J Dyn Diff Equat
DOI 10.1007/s10884-011-9224-3

Dynamics of a Periodically Pulsed Bio-Reactor Model With a Hydraulic Storage Zone

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Received: 28 April 2010

Abstract In this paper, we investigate a periodically pulsed bio-reactor model of a flowing water habitat with a hydraulic storage zone in which no flow occurs. The full system can be reduced to a limiting system based on a conservation principle. Then we obtain sufficient conditions in terms of principal eigenvalues for the persistence of single population and the coexistence of two competing populations for the limiting system by appealing to the theory of monotone dynamical systems. Finally, we use the theory of chain transitive sets to lift the dynamics of the limiting system to the full system.

Keywords Periodic bioreactor model · Hydraulic storage zone · Extinction and persistence · Periodic coexistence state

Mathematics Subject Classification (2010) 35K55 · 37C65 · 92D25

1 Introduction

The chemostat is a basic piece of laboratory apparatus, yet it plays an important role in most theoretical studies of microbial growth and competition [17]. Although it provides a simple model for many microbial habitats, the assumption of idealized mixing may be doubtful. Natural environments are usually spatially inhomogeneous and several models have been introduced where the habitat is not well mixed. For the unstirred chemostat, the authors in

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Published online: 02 September 2011

[6] removed the "well-mixed" hypothesis and considered a system of reaction-diffusion equations. Basically, the flow enters at one boundary supplying nutrient resource(s), and exits at another, removing nutrients and organisms, while diffusion transports organisms and nutrient across the habitat domain. A different environment for microbial growth and competition is the flow reactor model with advection [1,2,9,16]. Let us briefly introduce the flow reactor model of microbial competition for a nutrient in a riverine reservoir occupying a simple channel of longitudinally invariant cross-section that was formulated by Kung and Baltzis in [9]. The channel is assumed to have constant cross-sectional area A and length L, yielding volume V. A flow of water enters at the upstream end ($x = 0$), with discharge F (dimensions length^3 / time). An equal flow exits at the downstream end ($x = L$), which is assumed to be a dam. Based on this flow, a dilution rate D (dimensions time^{-1}) is defined as F/V. The advective flow within the channel is set to maintain water balance, by transporting water with a net velocity $\nu = DL$. The microbial populations $N_i, i = 1, 2$ compete for nutrient R. The competition is purely exploitative in the sense that organisms simply consume the nutrient, thereby making it unavailable for its competitor. A flow of medium in the channel with velocity ν in the direction of increasing x brings fresh nutrient at a a time-independent constant concentration into the reactor at $x = 0$ and carries medium, unutilized nutrient and organisms out of the reactor at $x = L$. Nutrient and organisms are assumed to diffuse throughout the channel with the same diffusivity δ.

However, if we consider the periodic time dependence in the nutrient concentration to account for seasonal or daily changes, then the model will become more realistic. The authors in [18] assume that the nutrient concentration in the medium is maintained at the periodically varying concentration $R^{(0)}(t + \tau) = R^{(0)}(t)$ at the up stream end of the channel ($x = 0$). These assumptions above lead to the following parabolic systems:

$$\begin{aligned}
\frac{\partial R}{\partial t} &= \delta \frac{\partial^2 R}{\partial x^2} - \nu \frac{\partial R}{\partial x} - q_1 f_1(R) N_1 - q_2 f_2(R) N_2, \\
\frac{\partial N_1}{\partial t} &= \delta \frac{\partial^2 N_1}{\partial x^2} - \nu \frac{\partial N_1}{\partial x} + f_1(R) N_1, \\
\frac{\partial N_2}{\partial t} &= \delta \frac{\partial^2 N_2}{\partial x^2} - \nu \frac{\partial N_2}{\partial x} + f_2(R) N_2, \ 0 < x < L, \ t > 0
\end{aligned} \tag{1.1}$$

with boundary conditions

$$\begin{aligned}
&\nu R(0, t) - \delta \frac{\partial R}{\partial x}(0, t) = \nu R^{(0)}(t), \\
&\nu N_i(0, t) - \delta \frac{\partial N_i}{\partial x}(0, t) = 0, \\
&\frac{\partial R}{\partial x}(L, t) = \frac{\partial N_i}{\partial x}(L, t) = 0, \qquad i = 1, 2,
\end{aligned} \tag{1.2}$$

and initial conditions

$$\begin{aligned}
&R(x, 0) = R^0(x) \geq 0, \\
&N_i(x, 0) = N_i^0(x) \geq 0, \quad 0 < x < L, \qquad i = 1, 2,
\end{aligned} \tag{1.3}$$

where q_i is the constant nutrient quota for species i; $R^{(0)}(t)$ satisfies

$$\begin{aligned}
&R^{(0)}(\cdot) \in C^2(\mathbb{R}_+, \mathbb{R}), R^{(0)}(t) \geq 0 \text{ but } R^{(0)}(\cdot) \not\equiv 0 \text{ on } \mathbb{R}_+ := [0, \infty), \\
&R^{(0)}(t + \tau) = R^{(0)}(t), \text{ for some real number } \tau > 0.
\end{aligned} \tag{1.4}$$

The nonlinear functions $f_i(R)$ describes the nutrient uptake rate and the growth rate of the organisms N_i at nutrient concentration R. We assume that these functions satisfy

$$f_i(0) = 0,\ \ f_i'(R) > 0,\ \ f_i \in C^2, i = 1, 2.$$

A usual example is the Monod function

$$f_i(R) = \frac{\mu_{\mathrm{max,i}} R}{K_{\mu,i} + R}.$$

The aim of this paper is to generalize (1.1)–(1.3) by adding a hydraulic storage zone in which there is no spatial transport. Models with hydraulic storage zones partition the cross-section of a channel into a flowing zone of area A, and a static zone of area A_S. Exchange of nutrient and populations between the flowing and storage zones occurs by Fickian diffusion with rate α (time^{-1}). Although nutrient concentration and population densities vary with location x in both the flowing channel and the storage zone, advective and diffusive transport occur only in the flowing zone, not the storage zone. Suppose $R(x,t)$, $N_i(x,t)$ denote nutrient concentration and population densities in the flowing channel; $R_S(x,t)$, $N_{S,i}$ denote nutrient concentration and population densities in the storage zone. Then the governing equations are

$$\begin{aligned}
\frac{\partial R}{\partial t} &= \delta\frac{\partial^2 R}{\partial x^2} - \nu\frac{\partial R}{\partial x} - q_1 f_1(R)N_1 - q_2 f_2(R)N_2 + \alpha(R_S - R),\\
\frac{\partial N_1}{\partial t} &= \delta\frac{\partial^2 N_1}{\partial x^2} - \nu\frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) + f_1(R)N_1,\\
\frac{\partial N_2}{\partial t} &= \delta\frac{\partial^2 N_2}{\partial x^2} - \nu\frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + f_2(R)N_2,\\
\frac{\partial R_S}{\partial t} &= -\alpha\frac{A}{A_S}(R_S - R) - q_1 f_1(R_S)N_{S,1} - q_2 f_2(R_S)N_{S,2},\\
\frac{\partial N_{S,1}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,1} - N_1) + f_1(R_S)N_{S,1},\\
\frac{\partial N_{S,2}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,2} - N_2) + f_2(R_S)N_{S,2},\ \ 0 < x < L,\ \ t > 0
\end{aligned} \tag{1.5}$$

with boundary conditions

$$\begin{aligned}
&\nu R(0,t) - \delta\frac{\partial R}{\partial x}(0,t) = \nu R^{(0)}(t),\\
&\nu N_i(0,t) - \delta\frac{\partial N_i}{\partial x}(0,t) = 0,\\
&\frac{\partial R}{\partial x}(L,t) = \frac{\partial N_i}{\partial x}(L,t) = 0, \qquad i = 1, 2,
\end{aligned} \tag{1.6}$$

and initial conditions

$$\begin{aligned}
R(x,0) &= R^0(x) \ge 0,\ \ N_i(x,0) = N_i^0(x) \ge 0,\ \ 0 < x < L,\\
R_S(x,0) &= R_S^0(x) \ge 0,\ \ N_{S,i}(x,0) = N_{S,i}^0(x) \ge 0,\ \ i = 1, 2,
\end{aligned} \tag{1.7}$$

where $R^{(0)}(t)$ satisfies (1.4). We should point out that the authors in [4] considered the system (1.5)–(1.7) under the assumption $R^{(0)}(t) \equiv R^{(0)}$.

One of the main technical difficulties in our analysis is the lack of compactness of solution maps of the model system. This is because some equations have no diffusion terms.

To overcome these problems, we first prove that the solution maps associated with a linearized system around the trivial (or semi-trivial) solution are κ-contractions, where κ is the Kuratowski measure of noncompactness (see, e.g., [3]). By a generalized Krein-Rutman Theorem, we can show that the principal eigenvalue of the associated eigenvalue problems exists, and hence, the stability of those trivial (or semi-trivial) solutions can be determined. Next, we prove the solution maps associated with our systems are asymptotically compact on any bounded set and then conclude that the associated Poincaré map is κ-contracting and admits a global attractor under some appropriate conditions by using the results in [10].

The organization of the paper is as follows. In Sect. 2, we study the well-posedness and the conservation principle for system (1.5)–(1.7). Due to this conservation law, (1.5)–(1.7) can be reduced to a limiting system which generates a monotone dynamical system. In Sect. 3, we consider the single population growth in the limiting system. We show that when the trivial solution is asymptotically stable, then the single population will be washed out; when the trivial solution is unstable, there is a unique periodic positive solution which attracts all solutions with nonzero initial data. Section 4 is devoted to the study of the limiting system of the two competing species model. We prove the existence of a positive periodic solution (i.e., a periodic coexistence state) if each species can invade the semi-trivial periodic state established by the other species. In Sect. 5, we lift the dynamics of the limiting system to the full system by using the theory of internal chain transitive sets.

2 The Conservation Principle

This section is devoted to the study of the well-posedness of the initial-boundary-value problem (1.5)–(1.7) and the conservation principle. Let $X^+ = C([0, L], \mathbb{R}^6_+)$ be the positive cone in the Banach space $X = C([0, L], \mathbb{R}^6)$ with the usual supremum norm. In order to simplify notations, we set $u_0 = R, u_1 = N_1, u_2 = N_2, u_3 = R_S, u_4 = N_{S,1}, u_5 = N_{S,2}$ and $\mathbf{u} = (u_0, u_1, u_2, u_3, u_4, u_5)$. We assume that the initial data in (1.7) satisfying $(u_0^0, u_1^0, u_2^0, u_3^0, u_4^0, u_5^0) := (R^0, N_1^0, N_2^0, R_S^0, N_{S,1}^0, N_{S,2}^0) \in X^+$. For the local existence and positivity of solutions in the space X^+, we appeal to the theory developed in [11] where existence and uniqueness and positivity are treated simultaneously (taking delay as zero). The idea is to view the system (1.5)–(1.7) as the abstract ordinary differential equation in X^+ and the so-called mild solutions can be obtained for any given initial data. More precisely,

$$\begin{cases} u_0(t) = V(t, 0)u_0^0 + \int_0^t T_0(t-s)B_0(\mathbf{u}(s))ds, \\ u_i(t) = T_i(t)u_i^0 + \int_0^t T_i(t-s)B_i(\mathbf{u}(s))ds, \ i = 1, 2, \\ u_i(t) = u_i^0 + \int_0^t B_i(\mathbf{u}(s))ds, \ i = 3, 4, 5, \end{cases} \tag{2.1}$$

where $T_i(t)$ is the positive, non-expansive, analytic semigroup on $C([0, L], \mathbb{R})$ (see, e.g., [16, Chap. 7]) such that $u = T_i(t)u_i^0, i = 0, 1, 2$, satisfies the linear initial value problem

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x}, \ t > 0, 0 < x < L, \\ \nu u(0, t) - \delta \frac{\partial u}{\partial x}(0, t) = \frac{\partial u}{\partial x}(L, t) = 0, \ t > 0, \\ u(x, 0) = u_i^0(x), \ i = 0, 1, 2. \end{cases} \tag{2.2}$$

$V(t, s), t > s$, is the family of affine operators on $C([0, L], \mathbb{R})$ (see, e.g., [13, Chap. 5]) such that $u = V(t, s)u_0^0$ satisfies the linear system with nonhomogeneous, periodic boundary conditions, with start time s, given by

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x}, \ t > s, \ 0 < x < L, \\ \nu u(0,t) - \delta \frac{\partial u}{\partial x}(0,t) = \nu R^{(0)}(t), \ \frac{\partial u}{\partial x}(L,t) = 0, \ t > s, \\ u(x,s) = u_0^0(x). \end{cases} \tag{2.3}$$

Since $R^{(0)}(t+\tau) = R^{(0)}(t)$, it follows that

$$V(t+\tau, s+\tau) = V(t,s), \ \forall \, t > s.$$

The nonlinear operator $B_i : C([0,L], \mathbb{R}_+) \to C([0,L], \mathbb{R})$ is defined by

$$\begin{cases} B_0(\mathbf{u}) = -q_1 f_1(u_0)u_1 - q_2 f_2(u_0)u_2 + \alpha(u_3 - u_0), \\ B_1(\mathbf{u}) = \alpha(u_4 - u_1) + f_1(u_0)u_1, \\ B_2(\mathbf{u}) = \alpha(u_5 - u_2) + f_2(u_0)u_2, \\ B_3(\mathbf{u}) = -\alpha \frac{A}{A_S}(u_3 - u_0) - q_1 f_1(u_3)u_4 - q_2 f_2(u_3)u_5, \\ B_4(\mathbf{u}) = -\alpha \frac{A}{A_S}(u_4 - u_1) + f_1(u_3)u_4, \\ B_5(\mathbf{u}) = -\alpha \frac{A}{A_S}(u_5 - u_2) + f_2(u_3)u_5. \end{cases} \tag{2.4}$$

By standard maximum principle arguments (see, e.g., [16, Chap. 7]), it follows that $V(t,s)C([0,L], \mathbb{R}_+) \subset C([0,L], \mathbb{R}_+)$, $\forall \ t > s$ and $T_i(t)C([0,L], \mathbb{R}_+) \subset C([0,L], \mathbb{R}_+)$, $\forall \, t > 0$. The operator V and semi-group T_0 are related to [11, Eq. (1.9)] by setting $\beta(x,t) = \nu R^{(0)}(t)$. Since $f_i(0) = 0$, it follows that $B_i(\mathbf{u}) \geq 0$ whenever $u_i \equiv 0, \forall \ 0 \leq i \leq 5$, and hence, $\mathbf{B} := (B_0, B_1, B_2, B_3, B_4, B_5)$ is quasipositive (see, e.g., [11, Remark 1.1]). By [11, Theorem 1 and Remark 1.1], we have the following results:

Lemma 2.1 *The system* (1.5)–(1.7) *has a unique noncontinuable solution and the solutions to* (1.5)–(1.7) *remain non-negative on their interval of existence if they are non-negative initially.*

In the followings, we demonstrate that (1.5)–(1.7) have mass conservation in the flow and storage zones. Let

$$\begin{aligned} W(x,t) &= R(x,t) + q_1 N_1(x,t) + q_2 N_2(x,t) \text{ and} \\ W_S(x,t) &= R_S(x,t) + q_1 N_{S,1}(x,t) + q_2 N_{S,2}(x,t). \end{aligned} \tag{2.5}$$

Then $W(x,t)$ and $W_S(x,t)$ satisfy the following coupled differential equations

$$\begin{aligned} \frac{\partial W}{\partial t} &= \delta \frac{\partial^2 W}{\partial x^2} - \nu \frac{\partial W}{\partial x} + \alpha W_S - \alpha W, \\ \frac{\partial W_S}{\partial t} &= -\alpha \frac{A}{A_S} W_S + \alpha \frac{A}{A_S} W, \ 0 < x < L, \ t > 0 \end{aligned} \tag{2.6}$$

with boundary conditions

$$\nu W(0,t) - \delta \frac{\partial W}{\partial x}(0,t) = \nu R^{(0)}(t), \ \frac{\partial W}{\partial x}(L,t) = 0, \tag{2.7}$$

and initial conditions

$$W(x,0) = W^0(x), \ W_S(x,0) = W_S^0(x). \tag{2.8}$$

Note that (1.5)–(1.7) reduces to (2.6)–(2.8) for $W = R$ and $W_S = R_S$ when $N_i = N_{S,i} = 0, i = 1, 2$.

