8

A Periodically Pulsed Bioreactor Model

In recent work of Ballyk et al. [27], it is argued that the plug-flow reactor, aside from its importance in chemical and bioengineering, is a good candidate as a surrogate model of the mammalian large intestine. In that work, a model of competition between different strains of microorganisms for a scarce nutrient in a plug-flow reactor, formulated by Kung and Baltzis [207], was studied with special attention given to the effects of random motility of the organisms on their ability to persist in the reactor and be good competitors in a mixed culture. The growth-limiting nutrient is assumed to enter the reactor tube at constant concentration at the upstream end of the reactor, so that the model equations take the form of a time-independent system of reaction–advection–diffusion equations. However, if the plug-flow reactor is to stand as a surrogate model of the intestine, then it is much more realistic to consider input nutrient concentration as being time-dependent. In the present chapter we consider this competition model with periodically varying input nutrient concentration, including pulsed input where the concentration may fall to zero over part of the cycle.

In Section 8.1 we briefly introduce the model and then discuss the well-posedness of the initial–boundary value problem and the positivity of its solutions. Section 8.2 is devoted to the special case of the model system with identical diffusivities and vanishing cell death rates. After consideration of the washout solution, we establish a conservation principle. We then consider single-population growth in the reactor, showing that when the washout solution is linearly stable, then it is globally stable, and when it is unstable, there is a unique, single-population periodic solution that attracts all solutions with nonzero initial data and is asymptotically stable in the linear approximation. Finally, we show that for two competing populations, where each single population periodic solution is unstable to invasion by the other population, we have persistence of both populations and the existence of a positive periodic solution representing coexistence. Section 8.3 is devoted to the perturbed system with different diffusivities and inclusion of cell death rates. We carry over

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the bulk of the results of Section 8.2 to the case where the random motility coefficients do not differ much from the diffusion constant of the nutrient and the cell death rates are small.

8.1 The Model

The plug-flow reactor may be thought of as a tube, of length L, through which a liquid medium flows with constant (small) velocity v. At the upstream end of the tube, $x = 0$, the nutrient concentration in the medium is maintained at the periodically varying concentration $S^0(t) = S^0(t + \omega)$. Downstream, bacteria consume nutrient, grow, divide, and die or leave the reactor at $x = L$. Bacteria are assumed to be motile, but their motility is random in the sense that it is modeled by an effective diffusion coefficient and is independent of nutrient concentration (chemotaxis is not considered here). The concentrations of nutrient S and microbial strains u_i, $i = 1, 2$, are governed by the equations (we have scaled variables so that $L = 1$)

$$\begin{aligned} \frac{\partial S}{\partial t} &= d_0 \frac{\partial^2 S}{\partial x^2} - v \frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S), \\ \frac{\partial u_i}{\partial t} &= d_i \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i(f_i(S) - k_i),\ i = 1, 2, \end{aligned} \tag{8.1}$$

where the d_i are the random motility coefficients of strain u_i, k_i is its death rate, and $f_i(S)$ is its uptake and growth rate. The quantity d_0 is the diffusion constant for nutrient S. Since the rate of change of the total nutrient concentration equals the difference between the inflow and outflow rates of the nutrient minus the consumption of the nutrient, we have

$$\frac{d}{dt} \int_0^1 S(x,t)dx = v\left(S^0(t) - S(1,t)\right) - \sum_{i=1}^{2} \int_0^1 u_i(x,t) f_i(S(x,t))dx.$$

On the other hand,

$$\begin{aligned} \frac{d}{dt} \int_0^1 S(x,t)dx &= \int_0^1 \frac{\partial S(x,t)}{\partial t} dx \\ &= \int_0^1 \left(d_0 \frac{\partial^2 S}{\partial x^2} - v \frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S) \right) dx \\ &= \left(d_0 \frac{\partial S(1,t)}{\partial x} - vS(1,t) \right) - \left(d_0 \frac{\partial S(0,t)}{\partial x} - vS(0,t) \right) \\ &\quad - \sum_{i=1}^{2} \int_0^1 u_i(x,t) f_i(S(x,t))dx. \end{aligned}$$

It then follows that

$$d_0 \frac{\partial S}{\partial x}(0,t) - vS(0,t) = -vS^0(t) \quad \text{and} \quad \frac{\partial S}{\partial x}(1,t) = 0.$$

Since the rate of change of the total concentration of species u_i is the difference between the natural growth and death rates of the species minus the washout rate of the species, we have

$$\frac{d}{dt}\int_0^1 u_i(x,t)dx = \int_0^1 u_i(x,t)(f_i(S(x,t)) - k_i)dx - vu_i(1,t).$$

On the other hand,

$$\begin{aligned}
\frac{d}{dt}\int_0^1 u_i(x,t)dx &= \int_0^1 \frac{\partial u_i(x,t)}{\partial t}dx \\
&= \int_0^1 \left(d_i \frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x} + u_i(f_i(S) - k_i)\right) dx \\
&= \left(d_i \frac{\partial u_i(1,t)}{\partial x} - vu_i(1,t)\right) - \left(d_i \frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t)\right) \\
&\quad + \int_0^1 u_i(x,t)(f_i(S(x,t)) - k_i)dx.
\end{aligned}$$

Thus we get

$$d_i \frac{\partial u_i}{\partial x}(0,t) - vu_i(0,t) = 0 \quad \text{and} \quad \frac{\partial u_i}{\partial x}(1,t) = 0.$$

Consequently, we impose on the model system the boundary conditions

$$\begin{aligned}
&d_0 \frac{\partial S}{\partial x}(0,t) - vS(0,t) = -vS^0(t), \\
&d_i \frac{\partial u_i}{\partial x}(0,t) - vu_i(0,t) = 0,\ i = 1,2, \\
&\frac{\partial S}{\partial x}(1,t) = \frac{\partial u_i}{\partial x}(1,t) = 0,\ i = 1,2,
\end{aligned} \tag{8.2}$$

and nonnegative initial conditions

$$S(x,0) = S_0(x), \quad u_i(x,0) = u_{0i}(x), \quad 0 \le x \le 1. \tag{8.3}$$

Next we discuss the well-posedness of the initial–boundary value problem (8.1)–(8.3) and the positivity of its solutions. Assume that the initial data in (8.3) satisfy $(S_0, u_{01}, u_{02}) \in X^+ = C([0,1], \mathbb{R}^3_+)$, the positive cone in the Banach space $X = C([0,1], \mathbb{R}^3)$ with uniform norm. For local existence and positivity of solutions in the space X^+, we follow [243], where existence and uniqueness and positivity are treated simultaneously, ignoring issues related to time delays treated there. The idea is to consider mild solutions of the system of abstract integral equations (we set $u_0 = S$ and $u_{00} = S_0$ to simplify notation)

$$\begin{aligned} u_0(t) &= V(t,0)u_{00} + \int_0^t T_0(t-r)B_0(u(r))dr, \\ u_i(t) &= T_i(t)u_{0i} + \int_0^t T_i(t-r)B_i(u(r))dr,\ i=1,2, \end{aligned} \tag{8.4}$$

where $u(t) = (u_0(t), u_1(t), u_2(t)) \equiv (S(\cdot,t), u_1(\cdot,t), u_2(\cdot,t)) \in X_+$. $T_i(t)$ is the positive, nonexpansive, analytic semigroup on $C([0,1],\mathbb{R})$ (see [326, Chapter 8]) such that $u = T_i(t)u_{0i}$ satisfies the linear initial value problem

$$\begin{aligned} &\frac{\partial u}{\partial t} = d_i \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x}, \\ &- d_i \frac{\partial u}{\partial x}(0,t) + vu(0,t) = 0 = \frac{\partial u}{\partial x}(1,t), \\ &u(x,0) = u_{0i}(x), \end{aligned} \tag{8.5}$$

$V(t,s)$, $t > s$, is the family of affine operators on $C([0,1],\mathbb{R})$ such that $u = V(t,s)u_{00}$ satisfies the linear system with inhomogeneous, periodic boundary conditions, with start time s, given by

$$\begin{aligned} &\frac{\partial u}{\partial t} = d_0 \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x},\ t > s, \\ &- d_0 \frac{\partial u}{\partial x}(0,t) + vu(0,t) = vS^0(t),\ t > s, \\ &\frac{\partial u}{\partial x}(1,t) = 0,\ t > s, \\ &u(x,s) = u_{00}(x). \end{aligned} \tag{8.6}$$

Due to the periodicity of the inhomogeneity in the boundary conditions, $S^0(t+\omega) = S^0(t)$, we have that $V(t,s) = V(t+\omega, s+\omega)$ for $t > s$. The nonlinear operator $B_i : C([0,1],\mathbb{R}_+) \to C([0,1],\mathbb{R})$ is defined by

$$\begin{aligned} B_0(u) &= -u_1 f_1(u_0) - f_2(u_0)u_2, \\ B_i(u) &= [f_i(u_0) - k_i]u_i,\ i = 1,2. \end{aligned}$$

The result [243, Theorem 1] can be used to give local existence and positivity of noncontinuable solutions of (8.1)–(8.3), although the elliptic operator in that setting is slightly different. The reason is that the semigroups T_i and evolution operator V defined above have the same properties as those in [243] (so [243, Corollary 4] may be applied). Indeed, $V(t,s)$ satisfies $V(t,s)C([0,1],\mathbb{R}_+) \subset C([0,1],\mathbb{R}_+)$ for $t > s$, by standard maximum principle arguments, and similarly (see [326, Chapter 8]), $T_i(t)C([0,1],\mathbb{R}_+) \subset C([0,1],\mathbb{R}_+)$ for $t > 0$. The operator V and semigroup T_0 are related as below (1.9) in [243] on setting $\gamma(x,t) = S^0(t)$. Since we assume that $f_i(0) = 0$, it follows that $B_i(u)(x) = 0$ whenever $u_i(x) = 0$ for some x; hence, $B = (B_0, B_1, B_2)$ is quasi-positive. Thus, [243, Theorem 1 and Remark 1.1] imply that (8.1)–(8.3) has a unique nonnegative noncontinuable solution that satisfies (8.1)–(8.2) in the classical sense for $t > 0$.

8.2 Unperturbed Model

Consider the system of equations with identical diffusivities and vanishing cell death rates

$$\begin{aligned}\frac{\partial S}{\partial t} &= d_0\frac{\partial^2 S}{\partial x^2} - v\frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S), \quad 0 < x < 1,\, t > 0,\\ \frac{\partial u_i}{\partial t} &= d_0\frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x} + u_i f_i(S), \quad i = 1,2,\ 0 < x < 1,\, t > 0,\end{aligned} \tag{8.7}$$

with boundary conditions

$$\begin{aligned}&d_0\frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t > 0,\\ &d_0\frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t) = 0, \quad i = 1,2,\, t > 0,\\ &\frac{\partial S(1,t)}{\partial x} = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad i = 1,2,\, t > 0,\end{aligned} \tag{8.8}$$

and initial value conditions

$$S(x,0) = S_0(x) \geq 0,\ u_i(x,0) = u_{0i}(x) \geq 0,\, i = 1,2,\, 0 \leq x \leq 1, \tag{8.9}$$

where $d_0 > 0$, $v > 0$, and $S^0(\cdot) \in C^2(\mathbb{R}_+,\mathbb{R})$, with $S^0(t) \geq 0, S^0(\cdot) \not\equiv 0$, $S^0(t+\omega) = S^0(t)$ for some real number $\omega > 0$, and $f_i(\cdot) \in C^2(\mathbb{R}_+,\mathbb{R}_+)$ satisfies

(H) $f_i(0) = 0, \quad f_i'(S) > 0, \forall S \in \mathbb{R}_+,\, i = 1,2.$

Let n be the outward normal to the boundary of $(0,1)$. Clearly, for any $\phi(\cdot) \in C^1([0,1],\mathbb{R})$,

$$\frac{\partial \phi(0)}{\partial n} = -\frac{\partial \phi(0)}{\partial x} \quad \text{and} \quad \frac{\partial \phi(1)}{\partial n} = \frac{\partial \phi(1)}{\partial x}.$$

Therefore, the boundary condition (8.8) is equivalent to the following one:

$$\begin{aligned}&d_0\frac{\partial S(0,t)}{\partial n} + vS(0,t) = vS^0(t), \qquad t > 0,\\ &d_0\frac{\partial u_i(0,t)}{\partial n} + vu_i(0,t) = 0, \qquad i = 1,2,\ t > 0,\\ &\frac{\partial S(1,t)}{\partial n} = \frac{\partial u_i(1,t)}{\partial n} = 0, \qquad i = 1,2,\ t > 0.\end{aligned} \tag{8.10}$$

Let $X^+ = C([0,1],\mathbb{R}^3_+)$. As mentioned in Section 8.1, [243, Theorem 1 and Remark 1.1] imply that for any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$, there exists a unique (mild) solution $(S(x,t,\phi), u_1(x,t,\phi), u_2(x,t,\phi))$ of (8.7)-(8.8), defined on its maximal interval of existence $[0,\sigma_\phi)$, satisfying

$$S(x,t,\phi) \geq 0,\ u_i(x,t,\phi) \geq 0,\, \forall x \in [0,1],\, t \in [0,\sigma_\phi),\, i = 1,2.$$

Moreover, $(S(x,t,\phi), u_1(x,t,\phi),\ u_2(x,t,\phi))$ is a classical solution of (8.7)–(8.8) for $t \in (0,\sigma_\phi)$.

