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Nonlinear Physiologically Structured Population Models with Two Internal Variables

Hao Kang¹ · Xi Huo¹ · Shigui Ruan¹

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Abstract

First-order hyperbolic partial differential equations with two internal variables have been used to model biological and epidemiological problems with two physiological structures, such as chronological age and infection age in epidemic models, age and another physiological character (maturation, size, stage) in population models, and cell-age and molecular content (cyclin content, maturity level, plasmid copies, telomere length) in cell population models. In this paper, we study nonlinear double physiologically structured population models with two internal variables by applying integrated semigroup theory and non-densely defined operators. We consider first a semilinear model and then a nonlinear model, use the method of characteristic lines to find the resolvent of the infinitesimal generator and the variation of constant formula, apply Krasnoselskii's fixed point theorem to obtain the existence of a steady state, and study the stability of the steady state by estimating the essential growth bound of the semigroup. Finally, we generalize the techniques to investigate a nonlinear age-size structured model with size-dependent growth rate.

Keywords Physiological structure · Cauchy problem with non-dense domain · Integrated semigroups · Infinitesimal generator · Spectrum theory · Stability

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Contents

1 Introduction	2848
2 Integrated Semigroup Setting	2850
3 Semilinear Double Physiologically Structured Models	2854
3.1 Existence of Nontrivial Steady States	2856
3.2 Stability	2862
4 Nonlinear Double Physiologically Structured Models	2866
4.1 Existence of Nontrivial Steady States	2868
4.2 Stability	2870
5 Age-Size Structured Models with Size-Dependent Growth Rate	2874
6 Discussion	2881
A Appendix: Positive Operators	2881
References	2883

1 Introduction

In modeling specific problems in biology and epidemiology, sometimes it is necessary to take into account more than one physiological structures of the population, such as chronological age and infection age of individuals (Gripenberg 1893; Hoppensteadt 1974; Inaba 2016; Laroche and Perasso 2016; Burie et al. 2017) in modeling infectious diseases; age and size structures (Sinko and Streifer 1967; Gyllenberg and Webb 1987; Webb 2008), age and maturation structures (Dyson et al. 2000a, b), and age and stage structures (McNair and Goulden 1991; Matucci 1995) in modeling population dynamics; age and pair age structures (Inaba 2017) in population pair formation models; age and an aggregated variable (Doumic 2007), age and cyclin content (Bekkal Brikci et al. 2008), age and maturity level (Bernard et al. 2003), age and plasmid copies (Stadler 2019), and age and telomere length (Kapitanov 2012) in modeling cell population kinetics. However, there are very few theoretical studies on the fundamental properties of such models with two physiological structures (Inaba 2016; Webb 1985).

Recently, we Kang et al. (2020) considered a *linear* first-order hyperbolic partial differential equation that models the single-species population dynamics with two physiological structures where both boundary conditions were non-trivial. By using semigroup theory, we studied the basic properties and dynamics of the model, including the solution flow and its semigroup with an infinitesimal generator. Moreover, we established the compactness of the solution trajectories, analyzed the spectrum of the infinitesimal generator, and investigated stability of the zero steady state with asynchronous exponential growth.

For the double physiologically structured population models, analyzing the infinitesimal generator seems complicated, in particular in solving the characteristic and resolvent equations. In this paper, we consider *nonlinear* physiologically structured population models with two internal variables and use different techniques, namely integrated semigroups and non-densely defined operators, which enable us to solve the characteristic equation directly and study the existence and stability of the steady states,

For the two physiological structures, define the state space by

$$E := L^1((0, a^+) \times (0, s^+)),$$

where a^+ and s^+ represent the maximums of two physiological structures respectively. Here we assume that they are finite. Consider the following nonlinear first-order hyperbolic partial differential equation with two internal variables a and s (representing two physiological structures):

$$\begin{cases} u_t(t, a, s) + u_a(t, a, s) + u_s(t, a, s) = G(u(t, \cdot, \cdot))(a, s), \\ u(t, a, 0) = F(u(t, \cdot, \cdot))(a), \\ u(t, 0, s) = H(u(t, \cdot, \cdot))(s), \\ u(0, a, s) = \phi(a, s), \end{cases} \quad (1.1)$$

where $u(t, a, s)$ denotes the density of a population at time t with age a and another physiological characteristic s , $\phi \in E$ is an initial data. Assume that $G : E \rightarrow E$, $F : E \rightarrow L^1(0, a^+)$ and $H : E \rightarrow L^1(0, s^+)$ are uniformly bounded and Lipschitz continuous functions. Notice that the second physiological characteristic s could be the chronological age or infection age if (1.1) is an epidemic model; the maturation, size, or stage variable if (1.1) is a population model; and cyclin content, maturity level, plasmid copies, or telomere length if (1.1) models cell population dynamics.

In most of the previously developed models, it is assumed that one boundary condition is trivial based on valid biological assumptions. For example, in the chronological age–infection age epidemic models, the infection age is always less than the chronological age, thus the boundary condition for those with zero chronological age but positive infection age would always be zero; in the age–size population models, no individuals would possess a positive age and a zero size; thus, the boundary condition for those with positive chronological age but zero size should be always zero. Therefore, it is natural for one to ask for the motivation of real-world applications with both boundaries being non-trivial. Here, we discuss two potential applications in modeling infectious diseases and cell population kinetics. (a) Hethcote (1988, 1997, 1999) used chronological age structured models to study the optimal age for vaccinations and boosters in preventing pertussis and measles; such models can be extended to a double physiologically structured system with one structure being the chronological age of human population and another being the immunity age (the age since last immunity build up). Under such consideration, the corresponding system would yield to two non-trivial boundary conditions: Newborns with maternal immunity would have a zero chronological age but a nonzero immunity age; people who take a booster vaccine can reset their immunity age to zero and thus would have a nonzero chronological age but a zero immunity age. (b) Kapitanov (2012) studied cancer stem cell lineage population dynamics by structuring the cell population with continuous cell age and discrete telomere length, such a model, once derived with both structures being continuous, would yield two non-trivial boundary conditions: since newly generated cells could have telomere with any length and some aged cells would have 0-length telomere due to telomere loss during cell differentiation.

To analyze such systems, the idea is to rewrite the initial-boundary value problem (1.1) as an abstract semilinear Cauchy problem with non-dense domain (Thieme 1990; Magal and Ruan 2018) and use integrated semigroup theory to discuss the problem. Then, we use the method of characteristic lines to find the resolvent of the infinitesimal generator and the variation of constant formula and apply the Krasnoselskii's fixed point theorem to obtain the existence of a steady state. Finally, we study the stability of the steady state by estimating the essential growth bound of the semigroup.

To present our idea and techniques, in next section we will set up the abstract semilinear Cauchy problem with non-dense domain by using integrated semigroups. In Sect. 3 we will study a semilinear model, and a nonlinear equation will be treated in Sect. 4. In Sect. 5 we will extend the methods to study an age-size structured model with size-dependent growth rate in two internal variables.

2 Integrated Semigroup Setting

We first recall some results on integrated semigroups and non-densely defined operators from Thieme (1990) and Magal and Ruan (2018). Let A be a differential operator acting on E defined by

$$A(\psi)(a, s) := -\psi_a - \psi_s, \quad D(A) := \{\psi \in E : \psi \in W^{1,1}((0, a^+) \times (0, s^+))\}.$$

Then, A is densely defined in E . Now we introduce an extended state space as

$$X := L^1(0, a^+) \times L^1(0, s^+) \times E$$

and its closed subspace $X_0 := \{0\} \times \{0\} \times E$. Define an operator \mathcal{A} acting on X such that

$$\mathcal{A} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} -\psi(a, 0) \\ -\psi(0, s) \\ -\psi_a - \psi_s \end{pmatrix} \text{ for } \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \in D(\mathcal{A}) := \{0\} \times \{0\} \times D(A).$$

Remark 2.1 Note that $\psi(a, 0)$ and $\psi(0, s)$ are well defined by the trace lemma for any $\psi \in W^{1,1}((0, a^+) \times (0, s^+))$.

Let $X_{0+} := \{0\} \times \{0\} \times E_+$ be the positive cone of X_0 . Define a bounded operator $\mathcal{B} : X_{0+} \rightarrow X$ by

$$\mathcal{B} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} = \begin{pmatrix} F(\psi) \\ H(\psi) \\ G(\psi) \end{pmatrix} \text{ for } \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \in X_{0+}.$$

Under the above definitions, we can formally rewrite system (1.1) as an abstract semilinear Cauchy problem with a non-densely defined operator on X :

$$\begin{cases} \frac{du(t)}{dt} = \mathcal{A}u(t) + \mathcal{B}u(t), \\ u(0) = \begin{pmatrix} 0 \\ 0 \\ \phi \end{pmatrix} \in X_{0+}. \end{cases} \tag{2.1}$$

Since u is the density of a population, we are interested in solutions of (2.1) such that $u(t) \in X_{0+}$, $t \geq 0$. Following Busenberg et al. (1991), we consider the following system which is equivalent to (2.1):

$$\begin{cases} \frac{du(t)}{dt} = (\mathcal{A} - \frac{1}{\epsilon}I)u(t) + \frac{1}{\epsilon}(I + \epsilon\mathcal{B})u(t), \\ u(0) = \begin{pmatrix} 0 \\ 0 \\ \phi \end{pmatrix} \in X_{0+}, \end{cases} \tag{2.2}$$

where ϵ is chosen so small that the operator $I + \epsilon\mathcal{B}$ maps X_{0+} into the positive cone of X , denoted by X_+ . It is easily shown that this choice of ϵ is possible for our system (2.1), since parameter functions G, F, H are assumed to be uniformly bounded. In the following, we mainly consider system (2.2) and for the sake of simplicity we use the following new notations:

$$\mathcal{A}_* = \mathcal{A} - \frac{1}{\epsilon}I, \quad \mathcal{B}_* = \frac{1}{\epsilon}(I + \epsilon\mathcal{B}).$$

Since the operator \mathcal{A}_* is not densely defined, we cannot apply the classical Hille–Yosida theory to solve (2.2) in the Banach space X . However, the operator \mathcal{A}_* can be proved to be a Hille–Yosida operator.

Lemma 2.2 \mathcal{A}_* is a closed linear operator with non-dense domain and the following holds: $\overline{D(\mathcal{A}_*)} = X_0$, \mathcal{A}_* satisfies the Hille–Yosida estimate such that for all $\lambda > -\frac{1}{\epsilon}$,

$$\|(\lambda I - \mathcal{A}_*)^{-1}\|_X \leq \frac{1}{\lambda + \frac{1}{\epsilon}} \tag{2.3}$$

and $(\lambda I - \mathcal{A}_*)^{-1}(X_+) \subset X_{0+}$ for $\lambda > 0$.

Proof Let us study the resolvent of operator \mathcal{A}_* , i.e.,

$$(\lambda I - \mathcal{A}_*) \begin{pmatrix} 0 \\ 0 \\ \varphi \end{pmatrix} = \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} \in X_+.$$

By the definition of \mathcal{A}_* ,

$$(\lambda I - \mathcal{A}_*) \begin{pmatrix} 0 \\ 0 \\ \varphi \end{pmatrix} = \begin{pmatrix} \varphi(a, 0) \\ \varphi(0, s) \\ \frac{\partial \varphi}{\partial a} + \frac{\partial \varphi}{\partial s} + (\lambda + \frac{1}{\epsilon}) \varphi \end{pmatrix},$$

we have

$$\frac{\partial \varphi}{\partial a} + \frac{\partial \varphi}{\partial s} + (\lambda + 1/\epsilon)\varphi = \phi(a, s), \tag{2.4}$$

$$\varphi(a, 0) = \alpha(a), \quad \varphi(0, s) = \eta(s). \tag{2.5}$$

By the method of characteristic lines, we obtain the solution of (2.4)-(2.5) as follows:

$$\varphi(a, s) = \begin{cases} \alpha(a - s)e^{-(\lambda+1/\epsilon)s} + \int_0^s e^{-\sigma(\lambda+1/\epsilon)}\phi(a - \sigma, s - \sigma)d\sigma, & a - s \geq 0, \\ \eta(s - a)e^{-(\lambda+1/\epsilon)a} + \int_0^a e^{-\sigma(\lambda+1/\epsilon)}\phi(a - \sigma, s - \sigma)d\sigma, & a - s < 0. \end{cases} \tag{2.6}$$

Thus,

$$(\lambda I - \mathcal{A}_*)^{-1} \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ \varphi(a, s) \end{pmatrix}$$

and

$$\begin{aligned} & \left\| (\lambda I - \mathcal{A}_*)^{-1} \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} \right\|_X = \|\varphi(a, s)\|_E \\ & \leq \left| \int_0^{a^+} \int_0^a \alpha(a - s)e^{-(\lambda+1/\epsilon)s} ds da \right| + \left| \int_0^{a^+} \int_0^a \int_0^s e^{-\sigma(\lambda+1/\epsilon)}\phi(a - \sigma, s - \sigma)d\sigma ds da \right| \\ & \quad + \left| \int_0^{s^+} \int_0^s \eta(s - a)e^{-(\lambda+1/\epsilon)a} da ds \right| + \left| \int_0^{s^+} \int_0^s \int_0^a e^{-\sigma(\lambda+1/\epsilon)}\phi(a - \sigma, s - \sigma)d\sigma da ds \right| \\ & \leq \int_0^{a^+} \int_0^a |\alpha(a - s)|e^{-(\lambda+1/\epsilon)s} ds da + \int_0^{a^+} \int_0^a \int_0^s e^{-\sigma(\lambda+1/\epsilon)}|\phi(a - \sigma, s - \sigma)|d\sigma ds da \\ & \quad + \int_0^{s^+} \int_0^s |\eta(s - a)|e^{-(\lambda+1/\epsilon)a} da ds + \int_0^{s^+} \int_0^s \int_0^a e^{-\sigma(\lambda+1/\epsilon)}|\phi(a - \sigma, s - \sigma)|d\sigma da ds \\ & \leq \frac{1}{\lambda + 1/\epsilon} \|\alpha\|_{L^1(0, a^+)} + \frac{1}{\lambda + 1/\epsilon} \|\eta\|_{L^1(0, s^+)} + \frac{1}{\lambda + 1/\epsilon} \|\phi\|_E \\ & \leq \frac{1}{\lambda + 1/\epsilon} \left\| \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} \right\|_X, \end{aligned} \tag{2.7}$$

which implies that

$$\|(\lambda I - \mathcal{A}_*)^{-1}\|_X \leq \frac{1}{\lambda + 1/\epsilon}$$

for $\lambda > -1/\epsilon$. Hence, \mathcal{A}_* is a Hille–Yosida operator with $M = 1$ and $\omega = -1/\epsilon < 0$. □