We first consider the following auxiliary system which will be used in our discussions later:

$$\frac{\partial U}{\partial t} = \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + \alpha U_S - \alpha U,$$
$$\frac{\partial U_S}{\partial t} = -\alpha \frac{A}{A_S} U_S + \alpha \frac{A}{A_S} U,\ 0 < x < L,\ t > 0 \tag{2.9}$$

with boundary conditions

$$\nu U(0,t) - \delta \frac{\partial U}{\partial x}(0,t) = 0,\ \frac{\partial U}{\partial x}(L,t) = 0, \tag{2.10}$$

and initial conditions

$$U(x,0) = U^0(x),\ U_S(x,0) = U_S^0(x). \tag{2.11}$$

It is easy to see that the system (2.9)–(2.11) is a linear and cooperative system. According to [16, pp. 147–148], the eigenvalue problem

$$\begin{cases} \lambda\phi(x) = \delta\phi''(x) - \nu\phi'(x),\ 0 < x < L, \\ \nu\phi(0) - \delta\phi'(0) = \phi'(L) = 0, \end{cases} \tag{2.12}$$

has a principal eigenvalue, denoted by λ^0, with an associated eigenvector $\phi^0 \gg 0$, and $\lambda^0 < 0$. This implies that $U = 0$ is globally asymptotically stable for $\frac{\partial U}{\partial t} = \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x}$ subject to (2.10).

Substituting $U(x,t) = e^{\lambda t}\phi(x)$ and $U_S(x,t) = e^{\lambda t}\varphi(x)$, we obtain the associated eigenvalue problem

$$\begin{cases} \lambda\phi(x) = \delta\phi''(x) - \nu\phi'(x) - \alpha\phi(x) + \alpha\varphi(x), \\ \lambda\varphi(x) = -\alpha \frac{A}{A_S}\varphi(x) + \alpha \frac{A}{A_S}\phi(x),\ 0 < x < L, \\ \nu\phi(0) - \delta\phi'(0) = \phi'(L) = 0. \end{cases} \tag{2.13}$$

Let $\mathcal{T}(t)$ be the solution semigroup generated by (2.9)–(2.11) on $C([0,L],\mathbb{R}^2)$. It is easy to see that $\mathcal{T}(t)$ is a strongly positive operator for each $t > 0$. By the similar arguments as in the proof of Lemma 3.3 (see also [8]), we can prove that for each $t > 0$, $\mathcal{T}(t)$ is an κ-contraction on $C([0,L],\mathbb{R}^2)$ in the sense that

$$\kappa(\mathcal{T}(t)B) \le e^{-\frac{\alpha A}{A_S}t}\kappa(B),$$

for any bounded subset B of $C([0,L],\mathbb{R}^2)$, where κ is the Kuratowski measure of noncompactness in the Banach space $C([0,L],\mathbb{R}^2)$. By the proof of [16, Theorem 7.6.1] and a generalized Krein-Rutman Theorem (see [12] or [8, Lemma 2.2]), it follows that the problem (2.13) has a principal eigenvalue, denoted by λ^*, with an associated eigenvector $(\phi^*, \varphi^*) \gg 0$. Further, for each $t > 0$, the spectrum radius of $\mathcal{T}(t)$, $r(\mathcal{T}(t))$, is the principal eigenvalue of $\mathcal{T}(t)$, and hence,

$$r(\mathcal{T}(t)) = e^{\lambda^* t},\ \forall\, t > 0. \tag{2.14}$$

Lemma 2.2 *Let λ^* be the principal eigenvalue of* (2.13). *Then*

$$\lambda^* = \frac{1}{2}\left[(\lambda^0 - \alpha - \frac{\alpha A}{A_S}) + \sqrt{(\lambda^0 - \alpha - \frac{\alpha A}{A_S})^2 + 4\lambda^0 \frac{\alpha A}{A_S}} \right],$$

and hence $\lambda^* < 0$.

Proof Our proof is essentially the same as that of [19, Lemma 3.1]. For the sake of completeness, we provide its details below. Suppose that λ^* and $(\phi^*, \varphi^*) \gg 0$ are the eigenvalue-eigenvector pair corresponding to (2.13). From the second equation of (2.13), it follows that

$$-\alpha\phi^*(x) + \alpha\varphi^*(x) = -\frac{\alpha\lambda^*}{\lambda^* + (\alpha A/A_S)}\phi^*(x).$$

From the first equation of (2.13), it follows that

$$\begin{cases} (\lambda^* + \frac{\alpha\lambda^*}{\lambda^*+(\alpha A/A_S)})\phi^*(x) = \delta\phi^{*\prime\prime}(x) - \nu\phi^{*\prime}(x), \ 0 < x < L, \\ \nu\phi^*(0) - \delta\phi^{*\prime}(0) = \phi^{*\prime}(L) = 0. \end{cases} \tag{2.15}$$

Since $\phi^*(x) > 0$ in $(0, L)$, it deduces that $\lambda^0 = \lambda^* + \frac{\alpha\lambda^*}{\lambda^*+(\alpha A/A_S)}$, and hence, λ^* is a real zero of the quadratic equation

$$P(\lambda) := \lambda^2 + \left(\frac{\alpha A}{A_S} + \alpha - \lambda^0\right)\lambda - \lambda^0\frac{\alpha A}{A_S} = 0. \tag{2.16}$$

It remains to show that λ^* is the maximum root of Eq. (2.15). Suppose that λ is a given zero of (2.15). Obviously, $P(-\frac{\alpha A}{A_S}) = -\frac{\alpha^2 A}{A_S} < 0$ and then $\lambda + \frac{\alpha A}{A_S} \neq 0$. By (2.16), it follows that $\lambda^0(\lambda + \frac{\alpha A}{A_S}) = \lambda[(\lambda + \frac{\alpha A}{A_S}) + \alpha]$, that is, $\lambda^0 = \lambda + \frac{\alpha\lambda}{\lambda+\frac{\alpha A}{A_S}}$. Note that $(\lambda^0, \phi^0(x))$ satisfies (2.12). Let $\varphi^0(x) = \frac{\frac{\alpha A}{A_S}}{\lambda+\frac{\alpha A}{A_S}}\phi^0(x)$. Hence, λ is an eigenvalue of (2.13) with eigenfunction $(\phi^0(x), \varphi^0(x))$. Thus, $\lambda \leq \lambda^*$ since λ^* is the principal eigenvalue of (2.13). Then λ^* is the maximum root of (2.15), and hence

$$\lambda^* = \frac{1}{2}\left[(\lambda^0 - \alpha - \frac{\alpha A}{A_S}) + \sqrt{(\lambda^0 - \alpha - \frac{\alpha A}{A_S})^2 + 4\lambda^0\frac{\alpha A}{A_S}}\right].$$

Since $\lambda^0 < 0$, the above equality implies that $\lambda^* < 0$. □

By Lemma 2.2 and (2.14), it follows that $r(\mathcal{T}(t)) < 1$ for each $t > 0$. This implies that $(0, 0)$ is globally asymptotically stable for (2.9)–(2.11), and hence, $(0, 0)$ is the unique steady-state solution for (2.9)–(2.11).

Lemma 2.3 *The system* (2.6)–(2.8) *admit a unique positive τ-periodic solution* $(W^*(x,t), W_S^*(x,t)) \gg 0$ *and for any* $(W_0(x), W_{0S}(x)) \in C([0, L], \mathbb{R}^2)$*, the unique mild solution* $(W(x,t), W_S(x,t))$ *of* (2.6)–(2.8) *with*

$$(W(x, 0), W_S(x, 0)) = (W_0(x), W_{0S}(x))$$

satisfies

$$\lim_{t\to\infty}((W(x,t), W_S(x,t)) - (W^*(x,t), W_S^*(x,t))) = (0, 0) \text{ uniformly for } x \in [0, L]. \tag{2.17}$$

Proof Let

$$U(x,t) = W(x,t) - R^{(0)}(t), \ \ U_S(x,t) = W_S(x,t).$$

Then $U(x,t)$ and $U_S(x,t)$ satisfy the following coupled differential equations

$$\begin{aligned} \frac{\partial U}{\partial t} &= \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + \alpha U_S - \alpha U + R_1(t), \\ \frac{\partial U_S}{\partial t} &= -\alpha \frac{A}{A_S} U_S + \alpha \frac{A}{A_S} U + R_2(t),\ 0 < x < L,\ t > 0 \end{aligned} \tag{2.18}$$

with boundary conditions

$$\nu U(0,t) - \delta \frac{\partial U}{\partial x}(0,t) = 0,\ \frac{\partial U}{\partial x}(L,t) = 0, \tag{2.19}$$

and initial conditions

$$U(x,0) = U^0(x),\ U_S(x,0) = U_S^0(x), \tag{2.20}$$

where $R_1(t) = -\frac{dR^0(t)}{dt} - \alpha R^{(0)}(t),\quad R_2(t) = \frac{\alpha A}{A_S} R^{(0)}(t)$.

The boundary condition (2.19) is homogeneous and we rewrite (2.18)–(2.20) as an abstract system of ordinary differential equations in $C([0,L],\mathbb{R}^2)$ given by

$$\frac{d}{dt}\begin{pmatrix} U \\ U_S \end{pmatrix} = \mathcal{A}\begin{pmatrix} U \\ U_S \end{pmatrix} + \begin{pmatrix} R_1(t) \\ R_2(t) \end{pmatrix},\ t > 0, \tag{2.21}$$

with initial condition

$$\begin{pmatrix} U(0) \\ U_S(0) \end{pmatrix} = \begin{pmatrix} U^0(x) \\ U_S^0(x) \end{pmatrix}, \tag{2.22}$$

where $\mathcal{A}$ is the closure in $C([0,L]) \times C([0,L])$ of

$$\mathcal{A}^0 = \begin{pmatrix} \delta \frac{\partial^2}{\partial x^2} - \nu \frac{\partial}{\partial x} - \alpha & \alpha \\ \alpha \frac{A}{A_S} & -\alpha \frac{A}{A_S} \end{pmatrix},$$

with domain

$$\begin{aligned} D(\mathcal{A}^0) = \{&(U^0, U_S^0) \in C^2((0,L),\mathbb{R}^2) \cap C^1([0,L],\mathbb{R}^2) : \mathcal{A}^0 \begin{pmatrix} U^0 \\ U_S^0 \end{pmatrix} \in C([0,L],\mathbb{R}^2), \\ &\nu U^0(0) - \delta (U^0)'(0) = (U^0)'(L) = 0\}. \end{aligned}$$

For any $(U^0, U_S^0) \in C([0,L],\mathbb{R}^2)$, the mild solution of (2.18)–(2.20) is express as

$$\begin{pmatrix} U(t) \\ U_S(t) \end{pmatrix} = \mathcal{T}(t)\begin{pmatrix} U^0 \\ U_S^0 \end{pmatrix} + \int_0^t \mathcal{T}(t-s)\begin{pmatrix} R_1(s) \\ R_2(s) \end{pmatrix} ds, \tag{2.23}$$

where $\mathcal{T}(t)$ is the analytic semigroup generated by $\mathcal{A}$ in $C([0,L],\mathbb{R}^2)$, that is, $\mathcal{T}(t)$ is the solution semigroup generated by (2.9)–(2.11). It is easy to see that $(U(t), U_S(t))$ is a τ-periodic solution of (2.21) if and only if $(U^0, U_S^0) = (U(0), U_S(0))$ and

$$(I - \mathcal{T}(\tau))\begin{pmatrix} U^0 \\ U_S^0 \end{pmatrix} = \int_0^\tau \mathcal{T}(\tau - s)\begin{pmatrix} R_1(s) \\ R_2(s) \end{pmatrix} ds. \tag{2.24}$$

By Lemma 2.2 and (2.14), it follows that $r(\mathcal{T}(\tau)) = e^{\lambda^* \tau} < 1$. This implies that $I - \mathcal{T}(\tau)$ is invertible, and hence, (2.21) admits a unique τ-periodic solution $(U^*(x,t), U_S^*(x,t))$.

Let $V(x,t) = U(x,t) - U^*(x,t)$ and $V_S(x,t) = U_S(x,t) - U_S^*(x,t)$. Then

$$\frac{d}{dt}\begin{pmatrix} V(t) \\ V_S(t) \end{pmatrix} = \mathcal{A}\begin{pmatrix} V(t) \\ V_S(t) \end{pmatrix}, \ t > 0, \tag{2.25}$$

with initial condition.

