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A PERIODIC-PARABOLIC DROOP MODEL FOR TWO SPECIES COMPETITION IN AN UNSTIRRED CHEMOSTAT

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Abstract. We study a periodic-parabolic Droop model of two species competing for a single-limited nutrient in an unstirred chemostat, where the nutrient is added to the culture vessel by way of periodic forcing function in time. For the single species model, we establish a threshold type result on the extinction/persistence of the species in terms of the sign of a principal eigenvalue associated with a nonlinear periodic eigenvalue problem. In particular, when diffusion rate is sufficiently small or large, the sign can be determined. We then show that for the competition model, when diffusion rates for both species are small, there exists a coexistence periodic solution.

1. **Introduction.** The Droop model, also known as the variable-yield model, plays a significant role in the study of resource competition theory in phytoplankton ecology. The growth of the phytoplankton species is assumed to be determined by the most basic limited nutrient(s) (e.g., nitrogen or phosphorus). The competition is purely exploitative in the sense that organisms simply consume the nutrient(s), thereby making them unavailable for other individuals. An earlier model for the growth of microorganisms proposed by Monod [26] in 1950 assumes that the growth rate is *constantly* proportional to the nutrient uptake rate. However, for many nutrients, yields of algal cells are not fixed but depend on the physiological state of the population. For instance, in spatially heterogeneous environments, cells can consume nutrients at rates which exceed immediate requirements for growth and store them as quota, which enhances the survival of the species since they can use the stored nutrient(s) when they travels to a poor zone [10, 11]. Thus the ecological system of variable-yield model leads to a great deal of studies among

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phytoplankton ecologists in both experimental and theoretical analysis. See e.g., the book by Nisbet and Gurney [28] and papers such as those by Sommer [35], Morel [27], Grover [7, 8, 9, 11] and the references therein. According to their study, the Droop model provides better predictions and performs better especially in nonequilibrium habitat than the Monod model.

Consider the following model formulated by Droop [4, 5] which describes the competition for a single nutrient which is stored within individuals of the phytoplankton in a well-mixed chemostat (see, e.g., [34]):

$$\begin{cases} \frac{dS}{dt} = (S^{(0)} - S)D - f_1(S, Q_1)u_1 - f_2(S, Q_2)u_2, \\ \frac{du_1}{dt} = (\mu_1(Q_1) - D)u_1, \\ \frac{dQ_1}{dt} = f_1(S, Q_1) - \mu_1(Q_1)Q_1, \\ \frac{du_2}{dt} = (\mu_2(Q_2) - D)u_2, \\ \frac{dQ_2}{dt} = f_2(S, Q_2) - \mu_2(Q_2)Q_2, \\ S(0) \geq 0,\ u_1(0) \geq 0,\ u_2(0) \geq 0,\ Q_1(0) \geq Q_{\min,1},\ Q_2(0) \geq Q_{\min,2}. \end{cases} \tag{1}$$

Here $S(t)$ is the concentration of nutrient, $u_i(t)$ $(i = 1, 2)$ represents the population density for the i-th species of phytoplankton, and $Q_i(t)$ $(i = 1, 2)$ is the average amount of stored nutrient per cell of the i-th population. The chemostat is supplied with nutrient at constant concentration $S^{(0)}$ from an external reservoir. A matching out flow is at dilution rate D whose reciprocal gives the residence time of a cell in the chemostat. $\mu_i(Q_i)$ is the growth rate of the i-th population as a function of cell quota Q_i, $f_i(S, Q_i)$ is the per capital nutrient uptake rate per cell of the i-th population as a function of nutrient concentration S and cell quota Q_i, and $Q_{\min,i}$ is the threshold cell quota below which no growth of the i-th population occurs.

Biologically, when the cell quota is above the minimal cell quota, the growth rate increases with cell quota and cells expressing a higher reproductive rate require a larger cell quota of resource. The nutrient uptake rate increases with nutrient concentration and decreases with cell quota. Typically, the following choices for the growth rate $\mu_i(Q_i)$ are made ([1, 2, 5]):

$$\mu_i(Q_i) = \mu_{i,\infty}\left(1 - \frac{Q_{\min,i}}{Q_i}\right), \forall\ Q \geq Q_{\min,i}, \tag{2}$$

or

$$\mu_i(Q_i) = \mu_{i,\infty}\frac{(Q_i - Q_{\min,i})_+}{a_i + (Q_i - Q_{\min,i})_+}, \forall\ Q \geq Q_{\min,i},$$

where $(Q_i - Q_{\min,i})_+$ is the positive part of $Q_i - Q_{\min,i}$, $\mu_{i,\infty}$ is the maximal growth rate of the i-th species and a_i is the relevant half-saturation constant. According to [9, 27], the uptake rate $f_i(S, Q_i)$ usually takes the form:

$$f_i(S, Q_i) = \rho_{\max,i}(Q_i)\frac{S}{K_i + S}, \tag{3}$$

where K_i is the relevant half-saturation constant. The function $\rho_{\max,i}(Q_i)$ is defined as follows:

$$\rho_{\max,i}(Q_i) = \rho^{\text{high}}_{\max,i} - (\rho^{\text{high}}_{\max,i} - \rho^{\text{low}}_{\max,i})\frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}}, \tag{4}$$

or

$$\rho_{\max,i}(Q_i) = \rho_{\max,i}\frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}. \tag{5}$$

where $Q_{\min,i} \leq Q_i \leq Q_{\max,i}$ and $Q_{\max,i}$ is the maximum cellular quota of the i-th species. In [1, 2], Cunningham and Nisbet took $\rho_{\max,i}(Q_i)$ to be a constant.

Complete mathematical analysis of (1) was carried out in [33]. It was shown that for most cases, competition exclusion holds for the two competing species. Later, Hsu et. al. [15] extended this result to the n-species case. Another modification of the basic chemostat model is to remove the well-mixed hypothesis and incorporate spatial variations. The authors in [19] mathematically investigated the Monod model including spatial heterogeneity in an unstirred chemostat in which two microbial populations compete for a single-limited nutrient. Inspired by the setting in [19], there has been a sequence of papers (see, e.g., [10, 11, 17, 16, 18]) studying variable-yield models in spatially variable habitats (e. g., an unstirred chemostat or a water column in oceans).

