zero λ of the characteristic equation. This result follows, however, immediately from Lemma 5.3 on grounds of the Intermediate Value Theorem since K is real on $\mathbb{R}$ and $K(0) > 1$ if $\tilde{R}'(P_*) > 0$. □

Remark 5.5. The condition of Theorem 5.4 has a simple natural interpretation: if the relative net reproduction rate $\tilde{R}(P)$ for an equilibrium total population $P = P_*$ increases, then the equilibrium is unstable. Note that Theorem 5.4 corresponds to an analogous result for the age-structured case, given that the relative net reproduction rate $\tilde{R}(P)$ plays the role of the net reproduction rate $R(P)$ in the age-structured case.

Remark 5.6. In [10] an analogous instability result was proven for a related size-structured model.

Stability results of nonzero stationary solutions for the kind of model discussed here are much harder to obtain than instability results since a rigorous linear stability proof requires to show that all zeros of the characteristic equation are in the left half-plane of $\mathbb{C}$. Hence it lies in the nature of the stability problem that any answer is generally hard to get by and is usually available for rather special or restricted cases only. Two such cases will be discussed in the following.

Theorem 5.7. *Let p_* be a nontrivial, stationary solution with corresponding population quantity P_*. Suppose that for $0 \leqslant a \leqslant m$,*

$$G(\mu, \gamma, a) \leqslant 0, \tag{5.15}$$

$$\beta(a, P_*) + \int_0^m \beta_P(\alpha, P_*)\, p_*(\alpha)\, d\alpha \geqslant 0, \tag{5.16}$$

$$\int_0^m p_*(a) \int_0^a G(\mu, \gamma, \alpha)\, d\alpha\, da \geqslant -1. \tag{5.17}$$

Then p_* is linearly asymptotically stable if and only if $\tilde{R}'(P_*) < 0$.

Proof. First we note that condition (3.9) holds since

$$p_*(a)G(\mu,\gamma,a)=\frac{\gamma_{aP}(a,P_*)p_*(a)+\mu_P(a,P_*)p_*(a)+\gamma_P(a,P_*)p_*'(a)}{\gamma(a,P_*)}. \tag{5.18}$$

Hence Theorem 3.3 and Corollary 3.5 apply. Thus we can restrict ourselves to $\lambda\in\mathbb{R}$. Next by Lemma 5.3 we have

$$\lim_{\lambda\to\infty}K(\lambda)=0 \tag{5.19}$$

and

$$K(0)=P_*\tilde{R}'(P_*)+1. \tag{5.20}$$

If $\tilde{R}'(P_*)\geqslant 0$, Eq. (4.1) has a solution $\lambda\geqslant 0$. Hence p_* is not linearly asymptotically stable. If $\tilde{R}'(P_*)<0$, p_* will be linearly asymptotically stable if we can show that the characteristic function K is nonincreasing for $\lambda>0$. To this end, we note that

$$K'=A_{11}'A_{22}+A_{11}A_{22}'-A_{12}'A_{21}-A_{12}A_{21}'+A_{12}'+A_{21}'. \tag{5.21}$$

In the following it is convenient to use the abbreviations:

$$\Gamma(a)=\int_0^a\frac{1}{\gamma(\alpha,P_*)}\,d\alpha, \tag{5.22}$$

$$f(\lambda,a)=F(\lambda,\mu,\gamma,a), \tag{5.23}$$

$$g(a)=G(\mu,\gamma,a), \tag{5.24}$$

$$T(\lambda,a)=\int_0^a\int_0^s g(r)\exp\left\{\int_0^r\frac{\lambda}{\gamma(x,P_*)}\,dx\right\}dr\,\frac{1}{\gamma(s)}\,ds$$

$$=\Gamma(a)\int_0^a g(\alpha)\exp\left\{\int_0^\alpha\frac{\lambda}{\gamma(x,P_*)}\,dx\right\}d\alpha \tag{5.25}$$

$$-\int_0^a\Gamma(\alpha)g(\alpha)\exp\left\{\int_0^\alpha\frac{\lambda}{\gamma(x,P_*)}\,dx\right\}d\alpha. \tag{5.26}$$