By [13, Theorem 4.4.3], there exist $M > 0$ and $\delta > 0$ such that $\| \ \mathcal{T}(t) \ \| < Me^{-\delta t}$, $t \geq 0$. Hence $\lim_{t\to\infty}(V(t), V_S(t)) = (0,0)$ uniformly in $C([0,L], \mathbb{R}^2)$, that is, $\lim_{t\to\infty}(V(x,t), V_S(x,t)) = (0,0)$ uniformly for $x \in [0,L]$. Then $\lim_{t\to\infty}(U(x,t) - U(x,t)^*, V_S(x,t) - V_S^*(x,t)) = (0,0)$ uniformly for $x \in [0,L]$.

Set $W^*(x,t) = U^*(x,t) + R^{(0)}(t)$ and $W_S^*(x,t) = U_S^*(x,t), x \in [0,L]$, and $t \geq 0$. It then follows that $(W^*(x,t), W_S^*(x,t))$ is a τ-periodic solution of (2.6)–(2.8). Moreover, for any $(W^0(\cdot), W_S^0(\cdot)) \in C([0,L], \mathbb{R}^2)$, the unique mild solution $(W(x,t), W_S(x,t))$ of (2.6)–(2.8) with $(W(\cdot,0), W_S(\cdot,0)) = (W^0(\cdot), W_S^0(\cdot))$ satisfies (2.17).

From [11, Theorem 1 and Remark 1.1], for any $(W^0(\cdot), W_S^0(\cdot)) \in C([0,L], \mathbb{R}_+^2)$, the unique solution $(W(x,t), W_S(x,t))$ of (2.6)–(2.8) with $(W(\cdot,0), W_S(\cdot,0)) = (W^0(\cdot), W_S^0(\cdot))$ satisfying

$$W(x,t) \geq 0, \ W_S(x,t)) \geq 0, \ x \in [0,L], \ t \geq 0.$$

It remains to show that

$$W^*(x,t) > 0, \ W_S^*(x,t) > 0, \ x \in [0,L], \ t \geq 0.$$

For any given $t \geq 0$, by (2.17), we have

$$\lim_{n\to\infty}[(W(x, t+n\tau), W_S(x, t+n\tau)) - (W^*(x,t), W_S^*(x,t))] = (0,0),$$

uniformly for $x \in [0,L]$. Then $W^*(x,t) = \lim_{n\to\infty} W(x, t+n\tau) \geq 0$ and $W_S^*(x,t) = \lim_{n\to\infty} W_S(x, t+n\tau) \geq 0$ uniformly for $x \in [0,L]$. It is easy to see that $R^{(0)}(t_0) > 0$, for some $t_0 > 0$. By the boundary condition of $U^*(x,t_0)$ at $x = 0$, it follows that $U^*(\cdot, t_0) \not\equiv -R^{(0)}(t_0)$. Thus, $W^*(\cdot, t_0) = U^*(\cdot, t_0) + R^{(0)}(t_0) \not\equiv 0$.

We first show that $W^*(x,t) > 0, \ x \in [0,L], \ t \geq t_0$. Suppose that $W^*(\hat{x}, \hat{t}) = 0$, for some $\hat{x} \in [0,L], \ \hat{t} \geq t_0$. By the first equation of (2.6), it follows that

$$-\frac{\partial W^*}{\partial t} + \delta\frac{\partial^2 W^*}{\partial x^2} - \nu\frac{\partial W^*}{\partial x} - \alpha W^* = -\alpha W_S^* \leq 0 \tag{2.26}$$

If $\hat{x} \in (0,L)$, then the strong maximum principle ([14, Chap. 3, Theorem 7]) implies that $W^*(x,t) \equiv 0$ on $x \in [0,L]$ and $\hat{t} \geq t_0$, which is impossible because $W^*(\cdot, t_0) \not\equiv 0$. Assume that $\hat{x} = 0$, that is, $W^*(0,\hat{t}) = 0$. Then by [14, Chap. 3, Theorem 3], it follows that $W_x^*(0,\hat{t}) > 0$, that is, $\nu W^*(0,\hat{t}) - \delta W_x^*(0,\hat{t}) < 0$, contradicting (2.7). Assume $\hat{x} = L$. By a similar argument, it follows that $W_x^*(L,\hat{t}) < 0$, contradicting (2.7) again. Thus, $W^*(x,t) > 0, \ x \in [0,L], \ t \geq t_0$. By the τ-periodicity of $W^*(x,\cdot)$, it follows that $W^*(x,t) > 0, \ x \in [0,L], \ t \geq 0$.

Next, we show that $W_S^*(x,t) > 0, \ x \in [0,L], \ t \geq 0$. Suppose that $W_S^*(\tilde{x}, \tilde{t}) = 0$, for some $\tilde{x} \in [0,L], \ \tilde{t} > 0$. By the second equation of (2.6), it follows that

$$\frac{\partial W_S}{\partial t}(\tilde{x}, \tilde{t}) = -\alpha\frac{A}{A_S}W_S(\tilde{x}, \tilde{t}) + \alpha\frac{A}{A_S}W(\tilde{x}, \tilde{t}) = \alpha\frac{A}{A_S}W(\tilde{x}, \tilde{t}) > 0. \tag{2.27}$$

Thus, $W_S^*(\tilde{x}, \tilde{t} - \delta) < W_S^*(\tilde{x}, \tilde{t}) = 0$ if $\delta > 0$ is sufficiently small. The above inequality contradicts that $W_S^*(x, t) \geq 0$ uniformly for $x \in [0, L]$, $t \geq 0$. This completes our proof. $\square$

By Lemma 2.1, together with the relation (2.5) and Lemma 2.3, it is easy to see that the following result hold.

Lemma 2.4 *Any solution of the system* (1.5)–(1.7) *exists globally on* $[0, \infty)$*. Moreover, solutions are ultimately bounded and uniformly bounded.*

Finally, we see from the relation (2.5) and Lemma 2.3 that the limiting systems of (1.5)–(1.7) take the forms:

$$\begin{aligned}
\frac{\partial N_1}{\partial t} &= \delta \frac{\partial^2 N_1}{\partial x^2} - \nu \frac{\partial N_1}{\partial x} + \alpha (N_{S,1} - N_1) + f_1(W^*(x,t) - q_1 N_1 - q_2 N_2) N_1, \\
\frac{\partial N_{S,1}}{\partial t} &= -\alpha \frac{A}{A_S} (N_{S,1} - N_1) + f_1(W_S^*(x,t) - q_1 N_{S,1} - q_2 N_{S,2}) N_{S,1}, \\
\frac{\partial N_2}{\partial t} &= \delta \frac{\partial^2 N_2}{\partial x^2} - \nu \frac{\partial N_2}{\partial x} + \alpha (N_{S,2} - N_2) + f_2(W^*(x,t) - q_1 N_1 - q_2 N_2) N_2, \\
\frac{\partial N_{S,2}}{\partial t} &= -\alpha \frac{A}{A_S} (N_{S,2} - N_2) + f_2(W_S^*(x,t) - q_1 N_{S,1} - q_2 N_{S,2}) N_{S,2},
\end{aligned} \tag{2.28}$$

in $(0, L) \times (0, \infty)$, with boundary conditions

$$\nu N_i(0,t) - \delta \frac{\partial N_i}{\partial x}(0,t) = 0, \quad \frac{\partial N_i}{\partial x}(L,t) = 0, \quad i = 1, 2, \tag{2.29}$$

and initial conditions

$$N_i(x,0) = N_i^0(x) \geq 0, \quad N_{S,i}(x,0) = N_{S,i}^0(x) \geq 0, \quad 0 < x < L, \ i = 1, 2. \tag{2.30}$$

From the biological view of point, the feasible domain $D(t)$ for (2.28)–(2.30) should be

$$\begin{aligned}
D(t) = \{ &(N_1, N_{S,1}, N_2, N_{S,2}) \in C([0, L], \mathbb{R}_+^4) : q_1 N_1(\cdot) + q_2 N_2(\cdot) \leq W^*(\cdot, t), \\
&q_1 N_{S,1}(\cdot) + q_2 N_{S,2}(\cdot) \leq W_S^*(\cdot, t) \}.
\end{aligned} \tag{2.31}$$

In the followings, we show that the set $D(t)$ is positively invariant for the solution maps associated with (2.28)–(2.30).

Lemma 2.5 *For any* $\phi := (\phi_1, \phi_2, \phi_3, \phi_4) \in D(0)$*, system* (2.28)–(2.30) *has a unique mild solution* $(N_1(\cdot, t), N_{S,1}(\cdot, t), N_2(\cdot, t), N_{S,2}(\cdot, t)) \in D(t)$*,* $\forall\ t \geq 0$*, whenever* $(N_1(\cdot, 0), N_{S,1}(\cdot, 0), N_2(\cdot, 0), N_{S,2}(\cdot, 0)) = \phi$*.*

Proof Our proof is similar to that of Lemma 3.1. We will give the proof of Lemma 3.1 in details, so we skip the proof here. $\square$

3 Single Species Growth

In this section, we investigate the single population model. Mathematically, it means that we set $(N_1, N_{S,1}) = (0, 0)$ or $(N_2, N_{S,2}) = (0, 0)$ in the model system (1.5)–(1.7). In order to simplify notations, we drop all subscripts in the remaining equations and then consider

$$\begin{aligned}
\frac{\partial R}{\partial t} &= \delta\frac{\partial^2 R}{\partial x^2} - \nu\frac{\partial R}{\partial x} - qf(R)N + \alpha(R_S - R),\\
\frac{\partial N}{\partial t} &= \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + f(R)N,\\
\frac{\partial R_S}{\partial t} &= -\alpha\frac{A}{A_S}(R_S - R) - qf(R_S)N_S,\\
\frac{\partial N_S}{\partial t} &= -\alpha\frac{A}{A_S}(N_S - N) + f(R_S)N_S,\ 0 < x < L,\ t > 0,
\end{aligned} \tag{3.1}$$

with boundary conditions

$$\begin{aligned}
&\nu R(0,t) - \delta\frac{\partial R}{\partial x}(0,t) = \nu R^{(0)}(t),\ \frac{\partial R}{\partial x}(L,t) = 0,\\
&\nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0,\ t > 0,
\end{aligned} \tag{3.2}$$

and initial conditions

$$\begin{aligned}
&R(x,0) = R^0(x) \geq 0,\ N(x,0) = N^0(x) \geq 0,\ 0 < x < L,\\
&R_S(x,0) = R_S^0(x) \geq 0,\ N_S(x,0) = N_S^0(x) \geq 0,
\end{aligned} \tag{3.3}$$

where $R^{(0)}(t)$ satisfies (1.4). By similar arguments as in Sect. 2, it follows that the limiting system of (3.1)–(3.3) takes the following form:

$$\begin{aligned}
\frac{\partial N}{\partial t} &= \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + f(W^*(x,t) - qN)N,\\
\frac{\partial N_S}{\partial t} &= -\alpha\frac{A}{A_S}(N_S - N) + f(W_S^*(x,t) - qN_S)N_S, 0 < x < L,\ t > 0,
\end{aligned} \tag{3.4}$$

with boundary conditions

$$\nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = 0,\ \frac{\partial N}{\partial x}(L,t) = 0,\ t > 0, \tag{3.5}$$

and initial conditions

$$N(x,0) = N^0(x) \geq 0,\ N_S(x,0) = N_S^0(x) \geq 0, \quad 0 < x < L. \tag{3.6}$$

From the biological view of point, the feasible domain $\Lambda(t)$ for (3.4)–(3.6) should be

$$\Lambda(t) = \{(N, N_S) \in C([0,L], \mathbb{R}_+^2) : qN(\cdot) \leq W^*(\cdot,t),\ qN_S(\cdot) \leq W_S^*(\cdot,t)\}. \tag{3.7}$$

Next, we prove some basic properties of the set $\Lambda(t)$.

Lemma 3.1 *For any $\phi := (\phi_1, \phi_2) \in \Lambda(0)$, system (3.4)–(3.6) has a unique mild solution $(N(\cdot,t), N_S(\cdot,t))$ with $(N(\cdot,0), N_S(\cdot,0)) = \phi$ and $(N(\cdot,t), N_S(\cdot,t)) \in \Lambda(t),\ \forall\, t \geq 0$.*

Proof Let $T(t)$ be the semigroup generated by

$$\begin{cases}
\frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} - \alpha N,\ 0 < x < L,\ t > 0,\\
\nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = 0,\ \frac{\partial N}{\partial x}(L,t) = 0,
\end{cases}$$

and $T_S(t)\phi_2 = e^{-\alpha\frac{A}{A_S}t}\phi_2$. From the system (3.4)–(3.6) with the initial condition $(N(x,0), N_S(x,0)) = \phi$, we have

$$\begin{cases}
N(\cdot,t,\phi) = T(t)\phi_1 + \int_0^t T(t-\theta)[\alpha N_S(\cdot,\theta) + f(W^*(\cdot,\theta) - qN(\cdot,\theta))N(\cdot,\theta)]d\theta,\\
N_S(\cdot,t,\phi) = T_S(t)\phi_2 + \int_0^t T_S(t-\theta)[\frac{\alpha A}{A_S}N(\cdot,\theta) + f(W_S^*(\cdot,\theta) - qN_S(\cdot,\theta))N_S(\cdot,\theta)]d\theta.
\end{cases}$$

It follows that (3.4)–(3.6) can be written as the following integral equation

$$\mathbf{u}(t) = \mathbf{T}(t)\phi + \int_0^t \mathbf{T}(t-\theta)B(\theta, \cdot, \mathbf{u}(\theta))d\theta, \tag{3.8}$$

where

$$\mathbf{u}(t) = \begin{pmatrix} N(t) \\ N_S(t) \end{pmatrix}, \mathbf{T}(t) = \begin{pmatrix} T(t) & 0 \\ 0 & T_S(t) \end{pmatrix},$$

and for any $\mathbf{v} := (v, v_s) \in \Lambda(t)$, $B(t, \cdot, \mathbf{v})$ is defined by

$$B(t, \cdot, \mathbf{v}) := \begin{pmatrix} B_1(t, \cdot, \mathbf{v}) \\ B_2(t, \cdot, \mathbf{v}) \end{pmatrix} = \begin{pmatrix} \alpha v_s + F(t, \cdot, v) \\ \alpha \frac{A}{A_S} v + G(t, \cdot, v_s) \end{pmatrix},$$

with $F(t, \cdot, v) = f(W^*(\cdot, t) - qv)v$ and $G(t, \cdot, v_s) = f(W_S^*(\cdot, t) - qv_s)v_s$.