In natural environments, nutrient levels can be expected to vary temporally as a result of diurnal or seasonal variations. Thus, motivated by the study of [32, 37, 20, 29], we intend to study a Droop model of two species competing in an unstirred chemostat for a single-limited nutrient, in which flow enters at one boundary supplying nutrient by way of periodic forcing function $S^{(0)}(t)$, and exits at another, removing nutrients and species, with diffusive transport of nutrient and species across the habitat. Thus, we consider the following system of reaction-diffusion equations:

$$\begin{cases} S_t = dS_{xx} - f_1\left(S, \frac{U_1}{u_1}\right)u_1 - f_2\left(S, \frac{U_2}{u_2}\right)u_2, & x \in (0,1),\ t > 0, \\ (u_1)_t = d(u_1)_{xx} + \mu_1\left(\frac{U_1}{u_1}\right)u_1, & x \in (0,1),\ t > 0, \\ (U_1)_t = d(U_1)_{xx} + f_1\left(S, \frac{U_1}{u_1}\right)u_1, & x \in (0,1),\ t > 0, \\ (u_2)_t = d(u_2)_{xx} + \mu_2\left(\frac{U_2}{u_2}\right)u_2, & x \in (0,1),\ t > 0, \\ (U_2)_t = d(U_2)_{xx} + f_2\left(S, \frac{U_2}{u_2}\right)u_2, & x \in (0,1),\ t > 0, \end{cases} \tag{6}$$

with boundary conditions

$$\begin{array}{ll} S_x(0,t) = -S^{(0)}(t), S_x(1,t) + \gamma S(1,t) = 0, & t > 0, \\ w_x(0,t) = 0, w_x(1,t) + \gamma w(1,t) = 0, & w = u_1, U_2, u_2, U_2, t > 0, \end{array} \tag{7}$$

and initial conditions

$$w(x,0) = w^0(x) \geq (\not\equiv) 0,\ \ w = S, U_2, u_2, U_2, x \in (0,1), \tag{8}$$

where the positive constant d in (6) is the diffusion coefficient and the positive constant γ in (7) represents the washout rate; $U_1(x,t) = u_1(x,t)Q_1(x,t)$ and $U_2(x,t) = u_2(x,t)Q_2(x,t)$ are the total amount of stored nutrient for species 1 and 2, respectively; $S^{(0)}(t)$ is positive and varies periodically in time with given period $T > 0$, i.e.,

$$S^{(0)}(t+T) = S^{(0)}(t) > 0 \text{ for all } t. \tag{9}$$

We assume that the initial data $u_1^0(x), U_1^0(x), u_2^0(x), U_2^0(x)$ satisfy

$$U_i^0(x) \geq Q_{\min,i}u^0(x) \text{ on } [0,1]. \tag{10}$$

By naturally extending the above functions $\mu_i(Q_i)$ and $f_i(S,Q_i)$ to be defined in $\mathbb{R}_+$ and $\mathbb{R}_+^2$ respectively, we assume that $\mu_i(Q_i)$ and $f_i(S,Q_i)$ satisfy the following assumptions for $i = 1,2$ (see also [17]) :

(H1) $\mu_i(Q_i)$ is Lipschitz continuous for $Q_i \geq 0$. Moreover, there exists $Q_{\min,i} > 0$ such that $\mu_i(Q_i) = 0$ for $Q_i \in [0, Q_{\min,i}]$ and $\mu_i'(Q_i) > 0$ for $Q_i > Q_{\min,i}$.

(H2) (i) $f_i(S,Q_i)$, $\frac{\partial f_i}{\partial S}(S,Q_i)$ and $\frac{\partial f_i}{\partial Q_i}(S,Q_i)$ are Lipschitz continuous in $S \geq 0$ and $Q_i \geq 0$;

(ii) $f_i(S,Q_i) \geq 0$, $\frac{\partial f_i}{\partial S}(S,Q_i) \geq 0$ and $\frac{\partial f_i}{\partial Q_i}(S,Q_i) \leq 0$ for a.e. $S > 0$ and $Q_i \geq 0$;

(iii) There exists $Q_{B,i} \in (Q_{\min,i}, +\infty]$ such that

$$f_i(S,Q_i) > 0, \frac{\partial f_i}{\partial S}(S,Q_i) > 0 \text{ in } \{(S,Q_i) \in \mathbb{R}^2_+ : S > 0 \text{ and } Q_i \in [0, Q_{B,i})\}$$
$$\text{and } f_i(S,Q_i) = 0 \text{ in } \{(S,Q_i) \in \mathbb{R}^2_+ : S = 0 \text{ or } Q_i \geq Q_{B,i}\}.$$

(When $Q_{B,i} = +\infty$, it is understood that $f_i(S,Q_i) = 0$ if and only if $S = 0$.)

The problem of understanding competition for resources in a both temporally and spatially varying environment is challenging and has received not as much attention as the temporally homogeneous but spatially varying case. This is our first attempt to study nonlinear periodic-parabolic Droop model and we hope to pursue further in this direction in future.

The rest of this paper is organized as follows. In Section 2, we study the single species model. We establish conditions for existence of positive periodic solutions and extinction. Moreover, we study the effects of diffusion rate on the persistence/extinction of the species. In Section 3, we study the competition for two populations. Using results in Section 2, we show that when both diffusion rates of the two competing species are small, there exists a coexistence periodic solution.

2. Population dynamics of single species model.

2.1. Well-posedness and essential boundedness of single species model.

In this section, we consider dynamics of the periodic Droop model of one species consuming one nutrient. Setting $u_2 = U_2 = 0$ and omitting all the subscripts in (6)-(8), we obtain the following system:

$$\begin{cases} S_t = dS_{xx} - f\left(S, \frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ u_t = du_{xx} + \mu\left(\frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ U_t = dU_{xx} + f\left(S, \frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ S_x(0,t) = -S^{(0)}(t),\ \ S_x(1,t) + \gamma S(1,t) = 0, & t > 0, \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u, U, t > 0, \\ w(x,0) = w^0(x) \geq (\not\equiv) 0, & w = S, u, U, x \in (0,1). \end{cases} \tag{11}$$

Let

$$Z = S + U. \tag{12}$$

It is easy to see that

$$\begin{cases} Z_t = dZ_{xx}, & x \in (0,1),\ t > 0, \\ Z_x(0,t) = -S^{(0)}(t),\ \ Z_x(1,t) + \gamma Z(1,t) = 0, & t > 0, \\ Z(x,0) = Z_0(x) \geq (\not\equiv) 0, & x \in [0,1]. \end{cases} \tag{13}$$

From [29, Lemma 3.2], we have the following result:

Lemma 2.1. *The system (13) admits a unique positive T-periodic solution $z^*(x,t)$ and for any $Z_0(x) \in C([0,1];\mathbb{R}_+) \setminus \{0\}$, the unique solution $Z(x,t)$ of (13) satisfies*

$$\lim_{t\to\infty} (Z(x,t) - z^*(x,t)) = 0 \text{ uniformly for } x \in [0,1]. \tag{14}$$

Let

$$\mathbf{Y} = \{(S^0, u^0, U^0) \in C([0,1]; \mathbb{R}^3_+) : \exists \tilde{Q} > 0 \text{ s.t.} \\ Q_{\min} u^0(x) \le U^0(x) \le \tilde{Q} u^0(x) \ \forall x \in [0,1]\}. \tag{15}$$

The following result is a direct consequence of Lemma 2.1 and parabolic comparison principle.