Then we have

$$A_{11}'(\lambda)=-\int_0^m\Gamma(\alpha)f(\lambda,\alpha)\,d\alpha, \tag{5.27}$$

$$A_{12}'(\lambda)=-\int_0^m\beta(\alpha,P_*)\Gamma(\alpha)f(\lambda,\alpha)\,d\alpha, \tag{5.28}$$

$$A_{21}'(\lambda)=p_*(0)\int_0^m f(\lambda,\alpha)T(\lambda,\alpha)\,d\alpha, \tag{5.29}$$

$$A_{22}'(\lambda)=p_*(0)\int_0^m\beta(\alpha,P_*)f(\lambda,\alpha)T(\lambda,\alpha)\,d\alpha. \tag{5.30}$$

Hence when using relation (1.10) we obtain

$$
\begin{aligned}
K'(\lambda) = &- \int_0^m \Gamma(a) f(\lambda, a)\left(\beta(a, P_*) + \int_0^m \beta_P(\alpha, P_*) p_*(\alpha)\, d\alpha\right) da \\
&+ p_*(0) \int_0^m f(\lambda, a) \int_0^a g(\alpha) \exp\left\{\int_0^\alpha \frac{\lambda}{\gamma(x, P_*)}\, dx\right\} d\alpha \\
&\times \left(\beta(a, P_*) \int_0^m \Gamma(\alpha) f(\lambda, \alpha)\, d\alpha - \int_0^m \beta(\alpha, P_*) \Gamma(\alpha) f(\lambda, \alpha)\, d\alpha\right) da \\
&+ p_*(0) \int_0^m f(\lambda, a) T(\lambda, a) \\
&\times \left(\beta(a, P_*) \int_0^m f(\lambda, \alpha)\, d\alpha - \int_0^m \beta(\alpha, P_*) f(\lambda, \alpha)\, d\alpha + 1\right) da. \qquad (5.31)
\end{aligned}
$$

Now observe that the last term in this sum is nonpositive because $T \leqslant 0$, $\beta \geqslant 0$, $f \geqslant 0$, the map $\lambda \mapsto \int_0^m \beta(\alpha, P_*) f(\lambda, \alpha)\, d\alpha$ is decreasing for $\lambda \geqslant 0$, and $\int_0^m \beta(\alpha, P_*) f(0, \alpha)\, d\alpha = 1$ by Eq. (1.11). Next we note that

$$
\begin{aligned}
&\int_0^m \beta(\alpha, P_*) \Gamma(\alpha) f(\lambda, \alpha)\, d\alpha - \beta(a, P_*) \int_0^m \Gamma(\alpha) f(\lambda, \alpha)\, d\alpha \\
&\quad \leqslant \int_0^m \Gamma(\alpha) f(\lambda, \alpha)\left(\beta(\alpha, P_*) + \int_0^m \beta_P(x, P_*) p_*(x)\, dx\right) d\alpha \qquad (5.32)
\end{aligned}
$$

because of condition (5.16). Hence since $g \leqslant 0$ the first two terms in the sum (5.31) are bounded above by

$$
\begin{aligned}
&\int_0^m \Gamma(a) f(\lambda, a)\left(\beta(a, P_*) + \int_0^m \beta_P(\alpha, P_*) p_*(\alpha)\, d\alpha\right) da \\
&\quad \times \left(-1 - p_*(0) \int_0^m f(\lambda, a) \int_0^a g(\alpha) \exp\left\{\int_0^\alpha \frac{\lambda}{\gamma(x, P_*)}\, dx\right\} d\alpha\, da\right). \qquad (5.33)
\end{aligned}
$$

The first term in this product is nonnegative, while the second term equals $-1 + A_{21}(\lambda)$. Since this latter term is decreasing for $\lambda \geqslant 0$, the claim follows from the condition

$$A_{21}(0) \leqslant 1. \qquad (5.34)$$

However, this is just condition (5.17). □

Remark 5.8. The positivity conditions (5.15)–(5.16) of Theorem 5.7 require that, for nonvanishing β_P, the fertility β has to be strictly positive for stability. Situations where individuals are initially infertile can be treated within the same framework considered here if the dynamics of infertile and fertile individuals are coupled through a population influx included in the boundary condition (1.2). This scenario is left for future work.