8.2.1 Conservation Principle

Since we have scaled the u_i in nutrient-equivalent units, the total nutrient $W(x,t) = S(x,t)+u_1(x,t)+u_2(x,t)$ should eventually come into balance with the input $S^0(t)$. Then $W(x,t)$ satisfies the following scalar linear equation

$$\begin{aligned} &\frac{\partial W}{\partial t} = d_0\frac{\partial^2 W}{\partial x^2} - v\frac{\partial W}{\partial x}, \quad 0 < x < 1,\, t > 0, \\ &d_0\frac{\partial W(0,t)}{\partial n} + vW(0,t) = vS^0(t), \quad t > 0, \\ &\frac{\partial W(1,t)}{\partial n} = 0, \quad t > 0. \end{aligned} \tag{8.11}$$

Note that equations (8.7)–(8.8) reduce to (8.11) for $W = S$ when $u_i = 0,\, i = 1,2$. In what follows, we use $B\phi = 0$ to denote the homogeneous boundary conditions $d_0\frac{\partial\phi(0)}{\partial n} + v\phi(0) = 0$ and $\frac{\partial\phi(1)}{\partial n} = 0$.

Proposition 8.2.1. *System (8.11) admits a unique positive ω-periodic solution $W^*(x,t) > 0$, and for any $W_0(\cdot) \in C([0,1],\mathbb{R})$, the unique (mild) solution $W(x,t)$ of (8.11) with $W(\cdot,0) = W_0(\cdot)$ satisfies $\lim_{t\to\infty}(W(x,t) - W^*(x,t)) = 0$ uniformly for $x \in [0,1]$.*

Proof. Let $u(x,t) = W(x,t) - S^0(t)$ and $S_1(t) = -\frac{dS^0(t)}{dt}$, $t \geq 0$. Then $u(x,t)$ satisfies

$$\begin{aligned} &\frac{\partial u}{\partial t} = d_0\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + S_1(t), \quad 0 < x < 1,\, t > 0, \\ &d_0\frac{\partial u(0,t)}{\partial n} + vu(0,t) = 0, \quad t > 0, \\ &\frac{\partial u(1,t)}{\partial n} = 0, \quad t > 0. \end{aligned} \tag{8.12}$$

Since the boundary conditions in (8.12) are homogeneous, (8.12) can then be written as an abstract ordinary differential equation in $C([0,1],\mathbb{R})$ given by

$$\begin{aligned} &\frac{du}{dt} = Au(t) + S_1(t), \quad t > 0, \\ &u(0) = \phi \in C([0,1]),\mathbb{R}), \end{aligned} \tag{8.13}$$

where A is the closure in $C([0,1],\mathbb{R})$ of $A^0 = d_0\partial/\partial x^2 - v\partial/\partial x$ with

$$D(A^0) = \left\{\phi \in C^2((0,1)) \cap C^1([0,1]) :\, A^0\phi \in C([0,1]), B\phi = 0\right\}.$$

For any $\phi \in C([0,1],\mathbb{R})$, the mild solution of (8.12) can be expressed as

$$u(t) = T(t)\phi + \int_0^t T(t-s)S_1(s)ds, \tag{8.14}$$

where $T(t)$ is the analytic semigroup generated by A in $C([0,1],\mathbb{R})$ (see, e.g., [272] and [326, Chapter 7.1]). It easily follows that $u(t)$ is an ω-periodic solution of (8.13) if and only if $u_0 = u(0)$ satisfies

$$(I - T(\omega))u_0 = \int_0^\omega T(t-s)S_1(s)ds. \tag{8.15}$$

By an argument similar to that in [326, Section 8.1], it follows that $\sigma = \sup\{\text{Re}\lambda : \lambda \in \sigma(A)\} < 0$. Then the radius of the spectrum of the compact operator $T(\omega)$ satisfies $r(T(\omega)) < 1$, and hence (8.13) admits a unique ω-periodic solution $u^*(t)$. Let $v(t) = u(t) - u^*(t)$. Then $v(t)$ satisfies

$$\frac{dv(t)}{dt} = Av(t), \quad t > 0. \tag{8.16}$$

By [272, Theorem 4.4.3], there exist $M > 0$ and $\mu > 0$ such that $\|T(t)\| \leq Me^{-\mu t}, t \geq 0$, and hence $\lim_{t\to\infty} v(t) = 0$ in $C([0,1],\mathbb{R})$. Then $\lim_{t\to\infty}(u(x,t) - u^*(x,t)) = 0$ uniformly for $x \in [0,1]$.

Let $W^*(x,t) = u^*(x,t) + S^0(t)$, $x \in [0,1], t \geq 0$. It then follows that $W^*(x,t)$ is an ω-periodic solution of (8.11), and for any $W_0(\cdot) \in C([0,1],\mathbb{R})$, the unique (mild) solution $W(x,t)$ of (8.11) with $W(\cdot,0) = W_0(\cdot)$ satisfies

$$\lim_{t\to\infty} (W(x,t) - W^*(x,t)) = 0, \text{ uniformly for } x \in [0,1]. \tag{8.17}$$

For any $W_0(\cdot) \in C([0,1],\mathbb{R}_+)$, by [243, Theorem 1 and Remark 1.1], the unique solution $W(x,t)$ of (8.11) with $W(\cdot,0) = W_0(\cdot)$ satisfies

$$W(x,t) \geq 0, \ \forall x \in [0,1], \ t \geq 0. \tag{8.18}$$

It remains to prove that $W^*(x,t) > 0$, for all $x \in [0,1]$ and $t \geq 0$. For any $t \geq 0$, by (8.17) we have $\lim_{n\to\infty}(W(x,t+n\omega) - W^*(x,t+n\omega)) = \lim_{n\to\infty}(W(x,t+n\omega) - W^*(x,t)) = 0$, uniformly for $x \in [0,1]$. Then $W^*(x,t) = \lim_{n\to\infty} W(x,t+n\omega) \geq 0, \forall x \in [0,1], t \geq 0$. Since $S^0(t) \geq 0, S^0(\cdot) \not\equiv 0$, there exists $t_0 > 0$ such that $S^0(t_0) > 0$. It is easy to see that $d_0\frac{\partial u^*(0,t_0)}{\partial n} + vu^*(0,t_0) = 0$ implies $u^*(\cdot,t_0) \not\equiv -S^0(t_0)$. Then $W^*(\cdot,t_0) = u^*(\cdot,t_0) + S^0(t_0) \not\equiv 0$. By the standard parabolic maximum principle, it follows that

$$W^*(x,t) > 0, \ \forall x \in [0,1], \ t > t_0. \tag{8.19}$$

Then, by the ω-periodicity of $W^*(x,\cdot)$, we have $W^*(x,t) > 0, \ \forall x \in [0,1]$, $t \geq 0$. ∎

8.2.2 Single Species Growth

If only one microbial species is present in the reactor, we have the single species model

$$\begin{aligned} \frac{\partial S}{\partial t} &= d_0\frac{\partial^2 S}{\partial x^2} - v\frac{\partial S}{\partial x} - uf(S), \quad 0 < x < 1, \ t > 0, \\ \frac{\partial u}{\partial t} &= d_0\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + uf(S), \quad 0 < x < 1, \ t > 0, \end{aligned} \tag{8.20}$$

with boundary conditions

$$\begin{aligned} &d_0 \frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t > 0, \\ &d_0 \frac{\partial u(0,t)}{\partial x} - vu(0,t) = 0, \quad t > 0, \\ &\frac{\partial S(1,t)}{\partial x} = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0, \end{aligned} \tag{8.21}$$

and initial conditions

$$S(x,0) = S_0(x) \geq 0,\ u(x,0) = u_0(x) \geq 0,\ \forall x \in [0,1], \tag{8.22}$$

where $d_0 > 0, v > 0,\ f(\cdot) \in C^2(\mathbb{R}_+, \mathbb{R}_+)$ satisfies (H) and $S^0(\cdot)$ is as in (8.8). Let $Y^+ = C([0,1], \mathbb{R}_+^2)$. It then follows that for any $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$, (8.20)–(8.22) admits a unique (mild) solution $(S(x,t,\phi), u(x,t,\phi))$, defined on its maximal interval of existence $[0, \sigma_\phi)$, satisfying $S(x,t,\phi) \geq 0, u(x,t,\phi) \geq 0$, $\forall x \in [0,1], t \in [0, \sigma_\phi)$. By the conservation principle in Subsection 8.2.1, for each $\phi \in Y^+, \sigma_\phi = \infty$.

We determine stability of periodic solutions in the following way. For any $m \in C^1([0,1] \times \mathbb{R}, \mathbb{R})$ with $m(x,t+\omega) = m(x,t), \forall x \in [0,1],\ t \in \mathbb{R}$, let $\mu(m(\cdot,\cdot))$ be the unique principal eigenvalue of the periodic–parabolic eigenvalue problem (see [152, Section II.14])

$$\begin{aligned} &\frac{\partial \varphi}{\partial t} = d_0 \frac{\partial \varphi}{\partial x^2} - v \frac{\partial \varphi}{\partial x} + m(x,t)\varphi + \mu\varphi, \qquad x \in (0,1),\ t \in \mathbb{R}, \\ &d_0 \frac{\partial \varphi(0,t)}{\partial x} - v\varphi(0,t) = \frac{\partial \varphi(1,t)}{\partial x} = 0, \quad t \in \mathbb{R}, \\ &\varphi\ \omega\text{-periodic in } t. \end{aligned} \tag{8.23}$$

The main result of this subsection says that if the washout periodic solution $(S,u) = (W^*, 0)$ is stable or neutrally stable in the linear approximation then it is globally stable, while if it is unstable then there exists a unique positive periodic solution representing survival of the population to which all other solutions with $u_0 \neq 0$ approach asymptotically.

Theorem 8.2.1. *Let $W^*(x,t)$ be as in Proposition 8.2.1.*

(a) If $\mu(f(W^*(x,t))) \geq 0$, then for any $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$, $\lim_{t\to\infty}(S(x,t,\phi) - W^*(x,t)) = 0$ and $\lim_{t\to\infty} u(x,t,\phi) = 0$ uniformly for $x \in [0,1]$;

(b) If $\mu(f(W^*(x,t))) < 0$, then (8.20)–(8.21) admits a unique positive ω-periodic solution $(S^*(x,t), u^*(x,t))$ and for any $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$ with $u_0(\cdot) \not\equiv 0$, $\lim_{t\to\infty}(S(x,t,\phi) - S^*(x,t)) = 0$ and $\lim_{t\to\infty}(u(x,t,\phi) - u^*(x,t)) = 0$ uniformly for $x \in [0,1]$. Moreover, $(S^*(x,t), u^*(x,t))$ is linearly asymptotically stable for (8.20)–(8.21).