Lemma 2.2. *Suppose* (H1) *and* (H2) *hold. Let* $(S(x,t), u(x,t), U(x,t))$ *be a solution of* (11) *for* $t \in [0, \tau)$. *If* $S^0(\cdot) \le z^*(\cdot, 0)$, *then* $S(\cdot, t) \le z^*(\cdot, t)$ *for all* $t \in [0, \tau)$. *Furthermore, there exists a constant* $C \ge 1$ *independent of* τ *and initial conditions* $(S^0(\cdot), u^0(\cdot), U^0(\cdot)) \in \mathbf{Y}$ *such that*

$$\sup_{t \in [0,\tau)} \|S(\cdot, t)\| \le C(1 + \|S^0(\cdot)\|),$$

where $\|\cdot\|$ *denotes for the sup-norm throughout this paper. Moreover, if* $\tau = \infty$, *then*

$$\limsup_{t \to \infty} (S(x,t) - z^*(x,t)) \le 0 \tag{16}$$

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

Define Q^* to be the unique positive number such that

$$Q^* = \inf\{Q > 0 : f(z^*(x,t), Q) - \mu(Q)Q \le 0 \text{ in } [0,1] \times [0,T]\}. \tag{17}$$

It is obvious that $Q_{\min} < Q^* < Q_B$, where $Q_{\min}$ and Q_B are given by (H1) and (H2) respectively.

Lemma 2.3. *Suppose* (H1) *and* (H2) *hold. Let* $(S(x,t), u(x,t), U(x,t))$ *be a solution of* (11) *for* $t \in [0, \tau)$, *with initial data* $(S^0, u^0, U^0) \in \mathbf{Y} \setminus \{(S^0, 0, 0) \mid S^0 \in C([0,1]; \mathbb{R}_+)\}$. *Then*

(i) It holds that

$$\inf_{x \in [0,1]} \frac{U(x,t)}{u(x,t)} \ge Q_{\min} \text{ for all } t \in (0, \tau). \tag{18}$$

(ii) There exists $\bar{Q} \in [Q^*, \infty)$ *depending on* $\|S^0\|$ *and* $\|U^0/u^0\|$ *such that*

$$\sup_{x \in [0,1]} \frac{U(x,t)}{u(x,t)} \le \bar{Q} \text{ for all } t \in (0, \tau). \tag{19}$$

Moreover, if $\tau = \infty$, *then for each* $Q > Q^*$,

$$\limsup_{t \to \infty} [\sup_{x \in [0,1]} (U(x,t) - Qu(x,t))] \le 0. \tag{20}$$

Furthermore, if $\|u(\cdot, t)\|$ *is bounded uniformly in* $t > 0$, *then* (20) *holds for* $Q = Q^*$.

Since the proof of the above lemma follows essentially from that of [17, Lemma 4.2] with mild modifications, we omit it here. Next, we apply Lemma 2.3 to show the global well-posedness results and eventual boundedness of solutions of (11).

Proposition 1. *Suppose* (H1) *and* (H2) *hold. Then for each initial condition in* $\mathbf{Y}$, *system* (11) *has a unique classical solution* (S, u, U) *that exists for all* $t > 0$. *Moreover, the solution satisfies* $(S(\cdot, t), u(\cdot, t), U(\cdot, t)) \in \mathbf{Y}$ *for all* $t > 0$. *There exists a constant* $C > 0$ *independent of initial conditions in* $\mathbf{Y}$ *such that for any solution* (S, u, U) *of system* (11), *we have*

$$\limsup_{t \to \infty} \|(S(\cdot, t), u(\cdot, t), U(\cdot, t))\| \le C. \tag{21}$$

Proof. We rewrite μ and f as follows:

$$\tilde{\mu}(u,U)=\begin{cases}0 & \text{when } u=0,\\ \mu(U/u)u & \text{when } u>0,\end{cases} \tag{22}$$

and

$$\tilde{f}(S,u,U)=\begin{cases}0 & \text{when } u=0,\\ f(S,U/u)u & \text{when } u>0.\end{cases} \tag{23}$$

Then (11) can be written as

$$\begin{cases}S_t=dS_{xx}-\tilde{f}(S,u,U), & x\in(0,1),\ t>0,\\ u_t=du_{xx}+\tilde{\mu}(u,U), & x\in(0,1),\ t>0,\\ U_t=dU_{xx}+\tilde{f}(S,u,U), & x\in(0,1),\ t>0,\\ S_x(0,t)=-S^{(0)}(t),\quad S_x(1,t)+\gamma S(1,t)=0, & t>0,\\ w_x(0,t)=0,\ w_x(1,t)+\gamma w(1,t)=0, & w=u,U,\ t>0,\\ w(x,0)=w^0(x)\geq(\not\equiv)0, & w=S,u,U,\ x\in(0,1).\end{cases} \tag{24}$$

Observe that $\tilde{\mu}$ and $\tilde{f}$, when regarded as mappings in $\mathbf{Y}$, are Lipchitz continuous. It follows from Lemma 2.3 and [3, Theorem 3.3.3] that for each initial condition $(S^0,u^0,U^0)\in\mathbf{Y}$, there exist $\tau>0$ and a unique solution (S,u,U) of (24) in $[0,\tau)$ satisfying that $(S(\cdot,t),u(\cdot,t),U(\cdot,t))\in\mathbf{Y}$ for all $t\in[0,\tau)$. Next we claim that every solution of (11) with initial condition $(u^0,U^0)\in\mathbf{Y}$ exists for all time, i.e., $\tau=\infty$. Indeed, by Lemmas 2.2 and 2.3, we see that $\|S\|$ and the ratio$\|U/u\|$ remain bounded uniformly in $t\in[0,\tau)$. Therefore if $\tau<\infty$, we must have $\lim_{t\nearrow\tau}\|(u(\cdot,t),U(\cdot,t))\|=\infty$. However, by regarding the equation for (u,U) in (11) as a linear equation with bounded coefficients, we deduce that

$$\sup_{t\in[0,\tau)}\|(u(\cdot,t),U(\cdot,t))\|<\infty \text{ if } \tau<\infty,$$

which is a contradiction. Hence, we must have $\tau=\infty$, i.e., solution to system (11) exists for all time.

It only remains to show (21). By (12), we see that $U(x,t)\leq Z(x,t)$. Hence, it follows from Lemma 2.1 that

$$\limsup_{t\to\infty}\|U(\cdot,t)\|\leq\|z^*\|+1.$$

Then it follows from Lemma 2.3 that

$$\limsup_{t\to\infty}\|u(\cdot,t)\|\leq\limsup_{t\to\infty}\|U(\cdot,t)\|/Q_{\min}\leq(\|z^*\|+1)/Q_{\min}.$$

This together with Lemma 2.2 finish the proof of (21). □

2.2. **Threshold dynamics of single species model.** To characterize the persistence/extinction of the single species model (11), we now consider the following system:

$$\begin{cases}u_t=du_{xx}+\mu\left(\frac{U}{u}\right)u, & x\in(0,1),t>0,\\ U_t=dU_{xx}+f\left(z^*(x,t),\frac{U}{u}\right)u, & x\in(0,1),t>0,\\ w_x(0,t)=0,\ w_x(1,t)+\gamma w(1,t)=0, & w=u,U,t>0,\\ w(x,0)=w^0(x)\geq(\not\equiv)0, & w=u,U,x\in(0,1),\end{cases} \tag{25}$$

where $z^*(x,t)$ is given by Lemma 2.1. Substituting $u(x,t) = e^{-\Lambda t}\phi(x,t)$ and $U(x,t) = e^{-\Lambda t}\varphi(x,t)$ into (25), we obtain the following associated nonlinear eigenvalue problem:

$$\begin{cases} \phi_t = d\phi_{xx} + \mu\left(\frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x,t) + \Lambda\phi(x,t), & x \in (0,1),\ t>0,\\ \varphi_t = d\varphi_{xx} + f\left(z^*(x,t), \frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x,t) + \Lambda\varphi(x,t), & x \in (0,1),\ t>0,\\ w_x(0,t)=0,\ w_x(1,t)+\gamma w(1,t)=0, & w=\phi,\varphi,\ t>0,\\ \phi,\varphi \text{ are } T\text{-periodic in } t. \end{cases} \tag{26}$$

