Asymptotic behavior of size structured populations via juvenile-adult interaction*

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Abstract

In this work a size structured juvenile-adult population model is considered. The linearized dynamical behavior of stationary solutions is analyzed using semigroup and spectral methods. The regularity of the governing linear semigroup allows to derive biologically meaningful conditions for the linear stability of stationary solutions. The main emphasis in this work is on juvenile-adult interaction and resulting consequences for the dynamics of the system. In addition, we investigate numerically the effect of a non-zero population inflow, due to an external source of newborns, on the dynamical behavior of the system in a special case of model ingredients.

Keywords: Structured population dynamics; juvenile-adult intraspecific interaction; linear stability; spectral analysis

1. Introduction

Population dynamics has been a central fixture in mathematical biology for more than two centuries, starting with Malthus' exponential model of population growth. The main focus of population dynamics has been a characterization of alterations in the numbers, sizes and age distribution of individuals and of potential internal or external causes provoking these changes. The last years have witnessed an invigorated interest in population dynamics, not the least

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because of its applicability in commercial endeavors (fisheries, crops), but also for environmental and medicinal purposes (reforesting, modeling the spread of infectious diseases and modeling tumour growth).

In [15] we gave a rigorous analysis of a linearized size structured population model. The objective of that study was to understand the linear stability of equilibrium solutions for a broad range of vital rates of individuals. Our analysis was primarily based on semigroup methods that allowed us to describe the linearized dynamical behavior of initially small perturbations of steady state via roots of an associated characteristic equation. We were able to formulate biologically meaningful conditions for the stability/instability of stationary solutions in terms of a modified inherent net reproduction function. The principal stability results in [15] were based on the assumption that newborns in the population are fertile from birth on. This assumption is justified for a large number of populations of primitive species, but is unrealistic in many other populations of multicellular organisms. The present paper will address this issue. Specifically, our model will separate the standing population into two parts: immature (non-reproducing) juveniles and fertile (reproducing) adults. The transition juvenile-adult is captured naively by assuming that a juvenile individual matures at a certain (fixed) critical size l (fertility size).

The dynamics of a juvenile-adult size structured population living in a closed territory is modeled by the following nonlinear system:

$$p_t(s,t) + (\gamma(s,J(t),A(t))\,p(s,t))_s = -\mu(s,J(t),A(t))\,p(s,t), \tag{1.1}$$

defined for $0 \leq s \leq m < \infty$ and $t > 0$, subject to the boundary condition

$$p(0,t) = \int_l^m \beta(s,J(t),A(t))\,p(s,t)\,ds, \quad t > 0, \tag{1.2}$$

and an initial condition of the form

$$p(s,0) = p_0(s), \quad 0 \leq s \leq m. \tag{1.3}$$

Here β, μ and γ denote the fertility, mortality and growth rate of individuals, respectively. We assume that these vital rates depend on size s and on both juvenile and adult population quantities J and A, defined by

$$J(t) = \int_0^l p(s,t)\,ds, \quad A(t) = \int_l^m p(s,t)\,ds. \tag{1.4}$$

The quantities l and m ($0 < l < m$) denote the fertility size and the maximum size of individuals, respectively. We make the following specific assumptions on the vital rate functions:

$$\mu = \mu(s,J,A) \in C([0,m];C^1([0,\infty)\times[0,\infty))), \quad \mu \geq 0, \tag{1.5}$$

$$\gamma = \gamma(s,J,A) \in C^1([0,m];C^1([0,\infty)\times[0,\infty))), \quad \gamma > 0, \tag{1.6}$$

$$\beta = \beta(s,J,A) \in C([l,m];C^1([0,\infty)\times[0,\infty))), \quad \beta \geq 0. \tag{1.7}$$

These assumptions are strong enough for the linear analysis presented in this work. They might, however, have to be strengthened to prove global existence results for the full nonlinear problem. Moreover, to make the model a reasonable description of real populations in a specific setting, one will have to impose additional biologically relevant assumptions (for example, one would possibly modify μ so that $\lim_{s\to m}\mu(s,.)=\infty$, thus modeling a gradual rather than instantaneous reduction in the numbers of individuals reaching maximum size m).

Equation (1.1) is usually equipped with a boundary condition of the form

$$\gamma(0,J(t),A(t))\,p(0,t)=\int_l^m \beta(s,J(t),A(t))\,p(s,t)\,ds, \tag{1.8}$$

since the population flux due to newborns (rate of change $\gamma(0,J(t),A(t))$ times population density $p(0,t)$) has to equal the rate at which the population gives birth to offspring. Condition (1.2) above is mathematically equivalent when the γ-term is incorporated in the fertility rate β on the right. We contend, however, that the choice (1.2) is better suited for analytical work, and hence we will use condition (1.2) instead of (1.8).

The governing equations (1.1)–(1.3) can be cast in an equivalent form, focusing on the evolution of juveniles (j) and adults (a) separately. Specifically, when setting

$$j=p|_{[0,l]} \quad \text{and} \quad a=p|_{[l,m]}, \tag{1.9}$$

we have the coupled system

$$j_t(s,t)+(\gamma(s,J(t),A(t))\,j(s,t))_s=-\mu(s,J(t),A(t))\,j(s,t), \tag{1.10}$$

$$j(0,t)=\int_l^m \beta(r,J(t),A(t))\,a(r,t)\,dr, \tag{1.11}$$

$$j(s,0)=p_0(s) \tag{1.12}$$

and

$$a_t(r,t)+(\gamma(r,J(t),A(t))\,a(r,t))_r=-\mu(r,J(t),A(t))\,a(r,t), \tag{1.13}$$

$$a(l,t)=j(l,t), \tag{1.14}$$

$$a(r,0)=p_0(r), \tag{1.15}$$

where

$$J(t)=\int_0^l j(s,t)\,ds \quad \text{and} \quad A(t)=\int_l^m a(r,t)\,dr. \tag{1.16}$$

The first boundary-initial value problem above is posed for $0\le s\le l$, $t\ge 0$, the second for $l\le r\le m$, $t\ge 0$. Although this formulation may seem unnecessary and clumsy, it allows in principal to treat the linear stability of stationary solutions in a way parallel to the one used for the simple size structured population model in [15]. We will, however, not follow this path here.

Age and size structured population models have been studied intensively in the literature. The general nonlinear stability analysis of equilibria in age structured population models was performed in the seminal works [23, 24]. For general reference we mention the well-known monographs [4, 11, 19, 21, 25]. Recent work on related population models can be found in [1, 2, 3, 9, 10, 13, 14]. The specific case of competition between juveniles and adults has been addressed in the literature, see for example the work [5] (and the references therein) where a McKendrick-type age structured model is treated. To our knowledge, the rather general model discussed here has not been analyzed before.

2. The linearized system

First we formulate the condition for the existence of positive equilibrium solutions of the problem (1.1)–(1.2).

