Stability results for a size-structured population model with resources-dependence and inflow

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Abstract

It is undoubted that the survival of individuals of populations is dependent on resources (e.g., foods). We formulate a system of integro-differential equations to model the dynamics of a size-structured and resources-dependent population, a kind of inflow of newborn individuals from external environment is considered. The resource-dependence is incorporated through the size growth, mortality, fertility and feeding rates of the target population. The existence of the stationary size distributions are discussed, and the linear stability is investigated by means of the semigroup theory and the characteristic equation technique, some sufficient conditions for stability/instability of stationary states are obtained, and two examples and the corresponding simulations are presented.

1. Introduction

In 1967, Sinko and Streifer established the first model for size-structured populations [1]. Similar models for the growth of procaryotic cell populations were formulated by Fredrickson, Ramkrishna and Tscuchiya [2]. A variant of the Bell–Anderson model in [3,4] for size-dependent cell population growth when reproduction occurs by fission was analyzed by Diekmann et al. [5,6]. Some physiologically structured population models were studied intensively in the literature, we just mention the Refs. [7–11] here. Tucker and Zimmerman, in [12], presented and investigated a general nonlinear model for populations in which individuals were characterized by chronological age and an arbitrary finite number of additional structure variables. The characteristic equation for a general system of multi-populations with age-dependent dynamics was introduced by Prüss [13]. In the studies of structured populations, the method of semigroups of linear and nonlinear operators in Banach spaces was applied by many researchers [5–7,12,14,15], which has the advantage of describing the population evolution processes as dynamical systems in a proper state space. By size we mean a continuous variable related to the target individuals, such as mass, length, volume, maturity, or any other quantity displaying their physiologic or demographic property. Generally speaking, size structure is more intuitive and practical than age structure. In recent years, some stability and regularity results for linear or nonlinear size-structured population models were obtained by M. Farkas, J.Z. Farkas and Hagen [16–19].

The resources species was considered at most implicitly in the researches mentioned above. In the present paper, however, we take the resources into account explicitly, as constituents of the size-structured species model. The organization of the paper is as follows. Firstly in Section 2, we propose the basic nonlinear model, which is a hybrid system of ordinary and partial differential equations and integral equations. Then in Section 3, we linearize the nonlinear system and derive some regularity properties for the simplified system by means of the semigroups theory [20,21], following that we deduce...
the characteristic equation and give some conditions for stability and instability of the stationary solution in Section 4. Section 5 consists of two examples and their computer simulations, which are used to show the effectiveness of the theoretical results. The final section contains some concluding remarks.

2. The basic model

In this paper, we propose the following size-structured population model with resources-dependence and inflow:

\[ p_t(s, t) + \left( g(s, R_1(t), R_2(t)) p(s, t) \right)_s = -\mu(s, R_1(t), R_2(t)) p(s, t), \quad (2.1) \]

\[ p(0, t) = I(R_1(t), R_2(t)) + \int_0^m \beta(s, R_1(t), R_2(t)) p(s, t) \, ds, \quad (2.2) \]

\[ \frac{dR_i(t)}{dt} = f_i(R_i(t)) - \int_0^m \omega_i(s, R_1(t), R_2(t), P(t)) p(s, t) \, ds, \quad i = 1, 2, \quad (2.3) \]

\[ p(s, 0) = p_0(s), \quad R_i(0) = R_{0i}, \quad i = 1, 2, \quad (2.4) \]

\[ P(t) = \int_0^m p(s, t) \, ds, \quad (2.5) \]

where the function \( p(s, t) \) denotes the density of individuals of size \( s \in [0, m] \) at time \( t \in [0, \infty) \), \( m > 0 \) is the (finite) maximum size of any individual in the population. The vital rates \( \mu(s, R_1(t), R_2(t)), \beta(s, R_1(t), R_2(t)) \) and \( g(s, R_1(t), R_2(t)) \) denote mortality, fertility and growth rates, respectively, which depend on the resources quantity \( R_1(t), R_2(t) \); The quantity \( \omega_i(s, R_1(t), R_2(t), P(t)) \) stands for the feeding rate at the \( i \)th resource of the individuals of size \( s \), which depends on the resources quantity and the total population quantity \( P(t) \); \( I(R_1(t), R_2(t)) \) represents an inflow of zero size individuals from an external source. Several biologically relevant situations arise when an external inflow of minimal size individuals is taken into account in the formulation of mathematical models of population dynamics (see [22] for some natural examples); The function \( f_i(R_i(t)) \) models the autonomous dynamics of the \( i \)th resource, i.e. \( f_i \) determines the dynamics of the \( i \)th non-consumed resource. Without loss of generality, we suppose that the size of newborns is zero.

In the present paper, we assume \( f_i \) is of the following form:

\[ f_i(R_i(t)) = r R_i(t) \left( 1 - \frac{R_i(t)}{K} \right), \quad r > 0, \quad i = 1, 2, \quad (2.6) \]

which marks the logistic growth of the resources with \( K > 0 \) denoting the carrying capacity of the environment.