We will rigorously show that the persistence/extinction of the phytoplankton species in system (11) is determined by the principal eigenvalue of the above nonlinear periodic parabolic eigenvalue problem. Hence, to study the existence of principal eigenvalue to (26), we introduce some notations (see also [17]). Let $(\tilde{\mathbf{X}}, \|\cdot\|)$ be a normed vector space (or NLS) over $\mathbb{R}$. We call a subset $C \subset \tilde{\mathbf{X}}$ a cone if (i) C is convex, (ii) $tC \subset C$ for all $t \geq 0$, and (iii) $C \cap (-C) = \{0\}$. A cone C is said to be solid if it has non-empty interior. If C is a cone and also a complete metric space in the metric induced by the norm on $\tilde{\mathbf{X}}$, we call C a complete cone. A cone C in an NLS $(\tilde{\mathbf{X}}, \|\cdot\|)$ induces a partial order $\leq_C$ on $\tilde{\mathbf{X}}$ by $x \leq_C y$ if and only if $y - x \in C$. If C is a solid cone, we say that $x \ll_C y$ if and only if $y - x \in \operatorname{Int} C$. We say the cone C is normal if there exists $M > 0$ such that $\|x\| \leq M\|y\|$ whenever $x \leq_C y$.

A mapping $\mathbf{T} : C \to C$ is *homogeneous of degree one* if, for each $t \geq 0$ and each $x \in C$,

$$\mathbf{T}(tx) = t\mathbf{T}(x).$$

Let $D \in \tilde{\mathbf{X}}$ be another cone such that $C \subset D$. A mapping $\mathbf{T} : C \to C$ is D-order-preserving if $\mathbf{T}(x) \leq_D T(y)$ whenever $x, y \in C$ satisfy $x \leq_D y$. Here $\leq_D$ is the partial order generated by the cone D. If D is a solid cone, we say that $\mathbf{T}$ is D-strongly-order-preserving if $\mathbf{T}(x) \ll_D \mathbf{T}(y)$ whenever $x, y \in C$ satisfy $x \leq_D y$ and $x \neq y$. Recall also the Bonsall cone spectral radius (see [22, 23, 36])

$$\tilde{r}_C(\mathbf{T}) := \lim_{m\to\infty} \|\mathbf{T}^m\|_C^{1/m} = \inf_{m\geq 1} \|\mathbf{T}^m\|_C^{1/m},$$

where $\|\mathbf{T}^m\|_C := \sup\{\|\mathbf{T}^m(x)\| : x \in C \text{ and } \|x\| \leq 1\}$. We assume that the following hold:

(**C**) Let $C \subset D$ be complete cones in an NLS $(\tilde{\mathbf{X}}, \|\cdot\|)$, D be normal, and $\mathbf{T} : C \to C$ be (i) continuous, (ii) compact, (iii) homogeneous of degree one, and (iv) D-order-preserving.

Proposition 2 ([17]). *Assume* (**C**) *holds. If, in addition, D is a solid cone and* $\mathbf{T}$ *is D-strongly-order-preserving, then*

(i) $\tilde{r} = \tilde{r}_C(\mathbf{T}) > 0$ and there is a non-zero eigenvector $\tilde{x} \in C \cap \operatorname{Int} D$ such that

$$\mathbf{T}\tilde{x} = \tilde{r}\tilde{x}.$$

(ii) If $x' \in C$ is another eigenvector of $\mathbf{T}$, *then $x' \in \operatorname{span}\{\tilde{x}\}$ and $\mathbf{T}x' = \tilde{r}x'$.*

We now show the existence of the principal eigenvalue of the nonlinear periodic-parabolic eigenvalue problem (26). From now on, let $D = C([0,1];\mathbb{R}^2_+)$ and $\leq_D$ be the partial order in $C([0,1];\mathbb{R}^2_+)$ induced by the cone D, i.e.,

$$(u_1(\cdot), v_1(\cdot)) \leq_D (u_2(\cdot), v_2(\cdot)) \text{ if } u_1(x) \leq u_2(x) \text{ and } v_1(x) \leq v_2(x),\ \forall x \in [0,1].$$

Let

$$C = \{(u,U) \in D : Q_{\min} u(x) \leq U(x) \leq Q^* u(x) \text{ for } x \in [0,1]\},$$

where Q^* is given in (17). It is easy to see that both C and D are complete cones and that D is both normal and solid.

By T-periodicity of $z^*(x,t)$ in t and similar arguments as in the proofs of Proposition 1, we deduce that system (25) generates periodic solution maps $\Pi(t)$ on C, i.e., $\Pi(t)$ satisfies that

$$\Pi(t+T) = \Pi(t) \circ \Pi(T), \ \forall t \geq 0.$$

Then we have the following result concerning the existence of the principal eigenvalue of system (26).

Lemma 2.4. *Suppose that* (H1) *and* (H2) *hold. For each $d > 0$, the eigenvalue problem* (26) *admits a unique principal eigenvalue $\Lambda^0 = \Lambda^0(d)$ corresponding to which there is a strongly positive eigenfunction $(\phi^0(x,t), \varphi^0(x,t)) \gg_D 0$.*

Proof. Recall that system (25) generates solution maps $\Pi(t)$ on C. It is easy to see that for all $t > 0$, $\Pi(t)$ is continuous, compact and homogeneous of degree one. By similar arguments as in the proof of [17, Lemma 5.1], we can show that for all $t > 0$, $\Pi(t) : C \to C$ is D-strongly-order-preserving. Hence, we may apply Proposition 2 to the operator $\Pi(T) : C \to C$ to obtain $\tilde{r}$ and $(\phi(x), \varphi(x)) \in C \cap \operatorname{Int} D$ such that

$$\Pi(T)(\phi(x), \varphi(x)) = \tilde{r}(\phi(x), \varphi(x)),$$

where $\tilde{r}$ is the Bonsall cone spectral radius of $\Pi(T) : C \to C$. Denote $\Lambda^0 = -\frac{1}{T}\log\tilde{r}$. Then we can verify that Λ^0 is the principal eigenvalue to (25) with

$$(\phi^0(x,t), \varphi^0(x,t)) = e^{\Lambda^0 t}\Pi(t)(\phi(x), \varphi(x))$$

being the associated eigenfunction. The uniqueness of Λ^0 follows from Proposition 2. □

We next study dynamics of the limiting system of (11):

$$\begin{cases} u_t = du_{xx} + \mu\left(\frac{U}{u}\right)u, & x \in (0,1), \ t > 0, \\ U_t = dU_{xx} + f\left(z^*(x,t) - U, \frac{U}{u}\right)u, & x \in (0,1), \ t > 0, \\ w_x(0,t) = 0, \ w_x(1,t) + \gamma w(1,t) = 0, & w = u, U, t > 0, \\ w(x,0) = w^0(x) \geq (\not\equiv) 0, & w = u, U, x \in (0,1). \end{cases} \tag{27}$$

The biologically feasible region for system (27) is defined by

$$\begin{aligned} \mathbf{D}(t) := \{(u,U) \in C([0,1];\mathbb{R}^2_+) : U(x) \leq z^*(x,t), \exists \tilde{Q} > 0 \text{ s.t.} \\ Q_{\min}u(x) \leq & U(x) \leq \tilde{Q}u(x) \ \forall x \in [0,1]\} \end{aligned}$$

Note that $\mathbf{D}(t)$ is T-periodic in t. We now show that the set $\mathbf{D}(t)$ is positively invariant for the solution map associated with (27).