Thus, we can seek solutions in the weak sense: A function $u(t) \in C^1(0, T; X) \cup D(\mathcal{A}_*)$ is called a *classical solution* of the Cauchy problem (2.2) if it is satisfied for all $t \in [0, T)$. $u(t) \in C(0, T; X_0)$ is called an *integral solution* of (2.2) if $\int_0^t u(s)ds \in D(\mathcal{A}_*)$ for all $t \in [0, T)$ and

$$u(t) = u(0) + \mathcal{A}_* \int_0^t u(s)ds + \int_0^t \mathcal{B}_*u(s)ds, \tag{2.8}$$

which was introduced by Da Prato and Sinestrari (1987) and B enilan et al. (1988). It can be shown that an integral solution becomes a classical solution if $u(0) \in D(\mathcal{A}_*)$, $\mathcal{A}_*u(0) + \mathcal{B}_*u(0) \in \overline{D(\mathcal{A}_*)}$ (Thieme 1990). Thus, in what follows, we are mainly concerned with the integral solutions of (2.2).

Define the *part* \mathcal{A}_0 of \mathcal{A}_* in X_0 by

$$\mathcal{A}_0 = \mathcal{A}_* \text{ on } D(\mathcal{A}_0) = \left\{ \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \in D(\mathcal{A}_*) : \mathcal{A}_* \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \in X_0 \right\}.$$

Then, the following result holds (Thieme 1990; Magal and Ruan 2018).

Lemma 2.3 *For the part \mathcal{A}_0 , $\overline{D(\mathcal{A}_0)} = X_0$ holds and \mathcal{A}_0 generates a strongly continuous semigroup $\{\mathcal{F}_0(t)\}_{t \geq 0}$ on X_0 and $\mathcal{F}_0(X_{0+}) \subset X_{0+}$.*

Using the semigroup $\{\mathcal{F}_0(t)\}_{t \geq 0}$, we can formulate an extended variation of constants formula for (2.2), see Thieme (1990) and Magal and Ruan (2018).

Proposition 2.4 *A positive function $u(t) \in C(0, T; X_0)$ is an integral solution for (2.2) if and only if $u(t)$ is the positive continuous solution of the variation of constants formula on X_0 :*

$$u(t) = \mathcal{F}_0(t)u(0) + \lim_{\lambda \rightarrow \infty} \int_0^t \mathcal{F}_0(t-s)\lambda(\lambda - \mathcal{A}_*)^{-1}\mathcal{B}_*u(s)ds. \tag{2.9}$$

From Proposition 2.4, it is sufficient to solve the extended variation of constants formula (2.9) to obtain an integral solution of (2.2). It can be seen from Inaba (2006) that without any essential modification to the proof for the classical variation of constants formula, if \mathcal{B}_* is a locally Lipschitz continuous and bounded perturbation, we can apply the contraction mapping principle to show the existence of positive local solutions for the extended variation of constants formula (2.9). Since the norm of the local solution grows at most exponentially, a local solution can be extended to a global solution. Hence, we conclude that problem (2.2) has a unique global positive integral solution.

Next let $\{\mathcal{F}(t)\}_{t \geq 0}$ be a semigroup on X_0 induced by setting $\mathcal{F}(t)u(0) = u(t)$, where $u(t)$ is an integral solution of (2.2). Then, it follows that $\{\mathcal{F}(t)\}_{t \geq 0}$ is a C_0 -semigroup generated by the part $\mathcal{A}_* + \mathcal{B}_*$ in $X_0 = \overline{D(\mathcal{A}_*)}$. Let $\mathcal{B}'_*[u^*]$ denote the Fréchet derivative at u^* , $\omega_0(A)$ and $\omega_1(A)$ represent the growth bound and the essential growth bound of the semigroup generated by A , respectively. Thus, the principle of linearized stability for this evolution system (2.2) with non-densely defined generator can be stated as follows (Thieme 1990):

Proposition 2.5 *Let \mathcal{B}_* be continuously Fréchet differentiable in X_0 , and let u^* be a steady state of problem (2.2). If $\omega_0(\mathcal{A}_* + \mathcal{B}'_*[u^*]) < 0$, then for any $\omega > \omega_0(\mathcal{A}_* + \mathcal{B}'_*[u^*])$, there exist numbers $M > 0$ and $\delta > 0$ such that*

$$\|\mathcal{F}(t)u - u^*\| \leq Me^{\omega t} \|u - u^*\|$$

for all $u \in X_0$ with $\|u - u^*\| \leq \delta, t \geq 0$.

Corollary 2.6 *Suppose that $\omega_1(\mathcal{A}_* + \mathcal{B}'_*[u^*]) < 0$. If all eigenvalues of $\mathcal{A}_* + \mathcal{B}'_*[u^*]$ have strictly negative real part, then there exist $\omega < 0, \delta > 0$, and $M > 0$ such that*

$$\|\mathcal{F}(t)u - u^*\| \leq Me^{\omega t} \|u - u^*\|$$

for all $u \in X_0$ with $\|u - u^*\| \leq \delta, t \geq 0$. If at least one eigenvalue of $\mathcal{A}_* + \mathcal{B}'_*[u^*]$ has strictly positive real part, then u^* is an unstable steady state.

In the following sections, we consider two nonlinear double physiologically structured populations models where the birth and death rates are dependent on the total population, which reduce to the classic nonlinear single age-structured models if one of the structures disappears, see Chapter 4 of Webb (1984), where the models with nonlinear death rate were referred to as *semilinear* and those with nonlinear death and birth rates were referred to as *nonlinear*. In fact, they are both semilinear in the PDE sense, but we keep using the notations in Webb (1984) for consistence. Moreover, such nonlinear models are common in population dynamics, in particular when the birth rates β, χ and mortality rate μ depend on the total population. In the following text, we put letters S and N in the superscripts to denote the semilinear and nonlinear cases, respectively.

3 Semilinear Double Physiologically Structured Models

In this section, we consider the following first-order semilinear hyperbolic equation with two internal variables:

$$\begin{cases} u_t(t, a, s) + u_a(t, a, s) + u_s(t, a, s) = -\mu(a, s, P(t))u(t, a, s), \\ u(t, a, 0) = \int_0^{a^+} \int_0^{s^+} \chi(a, x, s)u(t, x, s)dsdx, \\ u(t, 0, s) = \int_0^{s^+} \int_0^{a^+} \beta(a, x, s)u(t, a, x)dadx, \\ u(0, a, s) = \phi(a, s), \\ P(t) = \int_0^{s^+} \int_0^{a^+} u(t, a, s)dads, \end{cases} \quad (3.1)$$

where $\mu(a, s, P)$ denotes the mortality rate of the population at age a with characteristic s and total population $P(t)$; $\beta(a, x, s)$ and $\chi(a, x, s)$ describe the boundary conditions and are like birth rates in population dynamics or transmission rates in epidemic dynamics.

Assumption 3.1 Assume that

- (i) $\beta : [0, a^+) \times [0, s^+) \times [0, s^+) \rightarrow [0, \infty)$ and $\chi : [0, a^+) \times [0, a^+) \times [0, s^+) \rightarrow [0, \infty)$ are nonnegative L^1 integrable and Lipschitz continuous;
- (ii) $\mu : [0, a^+) \times [0, s^+) \rightarrow [0, \infty)$ is nonnegative L^1 integrable and Lipschitz continuous; $\mu(a, s, P\psi) \geq \mu(a, s, 0)$ for all $(a, s) \in (0, a^+) \times (0, s^+)$ and $\psi \in D(A)$, denote $\underline{\mu} := \inf_{(a,s) \in (0,a^+) \times (0,s^+)} \mu(a, s, 0) > 0$; $\mu(a, s, P)$ is differentiable with respect to P and denote

$$\mu_1(\cdot, \cdot, P) := \frac{\partial \mu(\cdot, \cdot, P)}{\partial P};$$

Moreover, μ_1 is also L_1 integrable and Lipschitz continuous;

- (iii) The following limits

$$\lim_{h \rightarrow 0} \int_0^{s^+} |\beta(a, x, s + h) - \beta(a, x, s)| ds = 0 \tag{3.2}$$

and

$$\lim_{h \rightarrow 0} \int_0^{a^+} |\chi(a + h, x, s) - \chi(a, x, s)| da = 0 \tag{3.3}$$

hold uniformly for $(a, x) \in (0, a^+) \times (0, s^+)$ and $(x, s) \in (0, a^+) \times (0, s^+)$, respectively;

- (iv) There exist two nonnegative functions $\epsilon_1(x), \epsilon_2(x)$ such that $\beta(a, x, s) \geq \epsilon_1(x) > 0$ and $\chi(a, x, s) \geq \epsilon_2(x) > 0$ for all $a, s \in (0, a^+) \times (0, s^+)$, respectively;
- (v) In addition,

$$\begin{aligned} \sup_{(a,x) \in (0,a^+) \times (0,s^+)} \beta(a, x, s) &\leq \bar{\beta}(s), \quad \text{where } \bar{\beta} \in L^1((0, s^+)), \\ \sup_{(x,s) \in (0,a^+) \times (0,s^+)} \chi(a, x, s) &\leq \bar{\chi}(a), \quad \text{where } \bar{\chi} \in L^1((0, a^+)). \end{aligned}$$

These assumptions and Lemma 2.2 guarantee the global existence of the integral solutions, see Thieme (1990). Thus, in what follows we mainly focus on the existence

and stability of the nontrivial steady states. Suppose that $\begin{pmatrix} 0 \\ 0 \\ \hat{\psi} \end{pmatrix}$ is a steady state, i.e.,

$$\mathcal{A} \begin{pmatrix} 0 \\ 0 \\ \hat{\psi} \end{pmatrix} + \mathcal{B} \begin{pmatrix} 0 \\ 0 \\ \hat{\psi} \end{pmatrix} = 0,$$

where

$$\mathcal{A} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} -\psi(a, 0) \\ -\psi(0, s) \\ -\psi_a - \psi_s \end{pmatrix}, \quad \mathcal{B} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} F(\psi) \\ H(\psi) \\ G(\psi) \end{pmatrix},$$

in which

$$F(\psi)(a) = \int_0^{a^+} \int_0^{s^+} \chi(a, x, s) \psi(x, s) ds dx, \tag{3.4}$$

$$H(\psi)(s) = \int_0^{s^+} \int_0^{a^+} \beta(a, x, s) \psi(a, x) da dx, \tag{3.5}$$

$$G(\psi)(a, s) = -\mu(a, s, P\psi) \psi(a, s), \quad P\psi := \int_0^{s^+} \int_0^{a^+} \psi(a, s) da ds. \tag{3.6}$$

3.1 Existence of Nontrivial Steady States

In this subsection, we study the existence of the nontrivial steady state $\hat{\psi} \neq 0$. From the definition, $\hat{\psi}$ satisfies the following equations:

$$\begin{cases} \psi_a + \psi_s + \mu(a, s, P\psi) \psi = 0 \\ \psi(a, 0) = F(\psi)(a) \\ \psi(0, s) = H(\psi)(s) \\ P\psi = \int_0^{a^+} \int_0^{s^+} \psi(a, s) ds da. \end{cases} \tag{3.7}$$

Solving the problem, we obtain

$$\hat{\psi}(a, s) = \begin{cases} \hat{\psi}(a - s, 0) \Pi_{\hat{P}}(a, s, s), & a - s \geq 0, \\ \hat{\psi}(0, s - a) \Pi_{\hat{P}}(a, s, a), & a - s < 0, \end{cases} \tag{3.8}$$

where $\Pi_{\hat{P}}(a, s, \sigma) = e^{-\int_0^\sigma \mu(a-\tau, s-\tau, \hat{P}) d\tau}$ and $\hat{P} = P\hat{\psi}$. Denote $\hat{\alpha}(s) = \hat{\psi}(0, s)$, $\hat{\eta}(a) = \hat{\psi}(a, 0)$. Plugging the solution into the boundary conditions, we get

$$\begin{aligned} \hat{\eta}(a) &= \int_0^{a^+} \int_0^x \chi(a, x, s) \hat{\eta}(x - s) \Pi_{\hat{P}}(x, s, s) ds dx \\ &\quad + \int_0^{s^+} \int_0^s \chi(a, x, s) \hat{\alpha}(s - x) \Pi_{\hat{P}}(x, s, x) dx ds, \end{aligned}$$

$$\hat{\alpha}(s) = \int_0^{s^+} \int_0^x \beta(a, x, s) \hat{\alpha}(x - a) \Pi_{\hat{p}}(a, x, a) da dx + \int_0^{a^+} \int_0^a \beta(a, x, s) \hat{\eta}(a - x) \Pi_{\hat{p}}(a, x, x) dx da.$$