Proposition 2.1 *For given vital rate functions β, μ, γ, there is a one-to-one correspondence between all positive stationary solutions p_* of problem* (1.1)–(1.2) *and all pairs (J_*, A_*) of positive numbers that satisfy the conditions*

$$\frac{J_*}{A_*} = \frac{\displaystyle\int_0^l \exp\left\{-\int_0^s \frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right\} ds}{\displaystyle\int_l^m \exp\left\{-\int_0^s \frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right\} ds} \tag{2.1}$$

and

$$R(J_*,A_*) = 1, \tag{2.2}$$

$$\text{where } R(J,A) = \int_l^m \gamma(0,J,A)\,\frac{\beta(s,J,A)}{\gamma(s,J,A)}\,\exp\left\{-\int_0^s \frac{\mu(r,J,A)}{\gamma(r,J,A)}\,dr\right\} ds. \tag{2.3}$$

In this case, the unique positive stationary solution p_* of problem (1.1)–(1.2) *is given by*

$$p_*(s) = \frac{(J_*+A_*)\,\exp\left(-\displaystyle\int_0^s \frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right)}{\displaystyle\int_0^m \exp\left(-\int_0^s \frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right) ds} \tag{2.4}$$

and J_*, A_* satisfy

$$J_* = \int_0^l p_*(s)\,ds, \qquad A_* = \int_l^m p_*(s)\,ds. \tag{2.5}$$

Proof. Suppose first that p_* is a positive stationary solution and define J_*, A_* by (2.5). Then we find immediately that

$$p_*(s) = p_*(0)\,\exp\left\{-\int_0^s \frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right\}, \tag{2.6}$$

which implies condition (2.1). Combining equation (2.6) with the boundary condition (1.2), we have

$$1 = \int_l^m \beta(s, J_*, A_*) \exp\left\{ - \int_0^s \frac{\mu(r, J_*, A_*) + \gamma_s(r, J_*, A_*)}{\gamma(r, J_*, A_*)} \, dr \right\} ds. \tag{2.7}$$

Hence we obtain

$$R(J_*, A_*) = 1. \tag{2.8}$$

Finally, integration of (2.6) gives the stationary solution in the form of (2.4). If, on the other hand, the pair (J_*, A_*) satisfies conditions (2.1)–(2.2) and p_* is defined by (2.4), then p_* is readily seen to be a positive stationary solution such that (2.5) holds true. □

It is straightforward to deduce the existence of positive stationary solutions for specific (nontrivial) vital rates by use of the Implicit Function Theorem. Therefore we will tacitly assume in the following that positive stationary solutions are available.

Remark 2.2 The quantity R is the inherent net reproduction rate: the expected number of newborns of an individual in her lifetime. Note that for a positive stationary solution p_*

$$1 = R(J_*, A_*) = \frac{1}{p_*(0)} \int_l^m \beta(s, J_*, A_*) \, p_*(s) \, ds. \tag{2.9}$$

Given a positive stationary solution p_*, we linearize p by introducing the perturbation $w = w(s,t)$ and making the ansatz $p = w + p_*$. Then w has to satisfy the equations

$$\begin{aligned} & w_t(s,t) + (\gamma(s, J(t), A(t)) \, w(s,t))_s + \mu(s, J(t), A(t)) \, w(s,t) \\ & \quad + (\gamma(s, J(t), A(t)) \, p_*(s))_s - \mu(s, J(t), A(t)) \, p_*(s) = 0, \end{aligned} \tag{2.10}$$

$$w(0,t) = \int_l^m \beta(s, J(t), A(t)) \, (w(s,t) + p_*(s)) \, ds - \gamma(0, J(t), A(t)) \, p_*(0), \tag{2.11}$$

where

$$J(t) = \int_0^l w(s,t) \, ds + \int_0^l p_*(s) \, ds, \quad A(t) = \int_l^m w(s,t) \, ds + \int_l^m p_*(s) \, ds. \tag{2.12}$$

When linearizing using expansions like

$$\begin{aligned} f(s, J, A) = {} & f(s, J_*, A_*) + f_J(s, J_*, A_*) \, (J - J_*) \\ & + f_A(s, J_*, A_*) \, (A - A_*) + \text{higher order terms} \end{aligned} \tag{2.13}$$

and omitting nonlinear terms, we obtain the linearized problem

$$\begin{aligned} & w_t(s,t) + \gamma(s, J_*, A_*) \, w_s(s,t) + (\gamma_s(s, J_*, A_*) + \mu(s, J_*, A_*)) \; w(s,t) \\ & \quad + (p_*(s) \, (\gamma_{sJ}(s, J_*, A_*) + \mu_J(s, J_*, A_*)) + p_*'(s) \, \gamma_J(s, J_*, A_*)) \; W_1(t) \\ & \quad + (p_*(s) \, (\gamma_{sA}(s, J_*, A_*) + \mu_A(s, J_*, A_*)) + p_*'(s) \, \gamma_A(s, J_*, A_*)) \; W_2(t) = 0, \end{aligned} \tag{2.14}$$

subject to the boundary condition

$$
\begin{aligned}
w(0,t) = &\int_l^m \beta(s,J_*,A_*)\,w(s,t)\,ds + W_1(t)\int_l^m \beta_J(s,J_*,A_*)\,p_*(s)\,ds \\
&+ W_2(t)\int_l^m \beta_A(s,J_*,A_*)\,p_*(s)\,ds,
\end{aligned}
\tag{2.15}
$$

where we have set

$$
W_1(t) = \int_0^l w(s,t)\,ds, \quad W_2(t) = \int_l^m w(s,t)\,ds. \tag{2.16}
$$

In addition we have an initial condition of the form

$$
w(s,0) = w_0(s). \tag{2.17}
$$

3. The linear semigroup and its positivity

Suppose p_* is a positive stationary solution of problem (1.1)–(1.2) and that

$$
J_* = \int_0^l p_*(s)\,ds, \quad A_* = \int_l^m p_*(s)\,ds. \tag{3.1}
$$

Let $\mathcal{X}$ be the Lebesgue space $L^1(0,m)$ with the usual L^1-norm $\|\cdot\|$, and let Λ be the bounded linear functional on $\mathcal{X}$, given by

$$
\begin{aligned}
\Lambda(w) = &\int_l^m \beta_J(s,J_*,A_*)\,p_*(s)\,ds \int_0^l w(s)\,ds \\
&+ \int_l^m \left(\beta(s,J_*,A_*) + \int_l^m \beta_A(r,J_*,A_*)\,p_*(r)\,dr\right) w(s)\,ds.
\end{aligned}
\tag{3.2}
$$