The following assumptions will be used throughout this paper \((i = 1, 2)\):

\[ \mu, \beta \in C^1([0, m] \times (0, \infty) \times (0, \infty)), \quad \mu \geq 0, \quad \beta \geq 0, \quad (2.7) \]

\[ g \in C^2([0, m] \times (0, \infty) \times (0, \infty)), \quad g \geq k > 0, \quad (2.8) \]

\[ \omega_i \in C^1([0, m] \times (0, \infty) \times (0, \infty) \times (0, \infty) \times (0, \infty)), \quad \omega_i \geq 0, \quad (2.9) \]

\[ f_i \in C^1(0, \infty), \quad l \in C^1((0, \infty) \times (0, \infty)), \quad l \geq 0. \quad (2.10) \]

Any stationary solution \((p^*(s), R_1^*, R_2^*)\) of system (2.1)-(2.5) satisfies the equations:

\[ \left( g(s, R_1^*, R_2^*) p^*(s) \right)_s = -\mu(s, R_1^*, R_2^*) p^*(s), \quad (2.11) \]

\[ p^*(0) = I(R_1^*, R_2^*) + \int_0^m \beta(s, R_1^*, R_2^*) p^*(s) \, ds, \quad (2.12) \]

\[ 0 = f_i(R_i^*) - \int_0^m \omega_i(s, R_1^*, R_2^*, P^*) p^*(s) \, ds, \quad i = 1, 2, \quad (2.13) \]

where \( P^* = \int_0^m p^*(s) \, ds \) denotes the total individuals of the stationary population \( p^* \). The general solution of Eq. (2.11) is found as

\[ p^*(s) = p^*(0) \Pi(s, R_1^*, R_2^*), \quad (2.14) \]
3. The linearized system and its regularity properties

Remark 2.2.

Proposition 2.1.

Actually, we are able to prove that there exist positive solutions to the system (2.18)–(2.19) in certain circumstances.

3. The linearized system and its regularity properties

Given a stationary distribution \( p^*(s) \) of system (2.1)–(2.5), in order to analyze its stability we linearize system (2.1)–(2.5) at \( p^*(s) \). We introduce \( T_1 \), \( T_2 \) and \( u \) for the perturbations of \( R_1^* \), \( R_2^* \) and \( p^* \), respectively. Dropping all of the nonlinear terms, we arrive at the following linearized system

\[
\begin{align*}
\Delta_1 & = g_{R_1}(s, R_1^*, R_2^*) p^*(s) + \mu_{R_1}(s, R_1^*, R_2^*) p^*(s) + g_{R_2}(s, R_1^*, R_2^*) p^*(s), \\
\Delta_2 & = I_{R_1}(R_1^*) + \int_{0}^{m} \beta_{R_1}(s, R_1^*, R_2^*) p^*(s) \, ds, \\
\gamma_1 & = f_{IR_1}(R_1^*) - \int_{0}^{m} \omega_{R_1}(s, R_1^*, R_2^*) p^*(s) \, ds,
\end{align*}
\]

where

\[
\Pi(s, R_1, R_2) = \left( \frac{\mu(s, R_1, R_2)}{g(s, R_1, R_2)} \right) \exp \left\{ - \int_{0}^{s} \frac{g_s(x, R_1, R_2) + \mu(x, R_1, R_2)}{g(x, R_1, R_2)} \, dx \right\}. \tag{2.15}
\]

By integration of Eq. (2.14) we obtain

\[
p^*(0) = \int_{0}^{m} \frac{\Pi(s, R_1^*, R_2^*)}{\Pi(s, R_1^*, R_2^*)} \, ds.
\]

Thus, we have shown that, to each positive solution \( (p^*, R_1^*, R_2^*) \) of Eqs. (2.18) and (2.19), there belongs a uniquely determined stationary size distribution \( p^*(s) \).

Proposition 2.1. For given model parameters \( \mu, \beta, g, l, \omega_1, \omega_2, f_1 \) and \( f_2 \), the function \( p^*(s) \) is a positive stationary distribution of system (2.1)–(2.5) if and only if \( p^*(s) \) is determined by Eq. (2.17) with the positive numbers \( P^*, R_1^*, R_2^* \) satisfying Eqs. (2.18) and (2.19).
\[ \Omega_i = \omega_i(s, R_1^*, R_2^*) + \int_0^m \omega_i\rho (s, R_1^*, R_2^*, P^*) p^*(s) \, ds, \quad (3.8) \]

together with the initial conditions
\[ T_i(0) = R_i(0) - R_i^* \overset{\text{def}}{=} T_{0i}, \quad i = 1, 2, \quad u(s, 0) = p_0(s) - p^*(0) \overset{\text{def}}{=} u_0(s). \quad (3.9) \]

Let \( \mathcal{X} \) be the product space \( L^1(0, m) \times (0, \infty) \times (0, \infty) \), where \( L^1(0, m) \) is the Lebesgue space, endowed with the usual \( L^1 \)-norm \( \| \cdot \| \). We introduce the bounded linear functional \( \Phi \) on \( \mathcal{X} \) by
\[ \Phi(u, T_1, T_2)^T = \Lambda_1 T_1 + \Lambda_2 T_2 + \int_0^m \beta(s, R_1^*, R_2^*) u(s) \, ds, \quad (3.10) \]

hereafter, \( (\cdot, \cdot)^T \) denotes the transpose of vectors. Define the operators
\[ A \begin{pmatrix} u \\ T_1 \\ T_2 \end{pmatrix} = \begin{pmatrix} -g(\cdot, R_1^*, R_2^*) u_0 \\ (\delta + \gamma_1) T_1 \\ (\delta + \gamma_2) T_2 \end{pmatrix}, \quad (3.11) \]

with \( \text{Dom}(A) = \{(u, T_1, T_2)^T \in W^{1,1}(0, m) \times (0, \infty) \times (0, \infty) \mid u(0) = \Phi(u, T_1, T_2)\} \).