Define $\Omega_0^S : \mathbb{R} \times L^1(0, a^+) \times L^1(0, s^+) \rightarrow \mathbb{R} \times L^1(0, a^+) \times L^1(0, s^+)$ by

$$\Omega_0^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} = \left(\Omega_{10}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix}, \Omega_{20}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix}, \Omega_{30}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} \right), \tag{3.9}$$

where

$$\begin{aligned} \Omega_{10}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} &= \int_0^{a^+} \int_0^a \hat{\eta}(a - s) \Pi_{\hat{p}}(a, s, s) ds da + \int_0^{s^+} \int_0^s \hat{\alpha}(s - a) \Pi_{\hat{p}}(a, s, a) da ds, \\ \Omega_{20}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} &= \int_0^{a^+} \int_0^x \chi(a, x, s) \hat{\eta}(x - s) \Pi_{\hat{p}}(x, s, s) ds dx + \int_0^{s^+} \int_0^s \chi(a, x, s) \hat{\alpha}(s - x) \Pi_{\hat{p}}(x, s, x) dx ds, \\ \Omega_{30}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} &= \int_0^{s^+} \int_0^x \beta(a, x, s) \hat{\alpha}(x - a) \Pi_{\hat{p}}(a, x, a) da dx + \int_0^{a^+} \int_0^a \beta(a, x, s) \hat{\eta}(a - x) \Pi_{\hat{p}}(a, x, x) dx da. \end{aligned}$$

It is obvious that Ω_0^S is bounded by Assumption 3.1-(v) and $\Omega_0^S \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$. Denote the positive cone of $\mathbb{R} \times L^1(0, a^+) \times L^1(0, s^+)$ by Y_+ , i.e., $Y_+ := \mathbb{R}_+ \times L_+^1(0, a^+) \times L_+^1(0, s^+)$. Now the existence of a nontrivial steady state is equivalent to the existence of a nontrivial fixed point of the map Ω_0^S . Note that Ω_0^S is a nonlinear operator, we cannot apply the theory in the linear case (Kang et al. 2020) to this one directly. Fortunately, we have a fixed point theorem of Inaba (1990), which can be regarded as a special case of the Krasnoselskii’s theorem, see (Krasnoselskii 1964, Theorem 4.11). The theorem is described as follows:

Theorem 3.2 (Inaba 1990) *Let E be a real Banach space and E_+ be its positive cone. Let Ψ be a positive operator from E_+ to itself and $T := \Psi'[0]$ be its Fréchet derivative at 0. If*

- (i) $\Psi(0) = 0$;
- (ii) Ψ is compact and bounded;
- (iii) T has a positive eigenvector $v_0 \in E_+ \setminus \{0\}$ associated with an eigenvalue $\lambda_0 > 1$;
- (iv) T has no eigenvector in E_+ associated with the eigenvalue 1,

then Ψ has at least one nontrivial fixed point in E_+ .

In case where T is a majorant of Ψ (that is, T is a linear operator such that $\Psi(\phi) \leq T\phi$ for any $\phi \in E_+$), the following theorem also holds (see Inaba 2014, Proposition 7.8).

Theorem 3.3 (Inaba 2014) *Let E be a real Banach space and E_+ be its positive cone. Let Ψ be a positive operator from E_+ to itself and T be its compact and semi-non-supporting majorant. Then, Ψ has no trivial fixed point in E_+ provided $r(T) \leq 1$.*

By some computations, we obtain the Fréchet derivative of Ω_0^S at $(0, 0, 0)^T$, where T represents the transpose,

$$T^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} := \Omega_0^{S'}(0, 0, 0)^T \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} = \begin{pmatrix} 0 \frac{\partial \Omega_{10}^S}{\partial \eta}(0, 0, 0)^T & \frac{\partial \Omega_{10}^S}{\partial \alpha}(0, 0, 0)^T \\ 0 \frac{\partial \Omega_{20}^S}{\partial \eta}(0, 0, 0)^T & \frac{\partial \Omega_{10}^S}{\partial \alpha}(0, 0, 0)^T \\ 0 \frac{\partial \Omega_{30}^S}{\partial \eta}(0, 0, 0)^T & \frac{\partial \Omega_{30}^S}{\partial \alpha}(0, 0, 0)^T \end{pmatrix} \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}, \tag{3.10}$$

where

$$T^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} = \left(T_1^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}, T_2^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} \right),$$

in which

$$\begin{aligned} T_1^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} &= \int_0^{a^+} \int_0^a \eta(a-s) \Pi_0(a, s, s) ds da \\ &\quad + \int_0^{s^+} \int_0^s \alpha(s-a) \Pi_0(a, s, a) dad s, \\ T_2^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} &= \int_0^{a^+} \int_0^x \chi(a, x, s) \eta(x-s) \Pi_0(x, s, s) ds dx \\ &\quad + \int_0^{s^+} \int_0^s \chi(a, x, s) \alpha(s-x) \Pi_0(x, s, x) dx ds, \\ T_3^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} &= \int_0^{a^+} \int_0^a \beta(a, x, s) \eta(a-x) \Pi_0(a, x, x) dx da \end{aligned}$$

$$+ \int_0^{s^+} \int_0^x \beta(a, x, s) \alpha(x - a) \Pi_0(a, x, a) da dx.$$

By Assumption 3.1-(ii), it is easy to check that $\Omega_0^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} \leq T^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}$, which implies that T^S is a majorant of Ω_0^S .

Proposition 3.4 *Let Ω_0^S and T^S be defined by (3.9) and (3.10), respectively.*

(ii) *If $r(T^S) \leq 1$, then Ω_0^S has only the trivial fixed point $\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$ in Y_+ ;*

(i) *If $r(T^S) > 1$, then Ω_0^S has at least one nontrivial fixed point $\begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix}$ in $Y_+ \setminus \{0\}$.*

Proof Note that Ω_0^S is bounded. First let us prove that Ω_0^S is compact. Consider a bounded set $K \subset \mathbb{R} \times L^1(0, a^+) \times L^1(0, s^+)$, note that

$$\left| \Omega_{10}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} \right| \leq \frac{1}{\underline{\mu}} \left(\|\hat{\eta}\|_{L^1(0, a^+)} + \|\hat{\alpha}\|_{L^1(0, s^+)} \right),$$

which is uniformly bounded in K . It follows that $\Omega_{10}^S : K \rightarrow \mathbb{R}$ is compact. We have

$$\begin{aligned} & \left\| \Omega_{20}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} (a+h) - \Omega_{20}^S \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} (a) \right\|_{L^1(0, a^+)} \\ & \leq \left| \int_0^{a^+} \int_0^{a^+} \int_0^x \chi(a+h, x, s) \hat{\eta}(x-s) \Pi_{\hat{p}}(x, s, s) ds dx da \right. \\ & \quad + \int_0^{a^+} \int_0^{s^+} \int_0^s \chi(a+h, x, s) \hat{\alpha}(s-x) \Pi_{\hat{p}}(x, s, x) dx ds da \\ & \quad - \int_0^{a^+} \int_0^{a^+} \int_0^x \chi(a, x, s) \hat{\eta}(x-s) \Pi_{\hat{p}}(x, s, s) ds dx da \\ & \quad \left. + \int_0^{a^+} \int_0^{s^+} \int_0^s \chi(a, x, s) \hat{\alpha}(s-x) \Pi_{\hat{p}}(x, s, x) dx ds da \right| \\ & \leq \int_0^{a^+} \int_0^{a^+} \int_0^x |\chi(a+h, x, s) - \chi(a, x, s)| \hat{\eta}(x-s) \Pi_{\hat{p}}(x, s, s) ds dx da \\ & \quad + \int_0^{a^+} \int_0^{s^+} \int_0^s |\chi(a+h, x, s) - \chi(a, x, s)| \hat{\alpha}(s-x) \Pi_{\hat{p}}(x, s, x) dx ds da \\ & \rightarrow 0 \text{ as } h \rightarrow 0 \end{aligned} \tag{3.11}$$

by Assumption 3.1-(iii). Similarly, we can show the convergence for Ω_{30}^S , which implies that Ω_0^S is a compact operator by Kolmogorov compactness criterion. Moreover, we can show that T^S is also compact by using similar steps.

Next given $r(T^S) > 1$, we show that T^S is semi-nonsupporting via proving that every proper eigenvector corresponding to the proper eigenvalue $r(T^S)$ lying in Y_+ is a quasi-interior point of Y_+ and every proper eigenvector corresponding to $r(T^S)$ lying in Y_+^* is strictly positive (see Proposition A.2 and the definitions of semi-nonsupporting, proper eigenvalue (eigenvector) and quasi-interior point in “Appendix”). If $\begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} = \begin{pmatrix} P \\ 0 \\ 0 \end{pmatrix}$ with $P > 0$, then $T^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$. It follows that

$\begin{pmatrix} P \\ 0 \\ 0 \end{pmatrix}$ is not a proper eigenvector corresponding to the proper eigenvalue $r(T^S)$, otherwise $\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} = T^S \begin{pmatrix} P \\ 0 \\ 0 \end{pmatrix} = r(T^S) \begin{pmatrix} P \\ 0 \\ 0 \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$ is a contradiction. Thus, we only consider the points in Y_+ which have the form of $\begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}$ with $\begin{pmatrix} \eta \\ \alpha \end{pmatrix} \neq \begin{pmatrix} 0 \\ 0 \end{pmatrix}$.

It is easy to see that $T_1^S : Y_+ \rightarrow \mathbb{R}$ is positive for all $\begin{pmatrix} \eta \\ \alpha \end{pmatrix} \in L_+^1(0, a^+) \times L_+^1(0, s^+) \setminus \left\{ \begin{pmatrix} 0 \\ 0 \end{pmatrix} \right\}$ and thus nonsupporting. Noting that $T_i^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}$ for $i = 2, 3$ do not contain the terms of P . Thus, we can reduce it into a two-dimensional operator \tilde{T}^S , i.e.,

$$\tilde{T}^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} = \left(T_2^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right).$$

Define a positive functional $\tilde{\mathcal{F}} = (\mathcal{F}_2, \mathcal{F}_3)$ by

$$\begin{aligned} \left\langle \mathcal{F}_2, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle &:= \int_0^{a^+} \int_0^x \epsilon_1(x) \Pi_0(x, s, s) \eta(x - s) ds dx \\ &\quad + \int_0^{s^+} \int_0^s \epsilon_1(x) \Pi_0(x, s, x) \alpha(s - x) dx ds, \\ \left\langle \mathcal{F}_3, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle &:= \int_0^{s^+} \int_0^x \epsilon_2(x) \Pi_0(a, x, a) \alpha(x - a) da dx \\ &\quad + \int_0^{a^+} \int_0^a \epsilon_2(x) \Pi_0(a, x, x) \eta(a - x) dx da. \end{aligned} \tag{3.12}$$

From Assumption 3.1-(iv), $\tilde{\mathcal{F}}$ is a strictly positive functional and we have

$$\tilde{T}^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} = \left(T_2^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right) \geq \left(\left\langle \mathcal{F}_2, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle e_2, \left\langle \mathcal{F}_3, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle e_3 \right), \tag{3.13}$$

where $\begin{pmatrix} e_2 \\ e_3 \end{pmatrix} \equiv 1$ is a quasi-interior point in $L^1(0, a^+) \times L^1(0, s^+)$. Moreover, we have

$$\begin{aligned} (\tilde{T}^S)^2 \begin{pmatrix} \eta \\ \alpha \end{pmatrix} &= \tilde{T}^S \left(T_2^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right) \\ &= \left(T_2^S \left(T_2^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right), T_3^S \left(T_2^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right) \right), \end{aligned}$$

where

$$\begin{aligned} T_i^S \left(T_2^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right) &\geq \left\langle \mathcal{F}_i, \left(T_2^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix}, T_3^S \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right) \right\rangle e_i \\ &\geq \left\langle \mathcal{F}_i, \left(\left\langle \mathcal{F}_2, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle e_2, \left\langle \mathcal{F}_3, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle e_3 \right) \right\rangle e_i \\ &\geq \min \left\{ \left\langle \mathcal{F}_2, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle, \left\langle \mathcal{F}_3, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle \right\} \left\langle \mathcal{F}_i, \begin{pmatrix} e_2 \\ e_3 \end{pmatrix} \right\rangle e_i \\ &:= \min \left\langle \tilde{\mathcal{F}}, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle \left\langle \mathcal{F}_i, \begin{pmatrix} e_2 \\ e_3 \end{pmatrix} \right\rangle e_i, \quad i = 2, 3. \end{aligned}$$

It follows that

$$\begin{aligned} (\tilde{T}^S)^2 \begin{pmatrix} \eta \\ \alpha \end{pmatrix} &\geq \min \left\langle \tilde{\mathcal{F}}, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle \left(\left\langle \mathcal{F}_2, \begin{pmatrix} e_2 \\ e_3 \end{pmatrix} \right\rangle e_2, \left\langle \mathcal{F}_3, \begin{pmatrix} e_2 \\ e_3 \end{pmatrix} \right\rangle e_3 \right) \\ &\geq \min \left\langle \tilde{\mathcal{F}}, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle \min \left\langle \tilde{\mathcal{F}}, \begin{pmatrix} e_2 \\ e_3 \end{pmatrix} \right\rangle \begin{pmatrix} e_2 \\ e_3 \end{pmatrix}. \end{aligned}$$

By induction for any integer n we have

$$(\tilde{T}^S)^{n+1} \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \geq \min \left\langle \tilde{\mathcal{F}}, \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle \left[\min \left\langle \tilde{\mathcal{F}}, \begin{pmatrix} e_2 \\ e_3 \end{pmatrix} \right\rangle \right]^n \begin{pmatrix} e_2 \\ e_3 \end{pmatrix}.$$

Then, we obtain

$$\left\langle \mathcal{F}, (\tilde{T}^S)^n \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \right\rangle > 0, n \geq 1$$

for every pair

$$\begin{pmatrix} \eta \\ \alpha \end{pmatrix} \in L^1_+(0, a^+) \times L^1_+(0, s^+) \setminus \left\{ \begin{pmatrix} 0 \\ 0 \end{pmatrix} \right\}, \mathcal{F} \in (L^1_+(0, a^+))^* \times (L^1_+(0, s^+))^* \setminus \left\{ \begin{pmatrix} 0 \\ 0 \end{pmatrix} \right\};$$

that is, we know that \tilde{T}^S is a nonsupporting operator, thus semi-nonsupporting, which implies that condition (A) holds in Proposition A.2 in ‘‘Appendix’’ for \tilde{T}^S . It follows that

$$\begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} = [r(T^S)]^{-1} T^S \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} \text{ is a quasi-interior point and } \mathcal{F} \text{ is strictly positive for } \begin{pmatrix} \eta \\ \alpha \end{pmatrix} \neq \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

implies that condition (A) also holds for T^S . In summary, T^S is a semi-nonsupporting operator.