We define the operators

$$
\mathcal{A}w = -\gamma(\cdot,J_*,A_*)\,w_s, \quad \mathrm{Dom}(\mathcal{A}) = \left\{ w \in W^{1,1}(0,m) \,|\, w(0) = \Lambda(w) \right\}, \tag{3.3}
$$

$$
\mathcal{B}w = -\left(\gamma_s(\cdot,J_*,A_*) + \mu(\cdot,J_*,A_*)\right)\,w \quad \text{on } \mathcal{X}, \tag{3.4}
$$

$$
\begin{aligned}
\mathcal{C}w = &-\left(p_*\left(\gamma_{sJ}(\cdot,J_*,A_*) + \mu_J(\cdot,J_*,A_*)\right) + p_*'\,\gamma_J(\cdot,J_*,A_*)\right)\int_0^l w(s)\,ds \\
&-\left(p_*\left(\gamma_{sA}(\cdot,J_*,A_*) + \mu_A(\cdot,J_*,A_*)\right) + p_*'\,\gamma_A(\cdot,J_*,A_*)\right)\int_l^m w(s)\,ds \quad \text{on } \mathcal{X}.
\end{aligned}
\tag{3.5}
$$

Then we can write the linearized system (2.14)–(2.17) in functional form as an initial value problem for an abstract ordinary differential equation on $\mathcal{X}$:

$$
\frac{d}{dt}\,w = \left(\mathcal{A} + \mathcal{B} + \mathcal{C}\right)\,w, \tag{3.6}
$$

together with the initial condition

$$
w(0) = w_0. \tag{3.7}
$$

The semigroup property for solutions of this problem will be proven in a way similar to the case discussed in [15].

Theorem 3.1 *The operator $\mathcal{A}+\mathcal{B}+\mathcal{C}$ generates a strongly continuous semigroup $\{\mathcal{T}(t)\}_{t\geq 0}$ of bounded linear operators on $\mathcal{X}$.*

Proof. We define the operator $\mathcal{A}_0$ by

$$\mathcal{A}_0 w = -\gamma(\cdot, J_*, A_*)\, w_s \quad \text{on } \mathrm{Dom}(\mathcal{A}_0) = \left\{ w \in W^{1,1}(0,m) \,|\, w(0) = 0 \right\}. \quad (3.8)$$

Since γ is positive, $\mathcal{A}_0$ is invertible and generates a nilpotent strongly continuous semigroup $\{\mathcal{T}_0(t)\}_{t\geq 0}$ on $\mathcal{X}$, given explicitly by

$$\left(\mathcal{T}_0(t)w\right)(s) = \begin{cases} w\left(\Gamma^{-1}\left(\Gamma(s)-t\right)\right) & \text{if } \Gamma(s) \geq t, \\ 0 \quad \text{otherwise,} \end{cases} \quad (3.9)$$

where

$$\Gamma(s) = \int_0^s \frac{1}{\gamma(r, J_*, A_*)}\, dr. \quad (3.10)$$

Next we denote the completion of $\mathcal{X}$ in the norm $\|\cdot\|_{-1} \overset{\text{def}}{=} \|\mathcal{A}_0^{-1}\cdot\|$ by $\mathcal{X}_{-1}$ and introduce the lifted semigroup $\{\mathcal{T}_{-1}(t)\}_{t\geq 0}$ on $\mathcal{X}_{-1}$ by

$$\mathcal{T}_{-1}(t) = \mathcal{A}_0\, \mathcal{T}_0(t)\, \mathcal{A}_0^{-1}. \quad (3.11)$$

The generator $\mathcal{A}_{-1}$ of the semigroup $\{\mathcal{T}_{-1}(t)\}_{t\geq 0}$ with domain $\mathrm{Dom}(\mathcal{A}_{-1}) = \mathcal{X}$ and range in $\mathcal{X}_{-1}$ is an extension of $\mathcal{A}_0$. Now we introduce the operator $\mathcal{P} \in L\left(\mathcal{X}, \mathcal{X}_{-1}\right)$, given by

$$\mathcal{P}w \overset{\text{def}}{=} -\Lambda(w)\, \mathcal{A}_{-1}1, \quad (3.12)$$

where $\mathcal{A}_{-1}1$ denotes the operator $\mathcal{A}_{-1}$ acting on the constant function $1(\cdot) = 1$ in $\mathcal{X}$. Then we recover the operator $\mathcal{A}$ as the part of the operator $\mathcal{A}_{-1} + \mathcal{P}$ in $\mathcal{X}$ (see [12])

$$\mathcal{A} = \left(\mathcal{A}_{-1} + \mathcal{P}\right)|_{\mathcal{X}}. \quad (3.13)$$

Next we have

$$\int_0^m \Lambda(f(t))\, \mathcal{T}_0(m-t)\, 1(\cdot)\, dt = \int_{m-\Gamma(\cdot)}^m \Lambda(f(t))\, dt \quad (3.14)$$

for any $f \in L^1([0,m];\mathcal{X})$. The function on the right belongs to $W^{1,1}(0,m)$ and vanishes at 0. Hence the Desch-Schappacher Perturbation Theorem[1] yields that $\mathcal{A}$ generates a strongly continuous semigroup on $\mathcal{X}$. Finally, since $\mathcal{B}+\mathcal{C}$ is a bounded perturbation of $\mathcal{A}$ on $\mathcal{X}$, the claim follows. □

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[1] Here we refer to the following version of the Desch-Schappacher Perturbation Theorem (see Corollary III.3.4 in [12]):
Theorem *Let $\mathcal{A}_0$ be the generator of a strongly continuous semigroup $\{\mathcal{T}_0(t)\}$ on the Banach space $\mathcal{X}$ and let $\mathcal{P} \in L(\mathcal{X}, \mathcal{X}_{-1})$. Moreover, assume that there exists $t_0 > 0$ and $p \in [1,\infty)$ such that*

$$\int_0^{t_0} \mathcal{T}_{-1}(t_0 - r)\, \mathcal{P}\, f(r)\, dr \in \mathcal{X}$$

for all functions $f \in L^p([0,t_0];\mathcal{X})$. Then $\mathcal{A} = (\mathcal{A}_{-1}+\mathcal{P})\,|_{\mathcal{X}}$ generates a strongly continuous semigroup on $\mathcal{X}$.

To study the linear stability of stationary solutions, we would like to extract all relevant information from the spectrum of the semigroup generator (spectrally determined growth condition, see [12]). This approach would be ideal if we could ascertain that linear stability is governed by a leading real eigenvalue. In the following we will show that both properties hold true under certain conditions on the vital rates. In the elementary size structured case this strategy proved successful (see [15]).