We first show that $B(t, \cdot, \mathbf{v})$ is quasi-monotone on $\Lambda(t)$ in the sense that

$$\lim_{h \to 0^+} \frac{1}{h} d(\mathbf{v} - \mathbf{w} + h(B(t, \cdot, \mathbf{v}) - B(t, \cdot, \mathbf{w})); C([0, L], \mathbb{R}_+^2)) = 0,$$

for all $\mathbf{v} := (v, v_s),\ \mathbf{w} := (w, w_s) \in \Lambda(t)$ with $\mathbf{w}(x) \le \mathbf{v}(x)$, $x \in [0, L]$. By the mean-value theorem and the fact that $\mathbf{v},\ \mathbf{w} \in \Lambda(t)$, it is easy to see that there is a constant $\delta > 0$ such that $B(t, \cdot, \mathbf{v}) - B(t, \cdot, \mathbf{w}) =$

$$\begin{pmatrix} F(t, \cdot, v) - F(t, \cdot, w) + \alpha(v_s - w_s) \\ G(t, \cdot, v_s) - G(t, \cdot, w_s) + \alpha \frac{A}{A_S}(v - w) \end{pmatrix} \ge \begin{pmatrix} -\delta(v - w) + \alpha(v_s - w_s) \\ -\delta(v_s - w_s) + \alpha \frac{A}{A_S}(v - w) \end{pmatrix}.$$

Hence, for any $h > 0$ satisfying $h\delta < 1$, it follows that

$$(\mathbf{v} - \mathbf{w}) + h(B(t, \cdot, \mathbf{v}) - B(t, \cdot, \mathbf{w})) \ge \begin{pmatrix} (1 - \delta h)(v - w) + h\alpha(v_s - w_s) \\ (1 - \delta h)(v_s - w_s) + h\alpha \frac{A}{A_S}(v - w) \end{pmatrix} \ge 0.$$

Thus, [11, Corallary 5] and the discussions above complete the proof. □

By Lemma 3.1, we can define solution maps $\Psi_t : \Lambda(0) \to \Lambda(t)$ associated with (3.4)–(3.6) by

$$\Psi_t(P) = (N(\cdot, t, P), N_S(\cdot, t, P)),\ \forall P := (N^0(\cdot),\ N_S^0(\cdot)) \in \Lambda(0),\ t \ge 0. \tag{3.9}$$

Note that $\Psi_\tau : \Lambda(0) \to \Lambda(\tau) = \Lambda(0)$ is the Poincaré map associated with (3.4)–(3.6).

For convenience, we let

$$Y^+ = \Lambda(0),\ Y_0 = Y^+ \backslash \{(0, 0)\},\ \partial Y_0 := Y^+ \backslash Y_0 = \{(0, 0)\}.$$

Since one equation in (3.4)–(3.6) has no diffusion term, its solution map Ψ_t is not compact. Due to the lack of compactness, we need to impose the following condition:

$$\alpha \frac{A}{A_S} > f(W_S^*(x, t)),\ \forall\, x \in [0, L],\ t \ge 0. \tag{3.10}$$

Remark 3.1 As in [4, Remark 3.3], if the Monod function $f(R) := \frac{\mu_{\max} R}{K_\mu + R}$ satisfies

$$\mu_{\max} < \alpha \frac{A}{A_S}, \tag{3.11}$$

then it follows that

$$f(W_S^*(x,t)) = \mu_{\max}\frac{W_S^*(x,t)}{K_\mu + W_S^*(x,t)} < \mu_{\max} < \alpha\frac{A}{A_S},$$

that is, (3.10) holds. We note that condition (3.11) means that the cross-section of the storage zone is small or the exchange rate is large.

Recall that the Kuratowski measure of noncompactness (see [3]), κ, is defined by

$$\kappa(B) := \inf\{r : B \text{ has a finite cover of diameter} < r\}, \tag{3.12}$$

for any bounded set B. We set $\kappa(B) = \infty$ whenever B is unbounded. It is easy to see that B is precompact(i.e., $\bar{B}$ is compact) if and only if $\kappa(B) = 0$.

Lemma 3.2 *Let (3.10) hold. Then Ψ_τ is κ-contracting in the sense that*

$$\lim_{n\to\infty} \kappa(\Psi_\tau^n B) = 0$$

for any bounded set $B \subset Y^+$.

Proof For the sake of convenience, we let $(u, v) := (N, N_S)$ and rewrite (3.4)–(3.6) as

$$\begin{cases} \frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} - \nu\frac{\partial u}{\partial x} + m(t,x,u,v), \\ \frac{\partial v}{\partial t} = g(t,x,u,v),\ \ x \in (0,L), t > 0, \\ \nu u(0,t) - d\frac{\partial u}{\partial x}(0,t) = 0,\ \ \frac{\partial u}{\partial x}(L,t) = 0, \\ u(\cdot,0) = \phi_1(\cdot), v(\cdot,0) = \phi_2(\cdot), \end{cases} \tag{3.13}$$

where $m(t,x,u,v) = \alpha(v-u) + f(W^*(x,t) - qu)u$ and $g(t,x,u,v) = -\alpha\frac{A}{A_S}(v-u) + f(W_S^*(x,t) - qv)v$. For any $\phi(\cdot) = (\phi_1(\cdot), \phi_2(\cdot)) \in Y^+$, the solution maps associated with system (3.13) are defined by

$$\Psi_t(\phi) = (u(\cdot,t,\phi), v(\cdot,t,\phi)),\ \forall\, \phi \in Y^+,\ t \geq 0.$$

Define

$$\tilde{\Lambda} = \{(t,x,u,v) \in \mathbb{R}_+^4 : x \in [0,L],\ qu \leq W^*(x,t),\ qv \leq W_S^*(x,t)\}.$$

From (3.10), it is easy to see that there exists a real number $r > 0$ such that

$$\frac{\partial g(t,x,u,v)}{\partial v} \leq -r < 0,\ \ \forall\,(t,x,u,v) \in \tilde{\Lambda}. \tag{3.14}$$

By (3.14) and the same arguments as in Lemma 4.1, it then follows that Ψ_τ is κ-contracting. □

Theorem 3.1 *Ψ_τ admits a global attractor on Y^+ provided that (3.10) holds.*

Proof By Lemma 3.2, it follows that Ψ_τ is κ-contracting on Y^+. Further, Lemma 2.4 implies that Ψ_τ is point dissipative on Y^+ and that the positive orbits of bounded subsets of Y^+ for Ψ_τ are bounded. By Theorem 2.6 in [10], Ψ_τ has a global attractor that attracts each bounded set in Y^+. □

Note that (0, 0) is a solution of (3.4)–(3.6). Linearizing system (3.4)–(3.6) at (0, 0), we have

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + f(W^*(x,t))N, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) + f(W_S^*(x,t))N_S,\ 0 < x < L,\ t > 0, \end{cases} \tag{3.15}$$

with boundary conditions (3.5) and initial conditions (3.6).

Substituting $N(x,t) = e^{-\mu t}\phi_1(x,t)$ and $N_S(x,t) = e^{-\mu t}\phi_2(x,t)$, we obtain the associated eigenvalue problem

$$\begin{cases} \frac{\partial \phi_1}{\partial t} = \delta \frac{\partial^2 \phi_1}{\partial x^2} - \nu \frac{\partial \phi_1}{\partial x} + \alpha(\phi_2 - \phi_1) + f(W^*(x,t))\phi_1 + \mu\phi_1,\ t > 0,\ x \in (0, L), \\ \frac{\partial \phi_2}{\partial t} = -\alpha \frac{A}{A_s}(\phi_2 - \phi_1) + f(W_S^*(x,t))\phi_2 + \mu\phi_2,\ t > 0,\ x \in (0, L), \\ \nu\phi_1(0,t) - \delta \frac{\partial \phi_1}{\partial x}(0,t) = \frac{\partial \phi_1}{\partial x}(L,t) = 0,\ t > 0, \\ \phi_1, \phi_2 \text{ are } \tau\text{-periodic in } t. \end{cases} \tag{3.16}$$

Lemma 3.3 *Let (3.10) hold. Then the eigenvalue problem (3.16) has a principal eigenvalue, denoted by μ^*, with an associated eigenvector $\phi^* = (\phi_1^*, \phi_2^*) \gg 0$.*

Proof Let $(u, v) := (N, N_S)$ and rewrite (3.15) as

$$\begin{cases} \frac{\partial u}{\partial t} = d \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x} + E_1(t, x, u, v), \\ \frac{\partial v}{\partial t} = -r(x,t)v + E_2(u),\ x \in (0, L), t > 0, \\ \nu u(0,t) - d\frac{\partial u}{\partial x}(0,t) = 0,\ \frac{\partial u}{\partial x}(L,t) = 0 \\ u(x,0) = \phi_1(x), v(x,0) = \phi_2(x), \end{cases} \tag{3.17}$$

where $E_1(t,x,u,v) = \alpha(v-u) + f(W^*(x,t))u$, $E_2(u) = \alpha\frac{A}{A_S}u$ and $r(x,t) = \alpha\frac{A}{A_S} - f(W_S^*(x,t))$. By (3.10), it follows that

$$r(x,t) \geq r_0,\ \forall\, x \in [0, L],\ t \geq 0,\ \text{and } r_0 \text{ is a positive number.} \tag{3.18}$$

Let $\mathbf{C} := C([0, L], \mathbb{R}^2)$. For every initial value functions $\phi = (\phi_1, \phi_2) \in \mathbf{C}$, one may use the comparison theorem to show that the solution $(u(x,t,\phi), v(x,t,\phi)) \in \mathbf{C}$, $\forall t \geq 0$. Thus, the linear semigroup $\Pi_t : \mathbf{C} \to \mathbf{C}$ associated with the linear system (3.17) is defined by

$$\Pi_t(\phi) = (u(x,t,\phi), v(x,t,\phi)),\ \forall\, \phi \in \mathbf{C},\ t \geq 0.$$

We first show that for each $t > 0$, Π_t is an κ-contraction on $\mathbf{C}$ in the sense that $\kappa(\Pi_t B) \leq e^{-r_0 t}\kappa(B)$ for any bounded set B in $\mathbf{C}$, where κ is the Kuratowski measure of noncompactness as defined in (3.12).

Let $T_1(t)$ be the analytic semigroup on $C([0, L], \mathbb{R})$ generated by

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} - \nu\frac{\partial u}{\partial x}$$

subject to the above boundary condition and $T_2(t)\phi_2 = e^{-\int_0^t r(\cdot,\eta)d\eta}\phi_2$, $\forall \phi_2 \in C([0, L], \mathbb{R})$. Obviously, $T(t) = (T_1(t), T_2(t))$ is a linear semigroup on $\mathbf{C}$.

Define a linear operator

$$L(t)\phi = (0, T_2(t)\phi_2),\ \forall \phi = (\phi_1, \phi_2) \in \mathbf{C}, \tag{3.19}$$

and a nonlinear operator

$$Q(t)\phi = (u(\cdot,t,\phi), \int_0^t T_2(t-s)E_2(u(\cdot,s,\phi))ds),\ \forall \phi = (\phi_1, \phi_2) \in \mathbf{C},$$

where

$$u(\cdot,t,\phi)=T_1(t)\phi_1+\int_0^t T_1(t-s)E_1(s,\cdot,u(\cdot,s,\phi),v(\cdot,s,\phi))ds.$$

It is easy to see that

$$\Pi_t(\phi)=L(t)\phi+Q(t)\phi,\ \forall\phi\in\mathbf{C},\ t\geq 0.$$

By (3.18) and (3.19), it follows that

$$\sup_{\phi\in\mathbf{C}}\frac{\|L(t)\phi\|}{\|\phi\|}\leq\sup_{\phi\in\mathbf{C}}\frac{\|e^{-\int_0^t r(\cdot,\eta)d\eta}\phi_2\|}{\|\phi\|}\leq\sup_{\phi\in\mathbf{C}}\frac{\|e^{-r_0t}\phi_2\|}{\|\phi\|}\leq e^{-r_0t},$$

and hence $\|L(t)\|\leq e^{-r_0t}$.

By the boundedness of Π_t and the compactness of $T_1(t)$ for $t>0$, it follows that $Q(t):\mathbf{C}\to\mathbf{C}$ is compact for each $t>0$. For any bounded set B in $\mathbf{C}$, there holds $\kappa(Q(t)B)=0$ since $Q(t)B$ is precompact, and consequently,

$$\kappa(\Pi_tB)\leq\kappa(L(t)B)+\kappa(Q(t)B)\leq\|L(t)\|\kappa(B)\leq e^{-r_0t}\kappa(B),\ \forall\, t>0.$$

Thus, Π_t is an κ-contraction on $\mathbf{C}$ with a contracting function e^{-r_0t}.