Now we prove (i). Since Ω_0^S is a positive operator from the positive cone Y_+ into itself and T^S is the positive linear majorant of Ω_0^S , we can apply Theorem 3.3 to conclude that Ω_0^S has no nontrivial fixed point in Y_+ provided $r(T^S) \leq 1$.

Next, we prove (ii). Conditions (i) and (ii) of Theorem 3.2 follow from the above arguments. We apply the theory of semi-nonsupporting operators (see Inaba 2014 or Marek 1970) to prove that $r(T^S) > 1$ is an eigenvalue of operator T^S with a corresponding positive nonzero eigenvector and T^S does not has any eigenvector associated with eigenvalue 1. Hence, conditions (iii) and (iv) of Theorem 3.2 follow and, consequently, Ω_0^S has at least one nontrivial fixed point in Y_+ . This completes the proof. \square

The existence of a nontrivial fixed point of Ω_0^S implies the existence of a nontrivial steady state solution $\hat{\psi} \in D(A) \setminus \{0\}$ of system (3.1). In conclusion, from Proposition 3.4, the following theorem can be obtained as one the main results of this paper.

Proposition 3.5 *Let T^S be defined in (3.10).*

- (i) *If $r(T^S) \leq 1$, then system (3.1) has only the trivial steady state 0 in $D(A)$;*
- (ii) *If $r(T^S) > 1$, then system (3.1) has at least one nontrivial steady state $\hat{\psi}$ in $D(A) \setminus \{0\}$.*

3.2 Stability

It is easy to see that

$$(G'(\hat{\psi})\psi)(a, s) = -\mu_1(a, s, P\hat{\psi})P\psi\hat{\psi}(a, s) - \mu(a, s, P\hat{\psi})\psi(a, s).$$

Now define

$$\mathcal{X}_1 \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} 0 \\ 0 \\ -\mu(a, s, P\hat{\psi})\psi \end{pmatrix} \text{ and } \mathcal{X}_2 \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} F(\psi) \\ H(\psi) \\ C(\psi) \end{pmatrix},$$

where $C(\psi) := -\mu_1(\cdot, \cdot, \hat{P})P\psi\hat{\psi}$, $\hat{P} = P\hat{\psi}$. Observe that C is a compact operator in E , thus \mathcal{X}_2 is also compact in X . By the method of characteristic lines, we see that $\mathcal{A} + \mathcal{X}_1$ generates a nilpotent semigroup and its perturbed semigroup by the compact operator \mathcal{X}_2 is eventually compact. Hence,

$$\omega_1(\mathcal{A} + \mathcal{B}'[\hat{\psi}]) = \omega_1(\mathcal{A} + \mathcal{X}_1 + \mathcal{X}_2) = \omega_1(\mathcal{A} + \mathcal{X}_1) = -\infty.$$

It follows that the stability of $\hat{\psi}$ is determined by the eigenvalues of $\mathcal{A} + \mathcal{B}'[\hat{\psi}]$. Accordingly, let $\lambda \in \mathbb{C}$ and let

$$\hat{B}^S \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} = \lambda \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \text{ for } \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \in D(\mathcal{A}) \text{ and } \psi \neq 0,$$

where $\hat{B}^S := \mathcal{A} + \mathcal{B}'[\hat{\psi}]$.

In the following, we study the stability of the steady state. From the definition of \hat{B}^S , we obtain

$$\begin{cases} \psi_a + \psi_s + \lambda\psi + \mu(a, s, \hat{P})\psi + \mu_1(a, s, \hat{P})P\psi\hat{\psi} = 0 \\ \psi(a, 0) = F(\psi)(a) \\ \psi(0, s) = H(\psi)(s) \\ P\psi = \int_0^{a^+} \int_0^{s^+} \psi(a, s)dsda, \end{cases} \tag{3.14}$$

where $\hat{P} = P\hat{\psi}$. Solving the problem, we get

$$\psi(a, s) = \begin{cases} \psi(a-s, 0)e^{-\lambda s} \Pi_{\hat{P}}(a, s, s) - \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma)P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma)d\sigma, & a-s \geq 0, \\ \psi(0, s-a)e^{-\lambda a} \Pi_{\hat{P}}(a, s, a) - \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma)P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma)d\sigma, & a-s < 0, \end{cases} \tag{3.15}$$

where $\Pi_{\hat{P}}(a, s, \sigma) = e^{-\int_0^\sigma \mu(a-\tau, s-\tau, \hat{P})d\tau}$. Denote $\alpha(s) = \psi(0, s)$, $\eta(a) = \psi(a, 0)$.

First we express $P\psi$ in terms of α and η . By the definition of $P\psi$, we obtain

$$\begin{aligned} P\psi &= \int_0^{a^+} \int_0^a \eta(a-s)e^{-\lambda s} \Pi_{\hat{P}}(a, s, s)dsda \\ &\quad - \int_0^{a^+} \int_0^a \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma)P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma)d\sigma dsda \\ &\quad + \int_0^{s^+} \int_0^s \alpha(s-a)e^{-\lambda a} \Pi_{\hat{P}}(a, s, a)dads \\ &\quad - \int_0^{s^+} \int_0^s \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma)P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma)d\sigma dads, \end{aligned}$$

which implies that

$$\begin{aligned}
 P\psi & \left[1 + \int_0^{a^+} \int_0^a \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma ds da \right. \\
 & \left. + \int_0^{s^+} \int_0^s \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma dads \right] \\
 & = \int_0^{a^+} \int_0^a \eta(a - s) e^{-\lambda s} \Pi_{\hat{P}}(a, s, s) ds da + \int_0^{s^+} \int_0^s \alpha(s - a) e^{-\lambda a} \Pi_{\hat{P}}(a, s, a) dad s \\
 & := B_\lambda(\eta, \alpha)
 \end{aligned} \tag{3.16}$$

where $B_\lambda : L^1(0, a^+) \times L^1(0, s^+) \rightarrow \mathbb{R}$ is a functional in $L^1(0, a^+) \times L^1(0, s^+)$ for all $\lambda \in \mathbb{R}$. Denote

$$\begin{aligned}
 A(\lambda) & = \int_0^{a^+} \int_0^a \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma ds da \\
 & \quad + \int_0^{s^+} \int_0^s \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma dads.
 \end{aligned} \tag{3.17}$$

It follows that $P\psi = (1 + A(\lambda))^{-1} B_\lambda(\eta, \alpha)$. Now plugging (3.15) into the boundary conditions, we obtain

$$\begin{aligned}
 \eta(a) & = \int_0^{a^+} \int_0^x \chi(a, x, s) \eta(x - s) e^{-\lambda s} \Pi_{\hat{P}}(x, s, s) ds dx \\
 & \quad - P\psi \int_0^{a^+} \int_0^x \int_0^s \chi(a, x, s) e^{-\lambda\sigma} \Pi_{\hat{P}}(x, s, \sigma) \\
 & \quad \mu_1(x - \sigma, s - \sigma, \hat{P}) \hat{\psi}(x - \sigma, s - \sigma) d\sigma ds dx \\
 & \quad + \int_0^{s^+} \int_0^s \chi(a, x, s) \alpha(s - x) e^{-\lambda x} \Pi_{\hat{P}}(x, s, x) dx ds \\
 & \quad - P\psi \int_0^{s^+} \int_0^s \int_0^x \chi(a, x, s) e^{-\lambda\sigma} \Pi_{\hat{P}}(x, s, \sigma) \\
 & \quad \mu_1(x - \sigma, s - \sigma, \hat{P}) \hat{\psi}(x - \sigma, s - \sigma) d\sigma dx ds, \\
 \alpha(s) & = \int_0^{s^+} \int_0^x \beta(a, x, s) \alpha(x - a) e^{-\lambda a} \Pi_{\hat{P}}(a, x, a) dad x \\
 & \quad - P\psi \int_0^{s^+} \int_0^x \int_0^a \beta(a, x, s) e^{-\lambda\sigma} \Pi_{\hat{P}}(a, x, \sigma) \\
 & \quad \mu_1(a - \sigma, x - \sigma, \hat{P}) \hat{\psi}(a - \sigma, x - \sigma) d\sigma dad x \\
 & \quad + \int_0^{a^+} \int_0^a \beta(a, x, s) \eta(a - x) e^{-\lambda x} \Pi_{\hat{P}}(a, x, x) dx da
 \end{aligned}$$

$$\begin{aligned}
 & -P\psi \int_0^{a^+} \int_0^a \int_0^x \beta(a, x, s)e^{-\lambda\sigma} \Pi_{\hat{p}}(a, x, \sigma) \\
 & \mu_1(a - \sigma, x - \sigma, \hat{P})\hat{\psi}(a - \sigma, x - \sigma)d\sigma dx da. \tag{3.18}
 \end{aligned}$$

Now define

$$\begin{aligned}
 \Omega_{1\lambda}^S(\eta, \alpha)(a) &= \int_0^{a^+} \int_0^x \chi(a, x, s)\eta(x - s)e^{-\lambda s} \Pi_{\hat{p}}(x, s, s)dsdx \\
 & \quad + \int_0^{s^+} \int_0^s \chi(a, x, s)\alpha(s - x)e^{-\lambda x} \Pi_{\hat{p}}(x, s, x)dxds, \\
 \Omega_{2\lambda}^S(\eta, \alpha)(s) &= \int_0^{s^+} \int_0^x \beta(a, x, s)\alpha(x - a)e^{-\lambda a} \Pi_{\hat{p}}(a, x, a)dadx \\
 & \quad + \int_0^{a^+} \int_0^a \beta(a, x, s)\eta(a - x)e^{-\lambda x} \Pi_{\hat{p}}(a, x, x)dx da, \\
 K_{1\lambda}^S(a) &= \int_0^{a^+} \int_0^x \int_0^s \chi(a, x, s)e^{-\lambda\sigma} \Pi_{\hat{p}}(x, s, \sigma) \\
 & \quad \mu_1(x - \sigma, s - \sigma, \hat{P})\hat{\psi}(x - \sigma, s - \sigma)d\sigma dsdx, \\
 K_{2\lambda}^S(a) &= \int_0^{s^+} \int_0^s \int_0^x \chi(a, x, s)e^{-\lambda\sigma} \Pi_{\hat{p}}(x, s, \sigma) \\
 & \quad \mu_1(x - \sigma, s - \sigma, \hat{P})\hat{\psi}(x - \sigma, s - \sigma)d\sigma dxds, \\
 K_{3\lambda}^S(s) &= \int_0^{s^+} \int_0^x \int_0^a \beta(a, x, s)e^{-\lambda\sigma} \Pi_{\hat{p}}(a, x, \sigma) \\
 & \quad \mu_1(a - \sigma, x - \sigma, \hat{P})\hat{\psi}(a - \sigma, x - \sigma)d\sigma dadx, \\
 K_{4\lambda}^S(s) &= \int_0^{a^+} \int_0^a \int_0^x \beta(a, x, s)e^{-\lambda\sigma} \Pi_{\hat{p}}(a, x, \sigma) \\
 & \quad \mu_1(a - \sigma, x - \sigma, \hat{P})\hat{\psi}(a - \sigma, x - \sigma)d\sigma dx da.
 \end{aligned}$$

Thus, the two equations in (3.18) become

$$\begin{cases} \eta(a) = \Omega_{1\lambda}^S(\eta, \alpha)(a) - (1 + A(\lambda))^{-1} B_\lambda(\eta, \alpha)(K_{1\lambda}^S(a) + K_{2\lambda}^S(a)), \\ \alpha(s) = \Omega_{2\lambda}^S(\eta, \alpha)(s) - (1 + A(\lambda))^{-1} B_\lambda(\eta, \alpha)(K_{3\lambda}^S(s) + K_{4\lambda}^S(s)). \end{cases} \tag{3.19}$$

Next, define

$$\Omega_\lambda^S := (\Omega_{1\lambda}^S, \Omega_{2\lambda}^S)$$

and

$$M_\lambda^S(a) = (1 + A(\lambda))^{-1}(K_{1\lambda}^S(a) + K_{2\lambda}^S(a)), \quad V_\lambda^S(s) = (1 + A(\lambda))^{-1}(K_{3\lambda}^S(s) + K_{4\lambda}^S(s)).$$

Then, it follows that

$$\begin{pmatrix} \eta \\ \alpha \end{pmatrix} = \left(\Omega_\lambda^S - \begin{pmatrix} M_\lambda^S(a) \\ V_\lambda^S(s) \end{pmatrix} B_\lambda \right) \begin{pmatrix} \eta \\ \alpha \end{pmatrix}.$$

Denote

$$\Theta_\lambda^S := \Omega_\lambda^S - \begin{pmatrix} M_\lambda^S(a) \\ V_\lambda^S(s) \end{pmatrix} B_\lambda.$$

Since $M_\lambda^S(a)B_\lambda$ and $V_\lambda^S(s)B_\lambda$ are compact by the L^1 compactness criterion and Ω_λ^S is compact under Assumption 3.1-(iii), Θ_λ^S is also compact in $L^1(0, a^+) \times L^1(0, s^+)$ for all $\lambda \in \mathbb{C}$.