Proof. Let $\hat{f}(\cdot) : \mathbb{R} \to \mathbb{R}$ be a smooth extension of $f(\cdot) : \mathbb{R}_+ \to \mathbb{R}_+$ such that $\hat{f}(0) = 0, \hat{f}'(s) > 0, \quad \forall s \in \mathbb{R}$, and $\hat{f}(s) = f(s), \forall s \in \mathbb{R}_+$. Let $W = S + u$. Then system (8.20) with (8.21) is equivalent to the system

$$\begin{aligned} \frac{\partial W}{\partial t} &= d_0 \frac{\partial^2 W}{\partial x^2} - v \frac{\partial W}{\partial x}, \quad 0 < x < 1,\, t > 0, \\ \frac{\partial u}{\partial t} &= d_0 \frac{\partial^2 u}{\partial x^2} - v \frac{\partial u}{\partial x} + u f(W - u), \quad 0 < x < 1,\, t > 0, \end{aligned} \tag{8.24}$$

with boundary conditions

$$\begin{aligned} & d_0 \frac{\partial W(0,t)}{\partial x} - v W(0,t) = -v S^0(t), \quad t > 0, \\ & d_0 \frac{\partial u(0,t)}{\partial x} - v u(0,t) = 0, \quad t > 0, \\ & \frac{\partial W(1,t)}{\partial x} = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0. \end{aligned} \tag{8.25}$$

Given $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$, let $(W(x,t), u(x,t))$ be the unique solution of (8.24)–(8.25) satisfying $(W(x,0), u(x,0)) = (S_0(x) + u_0(x), u_0(x)), x \in [0,1]$. Then $U(x,t) = u(x, t+\omega)$, $x \in [0,1]$, $t \geq 0$, satisfies the nonautonomous scalar parabolic equation

$$\begin{aligned} & \frac{\partial u}{\partial t} = d_0 \frac{\partial^2 u}{\partial x^2} - v \frac{\partial u}{\partial x} + u \hat{f}(W(x, t+\omega) - u), \quad 0 < x < 1,\, t > 0, \\ & d_0 \frac{\partial u(0,t)}{\partial x} - v u(0,t) = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0. \end{aligned} \tag{8.26}$$

By the conservation principle, $\lim_{t\to\infty}(W(x,t) - W^*(x,t)) = 0$ uniformly for $x \in [0,1]$, and hence (8.26) is asymptotic to the following periodic scalar parabolic equation

$$\begin{aligned} & \frac{\partial u}{\partial t} = d_0 \frac{\partial^2 u}{\partial x^2} - v \frac{\partial u}{\partial x} + u \hat{f}(W^*(x,t) - u), \quad 0 < x < 1,\, t > 0, \\ & d_0 \frac{\partial u(0,t)}{\partial x} - v u(0,t) = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0. \end{aligned} \tag{8.27}$$

Let $1 < p < \infty$, and let $X^0 = L^p(0,1)$ and $X^1 = W^2_{p,B}(0,1)$. For $\beta \in (1/2 + 1/(2p), 1)$, let X^β be the fractional power space of X^0 with respect to (A^0, B) (see, e.g., [150]). Then $X^1 \subset X^\beta \subset X^0$ and $X^\beta \hookrightarrow C^{1+\lambda}[0,1]$ for some $\lambda > 0$. Clearly, $U(\cdot, 0) = u(\cdot, \omega) \in X^1 \subset X^\beta$. By Theorem 3.2.2, it follows that

(a) If $\mu(f(W^*(x,t))) \geq 0$, $\lim_{t\to\infty} U(x,t) = 0$, and hence $\lim_{t\to\infty} u(x,t) = 0$, uniformly for $x \in [0,1]$;
(b) If $\mu(f(W^*(x,t))) < 0$, (8.27) admits a unique positive ω-periodic solution $u^*(x,t)$ and $\lim_{t\to\infty}(U(x,t) - u^*(x,t)) = 0$, and hence $\lim_{t\to\infty}(u(x,t) - u^*(x,t)) = \lim_{t\to\infty}(U(x,t-\omega) - u^*(x,t-\omega)) = 0$, uniformly for $x \in [0,1]$.

In case (a), $\lim_{t\to\infty}(S(x,t) - W^*(x,t)) = \lim_{t\to\infty}[(W(x,t) - W^*(x,t)) - u(x,t)] = 0$ uniformly for $x \in [0,1]$; In case (b), let $S^*(x,t) = W^*(x,t) - u^*(x,t)$. Then $\lim_{t\to\infty}(S(x,t) - S^*(x,t)) = \lim_{t\to\infty}[(W(x,t) - W^*(x,t)) - (u(x,t) - u^*(x,t))] = 0$ uniformly for $x \in [0,1]$. We further claim that $(S^*(x,t), u^*(x,t))$ is a positive ω-periodic solution of (8.20)–(8.21). It then suffices to prove that $W^*(x,t) > u^*(x,t)$, $\forall x \in [0,1], t \geq 0$. Since $d_0 \frac{\partial W^*(0,t)}{\partial n} + vW^*(x,t) = vS^0(t) \geq 0$ and $\frac{\partial W^*(1,t)}{\partial n} = 0, t > 0$, $W^*(x,t)$ is an upper solution of (8.27). Let $u_0(x,t)$ be the unique solution of (8.27) with $u_0(\cdot,0) = W^*(\cdot,0)$. Then $u_0(x,t) \leq W^*(x,t)$, $\forall x \in [0,1]$, $t \geq 0$. It then follows that

$$u_0(x, t + n\omega) \leq W^*(x, t + n\omega) = W^*(x,t),\ \forall t \geq 0,\ n \geq 0. \tag{8.28}$$

Since $\lim_{t\to\infty}(u_0(x,t) - u^*(x,t)) = 0$ uniformly for $x \in [0,1]$, letting $n \to \infty$ in (8.28), we have

$$u^*(x,t) \leq W^*(x,t), \quad \forall x \in [0,1],\ t \geq 0.$$

Let $t_0 > 0$ be such that $S^0(t_0) > 0$. Clearly, the boundary conditions for $W^*(x,t)$ and $u^*(x,t)$ in (8.11) and (8.27) imply that $u^*(\cdot,t_0) \not\equiv W^*(\cdot,t_0)$. Then, by the parabolic maximum principle, we get

$$u^*(x,t) < W^*(x,t), \quad \forall x \in [0,1],\ t > t_0,$$

and hence by the ω-periodicity of $u^*(x,t)$ and $W^*(x,t)$,

$$u^*(x,t) < W^*(x,t), \quad \forall x \in [0,1],\ t \geq 0.$$

Let $P : Y^+ \to Y^+$ be the Poincaré map associated with (8.20)–(8.21); that is, $P(\phi) = (S(\cdot,\omega,\phi), u(\cdot,\omega,\phi))$, $\forall \phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$. Let $\phi_0 = (S^*(\cdot,0), u^*(\cdot,0))$. Clearly, $P(\phi_0) = \phi_0$. It remains to prove the linear asymptotic stability of the positive periodic solution $(S^*(x,t), u^*(x,t))$ in the sense that $r(D_\phi P(\phi_0)) < 1$. Let $\bar{S} = S - S^*, \bar{u} = u - u^*$. We then get the linearization of (8.20)–(8.21) at $(S^*(x,t), u^*(x,t))$ given by

$$\begin{aligned} \frac{\partial \bar{S}}{\partial t} &= d_0 \frac{\partial^2 \bar{S}}{\partial x^2} - v\frac{\partial \bar{S}}{\partial x} - u^*(x,t) f'(S^*(x,t))\bar{S} - f(S^*(x,t))\bar{u}, \\ \frac{\partial \bar{u}}{\partial t} &= d_0 \frac{\partial^2 \bar{u}}{\partial x^2} - v\frac{\partial \bar{u}}{\partial x} + u^*(x,t) f'(S^*(x,t))\bar{S} + f(S^*(x,t))\bar{u}, \end{aligned} \tag{8.29}$$

with homogeneous boundary conditions

$$\begin{aligned} & d_0 \frac{\partial \bar{S}(0,t)}{\partial x} - v\bar{S}(0,t) = 0, \quad t > 0, \\ & d_0 \frac{\partial \bar{u}(0,t)}{\partial x} - v\bar{u}(0,t) = 0, \quad t > 0, \\ & \frac{\partial \bar{S}(1,t)}{\partial x} = \frac{\partial \bar{u}(1,t)}{\partial x} = 0, \quad t > 0. \end{aligned} \tag{8.30}$$

Let $\overline{U}(t,s)$, $t \geq s \geq 0$, be the evolution operator of linear system (8.29)–(8.30). It easily follows that $D_\phi P(\phi_0) = \overline{U}(\omega, 0)$. Under the change of variables $w = \bar{S} + \bar{u}$, $z = \bar{u}$, that is,

$$\begin{pmatrix} w \\ z \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} \bar{S} \\ \bar{u} \end{pmatrix},$$

(8.29)–(8.30) is then transformed into the system

$$\begin{aligned} \frac{\partial w}{\partial t} &= d_0 \frac{\partial^2 w}{\partial x^2} - v\frac{\partial w}{\partial x}, \quad 0 < x < 1,\, t > 0, \\ \frac{\partial z}{\partial t} &= d_0 \frac{\partial^2 z}{\partial x^2} - v\frac{\partial z}{\partial x} + u^*(x,t) f'(S^*(x,t)) w \\ &\quad + \left(f(S^*(x,t)) - u^*(x,t) f'(S^*(x,t))\right) z, \quad 0 < x < 1,\, t > 0, \end{aligned} \tag{8.31}$$

with boundary conditions

$$\begin{aligned} d_0 \frac{\partial w(0,t)}{\partial x} - v w(0,t) &= 0, \quad t > 0, \\ d_0 \frac{\partial z(0,t)}{\partial x} - v z(0,t) &= 0, \quad t > 0, \\ \frac{\partial w(1,t)}{\partial x} = \frac{\partial z(1,t)}{\partial x} &= 0, \quad t > 0. \end{aligned} \tag{8.32}$$

Let $U_1(t,s)$, $t \geq s \geq 0$, be the evolution operator of the linear equation

$$\begin{aligned} \frac{\partial w}{\partial t} &= d_0 \frac{\partial^2 w}{\partial x^2} - v\frac{\partial w}{\partial x}, \quad 0 < x < 1,\, t > 0, \\ d_0 \frac{\partial w(0,t)}{\partial x} - v w(0,t) &= \frac{\partial w(1,t)}{\partial x} = 0, \quad t > 0, \end{aligned} \tag{8.33}$$

and let $U_2(t,s)$, $t \geq s \geq 0$, be the evolution operator of the periodic linear equation

$$\begin{aligned} \frac{\partial z}{\partial t} &= d_0 \frac{\partial^2 z}{\partial x^2} - v\frac{\partial z}{\partial x} + \left(f(S^*(x,t)) - u^*(x,t) f'(S^*(x,t))\right) z, \\ d_0 \frac{\partial z(0,t)}{\partial x} - v z(0,t) &= \frac{\partial z(1,t)}{\partial x} = 0. \end{aligned} \tag{8.34}$$

Then

$$U(t,s) = \begin{pmatrix} U_1(t,s) & 0 \\ \int_s^t U_2(t,\tau) u^*(\cdot,\tau) f'(S^*(\cdot,\tau)) U_1(\tau,s) d\tau & U_2(t,s) \end{pmatrix} \tag{8.35}$$

is the evolution operator of periodic linear system (8.31)–(8.32). In particular,

$$U(\omega,0) = \begin{pmatrix} U_1(\omega,0) & 0 \\ \int_0^\omega U_2(\omega,\tau) u^*(\cdot,\tau) f'(S^*(\cdot,\tau)) U_1(\tau,0) d\tau & U_2(\omega,0) \end{pmatrix}. \tag{8.36}$$

As claimed in Subsection 8.2.1, $r(U_1(\omega,0)) < 1$. By the definition of principal eigenvalue (see [152, Proposition 14.4]), we have

$$\mu(f(S^*(x,t) - u^*(x,t)f'(S^*(x,t))) = -\frac{1}{\omega}\ln(r(U_2(\omega,0))).$$

Since $(S^*(x,t), u^*(x,t))$ is an ω-periodic solution of (8.20)–(8.21), $u^*(x,t)$ satisfies the periodic linear equation

$$\begin{aligned}
&\frac{\partial u}{\partial t} = d_0\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + f(S^*(x,t))u,\ 0 < x < 1,\ t > 0,\\
&d_0\frac{\partial u(0,t)}{\partial x} - vu(0,t) = \frac{\partial u(1,t)}{\partial x} = 0,\ t > 0.
\end{aligned} \tag{8.37}$$

Then, by the uniqueness of the principal eigenvalue, we have $\mu(f(S^*(x,t))) = 0$. Since $f(S^*(x,t)) - u^*(x,t)f'(S^*(x,t)) < f(S^*(x,t))$, by the monotonicity of the principal eigenvalue ([152, Lemma 15.5]),

$$\mu\left(f^*(S^*(x,t) - u^*(x,t)f'(S^*(x,t))\right) > \mu\left(f(S^*(x,t))\right) = 0.$$

Therefore, $r(U_2(\omega,0)) < 1$. Clearly, $U(\omega,0) : Y = C([0,1],R)\times C([0,1],\mathbb{R}^2) \to Y$ is a compact and positive operator. We further claim that $r(U(\omega,0)) < 1$. Indeed, let $\alpha = r(U(\omega,0))$. If $\alpha = 0$, obviously we have $r(U(\omega,0)) < 1$. In the case where $\alpha > 0$, by the Krein–Rutman theorem (see, e.g., [152, Theorem 7.1]), there exists $\phi = \begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} > 0$ in Y such that

$$U(\omega,0)\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} = \alpha\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix}.$$

Then $U_1(\omega,0)\phi_1 = \alpha\phi_1$. If $\phi_1 > 0$, then $\alpha = r(U_1(\omega,0)) < 1$. If $\phi_1 = 0$, then $\phi_2 > 0$ and $U_2(\omega,0)\phi_2 = \alpha\phi_2$, and hence, $\alpha = r(U_2(\omega,0)) < 1$. Clearly,

$$\overline{U}(\omega,0) = \begin{pmatrix}1 & -1\\ 0 & 1\end{pmatrix} U(\omega,0)\begin{pmatrix}1 & -1\\ 0 & 1\end{pmatrix}^{-1}.$$

It then follows that $r(D_\phi P(\phi_0)) = r(\overline{U}(\omega,0)) = r(U(\omega,0)) < 1$. ∎

8.2.3 Two-Species Competition

For any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$, let

$$\Phi(x,t,\phi) = (S(x,t), u_1(x,t), u_2(x,t))$$

be the unique (mild) solution of (8.7)–(8.8) with $\Phi(\cdot,0,\phi) = \phi$. Then $S(x,t) \geq 0, u_i(x,t) \geq 0$, $\forall x \in [0,1]$, $t \in [0,\sigma_\phi)$, $i = 1,2$. By the conservation principle, for each $\phi \in Y^+$, $\sigma_\phi = \infty$.