Proposition 3.2 *The resolvent operator of $\mathcal{A}+\mathcal{B}+\mathcal{C}$ is compact. Hence the spectrum of $\mathcal{A}+\mathcal{B}+\mathcal{C}$ can contain only isolated eigenvalues of finite multiplicity.*

Proof. It suffices to prove the result for the operator $\mathcal{A}$. To this end, note that the inverse operator $\mathcal{A}^{-1}$ maps $\mathcal{X}=L^1(0,m)$ into $W^{1,1}(0,m)$. Since $\mathcal{A}^{-1}$ is bounded and since $W^{1,1}(0,m)$ is compactly embedded in $L^1(0,m)$, the claim follows from Riesz-Schauder Theory. □

Theorem 3.3 *Suppose that*

$$p_*\left(\gamma_{sJ}(\cdot,J_*,A_*)+\mu_J(\cdot,J_*,A_*)\right)+p_*'\,\gamma_J(\cdot,J_*,A_*)\le 0, \tag{3.15}$$

$$p_*\left(\gamma_{sA}(\cdot,J_*,A_*)+\mu_A(\cdot,J_*,A_*)\right)+p_*'\,\gamma_A(\cdot,J_*,A_*)\le 0, \tag{3.16}$$

$$\int_l^m \beta_J(r,J_*,A_*)\,p_*(r)\,dr\ge 0, \tag{3.17}$$

$$\beta(\cdot,J_*,A_*)+\int_l^m \beta_A(r,J_*,A_*)\,p_*(r)\,dr\ge 0. \tag{3.18}$$

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

Proof. The operator $\mathcal{A}+\mathcal{B}$ generates a semigroup on $\mathcal{X}$. Hence, suppose that w is the solution of the initial value problem

$$\frac{d}{dt}\,w=(\mathcal{A}+\mathcal{B})\;w,\quad w(0)=w_0\in\mathrm{Dom}(\mathcal{A}). \tag{3.19}$$

Then the function u, defined by

$$u(s,t)=w(s,t)\,\exp\left\{\int_0^s\frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right\}, \tag{3.20}$$

solves the problem

$$u_t(s,t)+\gamma(s,J_*,A_*)\,u_s(s,t)=0, \tag{3.21}$$

$$u(0,t)=\Lambda\left(\frac{u(\cdot,t)}{E_*}\right), \tag{3.22}$$

$$u(s,0)=w_0(s), \tag{3.23}$$

where E_* is given by

$$E_*(s)=\exp\left\{\int_0^s\frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right\}. \tag{3.24}$$

This boundary-initial value problem corresponds the the abstract initial value problem

$$\frac{d}{dt}\,u = \mathcal{A}_M\,u, \quad u(0) = w_0 \tag{3.25}$$

with the modified semigroup generator $\mathcal{A}_M$, defined by

$$\begin{aligned} \mathcal{A}_M u &= -\,\gamma(\cdot, J_*, A_*)\,u_s \quad \text{on the domain} \\ \mathrm{Dom}(\mathcal{A}_M) &= \left\{ u \in W^{1,1}(0,m) \,|\, u(0) = \Lambda\left(\frac{u}{E_*}\right)\right\}. \end{aligned} \tag{3.26}$$

For $\lambda \geq 0$ sufficiently large and $f \in L^1(0,m)$, the resolvent equation

$$\lambda u - \mathcal{A}_M u = f \tag{3.27}$$

has the implicit solution

$$u(s) = e^{-\lambda\,\Gamma(s)}\,\Lambda\left(\frac{u}{E_*}\right) + \int_0^s e^{\lambda\,(\Gamma(r)-\Gamma(s))}\,\frac{f(r)}{\gamma(r, J_*, A_*)}\,dr. \tag{3.28}$$

Consequently, we deduce the equation

$$\Lambda\left(\frac{u}{E_*}\right) = \left(1 - \Lambda\left(\frac{e^{-\lambda\,\Gamma(\cdot)}}{E_*}\right)\right)^{-1} \Lambda\left(\int_0^{\cdot} e^{\lambda\,(\Gamma(r)-\Gamma(\cdot))}\,\frac{f(r)}{\gamma(r, J_*, A_*)}\,dr\,\frac{1}{E_*}\right). \tag{3.29}$$

If conditions (3.17), (3.18) hold true, Λ is a positive linear functional. Hence the solution u, given by Eq. (3.28), is nonnegative if λ is sufficiently large and f is nonnegative. In this case the resolvent operator of $\mathcal{A}_M$ (and consequently of $\mathcal{A}+\mathcal{B}$) is positive. Since $\mathcal{C}$ is a positive operator by conditions (3.15), (3.16), the claim follows. □

Finally, the theory of positive semigroups on Banach lattices gives us the following result (see [12, 22]).

Corollary 3.4 *Assume that conditions* (3.15)–(3.18) *are satisfied. Then the following hold true:*

- *The growth rate* $\omega_0 = \lim_{t\to\infty} t^{-1} \ln \|\mathcal{T}(t)\|$ *of the semigroup is equal to the spectral bound* $s(\mathcal{A}+\mathcal{B}+\mathcal{C}) = \sup\{\mathrm{Re}\,\lambda \,|\, \lambda \in \sigma(\mathcal{A}+\mathcal{B}+\mathcal{C})\} \in [-\infty, \infty)$ *of its generator.*[2]
- *If the spectrum of the generator* $\mathcal{A}+\mathcal{B}+\mathcal{C}$ *is nonempty, then the spectral bound* $s(\mathcal{A}+\mathcal{B}+\mathcal{C})$ *is an eigenvalue of the generator* $\mathcal{A}+\mathcal{B}+\mathcal{C}$.

Even stronger regularity results for the governing semigroup could be derived (see for example [17] for related developments in fluid mechanics).

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[2] For a Banach lattice $L^1(\Omega, \mu)$ this result is known as Derndinger's Theorem [6].

4. Stability

In this section we will give biologically relevant and intuitively interpretable conditions for the linear stability and instability of stationary solutions in two important cases where stability/instability conditions can be stated in a particularly simple form. Throughout we shall assume that the nonlinear system (1.1)–(1.2) has a positive stationary solution p_*. We emphasize that more general scenarios can be studied along the same lines by exploiting the positivity of the underlying semigroup. We suppose, however, that the resulting stability conditions will not be easy to verify. For the cases considered, our results refine, strengthen and exceed the analytical results for the simple size structured model discussed previously in [15].

4.1 Fertility controlled dynamics

We suppose that neither juvenile nor adult survival depends on the population size, but that the fertility of adults depends on both juvenile and adult population sizes. Hence we assume that the vital rates are of the form

$$\gamma = \gamma(s), \quad \mu = \mu(s), \quad \beta = \beta(s, J, A). \tag{4.1}$$

In this case the linearized system (2.14)–(2.17) reads

$$\begin{aligned}
&w_t(s,t) + \gamma(s)\, w_s(s,t) + (\gamma'(s) + \mu(s))\, w(s,t) = 0, && (4.2)\\
&w(0,t) = \int_l^m \beta(s, J_*, A_*)\, w(s,t)\, ds + W_1(t) \int_l^m \beta_J(s, J_*, A_*)\, p_*(s)\, ds && (4.3)\\
&\quad + W_2(t) \int_l^m \beta_A(s, J_*, A_*)\, p_*(s)\, ds, &&\\
&w(s,0) = w_0(s). && (4.4)
\end{aligned}$$