In addition, under Assumption 3.1-(iv), it is easy to show that Ω_λ^S and $M_\lambda^S(a)B_\lambda$, $V_\lambda^S(s)B_\lambda$ are nonsupporting, then Θ_λ^S is also nonsupporting in $L^1(0, a^+) \times L^1(0, s^+)$ for all $\lambda \in \mathbb{R}$. Thus, we have the following results (see Kang et al. 2020).

Proposition 3.6 *We have the following statements:*

- (i) $\Gamma^S := \{\lambda \in \mathbb{C} : 1 \in \sigma(\Theta_\lambda^S)\} = \{\lambda \in \mathbb{C} : 1 \in \sigma_P(\Theta_\lambda^S)\}$, where $\sigma(A)$ and $\sigma_P(A)$ denote the spectrum and point spectrum of the operator A , respectively;
- (ii) There exists a unique real number $\lambda_0^S \in \Gamma^S$ such that $r(\Theta_{\lambda_0^S}^S) = 1$ and $\lambda_0^S > 0$ if $r(\Theta_0^S) > 1$; $\lambda_0^S = 0$ if $r(\Theta_0^S) = 1$; and $\lambda_0^S < 0$ if $r(\Theta_0^S) < 1$;
- (iii) $\lambda_0^S > \sup\{\text{Re}\lambda : \lambda \in \Gamma^S \setminus \{\lambda_0^S\}\}$;
- (iv) λ_0^S is the dominant eigenvalue of \hat{B}^S , i.e., λ_0^S is greater than all real parts of the eigenvalues of \hat{B}^S . Moreover, it is a simple eigenvalue of \hat{B}^S ;
- (v) $\{\lambda \in \mathbb{C} : \lambda \in \rho(\hat{B}^S)\} = \{\lambda \in \mathbb{C} : 1 \in \rho(\Theta_\lambda^S)\}$, where $\rho(A)$ denotes the resolvent set of A ;
- (vi) $\lambda_0^S = s(\hat{B}^S) := \sup\{\text{Re}\lambda : \lambda \in \sigma(\hat{B}^S)\}$.

Next, we can state the result on the stability of the steady state.

Theorem 3.7 *The steady state $\hat{\psi} \neq 0$ is locally exponentially asymptotically stable if $r(\Theta_0^S) < 1$ and unstable if $r(\Theta_0^S) > 1$.*

Remark 3.8 When $\hat{\psi} = 0$, it reduces to the linear case considered in Kang et al. (2020) and $\Omega_\lambda^S = F_\lambda$.

4 Nonlinear Double Physiologically Structured Models

In this section, we consider the following nonlinear equation with two internal variables

$$\begin{cases} u_t(t, a, s) + u_a(t, a, s) + u_s(t, a, s) = -\mu(a, s, P(t))u(t, a, s) \\ u(t, a, 0) = \int_0^{a^+} \int_0^{s^+} \chi(a, x, s, P(t))u(t, x, s) ds dx \\ u(t, 0, s) = \int_0^{s^+} \int_0^{a^+} \beta(a, x, s, P(t))u(t, a, x) da dx \\ u(0, a, s) = \phi(a, s) \\ P(t) = \int_0^{s^+} \int_0^{a^+} u(t, a, s) da ds \end{cases} \quad (4.1)$$

Assume that μ , χ , and β are differentiable with respect to P , and denote their derivatives by $\mu_1(\cdot, \cdot, P)$, $\chi_1(\cdot, \cdot, \cdot, P)$ and $\beta_1(\cdot, \cdot, \cdot, P)$, respectively. Suppose that $\begin{pmatrix} 0 \\ 0 \\ \hat{\psi} \end{pmatrix}$ is a steady state, i.e.,

$$\mathcal{A} \begin{pmatrix} 0 \\ 0 \\ \hat{\psi} \end{pmatrix} + \mathcal{B} \begin{pmatrix} 0 \\ 0 \\ \hat{\psi} \end{pmatrix} = 0,$$

where

$$\mathcal{A} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} -\psi(a, 0) \\ -\psi(0, s) \\ -\psi_a - \psi_s \end{pmatrix} \text{ and } \mathcal{B} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} F(\psi) \\ H(\psi) \\ G(\psi) \end{pmatrix},$$

in which

$$\begin{aligned} F(\psi)(a) &= \int_0^{a^+} \int_0^{s^+} \chi(a, x, s, P\psi)\psi(x, s) ds dx, \\ H(\psi)(s) &= \int_0^{s^+} \int_0^{a^+} \beta(a, x, s, P\psi)\psi(a, x) da dx, \\ G(\psi)(a, s) &= -\mu(a, s, P\psi)\psi(a, s), \end{aligned}$$

where $P\psi := \int_0^{s^+} \int_0^{a^+} \psi(a, s) da ds$. Further, we make the following assumption.

Assumption 4.1 Assumption 3.1 holds with $\chi(a, x, s)$ and $\beta(a, x, s)$ being replaced by $\chi(a, x, s, P)$ and $\beta(a, x, s, P)$, respectively. Moreover, χ_1 and β_1 also satisfy Assumption 3.1. Furthermore, $\beta(a, x, s, P\psi) \leq \beta(a, x, s, 0)$ and $\chi(a, x, s, P\psi) \leq \chi(a, x, s, 0)$ for all $a, x, s \geq 0$ and $\psi \in D(A)$.

We can obtain the global existence of integral solutions of (4.1) under Assumption 4.1. Here, we are mainly concerned with the existence and stability of nontrivial steady states of (4.1).

4.1 Existence of Nontrivial Steady States

In this subsection, we study the existence of a nontrivial steady state $\hat{\psi} \neq 0$. From the definition, $\hat{\psi}$ satisfies the following equations:

$$\begin{cases} \psi_a + \psi_s + \mu(a, s, P\psi)\psi = 0 \\ \psi(a, 0) = F(\psi)(a) \\ \psi(0, s) = H(\psi)(s) \\ P\psi = \int_0^{a^+} \int_0^{s^+} \psi(a, s) ds da. \end{cases} \tag{4.2}$$

Solving the problem, we obtain

$$\hat{\psi}(a, s) = \begin{cases} \hat{\psi}(a - s, 0)\Pi_{\hat{P}}(a, s, s), & a - s \geq 0, \\ \hat{\psi}(0, s - a)\Pi_{\hat{P}}(a, s, a), & a - s < 0, \end{cases} \tag{4.3}$$

where $\Pi_{\hat{P}}(a, s, \sigma) = e^{-\int_0^\sigma \mu(a-\tau, s-\tau, \hat{P})d\tau}$ and $\hat{P} = P\hat{\psi}$. Denote $\hat{\alpha}(s) = \hat{\psi}(0, s)$, $\hat{\eta}(a) = \hat{\psi}(a, 0)$. Plugging the solution into the boundary conditions, we have

$$\begin{aligned} \hat{\eta}(a) &= \int_0^{a^+} \int_0^x \chi(a, x, s, \hat{P})\hat{\eta}(x - s)\Pi_{\hat{P}}(x, s, s) ds dx \\ &\quad + \int_0^{s^+} \int_0^s \chi(a, x, s, \hat{P})\hat{\alpha}(s - x)\Pi_{\hat{P}}(x, s, x) dx ds, \\ \hat{\alpha}(s) &= \int_0^{s^+} \int_0^x \beta(a, x, s, \hat{P})\hat{\alpha}(x - a)\Pi_{\hat{P}}(a, x, a) da dx \\ &\quad + \int_0^{a^+} \int_0^a \beta(a, x, s, \hat{P})\hat{\eta}(a - x)\Pi_{\hat{P}}(a, x, x) dx da. \end{aligned}$$

Define $\Omega_0^N : \mathbb{R} \times L^1(0, a^+) \times L^1(0, s^+) \rightarrow \mathbb{R} \times L^1(0, a^+) \times L^1(0, s^+)$ by

$$\Omega_0^N \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} = \left(\Omega_{10}^N \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix}, \Omega_{20}^N \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix}, \Omega_{30}^N \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} \right), \tag{4.4}$$

where

$$\begin{aligned} \Omega_{10}^N \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} &= \int_0^{a^+} \int_0^a \hat{\eta}(a - s)\Pi_{\hat{P}}(a, s, s) ds da \\ &\quad + \int_0^{s^+} \int_0^s \hat{\alpha}(s - a)\Pi_{\hat{P}}(a, s, a) da ds, \end{aligned}$$

$$\begin{aligned} \Omega_{20}^N \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} &= \int_0^{a^+} \int_0^x \chi(a, x, s, \hat{P}) \hat{\eta}(x-s) \Pi_{\hat{P}}(x, s, s) ds dx \\ &\quad + \int_0^{s^+} \int_0^s \chi(a, x, s, \hat{P}) \hat{\alpha}(s-x) \Pi_{\hat{P}}(x, s, x) dx ds, \\ \Omega_{30}^N \begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix} &= \int_0^{s^+} \int_0^x \beta(a, x, s, \hat{P}) \hat{\alpha}(x-a) \Pi_{\hat{P}}(a, x, a) da dx \\ &\quad + \int_0^{a^+} \int_0^a \beta(a, x, s, \hat{P}) \hat{\eta}(a-x) \Pi_{\hat{P}}(a, x, x) dx da. \end{aligned}$$

Now the existence of a nontrivial steady state is equivalent to the existence of a nontrivial fixed point of map Ω_0^N . Using a similar method as in dealing with the semilinear case, we apply Theorems 3.2 and 3.3. Noting that the Fréchet derivative of Ω_0^N at $(0, 0, 0)^T$ is given as follows:

$$T^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} := \Omega_0^{N'}(0, 0, 0) \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} = \left(T_1^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}, T_2^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}, T_3^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} \right), \tag{4.5}$$

in which

$$\begin{aligned} T_1^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} &= \int_0^{a^+} \int_0^a \eta(a-s) \Pi_0(a, s, s) ds da \\ &\quad + \int_0^{s^+} \int_0^s \alpha(s-a) \Pi_0(a, s, a) da ds, \\ T_2^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} &= \int_0^{a^+} \int_0^x \chi(a, x, s, 0) \eta(x-s) \Pi_0(x, s, s) ds dx \\ &\quad + \int_0^{s^+} \int_0^s \chi(a, x, s, 0) \alpha(s-x) \Pi_0(x, s, x) dx ds, \\ T_3^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} &= \int_0^{a^+} \int_0^a \beta(a, x, s, 0) \eta(a-x) \Pi_0(a, x, x) dx da \\ &\quad + \int_0^{s^+} \int_0^x \beta(a, x, s, 0) \alpha(x-a) \Pi_0(a, x, a) da dx. \end{aligned}$$

By Assumption 4.1, it is easy to check that $\Omega_0^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix} \leq T^N \begin{pmatrix} P \\ \eta \\ \alpha \end{pmatrix}$ which implies that T^N is a majorant of Ω_0^N .

Proposition 4.2 Let Ω_0^N and T^N defined by (4.4) and (4.5), respectively.

- (i) If $r(T^N) \leq 1$, then Ω_0^N has only the trivial fixed point $\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$ in Y_+ ;
- (ii) If $r(T^N) > 1$, then Ω_0^N has at least one nontrivial fixed point $\begin{pmatrix} \hat{P} \\ \hat{\eta} \\ \hat{\alpha} \end{pmatrix}$ in $Y_+ \setminus \{0\}$.

Proof The proof is similar to that of Proposition 3.4 once noting Assumption 4.1, so we omit it. □

Similarly, we have the following results on the existence of steady states.

Proposition 4.3 Let T^N be defined in (4.5).