In the case where $\mu(f_i(W^*(x,t))) < 0$, $i = 1,2$, according to Theorem 8.2.1, let $(S_i^*(x,t), u_i^*(x,t))$ be the unique positive ω-periodic solution of (8.20)–(8.21) with $f(\cdot) = f_i(\cdot)$, $i = 1,2$, respectively. As shown in the proof of Theorem 8.2.1, for each $1 \le i \le 2$,

$$W^*(x,t) > u_i^*(x,t), \quad S_i^*(x,t) = W^*(x,t) - u_i^*(x,t), \ \forall x \in [0,1],\ t \ge 0,$$

and $u_i^*(x,t)$ is the unique positive ω-periodic solution of the periodic-parabolic equation

$$\begin{aligned} &\frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x} + u_i f_i(W^*(x,t) - u_i), \quad 0 < x < 1,\ t > 0, \\ &d_0 \frac{\partial u_i(0,t)}{\partial x} - v u_i(0,t) = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad t \ge 0. \end{aligned}$$

We now show that if each population can survive in the bioreactor in the absence of competition and if each population can invade the other's single-population periodic solution, then there exist two, not necessarily distinct, positive periodic solutions, each representing coexistence of the two populations, and system (8.7)–(8.8) is uniformly persistent.

Theorem 8.2.2. *Assume that*

(1) $\mu(f_i(W^*(x,t))) < 0$, $\forall i = 1,2$*;*
(2) $\mu(f_1(S_2^*(x,t))) < 0$ *and* $\mu(f_2(S_1^*(x,t))) < 0$.

Then system (8.7)–(8.8) admits two positive ω-periodic solutions $(\bar{S}_1^*(x,t), \bar{u}_{1*}(x,t),\ \bar{u}_2^*(x,t))$ *and* $(\bar{S}_2^*(x,t), \bar{u}_1^*(x,t), \bar{u}_{2*}(x,t))$ *with*

$$\bar{u}_i^*(x,t) \ge \bar{u}_{i*}(x,t),\ \forall x \in [0,1], t \in \mathbb{R}_+, i = 1,2,$$

and for any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$ *with* $u_{0i}(\cdot) \not\equiv 0$, $\forall i = 1,2$, $\Phi(x,t,\phi) = (S(x,t), u_1(x,t), u_2(x,t))$ *satisfies*

$$\lim_{t\to\infty} d(u_i(x,t), [\bar{u}_{i*}(x,t), \bar{u}_i^*(x,t)]) = 0,\ i = 1,2,\ \text{uniformly for } x \in [0,1].$$

Proof. For each $1 \le i \le 2$, let $\hat{f}_i(\cdot) : \mathbb{R} \to \mathbb{R}$ be a smooth extension of $f_i(\cdot) : \mathbb{R}_+ \to \mathbb{R}$ such that $\hat{f}_i(0) = 0$, $\hat{f}_i'(s) > 0$, $\forall s \in \mathbb{R}$, and $\hat{f}_i(s) = f_i(s)$, $\forall s \in \mathbb{R}_+$. Let $W = S + u_1 + u_2$. Then system (8.7) with (8.8) is equivalent to the system

$$\begin{aligned} &\frac{\partial W}{\partial t} = d_0 \frac{\partial^2 W}{\partial x^2} - v\frac{\partial W}{\partial x}, \quad 0 < x < 1,\ t > 0, \\ &\frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x} \\ &\qquad + u_i f_i(W - u_1 - u_2), \quad i = 1,2,\ 0 < x < 1,\ t > 0, \end{aligned} \tag{8.38}$$

with boundary conditions

$$\begin{aligned} & d_0 \frac{\partial W(0,t)}{\partial x} - vW(0,t) = -vS^0(t), \quad t > 0, \\ & d_0 \frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t) = 0, \quad i = 1, 2,\, t > 0, \\ & \frac{\partial W(1,t)}{\partial x} = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad i = 1, 2,\, t > 0. \end{aligned} \tag{8.39}$$

Given $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$, let

$$\Phi(x, t, \phi) = (S(x, t), u_1(x, t), u_2(x, t)),\ \forall x \in [0, 1],\, t \geq 0,$$

and let

$$(U_1(x, t), U_2(x, t)) = (u_1(x, t + \omega), u_2(x, t + \omega)),\ \forall x \in [0, 1],\, t \geq 0.$$

Then $(U_1(x, t), U_2(x, t))$ satisfies the following nonautonomous parabolic system

$$\begin{aligned} & \frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i \hat{f}_i(W(x, t + \omega) - u_1 - u_2), \quad i = 1, 2, \\ & Bu_i = 0, \quad i = 1, 2. \end{aligned} \tag{8.40}$$

By the conservation principle, $\lim_{t\to\infty}(W(x, t) - W^*(x, t)) = 0$ uniformly for $x \in [0, 1]$, and hence (8.40) is asymptotic to the following periodic-parabolic system

$$\begin{aligned} & \frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i \hat{f}_i(W^*(x, t) - u_1 - u_2), \quad i = 1, 2, \\ & Bu_i = 0, \quad i = 1, 2. \end{aligned} \tag{8.41}$$

Let X^β be as in the proof of Theorem 8.2.1, let $Z = X^\beta \times X^\beta$, and let Z^+ be the usual positive cone of Z. Since $(U_1(\cdot, 0), U_2(\cdot, 0)) = (u_1(\cdot, \omega), u_2(\cdot, \omega)) \in Z$, we consider systems (8.40) and (8.41) with initial values in Z^+. Let $\Delta = \{(t, s) : 0 \leq s \leq t < \infty\}$. Define $\tilde{\Phi} : \Delta \times Z^+ \to Z^+$ by $\tilde{\Phi}(t, s, \psi) = \tilde{u}(\cdot, t, s, \psi), t \geq s \geq 0, \psi \in Z^+$, where $\tilde{u}(x, t, s, \psi) = (\tilde{u}_1(x, t, s, \psi), \tilde{u}_2(x, t, s, \psi))$ is the unique solution of (8.40) with $\tilde{u}(\cdot, s, s, \psi) = \psi$. Define $T_n : Z^+ \to Z^+, n \geq 0$, by $T_n(\psi) = \tilde{\Phi}(n\omega, 0, \psi), \psi \in Z^+$. Let $T(t) : Z^+ \to Z^+$, $t \geq 0$, be the periodic semiflow generated by periodic system (8.41), i.e., $T(t)\psi = u(\cdot, t, \psi)$, where $u(x, t, \psi)$ is the unique solution of (8.41) with $u(\cdot, 0, \psi) = \psi$. Clearly, $Q = T(\omega) : Z^+ \to Z^+$ is the Poincaré map associated with the periodic system (8.41). Then, by Proposition 3.2.1, $\tilde{\Phi} : \Delta \times Z^+ \to Z^+$ is an asymptotically periodic semiflow with limit ω-periodic semiflow $T(t) : Z^+ \to Z^+, t \geq 0$, and hence $T_n : Z^+ \to Z^+, n \geq 0$, is an asymptotically autonomous discrete process with limit $Q : Z^+ \to Z^+$. Moreover, for any $\psi \in Z^+$, $\gamma^+(\psi) = \{T_n(\psi) : n \geq 0\}$ is precompact in Z^+. Let (Z, P) be the ordered Banach space with the positive cone $P = X^\beta_+ \times (-X^\beta_+)$, where X^β_+ is the usual positive cone of X^β, and denote its order by $\leq_P$. It then follows that $T(t) : Z^+ \to Z^+$, $t \geq 0$, is monotone with respect to $\leq_P$ in the sense that if $\phi, \psi \in Z^+$ with $\phi \leq_P \psi$, then $T(t)\phi \leq_P T(t)\psi$, $\forall t \geq 0$.

Clearly, condition (2) implies $\mu(f_1(W^*(x,t) - u_2^*(x,t))) = \mu(f_1(S_2^*(x,t))) < 0$ and $\mu(f_2(W^*(x,t) - u_1^*(x,t))) = \mu(f_2(S_1^*(x,t))) < 0$. By Theorem 2.4.2, as applied to the Poincaré map associated with (8.41), or an argument similar to that in [152, Theorem 33.3], it then follows that (8.41) admits two positive ω-periodic solutions $(\bar{u}_{1*}(x,t), \bar{u}_2^*(x,t))$ and $(\bar{u}_1^*(x,t), \bar{u}_{2*}(x,t))$ with

$$\bar{u}_{i*}(x,t) \leq \bar{u}_i^*(x,t),\ \forall x \in [0,1],\ t \geq 0,$$

such that the compressive dynamics stated in Theorem 8.2.2 holds for (8.41) on Z^+. Let $E_1^* = (\bar{u}_{1*}(\cdot,0), \bar{u}_2^*(\cdot,0))$ and $E_2^* = (\bar{u}_1^*(\cdot,0), \bar{u}_{2*}(\cdot,0))$. Clearly, $Q(E_i^*) = E_i^*$, $i = 1,2$. Let $Z_0 := \{(\phi_1,\phi_2) \in Z^+ : \phi_i(\cdot) \not\equiv 0, i = 1,2\}$ and $\partial Z_0 := Z^+ \setminus Z_0$. Clearly, $Q : Z_0 \to Z_0$, and $Q : \partial Z_0 \to \partial Z_0$. It then follows that $Q : Z_0 \to Z_0$ admits a global attractor $A_0 \subset [E_1^*, E_2^*]_P$. Let $M_0 = (0,0)$, $M_1 = (u_1^*(\cdot,0),0)$, and $M_2 = (0, u_2^*(\cdot,0))$. It is easy to see that $\cup_{i=0}^2 M_i$ is an isolated and acyclic covering of $\cup_{\phi\in\partial Z_0}\omega(\phi)$ for $Q : \partial Z_0 \to \partial Z_0$. By our assumptions and Proposition 3.2.3, we have $\tilde{W}^s(M_i) \cap Z_0 = \emptyset$, $\forall i = 0,1,2$, where $\tilde{W}^s(M_i)$ is the stable set of M_i with respect to $T_n : Z^+ \to Z^+, n \geq 0$. By Lemma 1.2.2, every ω-limit set $\omega(\phi)$ of $\gamma^+(\phi) = \{T_n(\phi) : n \geq 0\}$ is internally chain transitive for $Q : Z^+ \to Z^+$. By Theorem 1.2.1, it then follows that $\omega(\psi) \subset A_0$, $\forall \psi \in Z_0$. By Theorem 3.2.1, $\lim_{t\to\infty} d(\tilde{u}(\cdot,t,0,\psi), T(t)A_0) = 0$. Since $E_1^* \leq_P A_0 \leq_P E_2^*$, by the monotonicity of $T(t) : Z^+ \to Z^+$, $t \geq 0$, we have

$$T(t)E_1^* \leq_P T(t)A_0 \leq_P T(t)E_2^*, \quad \forall t \geq 0. \tag{8.42}$$

Note that

$$T(t)E_1^* = (\bar{u}_{1*}(\cdot,t), \bar{u}_2^*(\cdot,t)), \quad \text{and} \quad T(t)E_2^* = (\bar{u}_1^*(\cdot,t), \bar{u}_{2*}(\cdot,t)),\ \forall t \geq 0.$$

For any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$ with $u_{0i}(\cdot) \not\equiv 0$, $\forall i = 1,2$, since $(U_1(\cdot,0), U_2(\cdot,0)) \in Z_0$, we have

$$\begin{aligned}&\lim_{t\to\infty} d(u_i(x,t), [\bar{u}_{i*}(x,t), \bar{u}_i^*(x,t)])\\ &\quad = \lim_{t\to\infty} d(U_i(x,t-\omega), [\bar{u}_{i*}(x,t-\omega), \bar{u}_i^*(x,t-\omega)]) = 0,\ \forall i = 1,2,\end{aligned}$$

uniformly for $x \in [0,1]$.