\[ B \begin{pmatrix} u \\ T_1 \\ T_2 \end{pmatrix} = -\begin{pmatrix} g_1(\cdot, R_1^*, R_2^*) u_0 \\ \delta T_1 + (\int_0^m \omega_0 R_2(s, R_1^*, R_2^*, P^*) p^*(s) \, ds) T_2 \end{pmatrix} \quad \text{on} \ \mathcal{X}, \quad (3.12) \]

\[ C \begin{pmatrix} u \\ T_1 \\ T_2 \end{pmatrix} = -\begin{pmatrix} \Delta_1 T_1 + \Delta_2 T_2 \\ \int_0^m \omega_0 \Omega_1 u(s) \, ds \\ \int_0^m \omega_0 \Omega_2 u(s) \, ds \end{pmatrix} \quad \text{on} \ \mathcal{X}, \quad (3.13) \]

where \( \delta \) is chosen such that
\[ Q_i^* \overset{\text{def}}{=} \delta + \gamma_i \neq 0, \quad i = 1, 2. \quad (3.14) \]

Then the linearized system (3.1)-(3.9) can be cast in the form of an abstract ordinary differential equation on \( \mathcal{X} \)
\[ \frac{d}{dt}(u, T_1, T_2)^T = (A + B + C)(u, T_1, T_2)^T, \quad (3.15) \]

with the initial condition
\[ (u(0), T_1(0), T_2(0))^T = (u_0, T_{01}, T_{02})^T. \quad (3.16) \]

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

**Proof.** Since the operator \( B + C \) is bounded on \( \mathcal{X} \), it suffices to prove that \( A \) generates a strongly continuous semigroup. To this end, we introduce the modified operator
\[ A_0(u, T_1, T_2)^T = (-g(\cdot, R_1^*, R_2^*) u_0, (\delta + \gamma_1) T_1, (\delta + \gamma_2) T_2)^T, \quad (3.17) \]

with \( \text{Dom}(A_0) = \{(u, T_1, T_2)^T \in W^{1,1}(0, m) \times (0, \infty) \times (0, \infty) \mid u(0) = 0\} \).

Since \( g \) is positive, it is obvious that \( A_0 \) is invertible and generates a strongly continuous semigroup \( \{T_0(t)\}_{t \geq 0} \) on \( \mathcal{X} \), given by
\[ (T_0(t)(u, T_1, T_2)^T)(s) = \begin{cases} (u(T^{-1}(\Gamma(s, R_1^*, R_2^*) - t)), \exp(Q_1^* t) T_1, \exp(Q_2^* t) T_2)^T, & \text{if } \Gamma(s, R_1^*, R_2^*) \geq t, \\ (0, \exp(Q_1^* t) T_1, \exp(Q_2^* t) T_2)^T, & \text{otherwise}, \end{cases} \quad (3.18) \]

where
\[ \Gamma(s, R_1, R_2) = \int_0^s \frac{1}{g(y, R_1, R_2)} \, dy. \quad (3.19) \]

Let \( \mathcal{X}_{-1} \) be the completion of \( \mathcal{X} \) in the norm \( \| \cdot \|_{-1} \overset{\text{def}}{=} \| A_0^{-1} \cdot \| \), define the extended semigroup \( \{T_{-1}(t)\}_{t \geq 0} \) on \( \mathcal{X}_{-1} \) by
\[ T_{-1}(t) = A_0 T_0(t) A_0^{-1}, \quad (3.20) \]
and denote its generator by \( A_{-1} \). Then \( A_{-1} \) is an extension of \( A_0 \) with \( \text{Dom}(A_{-1}) \) is \( \mathcal{X} \) and range in \( \mathcal{X}_{-1} \). Finally we define the perturbing operator \( \mathcal{P} \in \mathcal{L}(\mathcal{X}, \mathcal{X}_{-1}) \) by

\[
\mathcal{P} \begin{pmatrix} u \\ T_1 \\ T_2 \end{pmatrix} \overset{\text{def}}{=} \begin{pmatrix} -\Phi(u, T_1, T_2)T_0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} A_{-1} \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix},
\]

(3.21)

where \( 1 = 1(\cdot) \) is the constant function \( 1 \) in \( L^1(0, m) \). Then the operator \( \mathcal{A} \) is just the part of the operator \( A_{-1} + \mathcal{P} \) in \( \mathcal{X} \). If we could prove that operator \( \mathcal{P} \) generates a strongly continuous semigroup on \( \mathcal{X} \), then the theorem is also proved. To do so, we apply the Desch–Schappacher Perturbation Theorem (see [21] and also [18,19]). For given \( (h, h_1, h_2)^T \in L^1([0, m]; \mathcal{X}) \), we need to show that the following relation is true:

\[
\int_0^m T_{-1}(m-t)\mathcal{P}(h(t), h_1(t), h_2(t))^T \, dt = A_{-1} \int_0^m \left( \begin{array}{ccc} -\Phi(h(t), h_1(t), h_2(t))^T & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right) T_{-1}(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \\ 0 \end{pmatrix} \, dt \quad \text{on} \ \mathcal{X}.
\]

(3.22)

Since the above relation is equivalent to

\[
\int_0^m \left( \begin{array}{ccc} -\Phi(h(t), h_1(t), h_2(t))^T & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right) T_0(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \\ 0 \end{pmatrix} \, dt \in \text{Dom}(A_0),
\]

(3.23)

and

\[
\int_0^m \left( \begin{array}{ccc} -\Phi(h(t), h_1(t), h_2(t))^T & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right) T_0(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \\ 0 \end{pmatrix} \, dt = \int_{m-t}^m \left( \begin{array}{ccc} -\Phi(h(t), h_1(t), h_2(t))^T \\ 0 \\ 0 \end{array} \right) \, dr,
\]

(3.24)

the proof is complete. \( \square \)

Therefore, we have the following corollary.