To determine the spectrum of the semigroup generator, we take the standard approach: we substitute the ansatz $w(s,t) = e^{\lambda\, t}\, W(s)$ into the linearized system (4.2)–(4.3) to deduce

$$\begin{aligned}
W(s) =&W(0)\, \exp\left\{ - \int_0^s \frac{\lambda + \gamma'(r) + \mu(r)}{\gamma(r)}\, dr \right\}, && (4.5)\\
W(0) =& \int_l^m \beta(s, J_*, A_*)\, W(s)\, ds + \overline{W}_1 \int_{l_*}^m \beta_J(s, J_*, A_*)\, p_*(s)\, ds && (4.6)\\
&+ \overline{W}_2 \int_l^m \beta_A(s, J_*, A_*)\, p_*(s)\, ds, &&
\end{aligned}$$

where

$$\overline{W}_1 = \int_0^l W(s)\, ds, \quad \overline{W}_2 = \int_l^m W(s)\, ds. \tag{4.7}$$

Nonzero solutions W occur if and only if $\lambda \in \mathbb{C}$ is such that

$$1 = A_1(\lambda) + A_2(\lambda) + A_3(\lambda) \overset{\text{def}}{=} K(\lambda), \tag{4.8}$$

where

$$A_1(\lambda) = \int_l^m \beta(s, J_*, A_*)\, F(s,\lambda)\, ds, \tag{4.9}$$

$$A_2(\lambda) = \int_0^l F(s,\lambda)\, ds \int_l^m \beta_J(s, J_*, A_*)\, p_*(s)\, ds, \tag{4.10}$$

$$A_3(\lambda) = \int_l^m F(s,\lambda)\, ds \int_l^m \beta_A(s, J_*, A_*)\, p_*(s)\, ds \tag{4.11}$$

with

$$F(s,\lambda) = \exp\left\{ -\int_0^s \frac{\lambda + \gamma'(r) + \mu(r)}{\gamma(r)}\, dr \right\}. \tag{4.12}$$

To formulate our stability/instability result for a given positive stationary solution p_*, we introduce the function

$$R^*(J,A) \overset{\text{def}}{=} \frac{1}{p_*(0)} \int_l^m \beta(s, J, A)\, p_*(s)\, ds. \tag{4.13}$$

Then by (2.3) and (2.9)

$$R^*(J_*, A_*) = R(J_*, A_*) = 1. \tag{4.14}$$

Theorem 4.1 *The positive stationary solution p_* is linearly unstable if*

$$J_*\, R^*_J(J_*, A_*) + A_*\, R^*_A(J_*, A_*) > 0. \tag{4.15}$$

On the other hand, if

$$J_*\, R^*_J(J_*, A_*) + A_*\, R^*_A(J_*, A_*) < 0 \tag{4.16}$$

and

$$\beta(\cdot, J_*, A_*) + p_*(0)\, R^*_A(J_*, A_*) \geq 0, \quad R^*_J(A_*, J_*) \geq 0, \tag{4.17}$$

then the stationary solution p_* is linearly asymptotically stable.

Remark 4.2 By (4.13) conditions (4.15)–(4.17) are equivalent with the conditions

$$\int_l^m \left(J_*\, \beta_J(s, J_*, A_*) + A_*\, \beta_A(s, J_*, A_*) \right) p_*(s)\, ds > 0, \tag{4.18}$$

$$\int_l^m \left(J_*\, \beta_J(s, J_*, A_*) + A_*\, \beta_A(s, J_*, A_*) \right) p_*(s)\, ds < 0, \tag{4.19}$$

$$\beta(\cdot, J_*, A_*) + \int_l^m \beta_A(s, J_*, A_*)\, p_*(s)\, ds \geq 0, \quad \int_l^m \beta_J(s, J_*, A_*)\, p_*(s)\, ds \geq 0, \tag{4.20}$$

respectively.

Proof of Theorem 4.1 By definition of K, we have

$$\lim_{\lambda\to\infty} K(\lambda) = 0, \tag{4.21}$$

the limit being taken in $\mathbb{R}$. Next we note that

$$A_1(\lambda) = \int_l^m \gamma(0)\,\frac{\beta(s,J_*,A_*)}{\gamma(s)}\ \exp\left\{-\int_0^s \frac{\mu(r)}{\gamma(r)}\,dr\right\}\ \exp\left\{-\lambda\int_0^s \frac{1}{\gamma(r)}\,dr\right\}\,ds, \tag{4.22}$$

hence $A_1(0) = 1$ by (2.2). Also we obtain

$$\begin{aligned} A_2(0) &= \int_0^l F(s,0)\,ds \int_l^m \beta_J(s,J_*,A_*)\,p_*(s)\,ds \\ &= \frac{J_*}{p_*(0)} \int_l^m \beta_J(s,J_*,A_*)\,p_*(0)\,\frac{\gamma(0)}{\gamma(s)}\ \exp\left\{-\int_0^s \frac{\mu(r)}{\gamma(r)}\,dr\right\}\,ds \qquad (4.23)\\ &= J_*\,R_J^*(J_*,A_*), \\ A_3(0) &= \int_l^m F(s,0)\,ds \int_l^m \beta_A(s,J_*,A_*)\,p_*(s)\,ds \\ &= \frac{A_*}{p_*(0)} \int_l^m \beta_A(s,J_*,A_*)\,p_*(0)\,\frac{\gamma(0)}{\gamma(s)}\ \exp\left\{-\int_0^s \frac{\mu(r)}{\gamma(r)}\,dr\right\}\,ds \qquad (4.24)\\ &= A_*\,R_A^*(J_*,A_*). \end{aligned}$$

Thus

$$K(0) = 1 + J_*\,R_J^*(J_*,A_*) + A_*\,R_A^*(J_*,A_*). \tag{4.25}$$

Since K is real on $\mathbb{R}$, the Intermediate Value Theorem proves the existence of a positive solution λ of (4.8) if condition (4.15) holds true. Hence the stationary solution is linearly unstable. On the other hand, if conditions (4.16)–(4.17) are satisfied, then $K(\lambda) < 1$ on $\mathbb{R}_0^+$. To see this, we note that the functions

$$A_2(\lambda) = \int_0^l F(s,\lambda)\,ds \int_l^m \beta_J(s,J_*,A_*)\,p_*(s)\,ds, \tag{4.26}$$

$$A_1(\lambda) + A_3(\lambda) = \int_l^m \left(\beta(s,J_*,A_*) + \int_l^m \beta_A(r,J_*,A_*)\,p_*(r)\,dr\right)\,F(s,\lambda)\,ds \tag{4.27}$$

decrease monotonically on $\mathbb{R}_0^+$. Since

$$p_*(0)\,R_J^*(J_*,A_*) = \int_l^m \beta_J(s,J_*,A_*)\,p_*(s)\,ds, \tag{4.28}$$

$$p_*(0)\,R_A^*(J_*,A_*) = \int_l^m \beta_A(s,J_*,A_*)\,p_*(s)\,ds, \tag{4.29}$$

conditions (4.17) imply the positivity of the semigroup by Theorem 3.3. Consequently, we obtain from Corollary 3.4 that the stationary solution is linearly asymptotically stable. $\square$