From the discussions above, it is easy to see that the Poincaré map Π_τ generated by (3.17) is κ-condensing in the sense that

$$\kappa(\Pi_\tau B)<\kappa(B),\ \text{for any bounded set } B \text{ in } \mathbf{C} \text{ with } \kappa(B)>0.$$

Note that (3.17) is a cooperative system. By a generalized Krein-Rutman Theorem (see [12] or [8, Lemma 2.2]) and [5, Chap. II.14], it then follows that (3.16) has a principal eigenvalue, denoted by μ^*, with an associated eigenvector $\phi^*=(\phi_1^*,\phi_2^*)\gg 0$. □

Theorem 3.2 *Assume that* (3.10) *holds. For any* $P:=(N^0(\cdot),\ N_S^0(\cdot))\in Y^+$, *let* $(N(x,t),N_S(x,t))$ *be the solution of* (3.4)–(3.6). *Then the following statements are valid.*

(1) If $\mu^*>0$, *then* $\lim_{t\to\infty}\|(N(x,t),N_S(x,t))\|_\infty=0$ *uniformly for* $x\in[0,L]$;

(2) If $\mu^*<0$, *then* (3.4)–(3.6) *admit a unique positive* τ*-periodic solution* $(N^*(x,t),N_S^*(x,t))$ *and for any* $(N^0(\cdot),\ N_S^0(\cdot))\in Y_0$, *we have*

$$\lim_{t\to\infty}\|(N(x,t),N_S(x,t))-(N^*(x,t),N_S^*(x,t))\|_\infty=0,\ \textit{uniformly for } x\in[0,L].$$

Proof In the case where $\mu^*>0$, it follows that $\lim_{t\to\infty}\|(v(x,t,P),v_S(x,t,P))\|_\infty=0$ uniformly for $x\in[0,L]$, $\forall\,P\in Y^+$, where $(v(x,t,P),v_S(x,t,P))$ is the unique solution of (3.15) with $(v(x,0,P),v_S(x,0,P))=P$. For convenience, we rewrite the reaction terms in (3.4) as follows:

$$F(t,x,N,N_S)=\begin{pmatrix}\alpha(N_S-N)+f(W^*(x,t)-qN)N\\ -\alpha\frac{A}{A_S}(N_S-N)+f(W_S^*(x,t)-qN_S)N_S\end{pmatrix}. \tag{3.20}$$

It is easy to see that $F(t,x,\theta N,\theta N_S)\gg\theta F(t,x,N,N_S),\ \forall\,0<\theta<1,\ (N,N_S)\in Y^+$. Clearly, the solution $(N(x,t,P),N_S(x,t,P))$ of (3.4)–(3.6) satisfies

$$\begin{aligned}&\frac{\partial N}{\partial t}\leq\delta\frac{\partial^2N}{\partial x^2}-\nu\frac{\partial N}{\partial x}+\alpha(N_S-N)+f(W^*(x,t))N,\\&\frac{\partial N_S}{\partial t}\leq-\alpha\frac{A}{A_S}(N_S-N)+f(W_S^*(x,t))N_S,0<x<L,\ t>0,\end{aligned} \tag{3.21}$$

that is, $(N(x,t,P), N_S(x,t,P)) < (v(x,t,P), v_S(x,t,P))$. Thus, we have

$$\lim_{t\to\infty} \| (N(x,t,P), N_S(x,t,P)) \|_\infty = 0 \text{ uniformly for } x \in [0,L], \forall P \in Y^+.$$

For the case where $\mu^* < 0$, we first prove the following claim.
Claim. Zero is a uniform weak repeller for (3.4)–(3.6) in the sense that there exists $\delta > 0$ such that $\limsup_{t\to\infty} \| \Psi_t(P) \| \geq \delta, \forall P := (N^0(\cdot), N_S^0(\cdot)) \in Y_0$. Indeed, let μ_ϵ be the principal eigenvalue of

$$\begin{cases} \frac{\partial\phi_1}{\partial t} = \delta\frac{\partial^2\phi_1}{\partial x^2} - \nu\frac{\partial\phi_1}{\partial x} + \alpha(\phi_2-\phi_1) + (f(W^*(x,t))-\epsilon)\phi_1 + \mu\phi_1, \ t>0, \ x\in(0,L), \\ \frac{\partial\phi_2}{\partial t} = -\alpha\frac{A}{A_s}(\phi_2-\phi_1) + (f(W_S^*(x,t))-\epsilon)\phi_2 + \mu\phi_2, \ t>0, \ x\in(0,L) \\ \nu\phi_1(0,t) - \delta\frac{\partial\phi_1}{\partial x}(0,t) = \frac{\partial\phi_1}{\partial x}(L,t) = 0, \ t>0, \\ \phi_1, \phi_2 \text{ are } \tau\text{-periodic in } t, \end{cases} \tag{3.22}$$

with a positive eigenfunction $\phi_\epsilon^*(x,t) = (\phi_{1\epsilon}^*, \phi_{2\epsilon}^*) \gg 0$. Since $\lim_{\epsilon\to 0}\mu_\epsilon = \mu^*$, we can fix a sufficiently small number $\epsilon > 0$ such that $\mu_\epsilon < 0$. It is easy to see that

$$\lim_{N\to 0} f(W^*(x,t) - qN) = f(W^*(x,t)) \text{ and } \lim_{N_S\to 0} f(W_S^*(x,t) - qN_S) = f(W_S^*(x,t)),$$

uniformly for $x \in [0,L]$ and $t \geq 0$. Thus, we can choose $\delta_\epsilon > 0$ such that

$$f(W^*(x,t) - qN) > f(W^*(x,t)) - \epsilon \text{ and } f(W_S^*(x,t) - qN_S) > f(W_S^*(x,t)) - \epsilon,$$

for any $x \in [0,L]$, $t \geq 0$, and $(N, N_S) \in [0,\delta_\epsilon] \times [0,\delta_\epsilon]$.

Suppose, by contradiction, there exists $P_0 \in Y_0$ such that $\limsup_{t\to\infty} \| \Psi_t(P_0) \| < \delta_\epsilon$, thus, there exists $t_0 > 0$ such that $\| \Psi_t(P_0) \| < \delta_\epsilon, \forall t \geq t_0$. It then follows that $\Psi_t(P_0) = (N(x,t,P_0), N_S(x,t,P_0))$ satisfy

$$\begin{aligned} \frac{\partial N}{\partial t} &\geq \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(W^*(x,t)) - \epsilon]N, \\ \frac{\partial N_S}{\partial t} &\geq -\alpha\frac{A}{A_S}(N_S - N) + [f(W_S^*(x,t)) - \epsilon]N_S, \end{aligned} \tag{3.23}$$

for any $0 < x < L, \ t \geq t_0$. Note that $(N^\epsilon, N_S^\epsilon) := e^{-\mu_\epsilon t}\phi_\epsilon^*(x,t)$ is a solution of

$$\begin{aligned} \frac{\partial N^\epsilon}{\partial t} &= \delta\frac{\partial^2 N^\epsilon}{\partial x^2} - \nu\frac{\partial N^\epsilon}{\partial x} + \alpha(N_S^\epsilon - N) + [f(W^*(x,t)) - \epsilon]N^\epsilon, \\ \frac{\partial N_S^\epsilon}{\partial t} &= -\alpha\frac{A}{A_S}(N_S^\epsilon - N^\epsilon) + [f(W_S^*(x,t)) - \epsilon]N_S^\epsilon, 0 < x < L, \ t > 0, \end{aligned} \tag{3.24}$$

with boundary conditions (3.5). Since $\Psi_{t_0}(P_0) = (N(x,t_0,P_0), N_S(x,t_0,P_0)) \gg 0$ for all $x \in [0,L]$, there exists $a > 0$ such that

$$\Psi_{t_0}(P_0) \geq a\phi_\epsilon^*(x,t_0) \text{ for all } x \in [0,L].$$

By the comparison theorem, it follows that

$$\Psi_t(P_0) \geq a\phi_\epsilon^*(x,t_0)e^{-\mu_\epsilon(t-t_0)}, \forall t \geq t_0, \ x \in [0,L].$$

Since $\mu_\epsilon < 0$, we see that $\Psi_t(P_0)$ is unbounded, a contradiction.

By the claim above, Ψ_τ is weakly uniformly persistent with respect to $(Y_0, \partial Y_0)$. Since Ψ_τ admits a global attractor on Y^+, it follows from [20, Theorem 1.3.3] that Ψ_τ is uniformly persistent with respect to $(Y_0, \partial Y_0)$ in the sense that there exists $\eta > 0$ such that $\liminf_{t\to\infty} \parallel \Psi_t(P) \parallel \geq \eta, \forall\, P \in Y_0$.

Note that Ψ_τ is κ-contracting, point dissipative and uniformly persistent. It follows from [10, Theorem 3.8] that $\Psi_\tau : Y_0 \to Y_0$ admits a global attractor A_0. It is easy to see that Ψ_τ is strongly monotone, and strictly subhomogeneous in the sense that $\Psi_\tau(\theta N, \theta N_S) \gg \theta\Psi_\tau(N, N_S)$, $\forall\,(N, N_S) \gg 0$, $\theta \in (0, 1)$. Since $A_0 \subset Y_0$ and $A_0 = \Psi_\tau(A_0)$, we further have $A_0 \subset Int(C([0, L], \mathbb{R}^2_+))$. It then follows from [20, Theorem 2.3.2] with $K = A_0$ that Ψ_τ has a fixed point $e \gg 0$ such that $A_0 = \{e\}$. This implies that e is globally attractive for Ψ_τ in Y_0. Consequently, the statement (2) holds for solutions of (3.4)–(3.6). □

Remark 3.2 By Theorem 3.2 and the method of chain transitive sets, as illustrated in Sect. 5, we can also obtain a threshold type result on the global dynamics of the single species model (3.1)–(3.3).

4 Two Species Competition

In this section, we study the global dynamics of the limiting system (2.28)–(2.30). Let $\lambda_1(a(x,t), b(x,t))$ be the principal eigenvalue of the following eigenvalue problem:

$$\begin{cases} \frac{\partial\varphi}{\partial t} = \delta\frac{\partial^2\varphi}{\partial x^2} - \nu\frac{\partial\varphi}{\partial x} + \alpha(\psi - \varphi) + a(x,t)\varphi + \lambda\varphi,\ t > 0,\ x \in (0, L), \\ \frac{\partial\psi}{\partial t} = -\alpha\frac{A}{A_s}(\psi - \varphi) + b(x,t)\psi + \lambda\psi,\ t > 0,\ x \in (0, L), \\ \nu\varphi(0,t) - \delta\frac{\partial\varphi}{\partial x}(0,t) = \frac{\partial\varphi}{\partial x}(L,t) = 0,\ t > 0, \\ \varphi, \psi \text{ are } \tau\text{-periodic in } t. \end{cases} \tag{4.1}$$

Theorem 3.2 can be applied to either of the two systems obtained from (2.28)–(2.30) by setting one of the two ordered pairs $(N_1, N_{S,1})$ or $(N_2, N_{S,2})$ to be $(0, 0)$. Let

$$\mu_1^* := \lambda_1(f_1(W^*(x,t)), f_1(W_S^*(x,t))) \text{ and } \mu_2^* := \lambda_1(f_2(W^*(x,t)), f_2(W_S^*(x,t))). \tag{4.2}$$

Then we conclude that the system (2.28)–(2.30) has the following results:

(i) Trivial solution $\hat{0} := (0, 0, 0, 0)$ always exists;
(ii) Semi-trivial solution $(N_1^*(x,t), N_{S,1}^*(x,t), 0, 0)$ exists provided that $\mu_1^* < 0$;
(iii) Semi-trivial solution $(0, 0, N_2^*(x,t), N_{S,2}^*(x,t))$ exists provided that $\mu_2^* < 0$;
(iv) There may be additional τ-periodic solutions as well and these must be positive.

Here, $(N_i^*(x,t), N_{S,i}^*(x,t))$ denotes the unique positive τ-periodic solution of (3.4)–(3.6) resulting from putting $f = f_i$ and $q = q_i$. The two organisms can coexist if a positive τ-periodic solution exists.

Recall that $D(t)$ is the feasible domain for (2.28)–(2.30) and it is defined in (2.31). From Lemma 2.5, we may define the solution maps $\Phi_t : D(0) \to D(t)$ associated with (2.28)–(2.30) by

$$\Phi_t(P) = (N_1(\cdot, t, P), N_{S,1}(\cdot, t, P), N_2(\cdot, t, P), N_{S,2}(\cdot, t, P)),\ \forall\, t \geq 0, \tag{4.3}$$

where $P := (N_1^0(\cdot),\ N_{S,1}^0(\cdot), N_2^0(\cdot),\ N_{S,2}^0(\cdot)) \in D(0)$.

Let $K = C([0, L], \mathbb{R}_+^2) \times (-C([0, L], \mathbb{R}_+^2))$ and denote its induced order by $\leq_K$. Thus, the solution map Φ_t is monotone [16] with respect to the partial order $\leq_K$. Note that $\Phi_\tau : D(0) \to D(\tau) = D(0)$ and for the Poincaré map $S := \Phi_\tau$, we have $S^n(P) = \Phi_{n\tau}(P), \forall\, n \in \mathbb{Z}$.

For convenience, let $\mathbb{Y}^+ = D(0)$, $\mathbb{Y}_0 := \{(N_1, N_{S,1}, N_2, N_{S,2}) \in \mathbb{Y}^+ : (N_1, N_{S,1}) \neq (0, 0)$ and $(N_2, N_{S,2}) \neq (0, 0)\}$ and $\partial\mathbb{Y}_0 := \mathbb{Y}^+ \backslash \mathbb{Y}_0$.

Since two equations in (2.28)–(2.30) have no diffusion terms, its solution maps are not compact. So we require the following conditions in this section:

$$\alpha \frac{A}{A_S} > f_i(W_S^*(x, t)),\ \forall x \in [0, L],\ t \geq 0,\ i = 1, 2. \tag{4.4}$$

For convenience, we let $(u_i, v_i) := (N_i, N_{S,i}),\ i = 1, 2$, and define

$$m_i(t, x, u_1, u_2, v_1, v_2) = \alpha(v_i - u_i) + f_i(W^*(x, t) - q_1 u_1 - q_2 u_2)u_i, \quad i = 1, 2,$$

and

$$g_i(t, x, u_1, u_2, v_1, v_2) = -\alpha \frac{A}{A_S}(v_i - u_i) + f_i(W_S^*(x, t) - q_1 v_1 - q_2 v_2)v_i, \quad i = 1, 2.$$

Then (2.28)–(2.30) can be rewritten as

$$\begin{cases} \frac{\partial u_i}{\partial t} = d\frac{\partial^2 u_i}{\partial x^2} - \nu \frac{\partial u_i}{\partial x} + m_i(t, x, u_1, u_2, v_1, v_2), \\ \frac{\partial v_i}{\partial t} = g_i(t, x, u_1, u_2, v_1, v_2),\ x \in (0, L), t > 0, \\ \nu u_i(0, t) - d\frac{\partial u_i}{\partial x}(0, t) = 0,\ \frac{\partial u_i}{\partial x}(L, t) = 0 \\ u_i(x, 0) = \phi_i, v_i(x, 0) = \psi_i,\ i = 1, 2. \end{cases} \tag{4.5}$$

Let $\mathbf{u} := (u_1, u_2)$ and $\mathbf{v} := (v_1, v_2)$, and define

$$\mathcal{D} = \{(t, x, \mathbf{u}, \mathbf{v}) \in \mathbb{R}_+^6 : x \in [0, L], q_1 u_1 + q_2 u_2 \leq W^*(x, t), q_1 v_1 + q_2 v_2 \leq W_S^*(x, t)\}.$$

With the assumption (4.4), it is easy to see that whenever $\alpha \frac{A}{A_S}$ is sufficiently large, there exists a constant $r > 0$ such that

$$\mathbf{x}^T \left[\frac{\partial \mathbf{g}(t, x, \mathbf{u}, \mathbf{v})}{\partial \mathbf{v}} \right] \mathbf{x} \leq -r\mathbf{x}^T \mathbf{x}, \quad \forall\, \mathbf{x} \in \mathbb{R}^2,\ (t, x, \mathbf{u}, \mathbf{v}) \in \mathcal{D}, \tag{4.6}$$

where $\mathbf{g}(t, x, \mathbf{u}, \mathbf{v}) := (g_1(t, x, u_1, u_2, v_1, v_2), g_2(t, x, u_1, u_2, v_1, v_2))$.