The proof of Theorem 5.7 allows the following simple conclusion.

Corollary 5.9. *Let p_* be a nontrivial, stationary solution with corresponding population quantity P_*. Suppose that for $0 \leqslant a \leqslant m$,*

$$G(\mu, \gamma, a) \leqslant 0, \tag{5.35}$$

$$\beta_a(P_*) \equiv 0 \quad \text{and} \quad \beta(P_*) + \beta_P(P_*)P_* \geqslant 0. \tag{5.36}$$

Then p_* is linearly asymptotically stable if and only if $\tilde{R}'(P_*) < 0$.

Proof. The second term in the sum (5.31) vanishes. Hence $K' \leqslant 0$ is vacuously true for $\lambda \geqslant 0$. □

Remark 5.10. Let us finally give an example that there are vital rates for which the conditions of Theorem 5.7 and Corollary 5.9 hold true:

$$\mu \equiv \text{const}, \qquad \gamma \equiv 1 \tag{5.37}$$

and $\beta = \beta(P)$ a positive function in $C^1([0, \infty))$ such that

$$\beta(P) = \frac{1}{P} \quad \text{if } P \geqslant \frac{1}{2\mu}\left(1 - e^{-\mu m}\right). \tag{5.38}$$

It is readily seen that this choice of vital rates gives a stationary solution p_* with total population quantity

$$P_* = \frac{1 - e^{-\mu m}}{\mu} \tag{5.39}$$

such that $\tilde{R}'(P_*) < 0$ and such that conditions (5.15)–(5.17), (5.35)–(5.36) are satisfied.

6. Conclusion

We have given a careful analysis of an important linearized size-structured population model. Our analysis was primarily based on semigroup methods that allowed us to give a rigorous characterization of the linearized dynamical behavior of initially small perturbations of steady state via roots of the associated characteristic equation. Our positivity result for the semigroups under certain conditions for the vital rates allowed us to stay within the framework of elementary calculus when addressing stability/instability of stationary solutions. Even though comprehensive linear stability results for stationary solutions are not to be expected, this approach allowed us to analyze the stability of stationary solutions in cases where analytical progress is possible. In these cases we have given a simple stability criterion in terms of the relative net reproduction rate $\tilde{R}(P)$.

It should be evident that our analysis can be readily extended to more general cases of size-structured models, including the one where a population influx is accounted for and where the vital rates β, γ and μ are functionally dependent on the standing population p in a more general way (as it is the case, for instance, in hierarchical size-structured models, see [1,3]).

Our stability results strengthen, extend and exceed earlier results given in [9–11] and elsewhere for simpler population models. Moreover, our results are directly related to and in support of the work of Diekmann et al. [5] toward a general mathematical theory for physiologically structured population models (see [6,7]).

Finally we point out that it would be desirable to have a rigorous result establishing a link between the stability of equilibria of the nonlinear system and the stability of the linearized system (Principle of Linearized Stability). To our knowledge, such a result is not yet available for the model equations considered here, where all the vital rates depend on both size and population density. However, for the age-structured case such a result was established by Prüß in [24] and in a more general context by Kato [21]. Calsina and Sanchón analyzed a size-structured model where all the vital rates depend on the population density only (see [4]). In this situation the model can be reduced to the age-structured case. Diekmann et al. [5–7] have been working on the Principle of Linearized Stability for general, physiologically structured population models. Their work—once completed successfully—would rigorously link the linear and nonlinear stability of solutions for the model studied here.

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