- (i) If $r(T^N) \leq 1$, then system (4.1) has only the trivial steady state 0 in $D(A)$.
- (ii) If $r(T^N) > 1$, then system (4.1) has at least one nontrivial steady state $\hat{\psi}$ in $D(A) \setminus \{0\}$;

4.2 Stability

We can verify that

$$\begin{aligned}
 (F'(\hat{\psi})\psi)(a) &= P\psi \int_0^{a^+} \int_0^{s^+} \chi_1(a, x, s, \hat{P})\hat{\psi}(x, s)dsdx \\
 &\quad + \int_0^{a^+} \int_0^{s^+} \chi(a, x, s, \hat{P})\psi(x, s)dsdx, \\
 (H'(\hat{\psi})\psi)(s) &= P\psi \int_0^{s^+} \int_0^{a^+} \beta_1(a, x, s, \hat{P})\hat{\psi}(a, x)dadx \\
 &\quad + \int_0^{s^+} \int_0^{a^+} \beta(a, x, s, \hat{P})\psi(a, x)dadx, \\
 (G'(\hat{\psi})\psi)(a, s) &= -\mu_1(a, s, P\hat{\psi})P\psi\hat{\psi}(a, s) \\
 &\quad -\mu(a, s, P\hat{\psi})\psi(a, s).
 \end{aligned}$$

Now define

$$\mathcal{X}_1 \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} 0 \\ 0 \\ -\mu(a, s, P\hat{\psi})\psi \end{pmatrix}, \quad \mathcal{X}_2 \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} F'(\hat{\psi})\psi \\ H'(\hat{\psi})\psi \\ C(\psi) \end{pmatrix},$$

where $C(\psi) := -\mu_1(\cdot, \cdot, \hat{P})P\psi\hat{\psi}$, $\hat{P} = P\hat{\psi}$. Observe that C is a compact operator in E and F' , H' are also compact in $L^1(0, a^+)$, $L^1(0, s^+)$, respectively under Assumption 4.1, thus \mathcal{X}_2 is also compact in X . By the method of characteristic lines,

we see that $\mathcal{A} + \mathcal{X}_1$ generates a nilpotent semigroup and its perturbed semigroup by the compact operator \mathcal{X}_2 is eventually compact. Hence,

$$\omega_1(\mathcal{A} + \mathcal{B}'[\hat{\psi}]) = \omega_1(\mathcal{A} + \mathcal{X}_1 + \mathcal{X}_2) = \omega(\mathcal{A} + \mathcal{X}_1) = -\infty.$$

It follows that the stability of $\hat{\psi}$ is determined by the eigenvalues of $\mathcal{A} + \mathcal{B}'[\hat{\psi}]$. Let

$$\lambda \in \mathbb{C} \text{ and } \hat{B}^N \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} = \lambda \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \text{ for } \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \in D(\mathcal{A}) \text{ and } \psi \neq 0,$$

where $\hat{B}^N := \mathcal{A} + \mathcal{B}'[\hat{\psi}]$. Using the definition of \hat{B}^N , we obtain

$$\begin{cases} \psi_a + \psi_s + \lambda\psi + \mu(a, s, \hat{P})\psi + \mu_1(a, s, \hat{P})P\psi\hat{\psi} = 0 \\ \psi(a, 0) = (F'(\hat{\psi})\psi)(a) \\ \psi(0, s) = (H'(\hat{\psi})\psi)(s) \\ P\psi = \int_0^{a^+} \int_0^{s^+} \psi(a, s) ds da, \end{cases} \tag{4.6}$$

where $\hat{P} = P\hat{\psi}$. Solving the initial-boundary value problem, we obtain that

$$\psi(a, s) = \begin{cases} \psi(a-s, 0)e^{-\lambda s} \Pi_{\hat{P}}(a, s, s) \\ - \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma) d\sigma, & a-s \geq 0, \\ \psi(0, s-a)e^{-\lambda a} \Pi_{\hat{P}}(a, s, a) \\ - \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma) d\sigma, & a-s < 0, \end{cases} \tag{4.7}$$

where $\Pi_{\hat{P}}(a, s, \sigma) = e^{-\int_0^\sigma \mu(a-\tau, s-\tau, \hat{P}) d\tau}$. Denote $\alpha(s) = \psi(0, s)$, $\eta(a) = \psi(a, 0)$.

To evaluate $P\psi$, using the definition of $P\psi$ yields that

$$\begin{aligned} P\psi &= \int_0^{a^+} \int_0^a \eta(a-s)e^{-\lambda s} \Pi_{\hat{P}}(a, s, s) ds da \\ &\quad - \int_0^{a^+} \int_0^a \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma) d\sigma ds da \\ &\quad + \int_0^{s^+} \int_0^s \alpha(s-a)e^{-\lambda a} \Pi_{\hat{P}}(a, s, a) da ds \\ &\quad - \int_0^{s^+} \int_0^s \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) P\psi\mu_1(a-\sigma, s-\sigma, \hat{P})\hat{\psi}(a-\sigma, s-\sigma) d\sigma da ds, \end{aligned}$$

which implies that

$$\begin{aligned}
 P\psi & \left[1 + \int_0^{a^+} \int_0^a \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma ds da \right. \\
 & \left. + \int_0^{s^+} \int_0^s \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma dads \right] \\
 & = \int_0^{a^+} \int_0^a \eta(a - s) e^{-\lambda s} \Pi_{\hat{P}}(a, s, s) ds da + \int_0^{s^+} \int_0^s \alpha(s - a) e^{-\lambda a} \Pi_{\hat{P}}(a, s, a) dads \\
 & = B_\lambda(\eta, \alpha), \tag{4.8}
 \end{aligned}$$

where $B_\lambda : L^1(0, a^+) \times L^1(0, s^+) \rightarrow \mathbb{R}$ is a functional in $L^1(0, a^+) \times L^1(0, s^+)$ and for all $\lambda \in \mathbb{R}$. Define

$$\begin{aligned}
 A(\lambda) & = \int_0^{a^+} \int_0^a \int_0^s e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma ds da \\
 & \quad + \int_0^{s^+} \int_0^s \int_0^a e^{-\lambda\sigma} \Pi_{\hat{P}}(a, s, \sigma) \mu_1(a - \sigma, s - \sigma, \hat{P}) \hat{\psi}(a - \sigma, s - \sigma) d\sigma dads. \tag{4.9}
 \end{aligned}$$

It follows that $P\psi = (1 + A(\lambda))^{-1} B_\lambda(\eta, \alpha)$. Substituting (4.7) in the boundary conditions, we have

$$\begin{aligned}
 \eta(a) & = \int_0^{a^+} \int_0^x \chi(a, x, s, \hat{P}) \eta(x - s) e^{-\lambda s} \Pi_{\hat{P}}(x, s, s) ds dx \\
 & \quad - P\psi \int_0^{a^+} \int_0^x \int_0^s \chi(a, x, s, \hat{P}) e^{-\lambda\sigma} \Pi_{\hat{P}}(x, s, \sigma) \mu_1(x - \sigma, s - \sigma, \hat{P}) \hat{\psi}(x - \sigma, s - \sigma) d\sigma ds dx \\
 & \quad + \int_0^{s^+} \int_0^s \chi(a, x, s, \hat{P}) \alpha(s - x) e^{-\lambda x} \Pi_{\hat{P}}(x, s, x) dx ds \\
 & \quad - P\psi \int_0^{s^+} \int_0^s \int_0^x \chi(a, x, s, \hat{P}) e^{-\lambda\sigma} \Pi_{\hat{P}}(x, s, \sigma) \mu_1(x - \sigma, s - \sigma, \hat{P}) \hat{\psi}(x - \sigma, s - \sigma) d\sigma dx ds \\
 & \quad + P\psi \int_0^{a^+} \int_0^{s^+} \chi_1(a, x, s, \hat{P}) \hat{\psi}(x, s) ds dx, \\
 \alpha(s) & = \int_0^{s^+} \int_0^x \beta(a, x, s, \hat{P}) \alpha(x - a) e^{-\lambda a} \Pi_{\hat{P}}(a, x, a) dadx \\
 & \quad - P\psi \int_0^{s^+} \int_0^x \int_0^a \beta(a, x, s, \hat{P}) e^{-\lambda\sigma} \Pi_{\hat{P}}(a, x, \sigma) \mu_1(a - \sigma, x - \sigma, \hat{P}) \hat{\psi}(a - \sigma, x - \sigma) d\sigma dadx \\
 & \quad + \int_0^{a^+} \int_0^a \beta(a, x, s, \hat{P}) \eta(a - x) e^{-\lambda x} \Pi_{\hat{P}}(a, x, x) dx da \\
 & \quad - P\psi \int_0^{a^+} \int_0^a \int_0^x \beta(a, x, s, \hat{P}) e^{-\lambda\sigma} \Pi_{\hat{P}}(a, x, \sigma) \mu_1(a - \sigma, x - \sigma, \hat{P}) \hat{\psi}(a - \sigma, x - \sigma) d\sigma dx da \\
 & \quad + P\psi \int_0^{s^+} \int_0^{a^+} \beta_1(a, x, s, \hat{P}) \hat{\psi}(a, x) dadx.
 \end{aligned}$$

Denote

$$\begin{aligned} \Omega_{1\lambda}^N(\eta, \alpha)(a) &= \int_0^{a^+} \int_0^x \chi(a, x, s, \hat{P})\eta(x-s)e^{-\lambda s} \Pi_{\hat{p}}(x, s, s) ds dx \\ &\quad + \int_0^{s^+} \int_0^s \chi(a, x, s, \hat{P})\alpha(s-x)e^{-\lambda x} \Pi_{\hat{p}}(x, s, x) dx ds, \\ \Omega_{2\lambda}^N(\eta, \alpha)(s) &= \int_0^{s^+} \int_0^x \beta(a, x, s, \hat{P})\alpha(x-a)e^{-\lambda a} \Pi_{\hat{p}}(a, x, a) da dx \\ &\quad + \int_0^{a^+} \int_0^a \beta(a, x, s, \hat{P})\eta(a-x)e^{-\lambda x} \Pi_{\hat{p}}(a, x, x) dx da, \\ K_{1\lambda}^N(a) &= \int_0^{a^+} \int_0^x \int_0^s \chi(a, x, s, \hat{P})e^{-\lambda\sigma} \Pi_{\hat{p}}(x, s, \sigma) \\ &\quad \mu_1(x-\sigma, s-\sigma, \hat{P})\hat{\psi}(x-\sigma, s-\sigma) d\sigma ds dx, \\ K_{2\lambda}^N(a) &= \int_0^{s^+} \int_0^s \int_0^x \chi(a, x, s, \hat{P})e^{-\lambda\sigma} \Pi_{\hat{p}}(x, s, \sigma) \\ &\quad \mu_1(x-\sigma, s-\sigma, \hat{P})\hat{\psi}(x-\sigma, s-\sigma) d\sigma dx ds, \\ K_{3\lambda}^N(s) &= \int_0^{s^+} \int_0^x \int_0^a \beta(a, x, s, \hat{P})e^{-\lambda\sigma} \Pi_{\hat{p}}(a, x, \sigma) \\ &\quad \mu_1(a-\sigma, x-\sigma, \hat{P})\hat{\psi}(a-\sigma, x-\sigma) d\sigma da dx, \\ K_{4\lambda}^N(s) &= \int_0^{a^+} \int_0^a \int_0^x \beta(a, x, s, \hat{P})e^{-\lambda\sigma} \Pi_{\hat{p}}(a, x, \sigma) \\ &\quad \mu_1(a-\sigma, x-\sigma, \hat{P})\hat{\psi}(a-\sigma, x-\sigma) d\sigma dx da, \\ K_5(a) &= P\psi \int_0^{a^+} \int_0^{s^+} \chi_1(a, x, s, \hat{P})\hat{\psi} ds dx, \\ K_6(s) &= P\psi \int_0^{s^+} \int_0^{a^+} \beta_1(a, x, s, \hat{P})\hat{\psi} da dx. \end{aligned}$$

Thus, $\eta(s)$ and $\alpha(s)$ can be rewritten as follows:

$$\begin{cases} \eta(a) = \Omega_{1\lambda}^N(\eta, \alpha)(a) - (1 + A(\lambda))^{-1} B_\lambda(\eta, \alpha)(K_{1\lambda}^N(a) + K_{2\lambda}^N(a) - K_5(a)), \\ \alpha(s) = \Omega_{2\lambda}^N(\eta, \alpha)(s) - (1 + A(\lambda))^{-1} B_\lambda(\eta, \alpha)(K_{3\lambda}^N(s) + K_{4\lambda}^N(s) - K_6(s)). \end{cases} \tag{4.10}$$

Similarly, define

$$\Omega_\lambda^N := (\Omega_{1\lambda}^N, \Omega_{2\lambda}^N)$$

and

$$M_\lambda^N(a) = (1 + A(\lambda))^{-1}(K_{1\lambda}^N(a) + K_{2\lambda}^N(a) - K_5(a)),$$

$$V_\lambda^N(s) = (1 + A(\lambda))^{-1}(K_{3\lambda}^N(s) + K_{4\lambda}^N(s) - K_6(s)).$$

Then, system (4.10) becomes

$$\begin{pmatrix} \eta \\ \alpha \end{pmatrix} = \left(\Omega_\lambda^N - \begin{pmatrix} M_\lambda^N(a) \\ V_\lambda^N(s) \end{pmatrix} B_\lambda \right) \begin{pmatrix} \eta \\ \alpha \end{pmatrix}.$$

Further, define

$$\Theta_\lambda^N := \Omega_\lambda^N - \begin{pmatrix} M_\lambda^N(a) \\ V_\lambda^N(s) \end{pmatrix} B_\lambda.$$

Since Ω_λ^N , $M_\lambda^N(a)B_\lambda$, and $V_\lambda^N(s)B_\lambda$ are compact, Θ_λ^N is also compact in $L^1(0, a^+) \times L^1(0, s^+)$ for all $\lambda \in \mathbb{C}$ under Assumption 4.1. Also we can show that Ω_λ^N , $M_\lambda^N(a)B_\lambda$, and $V_\lambda^N(s)B_\lambda$ are nonsupporting under Assumption 4.1, then Θ_λ^N is also nonsupporting in $L^1(0, a^+) \times L^1(0, s^+)$ for all $\lambda \in \mathbb{R}$. Thus, similar to Proposition 3.6 we have the following results.