**Corollary 3.2.** For initial data \((u_0, T_{01}, T_{02})^T \in L^1((0, m) \times (0, \infty) \times (0, \infty)) \) the linear system (3.1)–(3.9) has a unique solution \((u, T_1, T_2)^T \) in \( C([0, \infty); L^1(0, m)) \), given by

\[
u(s, t) = \left( T(t)(u_0, T_{01}, T_{02})^T \right)(s).
\]

(3.25)

**Theorem 3.3.** The spectrum of the semigroup generator \( \mathcal{A} + \mathcal{B} + \mathcal{C} \) consists of isolated eigenvalues of finite multiplicity.

**Proof.** Since the operator \( \mathcal{B} + \mathcal{C} \) is compact on \( \mathcal{X} \) and the operator \( \mathcal{A} \) has a bounded resolvent mapping \( \mathcal{X} \) into \( W^{1,1}(0, m) \times \mathbb{C} \times \mathbb{C} \), where \( \mathbb{C} \) denotes the set of all complex numbers. Since \( W^{1,1}(0, m) \times \mathbb{C} \times \mathbb{C} \) can be compactly embedded in \( \mathcal{X} \), we obtain the conclusion by means of Riesz–Schauder theory. \( \square \)

Because of Theorem 3.3 the linear stability of the stationary solution is spectrally determined (see [20,21]). Our analysis would be much simpler if the eigenvalue with largest real part were real. The following result enables us to draw this conclusion in certain circumstances.

**Theorem 3.4.** Suppose that

\[
\Delta_i \leq 0, \quad A_i \geq 0, \quad \Omega_i \leq 0, \quad i = 1, 2,
\]

(3.26)

where \( A_i, \Delta_i, \Omega_i \) are given by (3.5), (3.6) and (3.8), respectively. Then the semigroup \( \{T(t)\}_{t \geq 0} \) generated by the operator \( \mathcal{A} + \mathcal{B} + \mathcal{C} \) is positive.

**Proof.** Condition (3.26) ensures that the operator \( \mathcal{C} \) is positive. Hence it suffices to prove that the operator \( \mathcal{A} + \mathcal{B} \) is non-negative. Suppose \( u \) is any solution of the following equation

\[
\frac{d}{dt} \begin{pmatrix} u \\ T_1 \\ T_2 \end{pmatrix} = \left( \begin{array}{ccc} \mathcal{A} + \mathcal{B} \end{array} \right) \begin{pmatrix} u \\ T_1 \\ T_2 \end{pmatrix}, \quad \begin{pmatrix} u(0) \\ T_1(0) \\ T_2(0) \end{pmatrix} = \begin{pmatrix} u_0 \\ T_{01} \\ T_{02} \end{pmatrix} \in \text{Dom}(\mathcal{A}).
\]

(3.27)
Then the function \( v \) defined by

\[
v(s, t) = u(s, t) \exp \left\{ \int_0^s \Theta(y, R_1^*, R_2^*) \, dy \right\}, \tag{3.28}\]

with

\[
\Theta(s, R_1, R_2) = \frac{g(s, R_1^*, R_2^*) + \mu(s, R_1, R_2)}{g(s, R_1, R_2)} \tag{3.29}\]

satisfies

\[
v_t(s, t) + g(s, R_1^*, R_2^*)v(s, t) = 0, \tag{3.30}\]

\[
v(0, t) = \Phi \left( \frac{v(\cdot, t) \exp \left\{ \int_0^t \Theta(y, R_1^*, R_2^*) \, dy \right\}}{T_1}, \frac{T_2}{T_2} \right) \tag{3.31}\]

\[
v(s, 0) = v_0(s), \tag{3.32}\]

which corresponds to the following modified semigroup generator

\[
A_m(v, T_1, T_2)^T = (-g(\cdot, R_1^*, R_2^*)v_s, T_1 T_1, T_2 T_2)^T, \tag{3.33}\]

with \( \text{Dom}(A_m) = \left\{ \left( \begin{array}{c} v \\ T_1 \\ T_2 \end{array} \right) \in W_{1,1}(0, m) \times C \times C \mid v(0) = \Phi \left( \begin{array}{c} v \\ T_1 \\ T_2 \end{array} \right) \right\}. \]

For \( \lambda > 0 \) sufficiently large and \( h \in L^1(0, m), h_1, h_2 \in C(0, \infty) \), the resolvent equation is

\[
\lambda(v, T_1, T_2)^T - A_m(v, T_1, T_2)^T = (h, h_1, h_2)^T. \tag{3.34}\]