Examples Let us now discuss some special cases. First we assume that

$$\beta = \beta(s, P) \quad \text{with} \quad P = \alpha\, J + A, \quad \alpha > 0. \tag{4.30}$$

This case was treated in Section 3 of [5] in the context of an age structured model. Here α measures the relative effect of the number of juvenile individuals versus adult individuals on the fertility. Of course, stationary solutions for different values of α will not be equal and, for certain values of α (or certain vital rates), no stationary solution need exist. Assuming that stationary solutions exist, we obtain with (4.30)

$$J_*\, R_J^*(J_*, A_*) + A_*\, R_A^*(J_*, A_*) = (\alpha\, J_* + A_*)\, r(J_*, A_*), \tag{4.31}$$

where

$$r(J_*, A_*) = \frac{1}{p_*(0)} \int_l^m \beta_P(s, \alpha\, J_* + A_*)\, p_*(s)\, ds. \tag{4.32}$$

Consequently, by condition (4.15) we have instability for any value of α if $\beta_P \geq 0$, $\beta_P \not\equiv 0$. Our result fails, however, to predict asymptotic stability of the stationary solution in case $\beta_P \leq 0$, $\beta_P \not\equiv 0$ since then the positivity condition (4.17) does not hold.

The second case we address arises for

$$\beta = \beta(s, Q) \quad \text{with} \quad Q = \frac{J^\alpha}{A}, \quad \alpha > 0,\ \alpha \neq 1. \tag{4.33}$$

Again this special functional dependence is designed to qualitatively describe the effect of juvenile versus adult population on the fertility for different values of α. In this case we find

$$J_*\, R_J^*(J_*, A_*) + A_*\, R_A^*(J_*, A_*) = (\alpha - 1)\, \frac{J_*^\alpha}{A_*}\, r(J_*, A_*), \tag{4.34}$$

where

$$r(J_*, A_*) = \frac{1}{p_*(0)} \int_l^m \beta_Q\left(s, \frac{J_*^\alpha}{A_*}\right) p_*(s)\, ds. \tag{4.35}$$

Hence if $\beta_Q \not\equiv 0$ and either $\beta_Q \leq 0$ and $\alpha < 1$ or $\beta_Q \geq 0$ and $\alpha > 1$, the stationary solution is unstable. If, however, $\beta_Q \geq 0$, $\beta_Q \not\equiv 0$ and $\alpha < 1$, the stationary solution is asymptotically stable by (4.16)–(4.17).

4.2 Adult-dependent juvenile survival

Now we assume that both the juvenile survival and the fertility depend on the adult population and size distribution only. Specifically, we consider the following situation:

$$\mu = \mu(s, A), \quad \gamma = \gamma(s, A), \quad \beta = \beta(s, A) \quad \text{and} \quad \mu_A = 0 = \gamma_A \quad \text{if } l \leq s \leq m. \tag{4.36}$$

The juvenile-adult interaction is given subtly through the separation of the interval $[0, m]$ into two parts. We apply the same strategy as before to determine the eigenvalues of the semigroup generator. The ansatz $w(s,t) = e^{\lambda\, t}\, W(s)$ gives the equations

$$\begin{aligned}&\gamma(s, A_*)\, W'(s) + (\lambda + \gamma_s(s, A_*) + \mu(s, A_*))\, W(s)\\ &+ \overline{W}_2\ (p_*(s)\ (\gamma_{sA}(s, A_*) + \mu_A(s, A_*)) + p_*'(s)\, \gamma_A(s, A_*)) = 0.\end{aligned} \tag{4.37}$$

Instead of imposing, however, the actual boundary condition, we solve this equation subject to the condition $W(0) = 1$ to find

$$W(s) = F(s,\lambda) \left(1 - \overline{W}_2 \int_0^s \frac{G(r)}{F(r,\lambda)}\, dr\right), \tag{4.38}$$

where the functions G and F are defined by

$$G(r) = \frac{p_*(r)\, (\gamma_{sA}(r, A_*) + \mu_A(r, A_*)) + p_*'(r)\, \gamma_A(r, A_*)}{\gamma(r, A_*)}, \tag{4.39}$$

$$F(s,\lambda) = \exp\left\{-\int_0^s \frac{\lambda + \gamma_s(r, A_*) + \mu(r, A_*)}{\gamma(r, A_*)}\, dr\right\}. \tag{4.40}$$

Integration of (4.38) yields

$$\overline{W}_2 = \int_l^m W(s)\, ds = \frac{\displaystyle\int_l^m F(s,\lambda)\, ds}{\displaystyle 1 + \int_l^m F(s,\lambda)\, ds \int_0^l \frac{G(s)}{F(s,\lambda)}\, ds}. \tag{4.41}$$

Here we have used the properties of the vital rates, given in (4.36). Finally imposing the actual boundary condition, we obtain the equation

$$W(0) = 1 = \int_l^m \beta(s, A_*)\, W(s)\, ds + \overline{W}_2 \int_l^m \beta_A(s, A_*)\, p_*(s)\, ds, \tag{4.42}$$

which gives a characteristic equation in the form

$$1 = A_1(\lambda) + A_2(\lambda)\, A_3(\lambda) \overset{\text{def}}{=} K(\lambda) \tag{4.43}$$

with

$$A_1(\lambda) = \int_l^m \beta(s, A_*)\, F(s,\lambda)\, ds, \tag{4.44}$$

$$A_2(\lambda) = \frac{\displaystyle\int_l^m F(s,\lambda)\, ds}{\displaystyle 1 + \int_l^m F(s,\lambda)\, ds \int_0^l \frac{G(s)}{F(s,\lambda)}\, ds}, \tag{4.45}$$

$$A_3(\lambda) = \int_l^m \beta_A(s, A_*)\, p_*(s)\, ds - \int_l^m \beta(s, A_*)\, F(s,\lambda)\, ds \int_0^l \frac{G(s)}{F(s,\lambda)}\, ds. \tag{4.46}$$

A straightforward calculation shows that K can be cast in the form

$$K(\lambda) = \frac{\displaystyle\int_l^m \left(\beta(s,A_*) + \int_l^m \beta_A(r,A_*)p_*(r)\,dr\right) F(s,\lambda)\,ds}{\displaystyle 1 + \int_l^m F(s,\lambda)\,ds \int_0^l \frac{G(s)}{F(s,\lambda)}\,ds}. \tag{4.47}$$

Next we observe that there can exist nontrivial solutions W of (4.37) that vanish at 0. Therefore imposing the condition $W(0) = 0$, we obtain

$$W(s) = -\overline{W}_2\, F(s,\lambda) \int_0^s \frac{G(r)}{F(r,\lambda)}\,dr, \tag{4.48}$$

where $\overline{W}_2$ is arbitrary and λ is a solution of the characteristic equation

$$0 = 1 + \int_l^m F(s,\lambda)\,ds \int_0^l \frac{G(s)}{F(s,\lambda)}\,ds \overset{\text{def}}{=} k(\lambda). \tag{4.49}$$

In conclusion, the set of eigenvalues of the linearized operator consists of all $\lambda \in \mathbb{C}$ which satisfy either Eq. (4.43) or Eq. (4.49).