Remark 4.1 As in [4, Remark 3.3], we choose $f_i(R) = \frac{\mu_{\max,i} R}{K_{\mu,i} + R}$ and assume that

$$\alpha \frac{A}{A_S} > \mu_{\max,i} + \frac{1}{2}\left[\frac{q_2}{q_1} \cdot \frac{\mu_{\max,1}}{K_{\mu,1}} + \frac{q_1}{q_2} \cdot \frac{\mu_{\max,2}}{K_{\mu,2}} \right] \cdot \overline{W}_S^*,\ \forall\, i = 1, 2, \tag{4.7}$$

where $\overline{W}_S^* := \max_{x \in [0,L],\ t \in [0,\tau]} W_S^*(x, t)$. It then follows that (4.7) implies (4.4) and (4.6). Biologically, two conditions in (4.7) mean that the cross-section of the storage zone is sufficiently small or the exchange rate is sufficiently large.

Lemma 4.1 *Let* (4.4) *and* (4.6) *hold. Then the map* Φ_τ *is* κ*-contracting in the sense that*

$$\lim_{n \to \infty} \kappa(\Phi_\tau^n(B)) = 0$$

for any bounded set $B \subset \mathbb{Y}^+$*, where* κ *is the Kuratowski measure of noncompactness as defined in* (3.12).

Proof Let B be a given bounded subset in $\mathbb{Y}^+$. We first show that Φ_t is asymptotically compact on B in the sense that for any sequences $\varphi_n \in B$ and $t_n \to \infty$, there exist subsequences φ_{n_k} and $t_{n_k} \to \infty$ such that $\Phi_{t_{n_k}}(\varphi_{n_k})$ converges in $C([0, L], \mathbb{R}^4)$ as $k \to \infty$. Note that the family of functions $\{\Phi_{t_n}(\varphi_n)(x)\}_{n\geq 1}$ is uniformly bounded on $[0, L]$ for all $n \geq 1$. In view of the Arzela-Ascoli theorem, it suffices to prove that $\{\Phi_{t_n}(\varphi_n)(x)\}_{n\geq 1}$ is equicontinuous in $x \in [0, L]$ for all $n \geq 1$.

Let $(\mathbf{u}_n(x,t), \mathbf{v}_n(x,t)) = \Phi_t(\varphi_n)(x), \ \forall \varphi_n \in \mathbb{Y}^+, \ t \geq 0, \ x \in [0, L]$. For simplicity, we define $\overline{\mathbf{u}}_n(x,t) := \mathbf{u}_n(x, t+t_n)$ and $\overline{\mathbf{v}}_n(x,t) := \mathbf{v}_n(x, t+t_n), \forall t \geq -t_n, \ x \in [0, L]$. Clearly, $(\overline{\mathbf{u}}_n(x,0), \overline{\mathbf{v}}_n(x,0)) = \Phi_{t_n}(\varphi_n)(x), \ \forall n \geq 1, \ x \in [0, L]$. Note that $\overline{\mathbf{u}}_n(x,t)$ and $\overline{\mathbf{v}}_n(x,t)$ are uniformly bounded, $\forall n \geq 1, \ x \in [0, L], \ t \geq 0$ (see also Lemma 2.4).

For each $i = 1, 2$, we define $f_i(s) = 0$ for all $s \leq 0$ so that $f_i(s)$ is a continuous function on $\mathbb{R}$, and hence, $\mathbf{g}(t, x, \mathbf{u}, \mathbf{v})$ is a continuous function on $\mathbb{R}_+ \times [0, L] \times \mathbb{R}^4$. By a direct computation, we see that for all $t \geq -t_n, \ x, \ y \in [0, L]$, there holds

$$
\begin{aligned}
&\frac{\partial}{\partial t}\left[(\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t))^T \cdot (\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t))\right] \\
&\quad = 2\,(\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t))^T \cdot \frac{\partial}{\partial t}(\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)) \\
&\quad = 2\,(\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t))^T \cdot \\
&\quad \left[\mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(x,t)) - \mathbf{g}(t+t_n, y, \overline{\mathbf{u}}_n(y,t), \overline{\mathbf{v}}_n(y,t))\right]. \qquad (4.8)
\end{aligned}
$$

In the case where $W_S^*(y, t+t_n) \leq W_S^*(x, t+t_n)$, we have $(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(y,t)) \in \mathcal{D}$, and hence,

$$
\begin{aligned}
&\left[\mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(x,t)) - \mathbf{g}(t+t_n, y, \overline{\mathbf{u}}_n(y,t), \overline{\mathbf{v}}_n(y,t))\right] \\
&= \left[\mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(x,t)) - \mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(y,t))\right] \\
&\quad + \left[\mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(y,t)) - \mathbf{g}(t+t_n, y, \overline{\mathbf{u}}_n(y,t), \overline{\mathbf{v}}_n(y,t))\right]. \\
&= \left[\int_0^1 \frac{\partial \mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(y,t) + \eta(\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t))}{\partial \mathbf{v}} d\eta\right] \cdot [\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)] \\
&\quad + \left[\mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(y,t)) - \mathbf{g}(t+t_n, y, \overline{\mathbf{u}}_n(y,t), \overline{\mathbf{v}}_n(y,t))\right]. \qquad (4.9)
\end{aligned}
$$

Set

$$
h_n(t,x,y) := \|\mathbf{g}(t+t_n, x, \overline{\mathbf{u}}_n(x,t), \overline{\mathbf{v}}_n(y,t)) - \mathbf{g}(t+t_n, y, \overline{\mathbf{u}}_n(y,t), \overline{\mathbf{v}}_n(y,t))\|.
$$

It then follows from (4.6), (4.8) and (4.9) that there exists a real number $M > 0$ such that

$$
\frac{\partial}{\partial t}\|\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)\|^2 \leq -2r\|\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)\|^2 + Mh_n(t,x,y). \qquad (4.10)
$$

In the case where $W_S^*(y, t+t_n) \geq W_S^*(x, t+t_n)$, we have $(t+t_n, y, \overline{\mathbf{u}}_n(y,t), \overline{\mathbf{v}}_n(x,t)) \in \mathcal{D}$. By exchanging the positions of x and y in (4.9) and (4.10), we then obtain

$$
\frac{\partial}{\partial t}\|\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)\|^2 \leq -2r\|\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)\|^2 + Mh_n(t,y,x). \qquad (4.11)
$$

Define $H_n(t,x,y) := h_n(t,x,y) + h_n(t,y,x)$. It then follows from (4.10) and (4.11) that

$$
\frac{\partial}{\partial t}\|\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)\|^2 \leq -2r\|\overline{\mathbf{v}}_n(x,t) - \overline{\mathbf{v}}_n(y,t)\|^2 + MH_n(t,x,y) \qquad (4.12)
$$

for all $t \geq -t_n, \ x, \ y \in [0, L]$.

By the constant variation formula and the comparison argument, we obtain

$$\|\overline{\mathbf{v}}_n(x,t)-\overline{\mathbf{v}}_n(y,t)\|^2 \le e^{-2r(t-s)}\|\overline{\mathbf{v}}_n(x,s)-\overline{\mathbf{v}}_n(y,s)\|^2 + M\int_s^t e^{-2r(t-\theta)}H_n(\theta,x,y)d\theta, \tag{4.13}$$

for all $t \ge s \ge -t_n$. Letting $t=0$ and $s=-t_n$ in (4.13), we further have

$$\|\overline{\mathbf{v}}_n(x,0)-\overline{\mathbf{v}}_n(y,0)\|^2 \le e^{-2rt_n}\|\overline{\mathbf{v}}_n(x,-t_n)-\overline{\mathbf{v}}_n(y,-t_n)\|^2 + M\int_{-t_n}^0 e^{2r\theta}H_n(\theta,x,y)d\theta,$$

and hence,

$$\|\mathbf{v}_n(x,t_n)-\mathbf{v}_n(y,t_n)\|^2 \le e^{-2rt_n}\|\mathbf{v}_n(x,0)-\mathbf{v}_n(y,0)\|^2 + M\int_{-t_n}^0 e^{2r\theta}H_n(\theta,x,y)d\theta, \tag{4.14}$$

for all $n \ge 1, x,\ y \in [0,L]$.

Note that $(\mathbf{u}_n(x,0),\mathbf{v}_n(x,0)) = \varphi_n$ and $\varphi_n \in B$, for all $n \ge 1$ and $x \in [0,L]$, and that $\{\mathbf{u}_n(x,t_n)\}_{n\ge1}$ is equicontinuous on $[0,L]$ for all $n \ge 1$. Thus, it suffices to prove that $\{\mathbf{v}_n(x,t_n)\}_{n\ge1}$ is equicontinuous on $[0,L]$ for all $n \ge 1$ in the sense that for any $\epsilon > 0$, there exists $\delta > 0$ such that

$$\|\mathbf{v}_n(x,t_n)-\mathbf{v}_n(y,t_n)\| < \epsilon,\ \forall\, n \ge 1,\ \forall\, x,y \in [0,L] \text{ with } \mid x-y \mid < \delta.$$

Suppose, by contradiction, that there exist an $\epsilon_0 > 0, n_k \to \infty, x_k,\ y_k \in [0,L]$ with $\mid x_k - y_k \mid < \frac{1}{k}$ such that $\|\mathbf{v}_{n_k}(x_k,t_{n_k})-\mathbf{v}_{n_k}(y_k,t_{n_k})\| \ge \epsilon_0,\ \forall\, k \ge 1$. Letting $x=x_k, y=y_k$ and $n=n_k$ in (4.14), we then obtain

$$\begin{aligned}\epsilon_0^2 &\le \limsup_{k\to\infty}\|\mathbf{v}_{n_k}(x_k,t_{n_k})-\mathbf{v}_{n_k}(y_k,t_{n_k})\|^2\\ &\le M\cdot\limsup_{k\to\infty}\int_{-t_{n_k}}^0 e^{2r\theta}H_{n_k}(\theta,x_k,y_k)d\theta.\end{aligned} \tag{4.15}$$

Note that for each $\theta \le 0$, there exists a large integer $n_0 > 0$ such that the sequence of functions $\{\overline{\mathbf{u}}_n(x,\theta) = \mathbf{u}_n(x,\theta+t_n)\}_{n\ge n_0}$ is equicontinuous on $[0,L]$, and that $\mathbf{g}(t,x,\mathbf{u},\mathbf{v})$ is uniformly continuous in $(t,x,\mathbf{u},\mathbf{v}) \in [0,\infty)\times[0,L]\times\mathcal{H}$, where $\mathcal{H}$ is any given compact subset of $\mathbb{R}^4_+$. Since $\lim_{k\to\infty}\|\overline{\mathbf{u}}_{n_k}(x_k,\theta)-\overline{\mathbf{u}}_{n_k}(y_k,\theta)\| = 0$, it follows that for any given $\theta \le 0$, we have $\lim_{k\to\infty} H_{n_k}(\theta,x_k,y_k) = 0$. Using Fatou's lemma in (4.15), we then obtain

$$\epsilon_0^2 \le M\cdot\int_{-\infty}^0 e^{2r\theta}\limsup_{k\to\infty} H_{n_k}(\theta,x_k,y_k)d\theta = 0,$$

a contradiction. Consequently, Φ_t is asymptotically compact on B.

Now we consider the omega limit set of B for the Poincaré map $S := \Phi_\tau$ on $\mathbb{Y}^+$, which is defined as

$$\omega(B) = \{\varphi \in \mathbb{Y}^+ : \lim_{k\to\infty} S^{n_k}(\varphi_k) = \varphi \text{ for some sequences } \varphi_k \in B \text{ and } n_k \to \infty\}.$$

From what we proved for Φ_t and the fact that $S^n = \Phi_{n\tau}$, $\forall n \geq 0$, we easily see that S^n is asymptotically compact on B in the sense that for any sequences $\varphi_k \in B$ and $n_k \to \infty$, there exist subsequences, which we label as φ_k and $n_k \to \infty$, such that $S^{n_k}(\varphi_k)$ converges in $C([0, L], \mathbb{R}^4)$ as $k \to \infty$. It then follows that $\omega(B)$ is a nonempty, compact, and invariant set for S in $\mathbb{Y}^+$, and $\omega(B)$ attracts B (see, e.g., the proof of [15, Lemma 23.1 (2)] for continuous-time semiflows). In view of [10, Lemma 2.1 (b)], we have

$$\kappa(S^n(B)) \leq \kappa(\omega(B)) + \delta(S^n(B), \omega(B)) = \delta(S^n(B), \omega(B)) \to 0 \text{ as } n \to \infty.$$

This completes the proof. □

Recall that $\lambda_1(a(x,t), b(x,t))$ is the principal eigenvalue of the eigenvalue problem (4.1). By the similar arguments as in Lemma 3.3, it follows that

$$\eta_1^* := \lambda_1(f_2(W^*(x,t) - q_1 N_1^*(x,t)),\ f_2(W_S^*(x,t) - q_1 N_{S,1}^*(x,t))) \text{ exists,} \tag{4.16}$$

with an associated eigenfunction

$$(\varphi_1^*(x,t), \psi_1^*(x,t)) \gg 0. \tag{4.17}$$

Similarly,

$$\eta_2^* := \lambda_1(f_1(W^*(x,t) - q_2 N_2^*(x,t)),\ f_1(W_S^*(x,t) - q_2 N_{S,2}^*(x,t))) \text{ exists,} \tag{4.18}$$

with an associated eigenfunction

$$(\varphi_2^*(x,t), \psi_2^*(x,t)) \gg 0. \tag{4.19}$$

For $P_1, P_2 \in \mathbb{Y}^+$ with $P_1 \ll_K P_2$, we define type$-K$ order intervals

$$[P_1, P_2]_K = \{P \in \mathbb{Y}^+ : P_1 \leq_K P \leq_K P_2\},$$

and

$$[[P_1, P_2]]_K = \{P \in \mathbb{Y}^+ : P_1 \ll_K P \ll_K P_2\}.$$

Let $\omega(P)$ be the omega limit set of P for the map $S := \Phi_\tau$.