Let $\bar{S}_1^*(x,t) = W^*(x,t) - \bar{u}_{1*}(x,t) - \bar{u}_2^*(x,t)$ and $\bar{S}_2^*(x,t) = W^*(x,t) - \bar{u}_1^*(x,t) - \bar{u}_{2*}(x,t)$. We need to confirm that

$$(\bar{S}_1^*(x,t), \bar{u}_{1*}(x,t), \bar{u}_2^*(x,t)) \quad \text{and} \quad (\bar{S}_2^*(x,t), \bar{u}_1^*(x,t), \bar{u}_{2*}(x,t))$$

are two positive ω-periodic solutions of (8.7)–(8.8). It suffices to prove that

$$W^*(x,t) > \bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t),\ W^*(x,t) > \bar{u}_{1*}(x,t) + \bar{u}_2^*(x,t),$$

for all $x \in [0,1]$ and $t \geq 0$. Since $u_1^*(\cdot,0) \ll_P W^*(\cdot,0)$, we can choose $\psi^0 = (\psi_1^0, \psi_2^0) \in Z_0$ such that

$$E_2^* \leq_P \psi^0 \ll_P M_1 = (u_1^*(\cdot,0),0) \text{ and } \psi_1^0(x) + \psi_2^0(x) \leq W^*(x,0),\ \forall x \in [0,1].$$

Let $(u_1^0(x,t), u_2^0(x,t))$ be the unique solution of (8.41) with $(u_1^0(\cdot,0), u_2^0(\cdot,0)) = \psi^0$, and let $\bar{f}(s) = \max\{\hat{f}_1(s), \hat{f}_2(s)\}$, $\forall s \in \mathbb{R}$. Then

$$V(x,t) = u_1^0(x,t) + u_2^0(x,t),\ x \in [0,1],\ t \geq 0,$$

satisfies $V(x,0) \leq W^*(x,0)$, $\forall x \in [0,1]$, and

$$\begin{aligned} &\frac{\partial V}{\partial t} \leq d_0 \frac{\partial^2 V}{\partial x^2} - v\frac{\partial V}{\partial x} + V\bar{f}(W^*(x,t) - V),\ 0 < x < 1,\ t > 0, \\ &BV = 0,\ t > 0. \end{aligned} \tag{8.43}$$

Note that $W^*(x,t)$ satisfies

$$\begin{aligned} &\frac{\partial W^*}{\partial t} = d_0 \frac{\partial^2 W^*}{\partial x^2} - v\frac{\partial W^*}{\partial x} + W^*\bar{f}(W^*(x,t) - W^*(x,t)), \\ &BW^* \geq 0 \end{aligned} \tag{8.44}$$

for $0 < x < 1$ and $t > 0$. By the standard comparison theorem, it follows that

$$u_1^0(x,t) + u_2^0(x,t) = V(x,t) \leq W^*(x,t),\ \forall x \in [0,1],\ t \geq 0. \tag{8.45}$$

By Theorem 2.4.2, $Q^n(\psi^0) = (u_1^0(\cdot,n\omega), u_2^0(\cdot,n\omega)) \to E_2^*$ as $n \to \infty$, and hence

$$\lim_{t\to\infty}(u_1^0(x,t) - \bar{u}_1^*(x,t)) = 0 \text{ and } \lim_{t\to\infty}(u_2^0(x,t) - \bar{u}_{2*}(x,t)) = 0$$

uniformly for $x \in [0,1]$. By (8.45), we have

$$u_1^0(x,t+n\omega) + u_2^0(x,t+n\omega) \leq W^*(x,t+n\omega) = W^*(x,t) \tag{8.46}$$

for all $x \in [0,1]$ and $t \geq 0$. Letting $n \to \infty$ in (8.46), we get

$$\bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t) \leq W^*(x,t),\ \forall x \in [0,1],\ t \geq 0. \tag{8.47}$$

Since $V^* = \bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t)$ satisfies (8.43) and $W^*(x,t)$ satisfies (8.11), as argued in the proof that $W^*(x,t) > u^*(x,t)$ in Subsection 8.2.2, we further have $\bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t) < W^*(x,t)$, $\forall x \in [0,1]$, $t \geq 0$. Similarly, we can prove that $\bar{u}_{1*}(x,t) + \bar{u}_2^*(x,t) < W^*(x,t)$, $\forall x \in [0,1]$, $t \geq 0$. ∎

8.3 Perturbed Model

In order to apply abstract perturbation-type results to periodic systems with parameters, we first consider the weak repellers uniform in parameters and the continuity of solutions on parameters uniformly for initial values.

8.3.1 Periodic Systems with Parameters

Let Λ be a subset of $\mathbb{R}^l$. We consider the periodic-parabolic system with parameter (E_λ):

$$\begin{aligned}\frac{\partial u_i}{\partial t} &= A_i(\lambda)u_i + F_i(x,t,u,\lambda) \quad \text{in } \Omega \times (0,\infty),\ 1 \le i \le m,\\ B_i u_i &= 0 \quad \text{on } \partial\Omega \times (0,\infty),\ 1 \le i \le m,\end{aligned} \tag{8.48}$$

where $u = (u_1, \ldots, u_m) \in \mathbb{R}^m, \lambda \in \Lambda$, $B_i u_i = \frac{\partial u_i}{\partial n} + \alpha_i u_i$, $\alpha_i \ge 0$, $A_i(\lambda)$ are uniform elliptic operators with coefficients continuous in (x, λ), F_i are smooth functions, and for some real number $\omega > 0$, $F_i(x, t + \omega, u, \lambda) = F_i(x, t, u, \lambda)$, $\forall 1 \le i \le m$. We assume that for any $\phi = (\phi_1, \ldots, \phi_m) \in C^+ = C(\overline{\Omega}, R^m_+)$, the unique (mild) solution $u(x, t, \phi, \lambda)$ of (E_λ) with $u(\cdot, 0, \phi, \lambda) = \phi$ exists globally on $[0,\infty)$ and $u_i(x, t, \phi, \lambda) \ge 0$, $\forall x \in \overline{\Omega}$, $t \ge 0$, $1 \le i \le m$.

For each $1 \le i \le m$ and any $m \in C^1([0, 1] \times \mathbb{R}, \mathbb{R})$ with $m(x, t + \omega) = m(x, t)$, $\forall x \in [0, 1]$, $t \in \mathbb{R}$, let $\mu(A_i(\lambda), m(\cdot, \cdot))$ be the unique principal eigenvalue of the periodic–parabolic eigenvalue problem (see [152, Chapter II])

$$\begin{aligned}&\frac{\partial \varphi}{\partial t} = A_i(\lambda)\varphi + m(x,t)\varphi + \mu\varphi, \quad x \in \overline{\Omega},\ t \in \mathbb{R},\\ &B_i\varphi = 0, \quad x \in \partial\Omega,\ t \in \mathbb{R},\\ &\varphi\ \omega\text{-periodic in}\, t.\end{aligned}$$

Then we have the following result on the uniform weak repeller .

Proposition 8.3.1. *Let $\lambda_0 \in \Lambda$ be fixed. Assume that there exists some $1 \le i \le m$ such that $F_i(x, t, u, \lambda) = u_i G_i(x, t, u, \lambda)$, and (E_λ) admits a nonnegative periodic solution*

$$u_0^*(x, t) = (u_{01}^*(x, t), \ldots, u_{0i-1}^*(x, t), 0, u_{0i+1}^*(x, t), \ldots, u_{0n}^*(x, t))$$

with $\mu(A_i(\lambda_0), G_i(x, t, u_0^*(x, t), \lambda_0)) < 0$. Then there exist $\eta > 0$ and $\delta > 0$ such that for any $|\lambda - \lambda_0| < \delta$ and any $\phi \in C^+$ with $\phi_i(\cdot) \not\equiv 0$, we have

$$\limsup_{n\to\infty} \|(u(\cdot, n\omega, \phi, \lambda) - u_0^*(\cdot, 0)\| \ge \eta.$$

Proof. Let $M = u_0^*(\cdot, 0)$ and let $B(M, r)$ denote the open ball in $C = C(\overline{\Omega}, R^m)$ centered at the point M and with radius r. By the definition of the principal eigenvalue in [152, Proposition 14.4] and the continuous dependence of evolution operators on parameters (see, e.g., [13] and [89, Section III.11]), we have

$$\lim_{\lambda\to\lambda_0} \mu(A_i(\lambda), G_i(x, t, u_0^*(x, t), \lambda_0)) = \mu(A_i(\lambda_0), G_i(x, t, u_0^*(x, t), \lambda_0)) < 0.$$

Then there exists $\delta_0 > 0$ such that for any $|\lambda - \lambda_0| < \delta_0$,

$$\mu(A_i(\lambda), G_i(x,t,u_0^*(x,t),\lambda_0)) < \frac{1}{2}\mu(A_i(\lambda_0), G_i(x,t,u_0^*(x,t),\lambda_0)).$$

Let $\epsilon_0 = -\frac{1}{2}\mu\left(A_i(\lambda_0), G_i(x,t,u_0^*(x,t),\lambda_0)\right)$. Then for any $|\lambda - \lambda_0| < \delta_0$,

$$-\mu(A_i(\lambda), G_i(x,t,u_0^*(x,t),\lambda_0)) > \epsilon_0 > 0.$$

Let $r = \max_{x\in\overline{\Omega},\, t\in[0,\omega]} |u_0^*(x,t)| + 1$. Therefore, the uniform continuity of $G_i(x,t,u,\lambda)$ on the compact set $\overline{\Omega} \times [0,\omega] \times \overline{B(0,r)} \times \overline{B(\lambda_0,\delta_0)}$ implies that there exist $\delta_1 \in (0,\delta_0)$ and $\eta_1 \in (0,1)$ such that for any $u,v \in \overline{B(0,r)}$ with $|u-v| < \eta_1$ and $|\lambda - \lambda_0| < \delta_1$,

$$|G_i(x,t,u,\lambda) - G_i(x,t,v,\lambda_0)| < \epsilon_0, \ \ \forall x \in \overline{\Omega},\ t \in [0,\omega]. \tag{8.49}$$

Since $\lim_{(\phi,\lambda)\to(M,\lambda_0)} u(\cdot,t,\phi,\lambda) = u(\cdot,t,M,\lambda_0) = u_0^*(\cdot,t)$ in C uniformly for $t \in [0,\omega]$, there exist $\delta_2 \in (0,\delta_1)$ and $\eta_2 > 0$ such that for any $\phi \in B(M,\eta_2) \subset C$, $|\lambda - \lambda_0| < \delta_2$,

$$|u(x,t,\phi,\lambda) - u_0^*(x,t)| < \eta_1, \ \forall x \in \overline{\Omega},\ t \in [0,\omega].$$

We claim that for any $|\lambda - \lambda_0| < \delta_2$ and $\phi \in B(M,\eta_2) \cap C^+$ with $\phi_i(\cdot) \not\equiv 0$, there exists $n_0 = n_0(\lambda,\phi) \geq 1$ such that

$$u(\cdot, n_0\omega, \phi, \lambda) \notin B(M,\eta_2). \tag{8.50}$$

Assume, by contradiction, that there exist $\phi_0 \in B(M,\eta_2)\cap C^+$ with $\phi_{0i}(\cdot) \not\equiv 0$ and $|\lambda_1 - \lambda_0| < \delta_2$ such that for all $n \geq 1$,

$$u(\cdot, n\omega, \phi_0, \lambda_1) \in B(M,\eta_2). \tag{8.51}$$

For any $t \geq 0$, let $t = n\omega + t'$, where $t' \in [0,\omega)$ and $n = [t/\omega]$ is the greatest integer less than or equal to t/ω. Then we have

$$|u(x,t,\phi_0,\lambda_1) - u_0^*(x,t)| = |u(x,t',u(\cdot,n\omega,\phi_0,\lambda_1),\lambda_1) - u_0^*(x,t')| < \eta_1 \tag{8.52}$$

for all $x \in \overline{\Omega}$, and hence

$$|u(x,t,\phi_0,\lambda_1)| < |u^*(x,t)| + \eta_1 \leq \max_{x\in\overline{\Omega},t\in[0,\omega]} |u_0^*(x,t)| + 1 = r$$

for all $t \geq 0$ and $x \in \overline{\Omega}$. Therefore, by (8.49) and the ω-periodicity of $G_i(x,t,u,\lambda_1)$ with respect to t,

$$G_i(x,t,u(x,t,\phi_0,\lambda_1),\lambda_1) > G_i(x,t,u_0^*(x,t),\lambda_0) - \epsilon_0, \ \forall x \in \overline{\Omega},\ t \geq 0. \tag{8.53}$$

Let $\psi_i(x,t)$ be a positive eigenfunction corresponding to the principal eigenvalue $\mu = \mu(A_i(\lambda_1), G_i(x,t,u_0^*(x,t),\lambda_0))$; that is, $\psi_i(x,t)$ satisfies

$$\begin{aligned} &\frac{\partial \psi_i}{\partial t} = A_i(\lambda_1)\psi_i + G_i(x,t,u_0^*(x,t),\lambda_0)\psi_i + \mu\psi_i \quad \text{in } \Omega \times \mathbb{R}, \\ &B_i\psi_i = 0 \quad \text{on } \partial\Omega \times \mathbb{R}, \\ &\psi_i \ \ \omega\text{-periodic in}\, t. \end{aligned} \tag{8.54}$$