Our proof is motivated by [11, 24, 17].

Lemma 2.5. *For any $(u^0, U^0) \in \mathbf{D}(0)$, system* (27) *has a unique solution $(u(\cdot,t), U(\cdot,t))$ with $(u(\cdot,0), U(\cdot,0)) = (u^0, U^0)$ and $(u(\cdot,t), U(\cdot,t)) \in \mathbf{D}(t), \ \forall \ t \geq 0$. Moreover, the solution $(u(x,t), U(x,t))$ satisfies*

$$U(x,t) < z^*(x,t), \ \text{for all } x \in [0,1], \ t > 0, \tag{28}$$

and

$$\limsup_{t\to\infty}[\sup_{x\in[0,1]}(U(x,t) - Q^*u(x,t))] \leq 0, \ \text{for all } (u^0, U^0) \in \mathbf{D}(0).$$

Proof. Let $(u(x,t),U(x,t))$ be a solution of (27) for $t\in[0,\tau)$, with initial data $(u^0,U^0)\in\mathbf{D}(0)$. We first claim that $U(x,t)\le z^*(x,t)$ for all $x\in[0,1]$ and $t\in[0,\tau)$. Let

$$Y(x,t)=z^*(x,t)-U(x,t),$$

then $Y(x,t)$ satisfies the following equation

$$\begin{cases} Y_t-dY_{xx}+\left[u\int_0^1\frac{\partial f}{\partial S}(\xi Y,\frac{U}{u})\,d\xi\right]Y=0 & x\in[0,1],t\in[0,\tau),\\ Y_x(0,t)=-S^{(0)}(t),\ Y_x(1,t)+\gamma Y(1,t)=0 & t\in[0,\tau).\end{cases}$$

Since $u\int_0^1\frac{\partial f}{\partial S}(\xi Y,\frac{U}{u})\,d\xi\ge 0$ on $[0,1]\times[0,\tau)$ by (H2) and $Y(x,0)=z^*(x,0)-U^0(x)\ge 0$ on $[0,1]$, we have by comparison principle for linear parabolic equations that, $Y(\cdot,t)\ge 0$ on $[0,1]$ for all $t\in[0,\tau)$. Thus $U(x,t)\le z^*(x,t)$ for all $t\in[0,\tau)$. Next, we show that (28) holds. Assume for contradiction that there exists $x_1\in[0,1]$ and $t_1\in(0,\infty)$ such that $Y(x_1,t_1)=0$. Then $(x_1,t_1)\in[0,1]\times(0,\tau]$ and Y attains its minimum on $[0,1]\times[0,\tau]$ at the point (x_1,t_1). In case $x_1=1$ (resp. $x_1=0$), we apply the Hopf boundary lemma (see, e.g., [30, p. 170, Theorem 3]) and get $\frac{\partial Y}{\partial x}(1,t_1)<0$ (resp. $-\frac{\partial Y}{\partial x}(0,t_1)<0$), which is a contradiction to the boundary condition. In case $x_1\in(0,1)$, we apply the strong maximum principle ([30, p. 174, Theorem 7]) and we obtain that $Y(x,t)\equiv Y(x_1,t_1)=0,\ \forall\,(x,t)\in[0,1]\times[0,\tau]$, which is a contradiction to the boundary condition at $x=0$. Therefore, (28) is valid.

Let $S(x,t)=z^*(x,t)-U(x,t)$. Then it is easy to see that $(S(x,t),u(x,t),U(x,t))\in\mathbf{Y}$ satisfies system (11), where $\mathbf{Y}$ is given in (15). Hence, the rest of the proof follows from similar arguments as in [17, Lemma 4.2] and Proposition 1 and is thus omitted. □

Lemma 2.6. *Assume that* (H1) *and* (H2) *hold. Let* Λ^0 *be the principal eigenvalue of* (26). *Then the following statements are valid:*

(i) If $\Lambda^0>0$, *then* $(0,0)$ *is globally attractive in* $\mathbf{D}(0)$ *for system* (27).
(ii) If $\Lambda^0<0$, *then system* (27) *has a unique positive* T*-periodic solution* $(\hat u(x,t),\hat U(x,t))$ *that attracts all trajectories in* $\mathbf{D}(0)\backslash\{(0,0)\}$.

Proof. By Lemma 2.5, $\limsup_{t\to\infty}\sup_{x\in[0,1]}\frac{U(x;t)}{u(x;t)}<\infty$ for any given nontrivial trajectory. It follows then by eventual boundedness of the trajectory and standard parabolic estimates [21, Section VII.8] that system (27) generates solution maps $\Phi_t:\mathbf{D}(0)\to\mathbf{D}(t)$ with precompact trajectories defined by

$$\Phi_t(u^0,\ U^0):=(u(\cdot,t,u^0,U^0),U(\cdot,t,u^0,U^0)),\quad\forall\,(u^0(\cdot),\ U^0(\cdot))\in\mathbf{D}(0),$$

where $(u(x,t,u^0,U^0),U(x,t,u^0,U^0))$ is the solution of system (27) with

$$(u(\cdot,0,u^0,U^0),U(\cdot,0,u^0,U^0))=(u^0(\cdot),U^0(\cdot)).$$

The Jacobian matrix of reaction terms in (27) with respect to (u,U) at $(u,U)\in\mathbb{R}^2_+$ takes the form

$$J=\begin{pmatrix} * & a_{12}\\ a_{21} & *\end{pmatrix},$$

where

$$
\begin{aligned}
a_{12} &= \mu'(\frac{U}{u}) > 0, \\
a_{21} &= f(z^*(x,t) - U, \frac{U}{u}) - \frac{U}{u}\frac{\partial f}{\partial Q}(z^*(x,t) - U, \frac{U}{u}) \geq 0.
\end{aligned}
$$

Thus Φ_t is monotone on $\mathbf{D}(0)$ under the partial order $\leq_D$ generated by the cone $D = C([0,1];\mathbb{R}^2_+)$ (see, e.g., [31]). By the property (28) in Lemma 2.5, we see that $U(x,t) < z^*(x,t)$ for $x \in [0,1]$ and $t > 0$. Then $a_{21} > 0$ and hence J is irreducible. This implies that Φ_t is strongly monotone in $\mathbf{D}(0)$, i.e., if $(u_i^0,\ U_i^0) \in \mathbf{D}(0)$ for $i = 1, 2$ and $(u_1^0,\ U_1^0) <_D (u_2^0,\ U_2^0)$, then $\Phi_t(u_1^0,\ U_1^0) \ll_D \Phi_t(u_2^0,\ U_2^0)$ for all $t > 0$.