Substituting Eq. (3.33) into Eq. (3.34) and applying \( \Phi\), we are able to obtain

\[
\Phi \left( \begin{array}{c} v \\ T_1 \\ T_2 \end{array} \right) = \left( 1 - \Phi \left( \begin{array}{c} e^{-\lambda T_1 (R_1^*, R_2^*)} \\ T_1 \\ T_2 \end{array} \right) \right)^{-1} \Phi \left( \int_0^t e^{\lambda (T_1 (R_1^*, R_2^*) - T_1 (R_1^*, R_2^*))} \frac{h(x)}{g(x, R_1^*, R_2^*)} \, dx \right). \tag{3.35}\]

By condition (3.26), it is obvious that \( \Phi\) is a positive operator, hence for such \( \lambda \) the resolvent operator of \( A_m \) (or equivalently of \( A + B \)) is positive. The proof is complete. \( \square \)

The following corollary can be proved by means of the theory of positive semigroups (see [20,21] and also [18,19] for relative results).

**Corollary 3.5.** Suppose that the condition (3.26) is satisfied, then \( s(A + B + C) \in \sigma(A + B + C) \) and \( s(A + B + C) \) is a dominant eigenvalue, where \( s(A + B + C) \) denotes the bound of the spectrum of the operator \( A + B + C \).

4. The characteristic equation and stability results

In the light of the positivity conditions deduced in the previous section, the linear stability of stationary solutions of system (3.1)-(3.9) is determined by the eigenvalues of the semigroup generator \( A + B + C \). In this section we derive a characteristic equation to discuss the eigenvalues of the operator \( A + B + C \).

Suppose that the linearized system (3.1)-(3.9) has solutions of the form \( (u(s, t), T_1(t), T_2(t))^T = (e^{\lambda t} U(s), e^{\lambda t} N_1, e^{\lambda t} N_2)^T \). Substituting this into Eqs. (3.1)-(3.4) and dividing by \( e^{\lambda t} \), we have

\[
\left[ \lambda + g_s(s, R_1^*, R_2^*) + \mu_s(s, R_1, R_2) \right] U(s) + g_s(s, R_1^*, R_2^*) U_s(s) + \Delta_1 N_1 + \Delta_2 N_2 = 0, \tag{4.1}\]

\[
U(0) = \Lambda_1 N_1 + \Lambda_2 N_2 + \int_0^m \beta_s(s, R_1^*, R_2^*) U(s) \, ds, \tag{4.2}\]

\[
(\lambda - \gamma_1) N_1 + \int_0^m \omega_1 R_2(s, R_1^*, R_2^*, P^* ) p^*(s) \, ds \cdot N_2 + \int_0^m \Omega_2 U(s) \, ds = 0, \tag{4.3}\]

\[
(\lambda - \gamma_2) N_2 + \int_0^m \omega_2 R_1(s, R_1^*, R_2^*, P^* ) p^*(s) \, ds \cdot N_1 + \int_0^m \Omega_1 U(s) \, ds = 0. \tag{4.4}\]
The solution of Eq. (4.1) is given by

\[
U(s) = \left( U(0) - N_1 \int_0^s \frac{\Delta_1}{g(\Psi)} \, dy - N_2 \int_0^s \frac{\Delta_2}{g(\Psi)} \, dy \right) \Psi(\lambda, s, R_1^*, R_2^*),
\]

where \( \Psi(\lambda, s, R_1, R_2) = \exp(-\lambda \int_0^s \Theta(y, R_1, R_2) \, dy) \), with \( \Gamma, \Theta \) defined by (3.19) and (3.29). Substituting Eq. (4.5) into Eqs. (4.2)-(4.4), respectively, and introducing the notations,

\[
A_{11}(\lambda) = 1 - \int_0^m \beta(s, R_1^*, R_2^*) \Psi(\lambda, s, R_1^*, R_2^*) \, ds,
\]

\[
A_{12}(\lambda) = \int_0^m \beta(s, R_1^*, R_2^*) \Psi(\lambda, s, R_1^*, R_2^*) \int_0^s \frac{\Delta_1(y, R_1^*, R_2^*)}{g(y, R_1^*, R_2^*)} \, dy \, ds - A_1,
\]

\[
A_{13}(\lambda) = \int_0^m \beta(s, R_1^*, R_2^*) \Psi(\lambda, s, R_1^*, R_2^*) \int_0^s \frac{\Delta_2(y, R_1^*, R_2^*)}{g(y, R_1^*, R_2^*)} \, dy \, ds - A_2,
\]

\[
A_{21}(\lambda) = \int_0^m \Omega_1(s, R_1^*, R_2^*, R^*) \Psi(\lambda, s, R_1^*, R_2^*) \, ds,
\]

\[
A_{22}(\lambda) = \lambda - \Omega_1 - \int_0^m \Omega_1(s, R_1^*, R_2^*, R^*) \Psi(\lambda, s, R_1^*, R_2^*) \int_0^s \frac{\Delta_1(y, R_1^*, R_2^*)}{g(y, R_1^*, R_2^*)} \, dy \, ds,
\]

\[
A_{23}(\lambda) = \int_0^m \Omega_2(s, R_1^*, R_2^*, R^*) \, ds - \int_0^m \Omega_1(\lambda, s, R_1^*, R_2^*) \int_0^s \frac{\Delta_2(y, R_1^*, R_2^*)}{g(y, R_1^*, R_2^*)} \, dy \, ds,
\]