Proposition 4.4 *We have the following statements*

- (i) $\Gamma^N := \{\lambda \in \mathbb{C} : 1 \in \sigma(\Theta_\lambda^N)\} = \{\lambda \in \mathbb{C} : 1 \in \sigma_P(\Theta_\lambda^N)\}$, where $\sigma(A)$ and $\sigma_P(A)$ denote the spectrum and point spectrum of the operator A , respectively;
- (ii) There exists a unique real number $\lambda_0^N \in \Gamma^N$ such that $r(\Theta_{\lambda_0}^N) = 1$ and $\lambda_0^N > 0$ if $r(\Theta_0^N) > 1$; $\lambda_0^N = 0$ if $r(\Theta_0^N) = 1$; and $\lambda_0^N < 0$ if $r(\Theta_0^N) < 1$;
- (iii) $\lambda_0^N > \sup\{\text{Re}\lambda : \lambda \in \Gamma^N \setminus \{\lambda_0^N\}\}$;
- (iv) λ_0^N is the dominant eigenvalue of \hat{B}^N , i.e., λ_0^N is greater than all real parts of the eigenvalues of \hat{B}^N . Moreover, it is a simple eigenvalue of \hat{B}^N ;
- (v) $\{\lambda \in \mathbb{C} : \lambda \in \rho(\hat{B}^N)\} = \{\lambda \in \mathbb{C} : 1 \in \rho(\Theta_\lambda^N)\}$, where $\rho(A)$ denote the resolvent set of A ;
- (vi) $\lambda_0^N = s(\hat{B}^N) := \sup\{\text{Re}\lambda : \lambda \in \sigma(\hat{B}^N)\}$.

Also similar to Theorem 3.7, we have the following result on the stability of the steady state.

Theorem 4.5 *The steady state $\hat{\psi}$ is locally exponentially asymptotically stable if $r(\Theta_0^N) < 1$ and unstable if $r(\Theta_0^N) > 1$.*

5 Age-Size Structured Models with Size-Dependent Growth Rate

Size is another very important physiological structure in population dynamics, and size-structured models have been investigated extensively in the literature, see Cushing (1985, 1987, 1989), Calsina and Saldana (1995), Chu et al. (2009), Chu and Magal

(2013), Farkas and Hagen (2007), Farkas et al. (2010), and Gwiazda et al. (2010). In this section, we apply our analytical methods to a nonlinear age-size structured model with a growth rate term $g(s)$ in front of u_s motivated by Heijmans (1986), where the function g accounts for the growth of the second variable which does not increase at the same rate as age. Kojiman and Metz (1984) considered a nonlinear age-size structured model for the development of *Daphnia magna* whose mortality depends on age, whereas whose fertility depends on the size. Later, Thieme (1988) formulated the model in Heijmans (1986) as integral equations and discussed the well-posedness of the problem. Tucker and Zimmerman (1988) studied a more general nonlinear age-size structured model and established the well-posedness, existence and stability of steady states. See also Sinko and Streifer (1967) and Webb (2008) for age-size structured single-species population models and Gyllenberg and Webb (1987) for age-size structure in populations with quiescence.

Once again, in the above-mentioned models, one zero boundary condition was assumed. Here, we analyze a nonlinear age-size structured model with size-dependent growth rate and with generalized boundary conditions. Biologically speaking, the classical age-size structured population would always yield a trivial boundary condition, but if the “size” structure represents telomere length or another physiological character as illustrated in the introduction, then it is natural to assume that the changing rate of telomere or physiological character has its own pace depending on the specific status. Therefore, we consider the following model

$$\begin{cases} u_t(t, a, s) + u_a(t, a, s) + g(s)u_s(t, a, s) = G(u(t, \cdot, \cdot))(a, s), \\ u(t, a, 0) = F(u(t, \cdot, \cdot))(a), \\ u(t, 0, s) = H(u(t, \cdot, \cdot))(s), \\ u(0, a, s) = \phi(a, s). \end{cases} \tag{5.1}$$

Following the idea of Heijmans (1986), the characteristic curve through (t, a, s) is determined by

$$x \rightarrow (T(x, t), A(x, a), S(x, s)),$$

where x is an independent variable and T, A, S are solutions of the ODEs

$$\frac{dT}{dx} = 1, T(0, t) = t; \quad \frac{dA}{dx} = 1, A(0, a) = a; \quad \frac{dS}{dx} = g(S), S(0, s) = s.$$

Thus,

$$T(x, t) = x + t, \quad A(x, a) = x + a, \quad S(x, s) = G^{-1}(x + G(s)),$$

where $G(s) = \int_0^s \frac{d\xi}{g(\xi)}$, $s \geq 0$, which can be interpreted as the time need to grow from 0 to s and G^{-1} denotes its inverse. Observe that $G^{-1}(a) = S(a, 0)$.

A classical technique to treat size-structured models is to formulate them as integral equations and apply corresponding theories to study the problems (Thieme 1988).

Recently, semigroup theories, including integrated semigroup theory, have been developed to study size-structured models (Farkas et al. 2010; Chu et al. 2009; Chu and Magal 2013). In this section, we employ the integrated semigroup method to treat the age-size structured model (5.1). To do so, first we make an assumption on $g(s)$. The function $g(s)$ represents the growth rate of size or volume for a population such as a cell population. It is assumed to be continuous and there exist two constants $M, m > 0$ such that $0 < m \leq g(s) \leq M$ for all $s \in [0, s^+]$. Obviously, $G(s)$ is an increasing positive function, and we assume that $G(s^+) \leq a^+$. Now let t, a, x be fixed and let $u(x) = u(T(x, t), A(x, a), S(x, s))$. Then

$$\frac{dm}{dx} = G(u(x))(x).$$

Define an operator \mathcal{A} acting on X by

$$\mathcal{A} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} := \begin{pmatrix} -\psi(a, 0) \\ -\psi(0, s) \\ -\psi_a - g(s)\psi_s \end{pmatrix} \quad \text{for} \quad \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} \in D(\mathcal{A}) := \{0\} \times \{0\} \times D(B),$$

where B is a differential operator acting on E defined by

$$B(\psi)(a, s) := \psi_a + g(s)\psi_s, \quad D(B) := \{\psi \in E : \psi \in W^{1,1}((0, a^+) \times (0, s^+))\}.$$

Then, B is densely defined in E . First, we claim that $\mathcal{A}_* := \mathcal{A} - \frac{1}{\epsilon}I$ is still a Hille–Yosida operator.

Lemma 5.1 \mathcal{A}_* is a closed linear operator with non-dense domain and the following holds: $\overline{D(\mathcal{A}_*)} = X_0$, \mathcal{A}_* satisfies the Hille–Yosida estimate such that for all $\lambda > -\frac{1}{\epsilon}$,

$$\|(\lambda I - \mathcal{A}_*)^{-1}\|_X \leq \frac{M}{\lambda + 1/\epsilon}$$

and $(\lambda - \mathcal{A}_*)^{-1}(X_+) \subset X_{0+}$ for $\lambda > 0$.

Proof Consider the resolvent of the operator \mathcal{A}_* as follows:

$$(\lambda I - \mathcal{A}_*) \begin{pmatrix} 0 \\ 0 \\ \varphi \end{pmatrix} = \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} \in X_+.$$

By the definition of \mathcal{A}_* ,

$$(\lambda I - \mathcal{A}_*) \begin{pmatrix} 0 \\ 0 \\ \varphi \end{pmatrix} = \begin{pmatrix} \varphi(a, 0) \\ \varphi(0, s) \\ \frac{\partial \varphi}{\partial a} + g(s)\frac{\partial \varphi}{\partial s} + (\lambda + \frac{1}{\epsilon})\varphi \end{pmatrix},$$

we have

$$\frac{\partial \varphi}{\partial a} + g(s) \frac{\partial \varphi}{\partial s} + (\lambda + 1/\epsilon)\varphi = \phi(a, s), \tag{5.2}$$

$$\varphi(a, 0) = \alpha(a), \quad \varphi(0, s) = \eta(s). \tag{5.3}$$

By the method of characteristic lines mentioned above, we have

$$\frac{d\varphi}{dx} = -(\lambda + 1/\epsilon)\varphi(x) + \phi(A(x, a), S(x, s)),$$

which has a solution

$$\varphi(x) = \varphi(0)e^{-(\lambda+1/\epsilon)x} + \int_0^x e^{-(x-\sigma)(\lambda+1/\epsilon)} \phi(A(\sigma, a), S(\sigma, s))d\sigma. \tag{5.4}$$

Let $a' = A(x, a)$, $s' = S(x, s)$. We consider two cases.

- (i) Choose $a = 0$, then $a' = x$, $S(-a', s') = G^{-1}(-a' + G(s')) = G^{-1}(-x + x + G(s)) = s$. We deduce from (5.4) that

$$\begin{aligned} \varphi(a', s') &= \varphi(0, S(-a', s'))e^{-(\lambda+1/\epsilon)a'} \\ &\quad + \int_0^{a'} e^{-(a'-\sigma)(\lambda+1/\epsilon)} \phi(\sigma, S(\sigma, S(-a', s'))))d\sigma, \quad a' < G(s'). \end{aligned}$$

- (ii) Choose $s = 0$, then $s' = S(x, 0) = G^{-1}(x + G(0)) = G^{-1}(x)$, i.e., $x = G(s')$ and $a' = x + a = G(s') + a$ which implies that $a = a' - G(s')$. Now we deduce from (5.4) that

$$\begin{aligned} \varphi(a', s') &= \varphi(a' - G(s'), 0)e^{-(\lambda+1/\epsilon)G(s')} \\ &\quad + \int_0^{G(s')} e^{-(G(s')-\sigma)(\lambda+1/\epsilon)} \phi(\sigma + a' - G(s'), G^{-1}(\sigma))d\sigma, \quad a' > G(s'). \end{aligned}$$

Thus, the solution of (5.2), (5.3) is

$$\varphi(a, s) = \begin{cases} \alpha(a - G(s))e^{-(\lambda+1/\epsilon)G(s)} + \int_0^{G(s)} e^{-(G(s)-\sigma)(\lambda+1/\epsilon)} \phi(\sigma + a - G(s), G^{-1}(\sigma))d\sigma, & a - G(s) \geq 0, \\ \eta(S(-a, s))e^{-(\lambda+1/\epsilon)a} + \int_0^a e^{-(a-\sigma)(\lambda+1/\epsilon)} \phi(\sigma, S(\sigma, S(-a, s)))d\sigma, & a - G(s) < 0. \end{cases} \tag{5.5}$$

Thus, we have

$$(\lambda I - \mathcal{A}_*)^{-1} \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ \varphi(a, s) \end{pmatrix}$$

and

$$\begin{aligned}
 & \left\| (\lambda I - \mathcal{A}_*)^{-1} \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} \right\|_X = \|\varphi(a, s)\|_E \\
 & \leq \left| \int_0^{s^+} \int_{G(s)}^{a^+} \alpha(a - G(s)) e^{-(\lambda+1/\epsilon)G(s)} \, d\mathbf{a} ds \right| \\
 & \quad + \left| \int_0^{s^+} \int_{G(s)}^{a^+} \int_0^{G(s)} e^{-(G(s)-\sigma)(\lambda+1/\epsilon)} \phi(\sigma + a - G(s), G^{-1}(\sigma)) \, d\sigma \, d\mathbf{a} ds \right| \\
 & \quad + \left| \int_0^{s^+} \int_0^{G(s)} \eta(S(-a, s)) e^{-(\lambda+1/\epsilon)a} \, d\mathbf{a} ds \right| \\
 & \quad + \left| \int_0^{s^+} \int_0^{G(s)} \int_0^a e^{-(a-\sigma)(\lambda+1/\epsilon)} \phi(\sigma, S(\sigma, S(-a, s))) \, d\sigma \, d\mathbf{a} ds \right| \\
 & \leq \int_0^{s^+} \int_0^{a^+} |\alpha(a - G(s))| e^{-(\lambda+1/\epsilon)s/M} \, d\mathbf{a} ds \\
 & \quad + \int_0^{s^+} \int_{G(s)}^{a^+} \int_0^{G(s)} e^{-(G(s)-\sigma)(\lambda+1/\epsilon)} |\phi(\sigma + a - G(s), G^{-1}(\sigma))| \, d\sigma \, d\mathbf{a} ds \\
 & \quad + \int_0^{s^+} \int_0^{a^+} |\eta(S(-a, s))| e^{-(\lambda+1/\epsilon)a} \, d\mathbf{a} ds \\
 & \quad + \int_0^{s^+} \int_0^{G(s)} \int_0^a e^{-(a-\sigma)(\lambda+1/\epsilon)} |\phi(\sigma, S(\sigma, S(-a, s)))| \, d\sigma \, d\mathbf{a} ds \\
 & \leq \frac{M}{\lambda + 1/\epsilon} \|\alpha\|_{L^1(0, a^+)} + \frac{1}{\lambda + 1/\epsilon} \|\eta\|_{L^1(0, s^+)} + \frac{1}{\lambda + 1/\epsilon} \|\phi\|_E \\
 & \leq \frac{\max\{1, M\}}{\lambda + 1/\epsilon} \left\| \begin{pmatrix} \alpha \\ \eta \\ \phi \end{pmatrix} \right\|_X, \tag{5.6}
 \end{aligned}$$

which implies that

$$\left\| (\lambda I - \mathcal{A}_*)^{-1} \right\|_X \leq \frac{\max\{1, M\}}{\lambda + 1/\epsilon}$$

for $\lambda > -1/\epsilon$. Hence, \mathcal{A}_* is a Hille–Yosida operator with $\omega = -1/\epsilon < 0$. □

Thus, by a similar argument as in Sect. 2, we can also establish the generalized variation of constant formula and obtain the global existence of the integral solution..