We now prove Part (i) of the theorem. Recall that $(\phi^0(x,t), \varphi^0(x,t))$ is the eigenfunction corresponding to Λ^0 in Lemma 2.4. For each $(u^0, U^0) \in \mathbf{D}(0)$, it is easy to see that there exists some constant $a > 0$ such that $(u^0, U^0) \leq_D a(\phi^0(\cdot,0), \varphi^0(\cdot,0))$. Let

$$
(\overline{u}(x,t), \overline{U}(x,t)) := ae^{-\Lambda^0 t}(\phi^0(x,t), \varphi^0(x,t)). \tag{29}
$$

Then $(\overline{u}(x,t), \overline{U}(x,t))$ satisfies the following cooperative system

$$
\begin{cases}
\overline{u}_t = d\overline{u}_{xx} + \mu\left(\frac{\overline{U}}{\overline{u}}\right)\overline{u}, & x \in (0,1),\ t > 0, \\
\overline{U}_t = d\overline{U}_{xx} + f\left(z^*(x,t), \frac{\overline{U}}{\overline{u}}\right)\overline{u}, & x \in (0,1),\ t > 0, \\
w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = \overline{u}, \overline{U}, t > 0,
\end{cases} \tag{30}
$$

and $(u^0, U^0) \leq_D (\overline{u}(\cdot,0), \overline{U}(\cdot,0))$. By comparison principle, we see that

$$
(u(\cdot,t,u^0,U^0), U(\cdot,t,u^0,U^0)) \leq_D (\overline{u}(\cdot,t), \overline{U}(\cdot,t)) \quad \forall t \geq 0.
$$

In view of (29) and the fact that $\Lambda^0 > 0$, we have

$$
\lim_{t\to\infty}(u(\cdot,t,u^0,U^0), U(\cdot,t,u^0,U^0)) = (0,0).
$$

This finishes the proof for Part (i).

It only remains to prove Part (ii) of the theorem. For convenience, we define $\mathbf{D}_0 := \{(u,U) \in \mathbf{D}(0) : u \not\equiv 0 \text{ in } [0,1]\}$ and its complementary set

$$
\begin{aligned}
\partial\mathbf{D}_0 :&= \mathbf{D}(0) - \mathbf{D}_0 = \{(u,U) \in \mathbf{D}(0) : u \equiv 0 \text{ in } [0,1]\} \\
&= \{(u,U) \in \mathbf{D}(0) : u \equiv U \equiv 0 \text{ in } [0,1]\} = \{(0,0)\}.
\end{aligned}
$$

Since $\Lambda^0 < 0$, we can find some $0 < \epsilon_0 \ll 1$ such that $\Lambda^{\epsilon_0} < 0$, where Λ^{ϵ_0} is the principal eigenvalue of the following eigenvalue problem:

$$
\begin{cases}
\phi_t = d\phi_{xx} + \mu\left(\frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x,t) + \Lambda\phi(x,t), & x \in (0,1),\ t > 0, \\
\varphi_t = d\varphi_{xx} + f\left(z^*(x,t) - \epsilon_0, \frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x,t) + \Lambda\varphi(x,t), & x \in (0,1),\ t > 0, \\
w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = \phi, \varphi,\ t > 0, \\
\phi, \varphi \text{ are } T\text{-periodic in } t.
\end{cases} \tag{31}
$$

It is easy to see by continuity that

$$
\exists\delta > 0 \text{ such that } \|\Phi_t(u^0,U^0)\| < \epsilon_0 \text{ for all } t \in [0,T] \text{ and } \|(u^0,U^0)\| < \delta. \tag{32}
$$

Claim 2.1. Let $\delta > 0$ be given as above. Then

$$
\limsup_{n\to\infty} \|\Phi_{nT}(u^0,U^0)\| \geq \delta,\ \forall\ (u^0,U^0) \in \mathbf{D}_0.
$$

We now prove Claim 2.1. Assume by contradiction that there exists some $P^0 \in \mathbf{D}_0$ and $n_0 \in \mathbb{N}$ such that

$$\|\Phi_{nT}(P^0)\| < \delta, \ \forall \ n \geq n_0.$$

For each $t \geq n_0 T$, we can rewrite $t = nT + t'$ with $n \geq n_0$ and $t' \in [0, T)$. Then by (32)

$$\|\Phi_t(P^0)\| = \|\Phi_{t'}(\Phi_{nT}(P^0))\| < \epsilon_0, \ \forall \ t \geq n_0 T.$$

Thus, $U(x,t,P^0) \leq \epsilon_0, \ \forall \ x \in [0,1], \ t \geq n_0 T$. This implies that $(u(x,t,P^0), U(x,t,P^0))$ satisfies

$$\begin{cases} u_t = du_{xx} + \mu\left(\frac{U}{u}\right)u, & x \in (0,1), \ t \geq n_0 T, \\ U_t \geq dU_{xx} + f\left(z^*(x,t) - \epsilon_0, \frac{U}{u}\right)u, & x \in (0,1), \ t \geq n_0 T, \\ w_x(0,t) = 0, \ w_x(1,t) + \gamma w(1,t) = 0, & w = u, U, \ t \geq n_0 T. \end{cases} \tag{33}$$

Since $P^0 \in \mathbf{D}_0$, it follows from maximum principle that $(u(\cdot,t,P^0), U(\cdot,t,P^0)) \gg_D (0,0)$ for all $t > 0$. Then there exists $b > 0$ such that

$$(u(\cdot, n_0T, P^0), U(\cdot, n_0T, P^0)) \geq_D b(\underline{\phi}(\cdot, n_0T), \underline{\varphi}(\cdot, n_0T),$$

where $(\underline{\phi}, \underline{\varphi})$ is the eigenfunction of (31) associated with Λ^{ϵ_0}. On the other hand,

$$(\underline{u}(x,t), \underline{U}(x,t)) := be^{-\Lambda^{\epsilon_0}(t - n_0T)}(\underline{\phi}(x,t), \underline{\varphi}(x,t)) \tag{34}$$

satisfies the following cooperative system:

$$\begin{cases} \underline{u}_t = d\underline{u}_{xx} + \mu\left(\frac{U}{\underline{u}}\right)\underline{u}, & x \in (0,1), \ t \geq n_0 T, \\ \underline{U}_t = d\underline{U}_{xx} + f\left(z^*(x,t) - \epsilon_0, \frac{U}{\underline{u}}\right)\underline{u}, & x \in (0,1), \ t \geq n_0 T, \\ w_x(0,t) = 0, \ w_x(1,t) + \gamma w(1,t) = 0, & w = \underline{u}, \underline{U}, \ t \geq n_0 T, \end{cases} \tag{35}$$

and $(u(\cdot, n_0T, P^0), U(\cdot, n_0T, P^0)) \geq_D (\underline{u}(\cdot, n_0T), \underline{U}(\cdot, n_0T))$. By comparison principal, we have

$$(u(\cdot, t, P^0), U(\cdot, t, P^0)) \geq_D (\underline{u}(\cdot, t), \underline{U}(\cdot, t)) \quad \forall t \geq n_0 T.$$

In view of (34) and the fact $\Lambda^{\epsilon_0} < 0$, it follows that $(u(\cdot,t,P^0), U(\cdot,t,P^0))$ is unbounded, which contradicts the fact that $\|\Phi_t(P^0)\| < \epsilon_0$ for all $t \geq n_0 T$. This finished the proof of Claim 2.1.