\[
A_{31}(\lambda) = \int_0^m \Omega_2(s, R_1^*, R_2^*, R^*) \Psi(\lambda, s, R_1^*, R_2^*) \, ds,
\]

\[
A_{32}(\lambda) = \int_0^m \Omega_2(s, R_1^*, R_2^*, R^*) \, ds - \int_0^m \Omega_2(\lambda, s, R_1^*, R_2^*) \int_0^s \frac{\Delta_1(y, R_1^*, R_2^*)}{g(y, R_1^*, R_2^*)} \, dy \, ds,
\]

\[
A_{33}(\lambda) = \lambda - \Omega_2 - \int_0^m \Omega_2(s, R_1^*, R_2^*, R^*) \Psi(\lambda, s, R_1^*, R_2^*) \int_0^s \frac{\Delta_2(y, R_1^*, R_2^*)}{g(y, R_1^*, R_2^*)} \, dy \, ds,
\]

we obtain the following conditions for the constants \( U(0), N_1 \) and \( N_2 \):

\[
A_{11}(\lambda)U(0) + A_{12}(\lambda)N_1 + A_{13}(\lambda)N_2 = 0,
\]

\[
A_{21}(\lambda)U(0) + A_{22}(\lambda)N_1 + A_{23}(\lambda)N_2 = 0,
\]

\[
A_{31}(\lambda)U(0) + A_{32}(\lambda)N_1 + A_{33}(\lambda)N_2 = 0,
\]

which has nonzero solutions \( (U(0), N_1, N_2) \) if and only if its determinant of coefficients vanishes. This way we have shown the following theorem:

**Theorem 4.1.** The spectrum of the semigroup generator \( A + B + C \) consists of all of the roots of the characteristic equation \( K(\lambda) = 0 \), where the function \( K \) is defined by

\[
K(\lambda) \overset{\text{def}}{=} \begin{vmatrix}
A_{11}(\lambda) & A_{12}(\lambda) & A_{13}(\lambda) \\
A_{21}(\lambda) & A_{22}(\lambda) & A_{23}(\lambda) \\
A_{31}(\lambda) & A_{32}(\lambda) & A_{33}(\lambda)
\end{vmatrix}.
\]
Now we introduce the following function

\[ R(R_1, R_2) = \int_0^m \beta(s, R_1, R_2) \Pi(s, R_1, R_2) \, ds, \]  

which is called the net reproduction rate and gives the number of newborns that an individual is expected to produce during its lifetime.

**Theorem 4.2.** Given a positive stationary solution \((p^*, R_1^*, R_2^*)\), suppose the condition (3.26) holds, then the stationary solution is linearly unstable if \(K(0) < 0\).

**Proof.** Due to the condition (3.26), we invoke Corollary 3.5 and restrict ourselves to \(\lambda \in \mathbb{R}\). It is easy to show that \(\lim_{\lambda \to +\infty} \Psi(\lambda, s, R_1^*, R_2^*) = 0\), hence it follows from (2.9) and the Lebesgue dominated convergence theorem that

\[ \lim_{\lambda \to +\infty} \Psi(\lambda, s, R_1^*, R_2^*) = 0, \]

Consequently, assumptions (2.7)–(2.10) and the dominated convergence theorem imply that

\[ \lim_{\lambda \to +\infty} K(\lambda) = \lim_{\lambda \to +\infty} \left\{ A_{11}(\lambda)A_{22}(\lambda)A_{33}(\lambda) - A_{11}(\lambda)A_{23}(\lambda)A_{32}(\lambda) \right\} = +\infty. \]

On the other hand, by assumptions (2.7)–(2.10), \(K(\lambda)\) is a continuous function. Hence \(K(\lambda) = 0\) has a positive root if \(K(0) < 0\), i.e., the semigroup generator has a positive eigenvalue. The proof is complete. \(\square\)

**Theorem 4.3.** For a positive stationary solution \((p^*, R_1^*, R_2^*)\), suppose that condition (3.26) and the following hold, \(i = 1, 2\),

\[
\left[ R(R_1^*, R_2^*) - 1 \right] \left[ \gamma_1 + \int_0^m \Omega_1(s, R_1^*, R_2^*, P^*) \Pi(s, R_1^*, R_2^*) \int_0^s \frac{\Delta_1(x, R_1^*, R_2^*)}{g(x, R_1^*, R_2^*)} \, dx \, ds \right] \\
\geq \left[ \int_0^m \beta(s, R_1^*, R_2^*) \Pi(s, R_1^*, R_2^*) \int_0^s \frac{\Delta_1(x, R_1^*, R_2^*)}{g(x, R_1^*, R_2^*)} \, dx \, ds - 1 \right] \\
\times \int_0^m \Omega_1(s, R_1^*, R_2^*, P^*) \Pi(s, R_1^*, R_2^*) \, ds,
\]