Theorem 4.1 *Let (4.4) and (4.6) hold. Then Φ_τ admits a global attractor on $\mathbb{Y}^+$.*

Proof By Lemma 4.1, it follows that Φ_τ is κ-contracting on $\mathbb{Y}^+$. By Lemma 2.4, it follows that Φ_τ is point dissipative on $\mathbb{Y}^+$ and positive orbits of bounded subsets of $\mathbb{Y}^+$ for $S = \Phi_\tau$ are bounded. By [10, Theorem 2.6], Φ_τ has a global attractor that attracts each bounded set in $\mathbb{Y}^+$. □

Let $E_1 = (N_1^*(x,0), N_{S,1}^*(x,0), 0, 0)$, $E_2 = (0, 0, N_2^*(x,0), N_{S,2}^*(x,0))$ and $\hat{0} = (0, 0, 0, 0)$.

Theorem 4.2 *Let (4.4) and (4.6) hold, and assume that $\mu_i^* < 0$ and $\eta_i^* < 0$, $i = 1, 2$. Then system (2.28)–(2.30) admits two positive τ-periodic solutions*

$$\begin{aligned} E^-(x,t) &:= (\underline{N}_1(x,t), \underline{N}_{S,1}(x,t), \overline{N}_2(x,t), \overline{N}_{S,2}(x,t)),\\ E^+(x,t) &:= (\overline{N}_1(x,t), \overline{N}_{S,1}(x,t), \underline{N}_2(x,t), \underline{N}_{S,2}(x,t)), \end{aligned} \tag{4.20}$$

such that $E^-(\cdot,t) \leq_K E^+(\cdot,t)$ for all $t \geq 0$, and for any $P \in \mathbb{Y}_0^+$, the solution $\Phi_t(P)$ of (2.28)–(2.30) satisfies

$$\lim_{t\to\infty} d(\Phi_t(P), [E^-(\cdot,t), E^+(\cdot,t)]_K) = 0.$$

Furthermore, for any compact internal chain transitive set $\mathcal{I}$ of the Poincaré map S with $\mathcal{I} \notin \left\{\{\hat{0}\}, \{E_1\}, \{E_2\}\right\}$, we have $\mathcal{I} \subset [E^-(\cdot, 0), E^+(\cdot, 0)]_K$.

Proof It is easy to see that the stability of the semi-trivial solution $E_1(x,t) := (N_1^*(x,t), N_{S,1}^*(x,t), 0, 0)$ for (2.28)–(2.30) is determined by the sign of η_1^*. More precisely, $E_1(x,t)$ is unstable if $\eta_1^* < 0$. Similarly, $E_2(x,t) := (0, 0, N_2^*(x,t), N_{S,2}^*(x,t))$ is unstable if $\eta_2^* < 0$. By the theory of abstract competitive systems (see, e.g., [7, Theorem A and Corollary 1]), it follows that (2.28)–(2.30) admits two positive τ-periodic solution $E^-(x,t)$ and $E^+(x,t)$ with $E^-(x,t) \leq_K E^+(x,t)$ for $x \in [0, L], t \geq 0$ such that the dynamics of (2.28)–(2.30) stated in the Theorem 4.2 holds.

Recall that $S = \Phi_\tau : \mathbb{Y}^+ \to \mathbb{Y}^+$ is the Poincaré map associated with (2.28)–(2.30). Thus, $\lim_{n\to\infty} d(S^n(P), [E^-(\cdot, 0), E^+(\cdot, 0)]_K) = 0, \forall P \in \mathbb{Y}_0$. Hence, $S : \mathbb{Y}^+ \to \mathbb{Y}^+$ is uniformly persistent with respect to $\mathbb{Y}_0$. By [10, Theorem 3.7], it follows that $S : \mathbb{Y}_0 \to \mathbb{Y}_0$ has a global attractor A_0. Clearly, $A_0 \subset [E^-(\cdot, 0), E^+(\cdot, 0)]_K$. By [20, Theorem 1.3.1 and Remark 1.3.1], it then follows that there exists $\sigma > 0$ such that for any compact internal chain transitive set $\mathcal{I}$ of S with $\mathcal{I} \notin \left\{\{\hat{0}\}, \{E_1\}, \{E_2\}\right\}$, we have $\inf_{P\in\mathcal{I}} d(P, \partial\mathbb{Y}_0) > \sigma$. This implies that $\mathcal{I} \subset \mathbb{Y}_0$, and hence, $\mathcal{I} \subset A_0$. Thus, $\mathcal{I} \subset [E^-(\cdot, 0), E^+(\cdot, 0)]_K$. □

5 Dynamics of the Full System

In this section, we discuss the global dynamics of the full system (1.5)–(1.7). Rewrite (1.5)–(1.7) as

$$\begin{aligned}
\frac{\partial N_1}{\partial t} &= \delta\frac{\partial^2 N_1}{\partial x^2} - \nu\frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) + f_1(W - q_1N_1 - q_2N_2)N_1,\\
\frac{\partial N_{S,1}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,1} - N_1) + f_1(W_S - q_1N_{S,1} - q_2N_{S,2})N_{S,1},\\
\frac{\partial N_2}{\partial t} &= \delta\frac{\partial^2 N_2}{\partial x^2} - \nu\frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + f_2(W - q_1N_1 - q_2N_2)N_2,\\
\frac{\partial N_{S,2}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,2} - N_2) + f_2(W_S - q_1N_{S,1} - q_2N_{S,2})N_{S,2},\\
\frac{\partial W}{\partial t} &= \delta\frac{\partial^2 W}{\partial x^2} - \nu\frac{\partial W}{\partial x} + \alpha W_S - \alpha W,\\
\frac{\partial W_S}{\partial t} &= -\alpha\frac{A}{A_S}W_S + \alpha\frac{A}{A_S}W,
\end{aligned} \tag{5.1}$$

in $(0, L) \times (0, \infty)$, with boundary conditions

$$\begin{aligned}
&\nu N_i(0,t) - \delta\frac{\partial N_i}{\partial x}(0,t) = 0,\ \frac{\partial N_i}{\partial x}(L,t) = 0,\ i = 1, 2,\\
&\nu W(0,t) - \delta\frac{\partial W}{\partial x}(0,t) = \nu R^{(0)}(t),\ \frac{\partial W}{\partial x}(L,t) = 0,
\end{aligned} \tag{5.2}$$

and nonnegative initial functions, where $W(x,t)$ and $W_S(x,t)$ are defined as in (2.5).

Let

$$\Sigma = \{(N_1, N_{S,1}, N_2, N_{S,2}, W, W_S) \in C([0, L], \mathbb{R}_+^6) : q_1N_1^0(\cdot) + q_2N_2^0(\cdot) \leq W(\cdot),$$
$$q_1N_{S,1}^0(\cdot) + q_2N_{S,2}^0(\cdot) \leq W_S(\cdot) \text{ on } [0, L]\},$$

and

$$\Sigma_0 = \{(N_1, N_{S,1}, N_2, N_{S,2}, W, W_S) \in \Sigma : (N_1, N_{S,1}) \neq (0,0) \text{ and } (N_2, N_{S,2}) \neq (0,0)\}.$$

Lemma 5.1 *If $\tilde{P} \in \Sigma$, then the solution of* (5.1)–(5.2) *through $\tilde{P}$ satisfies*

$$(N_1(\cdot,t,\tilde{P}), N_{S,1}(\cdot,t,\tilde{P}), N_2(\cdot,t,\tilde{P}), N_{S,2}(\cdot,t,\tilde{P}), W(\cdot,t,\tilde{P}), W_S(\cdot,t,\tilde{P})) \in \Sigma,\ \forall\, t \geq 0.$$

Proof Let $R(x,t) = W(x,t) - (q_1 N_1(x,t) + q_2 N_2(x,t))$ and $R_S(x,t) = W_S(x,t) - (q_1 N_{S,1}(x,t) + q_2 N_{S,2}(x,t))$. Then $(R(x,t), N_1(x,t), N_{S,1}(x,t), R_S(x,t), N_2(x,t), N_{S,2}(x,t))$ satisfies (1.5)–(1.7). By Lemma 2.1, it follows that

$$(R(x,t,\tilde{P}), N_1(x,t,\tilde{P}), N_{S,1}(x,t,\tilde{P}), R_S(x,t,\tilde{P}), N_2(x,t,\tilde{P}), N_{S,2}(x,t,\tilde{P})) \geq 0,\quad \forall\, t \geq 0.$$

This completes our proof. □

Let $\tilde{\Phi}_t : \Sigma \to \Sigma$ be the solution maps associated with (5.1)–(5.2). We denote the Poincaré map

$$\tilde{S} : \Sigma \to \Sigma \text{ by } \tilde{S} = \tilde{\Phi}_\tau. \tag{5.3}$$

Then $\tilde{S}^n(\tilde{P}) = \tilde{\Phi}_{n\tau}(\tilde{P})$, $\forall n \in \mathbb{Z}_+$. For any $\tilde{P} \in \Sigma$, let $\tilde{\omega}(\tilde{P})$ be the omega limit set of $\tilde{P}$ for $\tilde{S}$. Then we have the following observation.

Lemma 5.2 *Let* (4.4) *and* (4.6) *hold. Then for any $\tilde{P} \in \Sigma$, $\tilde{\omega}(\tilde{P})$ is a nonempty, compact and invariant set for $\tilde{S}$.*

Proof It suffices to prove that the forward orbit $\tilde{S}^n(\tilde{P})$ is asymptotically compact in the sense that for any sequence $n_k \to \infty$, there exists a subsequence, which we label as $n_k \to \infty$, such that $\tilde{S}^{n_k}(\tilde{P})$ converges in $C([0,L], \mathbb{R}^6)$ as $k \to \infty$. Let $(\mathbf{u}, \mathbf{v}) = (u_1, u_2, v_1, v_2) := (N_1, N_2, N_{S,1}, N_{S,2})$ and

$$(\mathbf{u}(x,t), \mathbf{v}(x,t), W(x,t), W_S(x,t)) := \tilde{\Phi}_t(\tilde{P})(x),\ \forall\, t \geq 0,\ x \in [0,L].$$

By Lemma 2.3, we have

$$\lim_{t\to\infty} ((W(x,t), W_S(x,t)) - (W^*(x,t), W_S^*(x,t))) = (0,0) \tag{5.4}$$

uniformly for $x \in [0,L]$. Note that for any given sequence $t_n \to \infty$, the sequence of functions $\{(\mathbf{u}(x,t_n), \mathbf{v}(x,t_n), W(x,t_n), W_S(x,t_n))\}_{n\geq 1}$ is uniformly bounded on $[0,L]$ for all $n \geq 1$. Further, $\{\mathbf{u}(x,t_n)\}_{n\geq 1}$ and $\{(W(x,t_n), W_S(x,t_n))\}_{n\geq 1}$ are equicontinuous on $[0,L]$ for all $n \geq 1$. It is easy to see that $(\mathbf{u}(x,t), \mathbf{v}(x,t))$ satisfies (4.5) with $m_i(t,x,u_1,u_2,v_1,v_2)$ and $g_i(t,x,u_1,u_2,v_1,v_2)$ replaced, respectively, by

$$\hat{m}_i(t,x,u_1,u_2,v_1,v_2) = \alpha(v_i - u_i) + f_i(W(x,t) - q_1u_1 - q_2u_2)u_i,\ i = 1,2,$$
$$\hat{g}_i(t,x,u_1,u_2,v_1,v_2) = -\alpha\frac{A}{A_S}(v_i - u_i) + f_i(W_S(x,t) - q_1v_1 - q_2v_2)v_i,\ i = 1,2.$$

Let $\hat{\mathbf{g}}(t,x,\mathbf{u},\mathbf{v}) = (\hat{g}_1(t,x,u_1,u_2,v_1,v_2), \hat{g}_2(t,x,u_1,u_2,v_1,v_2))$. Using the same continuous extensions of $f_1(s)$ and $f_2(s)$ onto $\mathbb{R}$ as in the proof of Lemma 4.1, we then see from (5.4) that

$$\lim_{t\to\infty} \|\hat{\mathbf{g}}(t,x,\mathbf{u},\mathbf{v}) - \mathbf{g}(t,x,\mathbf{u},\mathbf{v})\| = 0, \tag{5.5}$$

uniformly for $(x, \mathbf{u}, \mathbf{v}) \in [0, L] \times \mathcal{H}$, where $\mathcal{H}$ is any given compact subset of $\mathbb{R}^4_+$ and $\mathbf{g}(t, x, \mathbf{u}, \mathbf{v})$ is defined as in Sect. 4. By (4.4), (4.6) and (5.4), it follows that there exist two positive numbers a and t_0 such that

$$\mathbf{x}^T \left[\frac{\partial \hat{\mathbf{g}}(t, x, \mathbf{u}, \mathbf{v})}{\partial \mathbf{v}} \right] \mathbf{x} \le -a\mathbf{x}^T\mathbf{x}, \quad \forall \mathbf{x} \in \mathbb{R}^2,\ (t, x, \mathbf{u}, \mathbf{v}) \in \mathcal{W}, \tag{5.6}$$

where

$$\mathcal{W} = \{(t, x, \mathbf{u}, \mathbf{v}) \in \mathbb{R}^6_+ : t \ge t_0, x \in [0, L], q_1u_1 + q_2u_2 \le W(x, t), q_1v_1 + q_2v_2 \le W_S(x, t)\}.$$

By using (5.4), (5.5) and (5.6), and a slight modification of the proof in Lemma 4.1, we can show that the sequence $\{\mathbf{v}(x, t_n)\}_{n\ge1}$ is equicontinuous on $[0, L]$ for all $n \ge 1$. Thus, $\tilde{\Phi}_t(\tilde{P})$ is asymptotically compact, and hence, so is $\tilde{S}^n(\tilde{P})$. □

Now we are ready to prove the main result of this section.