By Claim 2.1, we see that $W^s(0,0) \cap \mathbf{D}_0 = \emptyset$, where $W^s(0,0)$ is the stable set of $(0,0)$ for the Pincaré map $\Phi_T : \mathbf{D}(0) \to \mathbf{D}(0)$. Moreover, Claim 2.1 implies that $\{(0,0)\}$ is isolated in $\mathbf{D}(0)$. It is obvious that there exists no homoclinic cycle from $\{(0,0)\}$ to $\{(0,0)\}$ in $\partial\mathbf{D}_0$. Since Φ_T is compact and point dissipative (i.e., the trajectory is eventual bounded, see, e.g., [12, section 2.4]), we conclude from [12, Theorem 2.4.7] that there exists a global attractor for Φ_T in $\mathbf{D}(0)$. We can then apply the uniform persistence results of [38, Theorem 1.3.1 and Remark 1.3.1] to the Pincaré map $\Phi_T : \mathbf{D}(0) \to \mathbf{D}(0)$ to show that Φ_T is uniformly persistent with respect to $(\mathbf{D}_0, \partial\mathbf{D}_0)$ in the sense that there exists an $\eta > 0$ such that

$$\liminf_{n\to\infty} \|\Phi_{nT}(u^0, U^0)\| \geq \eta, \ \forall \ (u^0, U^0) \in \mathbf{D}_0. \tag{36}$$

Denote the reaction terms of (27) by

$$\begin{cases} F_1(u,U) = \mu\left(\frac{U}{u}\right)u, \\ F_2(u,U) = f\left(z^*(x,t) - U, \frac{U}{u}\right)u. \end{cases} \tag{37}$$

For $0 < \alpha < 1$ and $(u,U) \in \mathbf{D}(0) \setminus \{(0,0)\}$, it is easy to see that

$$F_1(\alpha u, \alpha U) = \alpha F_1(u,U), \qquad F_2(\alpha u, \alpha U) > \alpha F_2(u,U).$$

Then we can adopt the arguments in [6, Theorem 2.2] with slight modifications to show the following claim:

Claim 2.2. For any $t > 0$, $\Phi_t : \mathbf{D}(0) \to \mathbf{D}(t)$ is strictly subhomogeneous in the sense that for any $\alpha \in (0, 1)$ and $(u^0(\cdot), U^0(\cdot)) \gg_D (0, 0)$, we have

$$\Phi_t(\alpha u^0(\cdot), \alpha U^0(\cdot)) >_D \alpha \Phi_t(u^0(\cdot), U^0(\cdot)).$$

We have proved that the Pincaré map $\Phi_T : \mathbf{D}(0) \to \mathbf{D}(0)$ is compact, point dissipative and uniformly persistent. It follows from [38, Theorem 1.3.6] that $\Phi_T : \mathbf{D}_0 \to \mathbf{D}_0$ admits a global attractor A_0. Since Φ_T is also strongly monotone and strictly subhomogeneous, $A_0 \subset \mathbf{D}_0$ and $A_0 = \Phi_T(A_0) \in \mathrm{Int}(\mathbf{D}(0))$. It then follows from [38, Theorem 2.3.2] with $K = A_0$ that $A_0 = \{e\}$, where $e \gg_D (0, 0)$ is a fixed point of Φ_T. This implies that e is globally attractive for Φ_T in $\mathbf{D}_0$. Corresponding to the fixed point of the Pincaré map Φ_T, system (27) has a globally attractive positive T-periodic solution $(\hat{u}(x, t), \hat{U}(x, t))$ in $\mathbf{D}_0$. This finishes the proof of the lemma. ☐

Remark 1. We note that the dynamics of system (27) is unclear when $\Lambda^0 = 0$.

Recall the definition of $\mathbf{Y}$ in (15). We now define $\mathbf{Y}_0 = \{(S^0, u^0, U^0) \in \mathbf{Y} : u^0 \not\equiv 0 \text{ in } [0, 1]\}$ and its complementary set

$$\begin{aligned}\partial \mathbf{Y}_0 :&= \mathbf{Y} - \mathbf{Y}_0 = \{(S^0, u^0, U^0) \in \mathbf{Y} : u^0 \equiv 0 \text{ in } [0, 1]\} \\ &= \{(S^0, u^0, U^0) \in \mathbf{Y} : u^0 \equiv U^0 \equiv 0 \text{ in } [0, 1]\},\end{aligned}$$

so that $\mathbf{Y} = \mathbf{Y}_0 \cup \partial \mathbf{Y}_0$.

We now state the following result concerning global dynamics of (11).

Theorem 2.7. *Under the hypotheses of* (H1) *and* (H2), *the eigenvalue problem* (26) *has a principal eigenvalue* Λ^0, *characterized as the unique eigenvalue of* (26) *with a strictly positive eigenfunction. Furthermore,*

(i) If $\Lambda^0 > 0$, *then* $(z^*(x, t), 0, 0)$ *attracts all trajectories in* $\mathbf{Y}$.
(ii) If $\Lambda^0 < 0$, *then* (11) *has a unique positive* T*-periodic solution* $(\hat{S}(x, t), \hat{u}(x, t), \hat{U}(x, t))$ *that attracts all trajectories in* $\mathbf{Y}_0$.

Proof. We are ready to lift the dynamics of the limiting system (27) to the full system (11). Let

$$W(x, t) = z^*(x, t) - (S(x, t) + U(x, t)). \tag{38}$$

Then it follows from (13) and Lemma 2.1 that system (11) can be rewritten as

$$\begin{cases} W_t = dW_{xx}, & x \in (0, 1),\ t > 0, \\ u_t = du_{xx} + \mu\left(\frac{U}{u}\right) u, & x \in (0, 1),\ t > 0, \\ U_t = dU_{xx} + f\left(z^*(x, t) - U - W, \frac{U}{u}\right) u, & x \in (0, 1),\ t > 0, \\ w_x(0, t) = 0, \quad w_x(1, t) + \gamma w(1, t) = 0, & w = u, U, W, t > 0, \\ w(x, 0) = w^0(x), & w = u, U, W, x \in (0, 1). \end{cases} \tag{39}$$

The relevant domain for system (39) is

$$\begin{aligned}\tilde{\mathbf{Y}}(t) = \{(W, u, U) \in C([0, 1]; \mathbb{R}) \times C([0, 1]; \mathbb{R}^2_+) : U(\cdot) + W(\cdot) \leq z^*(\cdot, t) \\ \exists \tilde{Q} > 0 \text{ such that } Q_{\min} u(x) \leq U(x) \leq \tilde{Q} u(x)\ \forall x \in [0, 1]\}.\end{aligned} \tag{40}$$