\[
\left[ \gamma_1 + \int_0^m \Omega_2(s, R_1^*, R_2^*, P^*) \Pi(s, R_1^*, R_2^*) \int_0^s \frac{\Delta_2(x, R_1^*, R_2^*)}{g(x, R_1^*, R_2^*)} \, dx \, ds \right] \\
\times \left[ \gamma_2 + \int_0^m \Omega_2(s, R_1^*, R_2^*, P^*) \Pi(s, R_1^*, R_2^*) \int_0^s \frac{\Delta_2(x, R_1^*, R_2^*)}{g(x, R_1^*, R_2^*)} \, dx \, ds \right] \\
\geq \left[ \omega_{1R_2}(s, R_1^*, R_2^*, P^*) p^*(s) - \Omega_1(s, R_1^*, R_2^*, P^*) \Pi(s, R_1^*, R_2^*) \int_0^s \frac{\Delta_2(x, R_1^*, R_2^*)}{g(x, R_1^*, R_2^*)} \, dx \right] \, ds \\
\times \left[ \omega_{2R_1}(s, R_1^*, R_2^*, P^*) p^*(s) - \Omega_2(s, R_1^*, R_2^*, P^*) \Pi(s, R_1^*, R_2^*) \int_0^s \frac{\Delta_1(x, R_1^*, R_2^*)}{g(x, R_1^*, R_2^*)} \, dx \right] \, ds,
\]

where

\[
\omega_{1R_2}(s, R_1, R_2, P) \leq 0, \quad \omega_{2R_1}(s, R_1, R_2, P) \leq 0.
\]

Then the stationary distribution \(p^*(s)\) is linearly asymptotically stable if \(K(0) > 0\).
Proof. Because of the condition (3.26), Corollary 3.5 works and We restrict ourselves to $\lambda \in \mathbb{R}$. It implies that the spectrum of the semigroup generator is either empty or contains a dominant real eigenvalue. If the dominant eigenvalue is negative, then the growth bound of the semigroup are contained in $[-\infty, 0]$. By the proof of Theorem 4.2 we have $\lim_{\lambda \to +\infty} K(\lambda) = +\infty$. When $K(0) > 0$, the stationary solution will be linearly asymptotically stable if we can show that $K(\lambda)$ is nondecreasing for $\lambda \geq 0$ due to Theorem 4.1. In what follows we show that $K(\lambda) \geq 0$, $\lambda \geq 0$. Let

$$
D_1(\lambda) = \begin{vmatrix}
A_{11} & A_{12} & A_{13} \\
A_{21} & A_{22} & A_{23} \\
A_{31}' & A_{32}' & A_{33}'
\end{vmatrix},
$$

$$
D_2(\lambda) = \begin{vmatrix}
A_{11} & A_{12} & A_{13} \\
A_{21} & A_{22} & A_{23} \\
A_{31} & A_{32} & A_{33}
\end{vmatrix},
$$

$$
D_3(\lambda) = \begin{vmatrix}
A_{11} & A_{12} & A_{13} \\
A_{21} & A_{22} & A_{23} \\
A_{31} & A_{32} & A_{33}'
\end{vmatrix}.
$$

Clearly, $K'(\lambda) = D_1(\lambda) + D_2(\lambda) + D_3(\lambda)$. We shall prove $D_i(\lambda) \geq 0$, $i = 1, 2, 3$. Firstly we show $D_1(\lambda) \geq 0$. From (2.18) we see $R(R_1^+, R_2^+) \leq 1$. Making the use of conditions (3.26), (4.11) and the assumptions (2.7)–(2.10), we get the following relations:

$$
A_{ij}(\lambda) \geq 0, \quad i, j = 1, 2, 3;
$$

$$
A_{11}(\lambda) \geq 0, \quad A_{12}(\lambda) \leq 0, \quad A_{13}(\lambda) \leq 0, \quad A_{21}(\lambda) \leq 0, \quad A_{31}(\lambda) \leq 0.
$$

From (4.14), we arrive at $\lim_{\lambda \to +\infty} A_{23}(\lambda) \leq 0$ and $\lim_{\lambda \to +\infty} A_{32}(\lambda) \leq 0$. Hence by (4.16), we have

$$
A_{23}(\lambda) \leq 0, \quad A_{32}(\lambda) \leq 0.
$$

It is should be noted that the conditions (4.12)–(4.14) are equivalent to

$$
D_{11}(0) \geq 0, \quad D_{12}(0) \geq 0, \quad \text{where} \quad D_{11}(\lambda) = \begin{vmatrix}
A_{11}(\lambda) & A_{12}(\lambda) \\
A_{21}(\lambda) & A_{22}(\lambda)
\end{vmatrix}, \quad D_{12}(\lambda) = \begin{vmatrix}
A_{11}(\lambda) & A_{13}(\lambda) \\
A_{31}(\lambda) & A_{33}(\lambda)
\end{vmatrix},
$$

and

$$
D_{13}(0) \geq 0, \quad \text{where} \quad D_{13}(\lambda) = \begin{vmatrix}
A_{22}(\lambda) & A_{23}(\lambda) \\
A_{32}(\lambda) & A_{33}(\lambda)
\end{vmatrix}.
$$

Combining (4.16) with (4.18), the relations $A_{22}(0) \geq 0$ and $A_{33}(0) \geq 0$ must be true. Thus we have

$$
A_{22}(\lambda) \geq 0, \quad A_{33}(\lambda) \geq 0.
$$

Furthermore, it follows from (4.16)–(4.20) that $D_i'(\lambda) \geq 0$, $D_i'(\lambda) \geq 0$, $D_i'(\lambda) \geq 0$, which implies that

$$
D_{11}(\lambda) \geq 0, \quad D_{12}(\lambda) \geq 0, \quad D_{13}(\lambda) \geq 0.
$$

Now the signs of all elements of $D_1(\lambda)$ are determined. Expanding the determinant $D_1(\lambda)$ in the first column, we see that all terms in the expansion are nonnegative by (4.16)–(4.21), which implies $D_1(\lambda) \geq 0$. Similarly, we can show $D_2(\lambda) \geq 0$ and $D_3(\lambda) \geq 0$. The proof is complete. \hfill \square

5. Examples and simulations

In this section, two examples and the corresponding simulations will be taken to demonstrate the stability results given in Theorems 4.2 and 4.3.