Theorem 5.1 *Let (4.4) and (4.6) hold, and assume that $\mu_i^* < 0$ and $\eta_i^* < 0$, $i = 1, 2$. Then system (5.1)–(5.2) admits at least one positive τ-periodic solutions. Moreover, if*

$$\tilde{\Phi}_t(\tilde{P}) := (N_1(\cdot, t, \tilde{P}), N_{S,1}(\cdot, t, \tilde{P}), N_2(\cdot, t, \tilde{P}), N_{S,2}(\cdot, t, \tilde{P}), W(\cdot, t, \tilde{P}), W_S(\cdot, t, \tilde{P}))$$

is the solution of (5.1)–(5.2) through $\tilde{P} \in \Sigma_0$, then

$$\lim_{t\to\infty} d\left((N_1(\cdot, t, \tilde{P}), N_{S,1}(\cdot, t, \tilde{P}), N_2(\cdot, t, \tilde{P}), N_{S,2}(\cdot, t, \tilde{P})), [E^-(\cdot, t), E^+(\cdot, t)]_K\right) = 0,$$

and

$$\lim_{t\to\infty} \left((W(\cdot, t), W_S(\cdot, t)) - (W^*(\cdot, t), W_S^*(\cdot, t))\right) = (0, 0).$$

Proof Let $\tilde{P} \in \Sigma_0$ be given, and let $\tilde{\omega} := \tilde{\omega}(\tilde{P})$. It is easy to see from Theorem 4.2 that $\left(E^+(x, t), W^*(x, t), W_S^*(x, t)\right)$ and $\left(E^-(x, t), W^*(x, t), W_S^*(x, t)\right)$ are positive τ-periodic solutions of system (5.1)–(5.2). By Lemma 2.3, we further have

$$\lim_{t\to\infty} ((W(x, t), W_S(x, t)) - (W^*(x, t), W_S^*(x, t))) = (0, 0)$$

uniformly for $x \in [0, L]$. It then follows that for any $P^0 \in C([0, L], \mathbb{R}^4_+)$ with $(P^0, W^0, W_S^0) \in \tilde{\omega}$, there holds $(W^0, W_S^0) = (W^*(\cdot, 0), W_S^*(\cdot, 0))$. Thus, there exists a set $\mathcal{I} \subset C([0, L], \mathbb{R}^4_+)$ such that $\tilde{\omega} = \mathcal{I} \times \{(W^*(\cdot, 0), W_S^*(\cdot, 0))\}$.

Since Σ is closed, it follows from Lemma 5.1 that $\tilde{\omega} \subset \Sigma$. For any given $(N_1, N_{S,1}, N_2, N_{S,2}) \in \mathcal{I}$, we have $(N_1, N_{S,1}, N_2, N_{S,2}, W^*(\cdot, 0), W_S^*(\cdot, 0)) \in \tilde{\omega} \subset \Sigma$. By the definition of Σ, it follows that $(N_1, N_{S,1}, N_2, N_{S,2}) \in D(0) := \mathbb{Y}^+$. Thus, $\mathcal{I} \subset \mathbb{Y}^+$.

By Lemma 5.2 and [20, Lemma 1.2.1′], $\tilde{\omega}$ is a compact, invariant and internal chain transitive set for $\tilde{S} = \tilde{\Phi}_\tau$. Moreover, if $P^0 \in C([0, L], \mathbb{R}^4_+)$ with $(P^0, W^0, W_S^0) \in \tilde{\omega}$, there holds

$$\tilde{S}\mid_{\tilde{\omega}} (P^0, W^0, W_S^0) = (S(P^0), W^*(\cdot, 0), W_S^*(\cdot, 0)),$$

where $S(P^0) = \Phi_\tau(P^0)$ is Poincaré map associated with (2.28)–(2.30) on $\mathbb{Y}^+$. It then follows that $\mathcal{I}$ is a compact, invariant and internal chain transitive set for $S = \Phi_\tau : \mathbb{Y}^+ \to \mathbb{Y}^+$.

By Theorem 4.2, if we can prove $\mathcal{I} \notin \left\{\{\hat{0}\}, \{E_1\}, \{E_2\}\right\}$, then we must have $\mathcal{I} \subset [E^-(\cdot, 0), E^+(\cdot, 0)]_K$, and hence,

$$\tilde{\omega} \subset [E^-(x, 0), E^+(x, 0)]_K \times \{(W^*(x, 0), W_S^*(x, 0))\},$$

which implies that solutions of (5.1)–(5.2) have the asymptotic behavior as stated in the theorem. So it remains to prove that $\mathcal{I} \notin \left\{\{\hat{0}\}, \{E_1\}, \{E_2\}\right\}$. We only prove the claim that $\mathcal{I} \neq \{E_1\}$ since other two claims can be proved in a similar way. Suppose, by contradiction, that $\mathcal{I} = \{E_1\}$, then

$$\tilde{\omega}(\tilde{P}) = (N_1^*(\cdot, 0), N_{S,1}^*(\cdot, 0), 0, 0, W^*(\cdot, 0), W_S^*(\cdot, 0)) := \tilde{E}.$$

Thus, we have $\lim_{n\to\infty}(\tilde{S})^n(\tilde{P}) = \tilde{E}$, or equivalently,

$$\lim_{t\to\infty}[\tilde{\Phi}_t(\tilde{P}) - (N_1^*(\cdot, t), N_{S,1}^*(\cdot, t), 0, 0, W^*(\cdot, t), W_S^*(\cdot, t)] = 0.$$

Since $\eta_1^* := \lambda_1\left(f_2(W^*(x,t) - q_1N_1^*(x,t)), f_2(W_S^*(x,t) - q_1N_{S,1}^*(x,t))\right) < 0$, it follows that there exists a sufficiently small $\epsilon > 0$ such that ([5, Lemma15.7])

$$\eta_1^\epsilon := \lambda_1\left(f_2(W^*(x,t) - q_1N_1^*(x,t)) - \epsilon,\ f_2(W_S^*(x,t) - q_1N_{S,1}^*(x,t)) - \epsilon\right) < 0.$$

There also exists $n_0 = n_0(\epsilon) > 0$ such that

$$\begin{aligned} f_2(W(x,t) - q_1N_1(x,t) - q_2N_2(x,t)) &> f_2(W^*(x,t) - q_1N_1^*(x,t)) - \epsilon, \\ f_2(W_S(x,t) - q_1N_{S,1}(x,t) - q_2N_{S,2}(x,t)) &> f_2(W_S^*(x,t) - q_1N_{S,1}^*(x,t)) - \epsilon, \end{aligned}$$

for all $x \in [0, L]$ and $t \geq n_0\tau$. Therefore, we obtain

$$\begin{aligned} \frac{\partial N_2}{\partial t} &= \delta\frac{\partial^2 N_2}{\partial x^2} - \nu\frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + f_2(W(x,t) - q_1N_1 - q_2N_2)N_2, \\ &> \delta\frac{\partial^2 N_2}{\partial x^2} - \nu\frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + \left[f_2(W^*(x,t) - q_1N_1^*(x,t)) - \epsilon\right]N_2, \\ \frac{\partial N_{S,2}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,2} - N_2) + f_2(W_S(x,t) - q_1N_{S,1} - q_2N_{S,2})N_{S,2}, \\ &> -\alpha\frac{A}{A_S}(N_{S,2} - N_2) + [f_2(W_S^*(x,t) - q_1N_{S,1}^*) - \epsilon]N_{S,2}, \end{aligned} \tag{5.7}$$

for all $x \in [0, L]$ and $t \geq n_0\tau$. Let $(\varphi_\epsilon(x,t), \psi_\epsilon(x,t)) \gg 0$ be the eigenfunction corresponding to η_1^ϵ, that is,

$$\begin{cases} \frac{\partial\varphi_\epsilon}{\partial t} = \delta\frac{\partial^2\varphi_\epsilon}{\partial x^2} - \nu\frac{\partial\varphi_\epsilon}{\partial x} + \alpha(\psi_\epsilon - \varphi_\epsilon) + \left[f_2(W^*(x,t) - q_1N_1^*(x,t)) - \epsilon\right]\varphi_\epsilon + \eta_1^\epsilon\varphi_\epsilon, \\ \frac{\partial\psi_\epsilon}{\partial t} = -\alpha\frac{A}{A_s}(\psi_\epsilon - \varphi_\epsilon) + \left[f_2(W_S^*(x,t) - q_1N_{S,1}^*(x,t)) - \epsilon\right]\psi_\epsilon + \eta_1^\epsilon\psi_\epsilon, \\ t > 0,\ x \in (0, L), \\ \nu\varphi_\epsilon(0,t) - \delta\frac{\partial\varphi_\epsilon}{\partial x}(0,t) = \frac{\partial\varphi_\epsilon}{\partial x}(L,t) = 0,\ t > 0, \\ \varphi_\epsilon, \psi_\epsilon \text{ are } \tau\text{-periodic in } t. \end{cases} \tag{5.8}$$

Since $\tilde{P} \in \Sigma_0$, it follows that $(N_2(\cdot, 0), N_{S,2}(\cdot, 0)) \neq (0, 0)$, and hence,

$$(N_2(\cdot, t), N_{S,2}(\cdot, t)) \gg 0,\ \forall t > 0.$$

In particular, $N_2(\cdot, n_0\tau) \gg 0$ and $N_{S,2}(\cdot, n_0\tau) \gg 0$ in Σ. Thus, there exists $\rho := \rho(\epsilon, E_1) > 0$ such that $N_2(\cdot, n_0\tau) \geq \rho\varphi_\epsilon(\cdot, n_0\tau) = \rho\varphi_\epsilon(\cdot, 0)$ and $N_{S,2}(\cdot, n_0\tau) \geq \rho\psi_\epsilon(\cdot, n_0\tau) = \rho\psi_\epsilon(\cdot, 0)$. By the comparison theorem, it follows that

$$N_2(\cdot, t) \geq \rho e^{-\eta_1^\epsilon t}\varphi_\epsilon(\cdot, t) \text{ and } N_{S,2}(\cdot, t) \geq \rho e^{-\eta_1^\epsilon t}\psi_\epsilon(\cdot, t),\ \forall t \geq n_0\tau.$$

In particular,

$$N_2(\cdot, n\tau) \geq \rho e^{-\eta_1^{\epsilon} n\tau} \varphi_{\epsilon}(\cdot, n\tau) \text{ and } N_{S,2}(\cdot, n\tau) \geq \rho e^{-\eta_1^{\epsilon} n\tau} \psi_{\epsilon}(\cdot, n\tau), \ \forall n \geq n_0,$$

that is,

$$N_2(\cdot, n\tau) \geq \rho e^{-\eta_1^{\epsilon} n\tau} \varphi_{\epsilon}(\cdot, 0) \text{ and } N_{S,2}(\cdot, n\tau) \geq \rho e^{-\eta_1^{\epsilon} n\tau} \psi_{\epsilon}(\cdot, 0), \ \forall n \geq n_0,$$

which contradicts that $\lim_{n\to\infty}(N_2(\cdot, n\tau), N_{S,2}(\cdot, n\tau)) = (0, 0)$. □

Acknowledgment Xiao-Qiang Zhao would like to thank the National Center for Theoretical Science, National Tsing-Hua University, Taiwan for its financial support and kind hospitality during his visit there. Sze-Bi Hsu and Feng-Bin Wang were partially supported by National Council of Science, Republic of China. Xiao-Qiang Zhao was supported in part by the NSERC of Canada and the MITACS of Canada.

References

1. Ballyk, M., Dung, L.E., Jones, D.A., Smith, H.L.: Effects of random motility on microbial growth and competition in a flow reactor. SIAM J. Appl. Math. **59**, 573–596 (1998)
2. Baxley, J.V., Robinson, S.B.: Coexistence in the unstirred chemostat. Appl. Math. Comput. **89**, 41–65 (1998)
3. Deimling, K.: Nonlinear Functional Analysis. Springer, Berlin (1988)
4. Grover, J.P., Hsu, S.-B., Wang, F.-B.: Competition and coexistence in flowing habitats with a hydraulic storage zone. Math. Biosci. **222**, 42–52 (2009)
5. Hess, P.: Periodic-Parabolic Boundary Value Problem and Positivity, Pitman Res. Notes Math., 247, Longman Scientific and Technical (1991)
6. Hsu, S.B., Waltman, P.: On a system of reaction-diffusion equations arising from competition in an unsirred chemostat. SIAM J. Appl. Math. **53**, 1026–1044 (1993)
7. Hsu, S.B., Smith, H.L., Waltman, P.: Competitive exclusion and coexistence for competitive system on ordered Banach space. Trans. Am. Math. Soc. **348**, 4083–4094 (1996)
8. Jiang, J., Liang, X., Zhao, X.-Q.: Saddle point behavior for monotone semiflows and reaction-diffusion models. J. Differ. Equ. 313–330 (2004)
9. Kung, C.M., Baltzis, B.: The growth of pure and simple microbial competitors in a moving distributed medium. Math. Biosci. **111**, 295–313 (1992)
10. Magal, P., Zhao, X.-Q.: Global attractors and steady states for uniformly persistent dynamical systems. SIAM. J. Math. Anal. **37**, 251–275 (2005)
11. Martin, R., Smith, H.L.: Abstract functional differential equations and reaction-diffusion systems. Trans. Am. Math. Soc. **321**, 1–44 (1990)
12. Nussbaum, R.D.: Eigenvectors of nonlinear positive operator and the linear Krein-Rutman theorem. In: Fadell, E., Fournier, G. (eds.) Fixed Point Theory, Lecture Notes in Mathematics, vol. 886, pp. 309–331. Springer, New York/Berlin (1981)
13. Pazy, A.: Semigroups of linear operators and application to partial differential equations. Springer, New York (1983)
14. Protter, M.H., Weinberger, H.F.: Maximum Principles in Differential Equations. Springer, New York (1984)
15. Sell, G.R., You, Y.: Dynamics of Evolutionary Equations. Springer, New York (2002)
16. Smith, H.L.: Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems, Math. Surveys Monogr 41, American Mathematical Society Providence, RI (1995)
17. Smith, H.L., Waltman, P.E.: The Theory of the Chemostat. Cambridge University Press, Cambridge (1995)
18. Smith, H.L., Zhao, X.-Q.: Dynamics of a periodically pulsed bio-reactor model. J. Differ. Equ. **155**, 368–404 (1999)
19. Zhang, F., Zhao, X.-Q.: Asymptotic behaviour of a reaction-diffusion model with a quiescent stage. Proc. R. Soc. A **463**, 1029–1043 (2007)
20. Zhao, X.-Q.: Dynamical Systems in Population Biology. Springer, New York (2003)