Remark 4.3 A similar strategy was employed to derive characteristic equations of problems arising in fluid mechanics (see [16, 18]).

To formulate our stability/instability conditions for the positive stationary solution p_* we introduce the quantities

$$R^*(A) \overset{\text{def}}{=} \frac{1}{p_*(0)} \int_l^m \beta(s,A)\,p_*(s)\,ds, \tag{4.50}$$

$$\delta \overset{\text{def}}{=} \min_{0\le s\le l} \frac{G(s)}{p_*(s)} \quad \text{and} \quad \Delta \overset{\text{def}}{=} \max_{0\le s\le l} \frac{G(s)}{p_*(s)}, \tag{4.51}$$

where the function G is given by (4.39).

Theorem 4.4 *The positive stationary solution p_* is linearly unstable if*

$$1 + l\,A_*\,\Delta < 0 \quad \textit{or} \tag{4.52}$$

$$1 + l\,A_*\,\delta > 0 \quad \textit{and} \quad R^*_A(A_*) > l\,\Delta. \tag{4.53}$$

On the other hand, if

$$1 + l\,A_*\,\delta > 0, \quad R^*_A(A_*) < l\,\delta \tag{4.54}$$

and

$$G \le 0, \quad \beta(\cdot,A_*) + p_*(0)\,R^*_A(A_*) \ge 0, \tag{4.55}$$

then the stationary solution p_* is linearly asymptotically stable.

Proof. First we note that

$$k(0) = 1 + \int_l^m F(s,0)\,ds \int_0^l \frac{G(s)}{F(s,0)}\,ds \tag{4.56}$$

$$\le 1 + \Delta \int_l^m F(s,0)\,ds \int_0^l \frac{p_*(s)}{F(s,0)}\,ds = 1 + l\,A_*\,\Delta \tag{4.57}$$

and

$$\lim_{\lambda\to\infty} k(\lambda) = 1, \tag{4.58}$$

the limit being taken in $\mathbb{R}$. Hence if condition (4.52) is satisfied, Eq. (4.49) has a positive solution. If, however, conditions (4.53) hold true, we obtain

$$\int_l^m \left(\beta(s,A_*) + \int_l^m \beta_A(r,A_*)p_*(r)\,dr\right) F(s,0)\,ds = 1 + R_A^*(A_*)\,A_* \tag{4.59}$$

$$> 1 + l\,A_*\,\Delta \ge 1 + \int_l^m F(s,0)\,ds \int_0^l \frac{G(s)}{F(s,0)}\,ds \ge 1 + l\,A_*\,\delta > 0. \tag{4.60}$$

Consequently, we conclude from (4.47) that

$$K(0) > 1. \tag{4.61}$$

Since

$$\lim_{\lambda\to\infty} K(\lambda) = 0, \tag{4.62}$$

where the limit is taken in $\mathbb{R}$, the characteristic equation (4.43) has a positive solution. Therefore the instability part is proven.

For the stability claim we note that conditions (4.55) imply the positivity of the semigroup. Hence Corollary 3.4 is applicable. First we have for $\lambda \ge 0$

$$k(\lambda) \ge 1 + \delta \int_l^m F(s,\lambda)\,ds \int_0^l \frac{p_*(s)}{F(s,\lambda)}\,ds \tag{4.63}$$

$$\ge 1 + \delta \int_l^m F(s,0)\,ds \int_0^l \frac{p_*(s)}{F(s,0)}\,ds = 1 + l\,A_*\,\delta > 0 \tag{4.64}$$

by monotonicity. Similarly, if conditions (4.54) and (4.55) hold, we find for $\lambda \ge 0$

$$0 \le \int_l^m \left(\beta(s,A_*) + \int_l^m \beta_A(r,A_*)\,p_*(r)\,dr\right) F(s,\lambda)\,ds \tag{4.65}$$

$$\le \int_l^m \left(\beta(s,A_*) + \int_l^m \beta_A(r,A_*)\,p_*(r)\,dr\right) F(s,0)\,ds \tag{4.66}$$

$$= 1 + R_A^*(A_*)\,A_* < 1 + l\,A_*\,\delta \tag{4.67}$$

$$\le 1 + \delta \int_l^m F(s,\lambda)\,ds \int_0^l \frac{p_*(s)}{F(s,\lambda)}\,ds \tag{4.68}$$

$$\le 1 + \int_l^m F(s,\lambda)\,ds \int_0^l \frac{G(s)}{F(s,\lambda)}\,ds. \tag{4.69}$$

Hence we obtain

$$K(\lambda) < 1 \quad \text{for } \lambda \geq 0. \tag{4.70}$$

Since both $k(\lambda) > 0$ and $K(\lambda) < 1$ for $\lambda \geq 0$, no nonnegative eigenvalue exists. Hence the stability part is proven. □

5. The model equations revisited: The effect of a population inflow

We consider the following slightly modified version of our population model

$$p_t(s,t) + (\gamma(s,J(t),A(t))\,p(s,t))_s = -\mu(s,J(t),A(t))\,p(s,t), \tag{5.1}$$

$$p(0,t) = C + \int_l^m \beta(s,J(t),A(t))\,p(s,t)\,ds, \tag{5.2}$$

$$p(s,0) = p_0(s). \tag{5.3}$$

This modification introduces a positive constant inflow C of newborns (individuals of minimal size). Observe, however, that we incorporate the inflow as a density rather than a rate as is usually done. More general cases where C is not constant can be handled within the same framework.

There are many biological motivations for having a population inflow of newborns from an external source. A natural example for such an inflow is the case of migratory fish populations that lie eggs and then move on. Later on the newly hatched fish join a different fish population. Another example underscoring the relevance of this model is the case of fisheries where replenishment of newborn fish is practiced. In fact, models with population inflow have been studied intensively – we just mention the works of [1], [2] and [20] and the references therein where various aspects of related size structured models were discussed.