Example 5.1. Let the parameters of system (2.1)–(2.5) be as follows:

$$
\mu(s, R_1(t), R_2(t)) = \frac{5}{5 + R_1(t) + R_2(t)}, \quad \beta(s, R_1(t), R_2(t)) = 2se^s,
$$

$$
g(s, R_1(t), R_2(t)) = \frac{R_1(t) + R_2(t)}{100}, \quad f_i(R_i) = \frac{1}{3} R_i \left(1 - \frac{R_i}{12}\right), \quad i = 1, 2,
$$

$$
\omega_1(s, R_1(t), R_2(t), P(t)) = \frac{2R_1(t)e^{-P(t)}}{R_2(t)}, \quad \omega_2(s, R_1(t), R_2(t), P(t)) = \frac{2R_2(t)e^{-P(t)}}{R_1(t)},
$$

$$
l(R_1, R_2) = 0, \quad m = 1.
$$

Substituting these parameters into Eqs. (2.18) and (2.19), we obtain that

$$
R_1^* = R_2^* \approx 10, \quad P^* \approx 2.
$$

By means of Maple 9, it is not hard to get the following relations:

$$
p^*(s) = \frac{2e^s}{1 - e^s},
$$

$$
\Delta_i = \frac{-7e^{-s}}{150(1 - e^{-1})} < 0, \quad A_i = 0, \quad \Omega_i \approx -0.27 < 0, \quad K(0) \approx -0.012 < 0.
$$
Fig. 1. Total population size $P(t)$ and the resources quantity $R_i(t)$, $i = 1, 2$, the initial conditions corresponding to curves $a$ to $d$ are: (a) $R_1(0) = 11$, $p_0(s) = s + \frac{1}{s^2}$; (b) $R_1(0) = 9$, $p_0(s) = 2s + \frac{1}{s^2}$; (c) $R_1(0) = 8$, $p_0(s) = 1 + \frac{1}{s^2} - 2s$; (d) $R_1(0) = 10$, $p_0(s) = \frac{22}{s^2}$.

It follows from (5.3) that the conditions of Theorem 4.2 hold. Thus the stationary solution $(p^*, R_1^*, R_2^*)$ is unstable, as shown by Fig. 1.

**Example 5.2.** following parameters are chosen for system (2.1)–(2.5):

$$\mu(s, R_1(t), R_2(t)) = \frac{5}{5 + R_1(t) + R_2(t)}, \quad \beta(s, R_1(t), R_2(t)) = se^s,$$

$$g(s, R_1(t), R_2(t)) = \frac{R_1(t) + R_2(t)}{100}, \quad f_i(R_i) = \frac{1}{3}R_i \left(1 - \frac{R_i}{12}\right), \quad i = 1, 2,$$

$$\omega_1(s, R_1(t), R_2(t), P(t)) = \frac{2R_1(t)e^{-p(t)}}{R_2(t)}, \quad \omega_2(s, R_1(t), R_2(t), P(t)) = \frac{2R_2(t)e^{-p(t)}}{R_1(t)},$$

$$I(R_1, R_2) = \frac{R_1(t) + R_2(t)}{20(1 - e^{-1})}, \quad m = 1.$$

By the same manner, we have

$$R_1^* = R_2^* \approx 10, \quad P^* \approx 2, \quad p^*(s) = \frac{2e^{-s}}{1 - e^{-1}}, \quad (5.4)$$

$$\Delta_1 = \frac{-7e^{-s}}{150(1 - e^{-1})} < 0, \quad \Lambda_1 = \frac{1}{20(1 - e^{-1})} > 0, \quad \Omega_1 \approx -0.27 < 0, \quad (5.5)$$

$$K(0) \approx 0.018 > 0, \quad D_{11}(0) = D_{12}(0) \approx 0.11 > 0, \quad D_{13}(0) \approx 0.056 > 0. \quad (5.6)$$

Therefore the conditions of Theorem 4.3 are satisfied, then the stationary solution $(p^*, R_1^*, R_2^*)$ is locally asymptotically stable, as shown by Fig. 2.

6. Concluding remarks

**Remark 6.1.** If the target population has the same dependence on resources $R_1$ and $R_2$, then the feeding rate at a resource is decreasing while the quantity of another resource is increasing. The condition (4.14) in Theorem 4.3 holds under such circumstances.

**Remark 6.2.** If the target population depends only on one kind of resource, then our results reduce to that of Farkas and Hagen [19].

**Remark 6.3.** Within the framework presented here, more general models such as

$$p_t(s, t) + \left(\frac{g(s, R_1(t), \ldots, R_n(t))}{p(s, t)}\right)_s = -\mu(s, R_1(t), \ldots, R_n(t))p(s, t),$$

$$p(0, t) = I(R_1(t), \ldots, R_n(t)) + \int_0^m \beta(s, R_1(t), \ldots, R_n(t))p(s, t)\, ds,$$
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