Now, we analyze the principal eigenvalue for the linear problem of (5.1). Suppose that

$$F(\psi)(a) = \int_0^{a^+} \int_0^{s^+} \chi(a, x, s) \psi(x, s) \, ds dx,$$

$$\begin{aligned}
 H(\psi)(s) &= \int_0^{s^+} \int_0^{a^+} \beta(a, x, s)\psi(a, x)dadx, \\
 G(\psi)(a, s) &= -\mu(a, s)\psi(a, s).
 \end{aligned}$$

For $\chi(a, x, s)$ and $\beta(a, x, s)$ satisfying Assumption 3.1-(v), denote

$$\chi_{\text{sup}} := \int_0^{a^+} \bar{\chi}(a)da, \quad \beta_{\text{sup}} := \int_0^{s^+} \bar{\beta}(s)ds.$$

Consider the operator \mathcal{A} defined by

$$\mathcal{A}\psi = \begin{pmatrix} \psi(a, 0) \\ \psi(0, s) \\ -\psi_a - g(s)\psi_s - \mu(a, s)\psi \end{pmatrix}.$$

To find the eigenvalue of \mathcal{A} , via the characteristic equation $\mathcal{A} \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix} = \lambda \begin{pmatrix} 0 \\ 0 \\ \psi \end{pmatrix}$, we have

$$\begin{cases} \psi_a + g(s)\psi_s + \mu(a, s)\psi + \lambda\psi = 0, \\ \psi(a, 0) = F(\psi)(a), \\ \psi(0, s) = H(\psi)(s). \end{cases} \tag{5.7}$$

Solving the equation by the method of characteristic curves as above, we obtain that

$$\psi(a, s) = \begin{cases} \alpha(a - G(s))e^{-\lambda G(s)}\Pi(G(s), a - G(s), 0), & a - G(s) \geq 0, \\ \eta(S(-a, s))e^{-\lambda a}\Pi(a, 0, S(-a, s)), & a - G(s) < 0, \end{cases} \tag{5.8}$$

where $\Pi(x, a, s) = e^{-\int_0^x \mu(A(\sigma, a), S(\sigma, s))d\sigma}$ and $\alpha(a) = \psi(a, 0)$, $\eta(s) = \psi(0, s)$. Plugging them into the boundary conditions, we get

$$\begin{aligned}
 \alpha(a) &= \int_0^{s^+} \int_0^{G(s)} \chi(a, x, s)\eta(S(-x, s))e^{-\lambda x}\Pi(x, 0, S(-x, s))dxds \\
 &\quad + \int_0^{s^+} \int_{G(s)}^{a^+} \chi(a, x, s)\alpha(x - G(s))e^{-\lambda G(s)}\Pi(G(s), x - G(s), 0)dxds, \\
 \eta(s) &= \int_0^{s^+} \int_0^{G(x)} \beta(a, x, s)\eta(S(-a, x))e^{-\lambda a}\Pi(a, 0, S(-a, x))dadx \\
 &\quad + \int_0^{s^+} \int_{G(x)}^{a^+} \beta(a, x, s)\alpha(a - G(x))e^{-\lambda G(x)}\Pi(G(x), a - G(x), 0)dadx.
 \end{aligned}$$

Next define $\Gamma_\lambda : L^1(0, a^+) \times L^1(0, s^+) \rightarrow L^1(0, a^+) \times L^1(0, s^+)$ by $\Gamma_\lambda(\alpha, \eta) = (\Gamma_{1\lambda}(\alpha, \eta), \Gamma_{2\lambda}(\alpha, \eta))$, where

$$\begin{aligned} \Gamma_{1\lambda}(\alpha, \eta)(a) &= \int_0^{s^+} \int_0^{G(s)} \chi(a, x, s) \eta(S(-x, s)) e^{-\lambda x} \Pi(x, 0, S(-x, s)) dx ds \\ &\quad + \int_0^{s^+} \int_{G(s)}^{a^+} \chi(a, x, s) \alpha(x - G(s)) e^{-\lambda G(s)} \Pi(G(s), x - G(s), 0) dx ds \\ \Gamma_{2\lambda}(\alpha, \eta)(s) &= \int_0^{s^+} \int_0^{G(x)} \beta(a, x, s) \eta(S(-a, x)) e^{-\lambda a} \Pi(a, 0, S(-a, x)) da dx, \\ &\quad + \int_0^{s^+} \int_{G(x)}^{a^+} \beta(a, x, s) \alpha(a - G(x)) e^{-\lambda G(x)} \Pi(G(x), a - G(x), 0) da dx. \end{aligned}$$

By using similar arguments as in the previous sections, we can conclude that Γ_λ is compact for all $\lambda \in \mathbb{C}$ and nonsupporting for all $\lambda \in \mathbb{R}$ in $L^1(0, a^+) \times L^1(0, s^+)$ under Assumption 3.1. It follows that \mathcal{A} has a principal eigenvalue λ_0 , which satisfies $r(\Gamma_{\lambda_0}) = 1$ and is simple, see Kang et al. (2020). Next, we want to study the relation between the basic reproduction number \mathcal{R}_0 and g or G , where $\mathcal{R}_0 := r(\Gamma_0)$, see also Kang et al. (2020).

We have the following estimates

$$\begin{aligned} \|\Gamma_{1\lambda}(\alpha, \eta)\| &= \int_0^{a^+} \int_0^{s^+} \int_0^{G(s)} \chi(a, x, s) \eta(S(-x, s)) e^{-\lambda x} \Pi(x, 0, S(-x, s)) dx ds da \\ &\quad + \int_0^{a^+} \int_0^{s^+} \int_{G(s)}^{a^+} \chi(a, x, s) \alpha(x - G(s)) e^{-\lambda G(s)} \Pi(G(s), x - G(s), 0) dx ds da \\ &\leq \int_0^{a^+} \bar{\chi}(a) da \int_0^{s^+} \eta(S(-x, s)) ds \int_0^{G(s)} e^{-(\lambda+\underline{\mu})x} dx \\ &\quad + \int_0^{a^+} \bar{\chi}(a) da \int_{G(s)}^{a^+} \alpha(x - G(s)) dx \int_0^{s^+} e^{-(\lambda+\underline{\mu})G(s)} ds \\ &\leq \frac{\chi_{\text{sup}}}{\lambda + \underline{\mu}} \|\eta\|_{L^1_+(0, s^+)} + \chi_{\text{sup}} \|\alpha\|_{L^1_+(0, a^+)} \frac{M}{\lambda + \underline{\mu}} \\ &\leq \frac{\max\{1, M\} \chi_{\text{sup}}}{\lambda + \underline{\mu}} \|(\alpha, \eta)\|. \end{aligned} \tag{5.9}$$

Similarly, we have

$$\|\Gamma_{2\lambda}(\alpha, \eta)\| \leq \frac{\max\{1, M\} \beta_{\text{sup}}}{\lambda + \underline{\mu}} \|(\alpha, \eta)\|.$$

Thus,

$$\|\Gamma_\lambda\| \leq \frac{\max\{1, M\} \max\{\beta_{\text{sup}}, \chi_{\text{sup}}\}}{\lambda + \underline{\mu}}.$$

It follows from the well-known Gelfand's formula that

$$r(\Gamma_0) \leq \frac{\max\{1, M\} \max\{\beta_{\text{sup}}, \chi_{\text{sup}}\}}{\mu}.$$

In summary, the basic reproduction number is bounded by the upper bound of g .

In this section, we only considered g dependent on the size s , which can be directly treated by integrated semigroup setup, so that we can easily perform the change of variables, solve the solution and give the estimate of basic reproduction number in terms of g . In fact, there are many single size structured models which deal with more complicated cases, see Cushing (1985, 1987, 1989), Calsina and Saldana (1995) and Gwiazda et al. (2010), where g is a multivariate function about both size and the total population. The methods adopted in this paper might not be directly applied to study systems with more complicated size operators. Thus, other methods such as formulating the size dynamics via integral operators could be used to treat such problems.

6 Discussion

In this paper, we studied nonlinear double physiologically structured population models with two internal variables via the theory of non-densely defined operators and integrated semigroups. Motivated by the theory of age-structured models with a single internal variable in Webb (1984), we considered semilinear and nonlinear equations and studied the existence and stability of nontrivial steady states for both kinds of nonlinear equations. Further, we generalized techniques to deal with a nonlinear age-size structured model with a growth rate term $g(s)$ in front of u_s and provided an analysis for the principal eigenvalue of the non-densely defined operator in terms of the bound of $g(s)$.

It would be interesting to employ or extend our techniques to investigate nonlinear systems with two physiological structures, such as the chronological-age and infection-age structured epidemic models (Hoppensteadt 1974; Inaba 2016; Laroche and Perasso 2016; Burie et al. 2017), age and another physiological (maturation, size, stage) structured population models (Dyson et al. 2000a, b; McNair and Goulden 1991; Matucci 1995), and cell-age and molecular content (cyclin content, maturity level, plasmid copies, telomere length) structured cell population kinetics models (Bekkal Briki et al. 2008; Bernard et al. 2003; Kapitanov 2012; Stadler 2019). We leave these for future consideration.

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A Appendix: Positive Operators

In this “Appendix”, we recall some definitions and results of positive operator theory on ordered Banach spaces from Inaba (2006). For more complete exposition, we refer to Heijmans (1986); Marek (1970), and Sawashima (1964).

Let E be a real or complex Banach space and E^* be its dual (the space of all linear functionals on E). Write the value of $f \in E^*$ at $\psi \in E$ as $\langle f, \psi \rangle$. A nonempty closed subset E_+ is called a *cone* if the following hold: (i) $E_+ + E_+ \subset E_+$, (ii) $\lambda E_+ \subset E_+$ for $\lambda \geq 0$, (iii) $E_+ \cap (-E_+) = \{0\}$. Define the *order* in E such that $x \leq y$ if and only if $y - x \in E_+$ and $x < y$ if and only if $y - x \in E_+ \setminus \{0\}$. The cone E_+ is called *total* if the set $\{\psi - \phi : \psi, \phi \in E_+\}$ is dense in E . The *dual cone* E_+^* is the subset of E^* consisting of all positive linear functionals on E ; that is, $f \in E_+^*$ if and only if $\langle f, \psi \rangle \geq 0$ for all $\psi \in E_+$. $\psi \in E_+$ is called a *quasi-interior point* if $\langle f, \psi \rangle > 0$ for all $f \in E_+^* \setminus \{0\}$. $f \in E_+^*$ is said to be *strictly positive* if $\langle f, \psi \rangle > 0$ for all $\psi \in E_+ \setminus \{0\}$. The cone E_+ is called *generating* if $E = E_+ - E_+$ and is called *normal* if $E^* = E_+^* - E_+^*$.

An ordered Banach space (E, \leq) is called a *Banach lattice* if (i) any two elements $x, y \in E$ have a supremum $x \vee y = \sup\{x, y\}$ and an infimum $x \wedge y = \inf\{x, y\}$ in E ; and (ii) $|x| \leq |y|$ implies $\|x\| \leq \|y\|$ for $x, y \in E$, where the modulus of x is defined by $|x| = x \vee (-x)$.

Let $B(E)$ be the set of bounded linear operators from E to E . $T \in B(E)$ is said to be *positive* if $T(E_+) \subset E_+$. For $T, S \in B(E)$, we say $T \geq S$ if $(T - S)(E_+) \subset E_+$. A positive operator $T \in B(E)$ is called *semi-nonsupporting* if for every pair $\psi \in E_+ \setminus \{0\}, f \in E_+^* \setminus \{0\}$, there exists a positive integer $p = p(\psi, f)$ such that $\langle f, T^p \psi \rangle > 0$. A positive operator $T \in B(E)$ is called *nonsupporting* if for every pair $\psi \in E_+ \setminus \{0\}, f \in E_+^* \setminus \{0\}$, there exists a positive integer $p = p(\psi, f)$ such that $\langle f, T^n \psi \rangle > 0$ for all $n \geq p$. The *spectral radius* of $T \in B(E)$ is denoted by $r(T)$. $\sigma(T)$ denotes the *spectrum* of T and $\sigma_P(T)$ denotes the *point spectrum* of T . If there exists a nonzero $x \in E$ which satisfies $Tx = \lambda x$, λ is called a *proper value* and x a *proper vector* corresponding to λ .

From results in Sawashima (1964) and Inaba (2006), we state the following propositions.

Proposition A.1 *Let E be a Banach space, and let $T \in B(E)$ be compact and semi-nonsupporting. Then, the following statements hold:*

- (i) $r(T) \in \sigma_P(T) \setminus \{0\}$ and $r(T)$ is a simple pole of the resolvent $\lambda I - T$; that is, $r(T)$ is an algebraically simple eigenvalue of T ;
- (ii) The eigenspace of T corresponding to $r(T)$ is one-dimensional and the corresponding eigenvector $\psi \in E_+$ is a quasi-interior point. The relation $T\phi = \mu\phi$ with $\phi \in E_+$ implies that $\phi = c\psi$ for some constant c ;
- (iii) The eigenspace of T^* corresponding to $r(T)$ is also a one-dimensional subspace of E^* spanned by a strictly positive functional $f \in E_+^*$.

Proposition A.2 *Let E be a Banach space with positive cone E_+ which is total. Let $T \in B(E)$ be positive and have the resolvent $\lambda I - T$ with the point $r(T)$ as its pole. Then, T is a semi-nonsupporting operator if and only if $r(T) > 0$ and T satisfies (A), where*

- (A) *Every proper eigenvector corresponding to the proper eigenvalue $r(T)$ lying in E_+ is a quasi-interior point of E_+ and every proper eigenvector corresponding to $r(T)$ lying in E_+^* is strictly positive.*

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