When solving (5.1)–(5.2) for a stationary solution p_*, we easily obtain a result similar to Proposition 2.1. Specifically, we find that p_* is a positive stationary solution if and only if J_*, A_* satisfy condition (2.1) and the condition

$$Q(J_*,A_*) = 1, \tag{5.4}$$

where

$$\begin{aligned} Q(J,A) &= \frac{C}{J+A}\int_0^m \exp\left\{-\int_0^s \frac{\mu(r,J,A)+\gamma_s(r,J,A)}{\gamma(r,J,A)}\,dr\right\} ds \\ &\quad + \int_l^m \beta(s,J,A)\,\exp\left\{-\int_0^s \frac{\mu(r,J,A)+\gamma_s(r,J,A)}{\gamma(r,J,A)}\,dr\right\} ds \\ &= \frac{C}{J+A}\int_0^m \exp\left\{-\int_0^s \frac{\mu(r,J,A)+\gamma_s(r,J,A)}{\gamma(r,J,A)}\,dr\right\} ds + R(J,A). \end{aligned} \tag{5.5}$$

In this case, p_* is given by

$$p_*(s) = \frac{C \, \exp\left\{ - \displaystyle\int_0^s \frac{\mu(r, J_*, A_*) + \gamma_s(r, J_*, A_*)}{\gamma(r, J_*, A_*)} \, dr \right\}}{1 - \displaystyle\int_l^m \beta(s, J_*, A_*) \, \exp\left\{ - \int_0^s \frac{\mu(r, J_*, A_*) + \gamma_s(r, J_*, A_*)}{\gamma(r, J_*, A_*)} \, dr \right\} ds} \tag{5.6}$$

and J_*, A_* satisfy (2.5). The trivial stationary solution $p_* \equiv 0$ does not arise as a solution anymore. Clearly, the net reproduction rate R at a stationary solution, defined by (2.3), will be smaller than 1. To see this, note that

$$p_*(0) = C + \int_l^m \beta(s, J_*, A_*) \, p_*(s) \, ds = C + p_*(0) \, R(J_*, A_*). \tag{5.7}$$

Hence when setting

$$D \overset{\text{def}}{=} \frac{C}{p_*(0)}, \tag{5.8}$$

we have

$$R(J_*, A_*) = 1 - D. \tag{5.9}$$

For the sake of simplicity, we will show how the population inflow affects the dynamics of the linearized system in case of the fertility controlled process treated in Section 4.1. It should, however, be clear how our stability conditions can be modified to analyze other scenarios of vital rates and also other models like the one in [15]. A more comprehensive study of the effects of a population inflow in general form is left for future work.

It is readily seen that the linearization of Eqs. (5.1)–(5.3) results again in Eqs. (2.14)–(2.17). Consequently, the corresponding characteristic equation will assume the form (4.8). The difference in the case of a population inflow arises, however, for the functions A_1, A_2 and A_3 in (4.9)–(4.11). Specifically, we note that

$$A_1(0) = R(J_*, A_*) = 1 - D. \tag{5.10}$$

Thus for stability it is enough to ensure that

$$A_2(0) + A_3(0) = J_* \, R^*_J(J_*, A_*) + A_* \, R^*_A(J_*, A_*) < D, \tag{5.11}$$

where we define R^* by (4.13). We close our discussion with a numerical example demonstrating the impact of a nonzero inflow on the stability/instability of population equilibria.

Example For the choice of vital rates

$$\beta(s, J, A) = \begin{cases} 0 & \text{if } s \in [0, 0.5], \\ \dfrac{(s - 0.5)}{2}(J + A) & \text{if } s \in (0.5, 1], \end{cases} \tag{5.12}$$

$$\mu(s, J, A) \equiv 1, \quad \gamma(s, J, A) \equiv 1, \quad s \in [0, 1], \quad l = 0.5, \tag{5.13}$$

the population model is age structured with a unique positive stationary solution given by

$$p_*(s) = 36.5553(1-e^{-1})^{-1}e^{-s}, \tag{5.14}$$

together with the (approximate) population sizes

$$J_* = 22.7542, \quad A_* = 13.8011. \tag{5.15}$$

It is readily observed that

$$J_*\, R_J^*(J_*, A_*) + A_*\, R_A^*(J_*, A_*) = 6.7840 > 0. \tag{5.16}$$

According to Theorem 4.1, the stationary solution is unstable. This result is confirmed numerically since the characteristic equation (4.8) has the dominant real root

$$\lambda^* = 12.9237. \tag{5.17}$$

In passing, we note that it follows from stability results for the general age structured case in [19] that the trivial equilibrium solution $p^* \equiv 0$ is asymptotically stable since$R(0,0) = 0 < 1$.

Now for a positive inflow C we have

$$\begin{aligned} Q(J,A) =& \frac{C}{J+A}\int_0^1 e^{-s}ds + R(J,A) & (5.18)\\ =& \frac{C}{J+A}\,(1-e^{-1}) + 0.0273\,(J+A). & (5.19)\end{aligned}$$

For $C \in (0, 14.4869)$ the equation $Q(J,A) = 1$ has exactly two solutions. When we choose $C = 10$, we find the two positive stationary solutions

$$p_*^1(s) = 8.1288\,(1-e^{-1})^{-1}\,e^{-s}, \quad p_*^2(s) = 28.4265\,(1-e^{-1})^{-1}\,e^{-s}, \tag{5.20}$$

attained at the population sizes

$$J_*^1 = \int_0^{0.5} p_*^1(s)\,ds = 5.0598, \quad A_*^1 = \int_{0.5}^1 p_*^1(s)\,ds = 3.0689$$

and

$$J_*^2 = \int_0^{0.5} p_*^2(s)\,ds = 17.6943, \quad A_*^2 = \int_{0.5}^1 p_*^2(s)\,ds = 10.7321,$$

respectively. In either case it is easily seen that the (zero inflow) instability criterion of Theorem 4.1

$$J_*^m\, R_J^*(J_*^m, A_*^m) + A_*^m\, R_A^*(J_*^m, A_*^m) > 0, \quad m \in \{1,2\} \tag{5.21}$$

holds true. While in the case $m = 2$ the characteristic equation (4.8) has indeed the dominant real root

$$\lambda^* = 0.7560, \tag{5.22}$$

the dominant real root in the case $m = 1$ is

$$\lambda^* = -1.5185, \tag{5.23}$$

thus proving instability of p_*^2 and asymptotic stability of p_*^1. Finally we also observe that

$$Q_J(J_*^1, A_*^1) = Q_A(J_*^1, A_*^1) < 0, \tag{5.24}$$

$$Q_J(J_*^2, A_*^2) = Q_A(J_*^2, A_*^2) > 0, \tag{5.25}$$

which suggests a possible modification of Theorem 4.1 in case of a positive inflow. A thorough discussion of population models with inflow is left for future work.

6. Conclusion

We have given a careful analysis of a juvenile-adult size structured population model. In our analysis we used semigroup and spectral methods that allowed us to formulate stability/instability conditions of stationary solutions in several biologically relevant situations. Our main focus was the intraspecific interaction of juveniles and adults. The stability results of Section 4 strengthen and improve previous results obtained in [15]. We have also briefly explored the effects of a positive constant inflow on the dynamical behavior of the population in a special case of model ingredients.

The results presented in this work address the linear stability/instability of equilibrium solutions. While one might hope that these results shed light on the nonlinear dynamical behavior of the governing equations, there is, in general, no guarantee that this is so. We note, however, that Diekmann et al. [8, 7] have recently proved that linear stability/instability of stationary solutions dictates nonlinear stability/instability for general classes of quasilinear size structured population models. These important findings emphasize and corroborate our objective to formulate straightforward and biologically interpretable conditions for the stability/instability of equilibria of physiologically structured population models.

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