Then $\psi(\cdot,0) \gg 0$ in $C(\overline{\Omega},\mathbb{R})$. Let

$$u(x,t,\phi_0,\lambda_1) = (u_1(x,t,\phi_0,\lambda_1),\ldots,u_m(x,t,\phi_0,\lambda_1)).$$

Since $\phi_{0i}(\cdot) > 0$ in $C(\overline{\Omega},\mathbb{R})$, by applying the parabolic maximum principle to the ith component of (E_{λ_1}), we have $u_i(\cdot,t,\phi_0,\lambda_1) \gg 0$ in $C(\overline{\Omega},\mathbb{R})$ for all $t > 0$. Let $u_i(x,t) = u_i(x,t+\omega,\phi_0,\lambda_1)$. Then $u_i(\cdot,0) = u_i(\cdot,\omega,\phi_0,\lambda_1) \gg 0$ in $C(\overline{\Omega},\mathbb{R})$, and hence there exists $k > 0$ such that $u_i(\cdot,0) \geq k\psi_i(\cdot,0)$. Therefore, by (8.53), $u_i(x,t)$ satisfies

$$\begin{aligned}
&\frac{\partial u_i}{\partial t} \geq A_i(\lambda_1)u_i + u_i\left(G_i(x,t,u_0^*(x,t),\lambda_0) - \epsilon_0\right) \quad \text{in } \Omega \times (0,\infty),\\
&B_i u_i = 0 \quad \text{on } \partial\Omega \times (0,\infty),\\
&u_i(x,0) \geq k\psi_i(x,0) \quad \text{on } \overline{\Omega}.
\end{aligned} \tag{8.55}$$

By (8.54), it easily follows that $v(x,t) = ke^{(-\mu-\epsilon_0)t}\psi_i(x,t)$ satisfies

$$\begin{aligned}
&\frac{\partial v}{\partial t} = A_i(\lambda_1)v + v\left(G_i(x,t,u_0^*(x,t),\lambda_0) - \epsilon_0\right) \quad \text{in } \Omega \times (0,\infty),\\
&B_i v = 0 \quad \text{on } \partial\Omega \times (0,\infty),\\
&v(x,0) = k\psi_i(x,0) \quad \text{on } \overline{\Omega}.
\end{aligned} \tag{8.56}$$

By (8.55), (8.56), and the standard comparison theorem, we get

$$u_i(x,t) \geq ke^{(-\mu-\epsilon_0)t}\psi_i(x,t), \quad \forall t \geq 0,\ x \in \Omega.$$

Then $\lim_{t\to\infty} u_i(x,t) = \infty$ for any $x \in \Omega$, which contradicts (8.51). It follows that for any $|\lambda - \lambda_0| < \delta_2$ and any $\phi \in C^+$ with $\phi_i(\cdot) \not\equiv 0$, $\limsup_{n\to\infty} d(u(\cdot,n\omega,\phi,\lambda),M) \geq \eta_2$. ∎

By the continuous dependence of the evolution operator on parameters (see, e.g., [13] and [89, Section III.11]), the variation of constants formula, and a generalized Gronwall's inequality argument (see, e.g., [152, Lemma 19.4] and the proof of Proposition 3.2.1), we can prove the following result on the continuity of solutions on parameters uniformly for initial values.

Proposition 8.3.2. *Assume that solutions of (E_λ) are uniformly bounded uniformly for $\lambda \in \Lambda$; that is, for any $r > 0$, there exists $B = B(r) > 0$ such that for any $\phi \in C^+$ with $\|\phi\| \leq r$, $\|u(\cdot,t,\phi,\lambda)\| \leq B(r), \forall t \geq 0$, $\lambda \in \Lambda$. Then for any $\lambda_0 \in \Lambda$ and any integer $k > 0$,*

$$\lim_{\lambda\to\lambda_0} \|u(\cdot,t,\phi,\lambda) - u(\cdot,t,\phi,\lambda_0)\| = 0$$

uniformly for $t \in [\omega,k\omega]$ and ϕ in any bounded subset of C^+.

8.3.2 Single Species Growth

Consider the single species growth model with not necessarily identical diffusivities and nonvanishing cell death rate

$$\begin{aligned}\frac{\partial S}{\partial t}&=d_0\frac{\partial^2 S}{\partial x^2}-v\frac{\partial S}{\partial x}-uf(S),\quad 0<x<1,\, t>0,\\ \frac{\partial u}{\partial t}&=d\frac{\partial^2 u}{\partial x^2}-v\frac{\partial u}{\partial x}+u(f(S)-k),\quad 0<x<1,\, t>0,\end{aligned}\tag{8.57}$$

with boundary conditions

$$\begin{aligned}&d_0\frac{\partial S(0,t)}{\partial x}-vS(0,t)=-vS^0(t),\quad t>0,\\ &d\frac{\partial u(0,t)}{\partial x}-vu(0,t)=0,\quad t>0,\\ &\frac{\partial S(1,t)}{\partial x}=\frac{\partial u(1,t)}{\partial x}=0,\quad t>0,\end{aligned}\tag{8.58}$$

where $d_0>0, d>0, v>0$, and $k\geq 0$, and $S^0(\cdot)$ and $f(\cdot)$ are as in (8.20)–(8.21). Let $Y^+=C([0,1],\mathbb{R}^2_+)$. Let $d_0>0$ and $v>0$ be fixed and let $\lambda=(d,k), d>0, k\geq 0$. As argued in Section 8.1, [243, Theorem 1 and Remark 1.1] imply that for any $\phi=(S_0(\cdot),u_0(\cdot))\in Y^+$, (8.57)–(8.58) has a unique solution $(S(x,t,\phi,\lambda),u(x,t,\phi,\lambda))$, defined on its maximal interval of existence $[0,\sigma_\phi)$, satisfying $(S(\cdot,0,\phi,\lambda),u(\cdot,0,\phi,\lambda))=\phi$. Moreover,

$$S(x,t,\phi,\lambda)\geq 0,\qquad u(x,t,\phi,\lambda)\geq 0,\ \forall x\in[0,1],\, t\in[0,\sigma_\phi).$$

We further have the following result.

Lemma 8.3.1. *Let $\Lambda=\{(d,k):\frac{d_0}{2}\leq d\leq 2d_0,\ k\geq 0\}$. Then for each $\lambda\in\Lambda$, $\phi\in Y^+$, $(S(x,t,\phi,\lambda),u(x,t,\phi,\lambda))$ exists globally on $[0,\infty)$, and solutions of (8.57)–(8.58) are uniformly bounded and ultimately bounded uniformly for $\lambda\in\Lambda$.*

Proof. Given $\phi=(S_0(\cdot),u_0(\cdot))\in Y^+$, for convenience, let

$$(S(x,t),u(x,t))=(S(x,t,\phi,\lambda),u(x,t,\phi,\lambda)),\quad \forall x\in[0,1],\, t\in[0,\sigma_\phi).$$

Then $S(x,t)$ satisfies

$$\begin{aligned}&\frac{\partial S}{\partial t}\leq d_0\frac{\partial^2 S}{\partial x^2}-v\frac{\partial S}{\partial x},\quad 0<x<1,\, t>0,\\ &d_0\frac{\partial S(0,t)}{\partial x}-vS(0,t)=-vS^0(t),\quad t>0,\\ &\frac{\partial S(1,t)}{\partial x}=0,\quad t>0.\end{aligned}\tag{8.59}$$

By the parabolic comparison theorem, we have

$$S(x,t) \le \bar{S}(x,t), \quad \forall x \in [0,1],\, t \in [0,\sigma_\phi), \tag{8.60}$$

where $\bar{S}(x,t)$ is the unique solution of (8.11) with $\bar{S}(x,0) = S(x,0)$. By Proposition 8.2.1, $\bar{S}(x,t)$ exists globally on $[0,\infty)$ and $\lim_{t\to\infty}(\bar{S}(x,t) - W^*(x,t)) = 0$ uniformly for $x \in [0,1]$.

Let μ be the unique positive solution to equation $\tan\mu = \frac{v}{2\mu d_0}$ on the interval $[0,\frac{\pi}{2})$. Clearly, $\sin(\mu x) \ge 0, \cos(\mu x) > 0, x \in [0,1]$. Then for any $\lambda \in \Lambda$, by using (8.57) and (8.58) and integration by parts, we have

$$\begin{aligned}
&\frac{d}{dt}\int_0^1 S(x,t)\cos(\mu x)dx = \int_0^1 \frac{\partial S}{\partial t}\cos(\mu x)dx \\
&\quad = vS^0(t) - S(1,t)(v\cos\mu - \mu d_0 \sin\mu) - \mu v\int_0^1 S(x,t)\sin(\mu x)dx \\
&\qquad - d_0\mu^2\int_0^1 S(x,t)\cos(\mu x)dx - \int_0^1 u(x,t)f(S(x,t))\cos(\mu x)dx \\
&\quad \le vS^0(t) - d_0\mu^2\int_0^1 S(x,t)\cos(\mu x)dx \\
&\qquad - \int_0^1 u(x,t)f(S(x,t))\cos(\mu x)dx
\end{aligned} \tag{8.61}$$

and

$$\begin{aligned}
&\frac{d}{dt}\int_0^1 u(x,t)\cos(\mu x)dx = \int_0^1 \frac{\partial u}{\partial t}\cos(\mu x)dx \\
&\quad = -u(x,t)[v\cos\mu - \mu d\sin\mu] - v\int_0^1 u(x,t)\sin(\mu x)dx \\
&\qquad - d\mu^2\int_0^1 u(x,t)\cos(\mu x)dx + \int_0^1 u(x,t)(f(S(x,t) - k)\cos(\mu x)dx \\
&\quad \le -d\mu^2\int_0^1 u(x,t)\cos(\mu x)dx + \int_0^1 u(x,t)f(S(x,t))\cos(\mu x)dx.
\end{aligned} \tag{8.62}$$

Let $y(t) = \int_0^1 (S(x,t) + u(x,t))\cos(\mu x)dx$, $\forall t \in [0,\sigma_\phi)$. Then we get

$$\frac{dy(t)}{dt} \le vS^0(t) - \frac{d_0\mu^2}{2}y(t), \quad t \in [0,\sigma_\phi).$$

By the standard comparison theorem for ordinary differential equations, it then follows that for all $t \in [0,\sigma_\phi)$,

$$y(t) \le y^*(t) - \exp\left(-\frac{d_0\mu^2 t}{2}\right)y^*(0) + \exp\left(-\frac{d_0\mu^2 t}{2}\right)y(0), \tag{8.63}$$

where $y^*(t)$ is the unique positive ω-periodic solution of linear ordinary differential equations

$$\frac{dy}{dt} = vS^0(t) - \frac{d_0\mu^2}{2}y(t).$$

Since $S(x,t) \geq 0, u(x,t) \geq 0$, and $\cos(\mu x) \geq \min_{x\in[0,1]} \cos(\mu x) = m > 0$, $\forall x \in [0,1]$, (8.63) implies that for all $t \in [0, \sigma_\phi)$,

$$\int_0^1 u(x,t)dx \leq \frac{1}{m}\left[y^*(t) - exp\left(-\frac{d_0\mu^2 t}{2}\right)y^*(0) + \exp\left(-\frac{d_0\mu^2 t}{2}\right)\int_0^1 (S_0(x)+u_0(x))\cos(\mu x)dx\right]. \tag{8.64}$$

Then $u(\cdot,t)$ is L_1-bounded on $[0,\sigma_\phi)$. By (8.60), (8.64), and an argument similar to that in [6, Theorem 3.1], [186, Lemma 3.13], and [215, Proposition 2.4 and Theorem 2.5], it follows that for each $\phi \in Y^+$, $(S(x,t,\phi,\lambda), u(x,t,\phi,\lambda))$ is L^∞-bounded, and hence $\sigma_\phi = \infty$, and solutions of (8.57)–(8.58) are uniformly L^∞-bounded and ultimately L^∞-bounded uniformly for $\lambda \in \Lambda$. ∎

Now we show that the hypothesis of Theorem 8.2.1(b) for the unperturbed system implies the existence of a globally attracting single-population periodic solution for the perturbed system at least when the perturbation is small.

Theorem 8.3.1. *Let* $\lambda = (d,k)$, $\lambda_0 = (d_0, 0)$, *and* $W^*(x,t)$ *and* $\mu(m(\cdot,\cdot))$ *be as in Section 8.2. Assume that* $\mu(f(W^*(x,t))) < 0$ *and let* $(S^*(x,t), u^*(x,t))$ *be as in Theorem 8.2.1. Then there exists* $\delta_0 > 0$ *such that for any* $|\lambda - \lambda_0| < \delta_0$, *(8.57)–(8.58) admits a unique positive ω-periodic solution* $(S^*(x,t,\lambda), u^*(x,t,\lambda))$ *with*

$$(S^*(x,t,\lambda_0), u^*(x,t,\lambda_0)) = (S^*(x,t), u^*(x,t)), \ \forall x \in [0,1],\ t \geq 0,$$

and such that the map $\lambda \to (S^*(\cdot,\cdot,\lambda), u^*(\cdot,\cdot,\lambda))$ *is continuous. Moreover, for any* $(S_0(\cdot), u_0(\cdot)) \in Y^+$ *with* $u_0(\cdot) \not\equiv 0$,

$$\lim_{t\to\infty}(S(x,t,\phi,\lambda) - S^*(x,t,\lambda)) = 0 \ \textit{and} \ \lim_{t\to\infty}(u(x,t,\phi,\lambda) - u^*(x,t,\lambda)) = 0,$$

uniformly for $x \in [0,1]$.

Proof. Let $k_0 > 0$ be given and let $\Lambda_0 = \{(d,k) : \frac{d_0}{2} \leq d \leq 2d_0, 0 \leq k \leq k_0\}$. For any $\lambda \in \Lambda_0$, let $S_\lambda = S(\lambda,\cdot) : Y^+ \to Y^+$ be the Poincaré map associated with (8.57)–(8.58); that is, $S(\lambda,\phi) = (S(\cdot,\omega,\phi,\lambda), u(\cdot,\omega,\phi,\lambda))$, $\phi \in Y^+$. Then $S(\cdot,\cdot) : \Lambda_0 \times Y^+ \to Y^+$ is continuous. By Lemma 8.3.1, it follows that for each $\lambda \in \Lambda_0$, $S_\lambda : Y^+ \to Y^+$ is compact and point dissipative uniformly for $\lambda \in \Lambda_0$; that is, there exists a bounded and closed subset B_0 of Y^+, independent of $\lambda \in \Lambda_0$, such that for any $\phi \in Y^+$, $\lambda \in \Lambda_0$, there exists $N = N(\phi,\lambda)$ such that $S_\lambda^n(\phi) \in B_0$ for all $n \geq N$. Then, by Theorem 1.1.3, for each $\lambda \in \Lambda_0$, there exists a global attractor A_λ for $S_\lambda : Y^+ \to Y^+$. Clearly, $A_\lambda \subset B_0$. By a change of variables

$$\bar{S}(x,t) = S(x,t) - W^*(x,t), \ \ \bar{u}(x,t) = \exp\left(\frac{v(x-1)^2}{2d}\right)u(x,t),$$

the boundary conditions (8.58) then become the homogeneous ones

$$d_0 \frac{\partial \bar{S}(0,t)}{\partial x} - v\bar{S}(0,t) = \frac{\partial \bar{S}(1,t)}{\partial x} = 0, \quad t > 0,$$
$$\frac{\partial \bar{u}(0,t)}{\partial x} = \frac{\partial \bar{u}(1,t)}{\partial x} = 0, \quad t > 0,$$

which is independent of parameter λ. By Lemma 8.3.1 and Proposition 8.3.2, when applied to the resulting system with parameter λ under the above change of variables and the above boundary conditions, it then follows that $S(\cdot,\phi) : \Lambda_0 \to Y^+$ is continuous uniformly for ϕ in any bounded subset of Y^+. We further have the following claim:

Claim. For any bounded subset $B \subset Y^+$, $\overline{\cup_{\lambda\in\Lambda_0} S_\lambda(B)}$ is compact in Y^+.

Indeed, for any sequence $\{\psi_n\}$ in $\cup_{\lambda\in\Lambda_0} S_\lambda(B)$, we have $\psi_n = S_{\lambda_n}(\phi_n)$, $\lambda_n \in \Lambda_0, \phi_n \in B, n \geq 0$. By the compactness of Λ_0, without loss of generality we can assume that for some $\lambda_1 \in \Lambda_0$, $\lambda_n \to \lambda_1$ as $n \to \infty$. Since $S_{\lambda_1}(B)$ is precompact, there exist $\psi_0 \in Y^+$ and a subsequence $n_k \to \infty$ such that $S_{\lambda_1}(\phi_{n_k}) \to \psi_0$ as $k \to \infty$. Combining the continuity of $S(\cdot,\phi) : \Lambda_0 \to Y^+$ uniformly for $\phi \in B$ and the inequality

$$\begin{aligned}\|\psi_{n_k} - \psi_0\| &= \left\| S_{\lambda_{n_k}}(\phi_{n_k}) - \psi_0 \right\| \\ &\leq \left\| S_{\lambda_{n_k}}(\phi_{n_k}) - S_{\lambda_1}(\phi_{n_k}) \right\| + \left\| S_{\lambda_1}(\phi_{n_k}) - \psi_0 \right\|,\end{aligned}$$

we get $\psi_{n_k} \to \psi_0$, $k \to \infty$. Therefore, $\cup_{\lambda\in\Lambda_0} S_\lambda(B)$ is precompact.

Let

$$Y_0 := \left\{ (S(\cdot), u(\cdot)) \in Y^+ : \quad u(\cdot) \not\equiv 0 \right\} \text{ and } \partial Y_0 := Y^+ \setminus Y_0.$$

Then $S_\lambda : Y_0 \to Y_0$ and $S_\lambda : \partial Y_0 \to \partial Y_0$. Let $\phi_0 = (S^*(\cdot,0), u^*(\cdot,0))$. Then $S_{\lambda_0}(\phi_0) = \phi_0$. By Theorem 8.2.1, $r(D_\phi S(\lambda_0,\phi_0)) < 1$, and $\lim_{n\to\infty} S_{\lambda_0}^n \phi = \phi_0$ for every $\phi \in Y_0$. For each $\lambda \in \Lambda_0$, by Proposition 8.2.1,

$$\lim_{n\to\infty} S_\lambda^n(\phi) = (W^*(\cdot,0),0), \ \forall \phi \in \partial Y_0.$$

Clearly, $M = (W^*(\cdot,0),0)$ is a global attractor for $S_\lambda : \partial Y_0 \to \partial Y_0$. Note that $(W^*(x,t),0)$ is a nonnegative ω-periodic solution of (8.57)–(8.58) and $\mu(f(W^*(x,t))) < 0$. By a change of variables

$$\bar{S}(x,t) = S(x,t) - W^*(x,t), \quad \bar{u}(x,t) = \exp\left(\frac{v(x-1)^2}{2d}\right) u(x,t),$$

and Proposition 8.3.1, as applied to the resulting system, it then follows that there exist $\delta_1 > 0$ and $\eta_1 > 0$ such that for any $|\lambda - \lambda_0| < \delta_1$ and any $\phi \in Y_0$, we have

$$\limsup_{n\to\infty} d\left(S_\lambda^n(\phi), M\right) = \limsup_{n\to\infty} d\left((S(\cdot, n\omega, \phi, \lambda), u(\cdot, n\omega, \phi, \lambda)), M\right) \geq \eta_1,$$

which implies that M is isolated for $S_\lambda : Y^+ \to Y^+$, and $W_\lambda^s(M) \cap Y_0 = \emptyset$, $|\lambda - \lambda_0| < \delta_1$, where $W_\lambda^s(M)$ is the stable set of M with respect to S_λ. By Theorem 1.3.1, S_λ is uniformly persistent with respect to $(Y_0, \partial Y_0)$ for each $|\lambda - \lambda_0| < \delta_1$. Therefore, there exists a global attractor $A_\lambda^0 \subset Y_0$ for $S_\lambda : Y_0 \to Y_0$ (see, e.g., Theorem 1.3.6). Clearly, $A_\lambda^0 \subset B_0$, and $\overline{\cup_{\lambda\in\Lambda_0,\phi\in Y^+}\omega_\lambda(\phi)} \subset \overline{\cup_{\lambda\in\Lambda_0} S_\lambda(B_0)}$. Then by the previous claim, $\overline{\cup_{\lambda\in\Lambda_0,\phi\in Y^+}\omega_\lambda(\phi)}$ is compact. By Theorem 1.4.2, it follows that there exist $\delta_2 > 0$ and $\eta_2 > 0$ such that for any $|\lambda - \lambda_0| \leq \delta_2$, $\phi \in Y_0$, $\liminf_{n\to\infty} d(S_\lambda^n \phi, \partial Y_0) \geq \eta_2$. Then there exists a bounded and closed subset B_0^* of Y_0 such that $A_\lambda^0 \subset B_0^*$ for all $|\lambda - \lambda_0| \leq \delta_2$. Let $\Lambda_1 = \Lambda_0 \cap \overline{B(\lambda_0, \delta_2)}$, where $B(\lambda_0, \delta_2) = \{\lambda : |\lambda - \lambda_0| < \delta_2\}$. Since $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(A_\lambda^0)} \subset \overline{\cup_{\lambda\in\Lambda_1} S_\lambda(B_0^*)}$, by the previous claim $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(A_\lambda^0)}$ is compact. Moreover, $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(A_\lambda^0)} = \overline{\cup_{\lambda\in\Lambda_1} A_\lambda^0} \subset \overline{B_0^*} = B_0^* \subset Y_0$. By applying Theorem 1.4.1 on the perturbation of a globally stable fixed point to $S_\lambda(\cdot) : Y^+ \to Y^+$ with $U = Y_0$ and $B_\lambda = A_\lambda^0, \lambda \in \Lambda_1$, we complete the proof. ∎

8.3.3 Two-Species Competition

Consider two-species competition with unequal diffusivities and nonvanishing cell death rates

$$\begin{aligned}
\frac{\partial S}{\partial t} &= d_0 \frac{\partial^2 S}{\partial x^2} - v\frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S), \quad 0 < x < 1,\, t > 0, \\
\frac{\partial u_i}{\partial t} &= d_i \frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x} + u_i(f_i(S) - k_i), \quad i = 1, 2,\, 0 < x < 1,\, t > 0,
\end{aligned} \tag{8.65}$$

with boundary conditions

$$\begin{aligned}
& d_0 \frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t > 0, \\
& d_i \frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t) = 0, \quad i = 1, 2,\, t > 0, \\
& \frac{\partial S(1,t)}{\partial x} = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad i = 1, 2,\, t > 0,
\end{aligned} \tag{8.66}$$

where $d_0 > 0, v > 0, d_i > 0$, and $k_i \geq 0$, and $S^0(\cdot)$ and $f_i(\cdot)$, $i = 1, 2$, are as in (8.7)–(8.8). Let $X^+ = C([0,1], \mathbb{R}_+^3)$. Let $d_0 > 0$ and $v > 0$ be fixed and let $\lambda = (d_1, d_2, k_1, k_2), d_i > 0, k_i \geq 0, i = 1, 2$. As mentioned in Section 8.1, for any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$, (8.65)–(8.66) has a unique solution $(S(x,t,\phi,\lambda), u_1(x,t,\phi,\lambda), u_2(x,t,\phi,\lambda))$, defined on its maximal interval of existence $[0, \sigma_\phi)$, satisfying $(S(\cdot,0,\phi,\lambda), u_1(\cdot,0,\phi,\lambda), u_2(\cdot,0,\phi,\lambda)) = \phi$. Moreover,

$$S(x,t,\phi,\lambda) \geq 0, \quad u_i(x,t,\phi,\lambda) \geq 0,\ \forall x \in [0,1],\ t \in [0,\sigma_\phi),\ i = 1, 2.$$

By a similar argument as in Lemma 8.3.1, we have the following result on the boundedness of solutions uniformly for λ.

Lemma 8.3.2. *Let* $\Lambda = \{(d_1, d_2, k_1, k_2) : \frac{d_0}{2} \le d_i \le 2d_0,\ k_i \ge 0,\ i = 1, 2\}$. *Then for each* $\lambda \in \Lambda$, $\phi \in X^+$, $(S(x, t, \phi, \lambda), u_1(x, t, \phi, \lambda), u_2(x, t, \phi, \lambda))$ *exists globally on* $[0, \infty)$, *and solutions of (8.65)–(8.66) are uniformly bounded and ultimately bounded uniformly for* $\lambda \in \Lambda$.

Now we can state one of the main results of this chapter. It says that both species persist for the perturbed system and there exists a positive periodic solution when the hypotheses of Theorem 8.2.2 hold for the unperturbed system and the perturbation is sufficiently small.

Theorem 8.3.2. *Let* $\lambda = (d_1, d_2, k_1, k_2)$ *and* $\lambda_0 = (d_0, d_0, 0, 0)$. *Assume that all conditions in Theorem 8.2.2 hold. Then there exist* $\delta > 0$ *and* $\beta > 0$ *such that for any* $|\lambda - \lambda_0| < \delta$, *(8.65)–(8.66) admits at least one positive* ω*-periodic solution, and for any* $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$ *with* $u_{0i}(\cdot) \not\equiv 0$, $\forall i = 1, 2$, *there exists* $t_0 = t_0(\phi, \lambda)$ *such that*

$$u_i(x, t, \phi, \lambda) \ge \beta, \quad \forall x \in [0, 1],\ t \ge t_0,\ i = 1, 2.$$

Proof. Let $k_0 > 0$ be given and let

$$\Lambda_0 = \{(d_1, d_2, k_1, k_2) : \frac{d_0}{2} \le d_i \le 2d_0,\ 0 \le k_i \le k_0,\ i = 1, 2\}.$$

For each $\lambda \in \Lambda_0$, let $S_\lambda(\cdot) = S(\lambda, \cdot) : X^+ \to X^+$ be the Poincaré map associated with (8.65)–(8.66); that is,

$$S(\lambda, \phi) = (S(\cdot, \omega, \phi, \lambda), u_1(\cdot, \omega, \phi, \lambda), u_2(\cdot, \omega, \phi, \lambda)),\ \forall \phi \in X^+.$$

Then $S(\cdot, \cdot) : \Lambda_0 \times X^+ \to X^+$ is continuous. By Lemma 8.3.2, for each $\lambda \in \Lambda_0$, $S_\lambda : X^+ \to X^+$ is compact and point dissipative uniformly for $\lambda \in \Lambda_0$, and hence, by Theorem 1.1.3, there exists a global attractor A_λ for $S_\lambda : X^+ \to X^+$. Let

$$X_0 := \left\{(S(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+ :\ u_{0i}(\cdot) \not\equiv 0,\ \forall i = 1, 2\right\}$$

and $\partial X_0 := X^+ \setminus X_0$. Then $S_\lambda : X_0 \to X_0$ and $S_\lambda : \partial X_0 \to \partial X_0$. By Theorem 8.2.1, $(S_i^*(x, t), u_i^*(x, t))$ is the unique positive ω-periodic solution of (8.20)–(8.21) with $f(\cdot) = f_i(\cdot)$, $i = 1, 2$, respectively. Clearly, $(W^*(x, t), 0, 0)$, $(S_1^*(x, t), u_1^*(x, t), 0)$ and $(S_2^*(x, t), 0, u_2^*(x, t))$ are nonnegative periodic solutions of (8.65)–(8.66) with $\lambda = \lambda_0$. Let

$$M_0 = (W^*(\cdot, 0), 0, 0),\ M_1^0 = (S_1^*(\cdot, 0), u_1^*(\cdot, 0), 0),\ M_2^0 = (S_2^*(\cdot, 0), 0, u_2^*(\cdot, 0)).$$

Then $S_{\lambda_0}(M_0) = M_0$, $S_{\lambda_0}(M_i^0) = M_i^0$, $\forall i = 1, 2$. By a change of variables

$$\bar{S}(x, t) = S(x, t) - W^*(x, t),\ \bar{u}_i(x, t) = \exp\left(\frac{v(x-1)^2}{2d_i}\right) u_i(x, t),\ i = 1, 2,$$

and Proposition 8.3.1, as applied to the resulting system, it follows that there exist $\delta_0 > 0$ and $\eta_0 > 0$ such that for any $\lambda \in \Lambda_0$ with $|\lambda - \lambda_0| < \delta_0$, and for any $\phi \in X_0$,

$$\limsup_{n\to\infty} d(S_\lambda^n(\phi), M_0) \geq \eta_0, \ \limsup_{n\to\infty} d(S_\lambda^n(\phi), M_i^0) \geq \eta_0, \ i = 1, 2. \qquad (8.67)$$

By Proposition 8.2.1 and Theorem 8.2.1, it follows that M_0, M_1^0, and M_2^0 are acyclic for S_{λ_0} in ∂X_0, and $\cup_{\phi\in\partial X_0}\omega_{\lambda_0}(\phi) = M_0 \cup M_1^0 \cup M_2^0$, where $\omega_{\lambda_0}(\phi)$ is the omega limit set of ϕ for S_{λ_0}. Moreover, (8.67) implies that $M_0 \cup M_1^0 \cup M_2^0$ is an isolated covering of $\overline{\cup_{\phi\in\partial X_0}\omega_{\lambda_0}(\phi)}$ for S_{λ_0} in ∂X_0 and that $W_{\lambda_0}^s(M_0) \cap X_0 = \emptyset$ and $W_{\lambda_0}^s(M_i^0) \cap X_0 = \emptyset$, $\forall i = 1, 2$, where $W_{\lambda_0}^s(M)$ denotes the stable set of M with respect to S_{λ_0}. By Theorem 1.3.1 and Remark 1.3.1, it follows that $S_{\lambda_0} : X^+ \to X^+$ is uniformly persistent with respect to $(X_0, \partial X_0)$, and hence there exists a global attractor $A_{\lambda_0}^0 \subset X_0$ for $S_{\lambda_0} : X_0 \to X_0$ (see, e.g., Theorem 1.3.6).

Let $\Lambda_1 = \Lambda_0 \cap \overline{B(\lambda_0, \delta_0)}$. Again by a change of variables

$$\bar{S}(x, t) = S(x, t) - W^*(x, t), \ \bar{u}_i(x, t) = \exp\left(\frac{v(x-1)^2}{2d_i}\right) u_i(x, t), \ i = 1, 2,$$

Lemma 8.3.2, and Proposition 8.3.2, as applied to the resulting system, it follows that $S_\lambda : X^+ \to X^+$ is point dissipative uniformly for $\lambda \in \Lambda_1$ and $S(\cdot, \phi) : \Lambda_1 \to X^+$ is continuous uniformly for ϕ in any bounded subset of X^+. Therefore, by the same argument as in the claim in the proof of Theorem 8.3.1, for any bounded subset B of X^+, $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(B)}$ is compact. It then follows that, as argued in Theorem 8.3.1, $\overline{\cup_{\lambda\in\Lambda_1,\phi\in X^+}\omega_\lambda(\phi)}$ is compact. Therefore, by (8.67) and Theorem 1.4.2, there exist $\delta_1 \in (0, \delta_0)$ and $\eta > 0$ such that for any $\lambda \in \Lambda_0$ with $|\lambda - \lambda_0| \leq \delta_1$, and any $\phi \in X_0$, $\liminf_{n\to\infty} d(S_\lambda^n\phi, \partial X_0) \geq \eta$. Moreover, by Theorem 1.3.10, S_λ admits a fixed point $S_\lambda(\phi_\lambda) = \phi_\lambda \in X_0$, and hence (8.65)–(8.66) with $|\lambda - \lambda_0| \leq \delta_1$ admits a nonnegative ω-periodic solution $(S(x, t, \phi_\lambda, \lambda), u_1(x, t, \phi_\lambda, \lambda), u_2(x, t, \phi_\lambda, \lambda))$ with $u_i(\cdot, t, \phi_\lambda, \lambda) \gg 0$ in $C([0, 1], \mathbb{R})$, $\forall t \geq 0, i = 1, 2$. By parabolic maximum principle and the fact that $S^0(\cdot) \geq 0$ with $S^0(\cdot) \not\equiv 0$, it then easily follows that $S(\cdot, t, \phi_\lambda, \lambda) \gg 0$ in $C([0, 1], \mathbb{R})$, $\forall t \geq 0$. Thus, $(S(x, t, \phi_\lambda, \lambda), u_1(x, t, \phi_\lambda, \lambda), u_2(x, t, \phi_\lambda, \lambda))$ is a positive ω-periodic solution of (8.65)–(8.66).

It remains to prove the practical persistence claimed in the theorem. Let $\Lambda_2 = \Lambda_0 \cap \overline{B(\lambda_0, \delta_1)}$. By both the point dissipativity and the uniform persistence of S_λ with respect to $(X_0, \partial X_0)$ uniformly for $\lambda \in \Lambda_2$, it follows that there exists a closed and bounded set $B_0 \subset X_0$, independent of λ, such that $\underline{d}(B_0, \partial X_0) = \inf_{\phi\in B_0} d(\phi, \partial X_0) > 0$ and B_0 attracts points in X_0. As argued in Theorem 8.3.1, for each $\lambda \in \Lambda_2$, $S_\lambda : X_0 \to X_0$ admits a global attractor $A_\lambda^0 \subset X_0$, and hence A_λ^0 attracts any compact subset of X_0. Clearly, for each $\lambda \in \Lambda_2$, $A_\lambda^0 \subset B_0$, and hence B_0 attracts compact subsets of X_0 under S_λ. Since for each $\lambda \in \Lambda_2$, $S_\lambda : X^+ \to X^+$ is compact, and for any bounded subset B of X^+, as claimed in the previous paragraph, $\cup_{\lambda\in\Lambda_2} S_\lambda(B)$ is precompact, it follows that $\{S_\lambda : \lambda \in \Lambda_2\}$ is collectively compact. By Theorem 1.1.5, it then follows that A^0_λ is upper semicontinuous in $\lambda \in \Lambda_2$. In particular,

$$\lim_{\lambda\to\lambda_0} \sup_{\phi\in A^0_\lambda} d(\phi, A^0_{\lambda_0}) = 0. \tag{8.68}$$

Let $\Phi_\lambda(t,\cdot) : X^+ \to X^+$ be defined by

$$\Phi_\lambda(t,\phi) = (S(\cdot,t,\phi,\lambda), u_1(\cdot,t,\phi,\lambda), u_2(\cdot,t,\phi,\lambda)), \ \phi \in X^+.$$

Clearly, $S_\lambda = \Phi_\lambda(\omega,\cdot)$ and $S^n_\lambda = \Phi_\lambda(n\omega,\cdot)$. It then follows that $\Phi_\lambda : \mathbb{R}_+ \times X^+ \to X^+$ is a periodic semiflow. Moreover, by Theorem 3.1.1, $\lim_{t\to\infty} d(\Phi_\lambda(t,\phi),\ \tilde{A}^0_\lambda) = 0, \quad \forall \phi \in X_0$, where $\tilde{A}^0_\lambda = \cup_{t\in[0,\omega]}\Phi_\lambda(t, A^0_\lambda) \subset X_0$. Since $A^0_\lambda = S_\lambda(A^0_\lambda)$, $\tilde{A}^0_\lambda = \cup_{t\in(0,\omega]}\Phi_\lambda(t, A^0_\lambda)$. By the compactness of $\tilde{A}^0_{\lambda_0}$ and the parabolic maximum principle, it then follows that there exists $\beta_0 > 0$ such that for any $\phi = (\phi_0,\phi_1,\phi_2) \in \tilde{A}^0_{\lambda_0}$, $\phi_i(x) \geq \beta_0$, $\forall x \in [0,1]$, $i = 1,2$. By (8.68), we have $\lim_{\lambda\to\lambda_0} \sup_{\phi\in\tilde{A}^0_\lambda} d(\phi, \tilde{A}^0_{\lambda_0}) = 0$. Consequently, there exist $\delta_2 \in (0,\delta_1)$ and $\beta_1 > 0$ such that for any $|\lambda-\lambda_0| < \delta_2$, and any $\phi = (\phi_0,\phi_1,\phi_2) \in \tilde{A}^0_\lambda$, we have $\phi_i(x) \geq \beta_1$, $\forall x \in [0,1]$, $i = 1,2$. Now the global attractivity of $\tilde{A}^0_\lambda$ in X_0 for Φ_λ completes the proof. ∎

Remark 8.3.1. In the case where the velocity of the flow of medium in the bioreactor varies periodically as well, that is, $v = v(t) = v(t+\omega)$, a change of variables

$$\bar{S}(x,t) = \exp\left(\frac{v(t)(x-1)^2}{2d_0}\right)(S(x,t) - W^*(x,t)),$$
$$\bar{u}_i(x,t) = \exp\left(\frac{v(t)(x-1)^2}{2d_i}\right)u_i(x,t),\ i = 1,2,$$

results in the boundary conditions becoming homogeneous Neumann boundary conditions, and using similar ideas as in Sections 8.2 and 8.3, we can also discuss the global dynamics of the modified model systems.

Remark 8.3.2. In the case of constant nutrient input, that is, $S^0(\cdot) \equiv S^0$, it follows that the ω-periodic solutions in Sections 8.2 and 8.3 reduce to steady states of the corresponding autonomous reaction–diffusion systems, and hence we have the analogous results of Theorems 8.2.1, 8.2.2, 8.3.1, and 8.3.2.

8.4 Notes

This chapter is adapted from Smith and Zhao [336]. The model with constant nutrient input was formulated by Kung and Baltzis [207], and was studied in Ballyk, Le, Jones and Smith [27]. Smith and Zhao [341] established the existence of traveling waves for this model in the case of single species growth. The transformations in Section 8.3 converting Robin-type boundary conditions to Neumann boundary conditions were motivated by Pilyugin and Waltman [278]. Similar perturbation ideas as in Section 8.3 were used for two-species periodic competitive parabolic systems under perturbations in Zhao [437].

Hsu, Wang and Zhao [175] studied a periodically pulsed bioreactor model in a flowing water habitat with a hydraulic storage zone in which no flow occurs, and obtained sufficient conditions in terms of principal eigenvalues for the persistence of single population and the coexistence of two competing populations. Yu and Zhao [422] investigated the spatial dynamics of a periodic reaction–advection–diffusion model for a stream population, and established a threshold-type result on the global stability of either zero or the positive periodic solution in the case of a bounded domain.