Since systems (11) and (39) are equivalent, it suffices to study system (39) with initial data in $\tilde{\mathbf{Y}}(0)$. Note that

$$(S^0, u^0, U^0) \in \mathbf{Y} \text{ iff } (W^0, u^0, U^0) = (z^*(x,0) - S^0 - U^0, u^0, U^0) \in \tilde{\mathbf{Y}}(0).$$

By similar arguments as in Lemma 2.5, we can show that for any $(W^0, u^0, U^0) \in \tilde{\mathbf{Y}}(0)$, system (39) has a unique solution $(W(\cdot,t), u(\cdot,t), U(\cdot,t))$ with $(W(\cdot,0), u(\cdot,0), U(\cdot,0)) = (W^0, u^0, U^0)$ and $(W(\cdot,t), u(\cdot,t), U(\cdot,t)) \in \tilde{\mathbf{Y}}(t),\ \forall\, t \geq 0$. Moreover, the solution $(W(x,t), u(x,t), U(x,t))$ satisfies

$$\limsup_{t\to\infty}[\sup_{x\in[0,1]}(U(x,t) - Q^* u(x,t))] \leq 0. \tag{41}$$

Therefore, we can define the solution maps $\tilde{\Phi}_t : \tilde{\mathbf{Y}}(0) \to \tilde{\mathbf{Y}}(t)$ associated with (39) by

$$\tilde{\Phi}_t(\mathbf{u}^0) = (W(\cdot,t,\mathbf{u}^0), u(\cdot,t,\mathbf{u}^0), U(\cdot,t,\mathbf{u}^0))\ \forall t \geq 0,$$

where $\mathbf{u}^0 := (W^0, u^0, U^0) \in \tilde{\mathbf{Y}}(0)$ and the associated Pincaré map $\tilde{\mathbf{P}} : \tilde{\mathbf{Y}}(0) \to \tilde{\mathbf{Y}}(0)$ as follows:

$$\tilde{\mathbf{P}} = \tilde{\Phi}_T. \tag{42}$$

Define $\tilde{\mathbf{Y}}_0 := \{(W,u,U) \in \tilde{\mathbf{Y}}(0) : u \not\equiv 0\}$ and its complementary set

$$\begin{aligned}\partial\tilde{\mathbf{Y}}_0 :&= \tilde{\mathbf{Y}}(0) - \tilde{\mathbf{Y}}_0 = \{(W,u,U) \in \tilde{\mathbf{Y}}(0) : u \equiv 0 \text{ in } [0,1]\} \\ &= \{(W,u,U) \in \tilde{\mathbf{Y}}(0) : u \equiv U \equiv 0 \text{ in } [0,1]\}.\end{aligned}$$

Fix $\mathbf{u}^0 \in \tilde{\mathbf{Y}}(0)$, and let $\tilde{\omega}(\mathbf{u}^0)$ be the omega limit set of $\mathbf{u}^0$ for the Pincaré map $\tilde{\mathbf{P}}$.

By Lemma 2.1, we see that the equation of W in (39) satisfies

$$\lim_{t\to\infty} W(x,t) = 0 \text{ uniformly for } x \in [0,1], \tag{43}$$

regardless of initial condition $\mathbf{u}^0 \in \tilde{\mathbf{Y}}(0)$. It follows that there exists a set $\mathcal{I} \in C([0,1];\mathbb{R}^2_+)$ such that $\tilde{\omega} := \tilde{\omega}(\mathbf{u}^0) = \{0\} \times \mathcal{I}$.

Claim 2.3. $\mathcal{I} \subset \mathbf{D}(0)$.

For each $(u^0, U^0) \in \mathcal{I}$, we have $(0, u^0, U^0) \in \tilde{\omega} \subset \tilde{\mathbf{Y}}(0)$. By definition of $\tilde{\mathbf{Y}}(0)$, we deduce that $(u^0, U^0) \in \mathbf{D}(0)$. This proves the claim.

Claim 2.4. $\mathcal{I}$ is compact, invariant and internal chain transitive for the Pincaré map $\mathbf{P} = \Phi_T : \mathbf{D}(0) \to \mathbf{D}(0)$ associated with system (27).

It is straight forward to see that $\{0\} \times \mathcal{I}$ is compact and invariant with respect to $\tilde{\mathbf{P}}$ iff $\mathcal{I}$ is compact and invariant with respect to $\mathbf{P}$. Next, we show that $\mathcal{I}$ is internal chain transitive for the Pincaré map $\mathbf{P}$. For any $(u(\cdot), U(\cdot)) \in C([0,1], \mathbb{R}^2_+)$ with $(0, u(\cdot), U(\cdot)) \in \tilde{\omega}$, there holds

$$\tilde{\mathbf{P}}|_{\tilde{\omega}}((0, u(\cdot), U(\cdot))) = (0, \mathbf{P}(u(\cdot), U(\cdot))). \tag{44}$$

Given any $a, b \in \mathcal{I}$ and any $\epsilon > 0$. Since $(0,a), (0,b) \in \{0\} \times \mathcal{I} = \tilde{\omega}$ and $\tilde{\omega}$ is a compact, invariant and internal chain transitive set for $\tilde{\mathbf{P}}$ (see, e. g., [14, Lemma 2.1] or [38, Lemma 1.2.1′]), it follows from the definition (see, e. g., [14] or [38, Page 8]) that there is a finite sequence $\{(0,\chi_i)\}_{i=1}^n \subset \tilde{\omega} = \{0\} \times \mathcal{I}$ with $(0,\chi_1) = (0,a)$ and $(0,\chi_n) = (0,b)$ such that

$$\text{dist}(\tilde{\mathbf{P}}(0,\chi_{i-1}), (0,\chi_i)) < \epsilon,\ \forall\ 2 \leq i \leq n. \tag{45}$$

From (44) and (45), we see that the sequence $\{\chi_i\}_{i=1}^n \subset \mathcal{I}$ with $\chi_1 = a$ and $\chi_n = b$ satisfies that

$$\mathrm{dist}(\mathbf{P}(\chi_{i-1}), \chi_i) < \epsilon,\ \forall\ 2 \le i \le n.$$

This shows that $\mathcal{I}$ is a compact, invariant and internal chain transitive set for the Pincaré map $\mathbf{P} : \mathbf{D}(0) \to \mathbf{D}(0)$, which finishes the proof of Claim 2.4.

For the case $\Lambda^0 > 0$, it follows from Lemma 2.6(i) that $(0, 0)$ is globally attractive for system (27), which implies that $\mathcal{I} = \{(0, 0)\}$ by [38, Thm. 1.2.2]. Hence, $\tilde{\omega} = \{0\} \times \mathcal{I} = \{(0, 0, 0)\}$. This implies that $(0, 0, 0)$ is globally attractive for $\tilde{\mathbf{P}}$ in $\tilde{\mathbf{Y}}(0)$. Therefore, $(0, 0, 0)$ is globally attractive for system (39) in $\tilde{\mathbf{Y}}(0)$. In view of (38), we finish the proof of Part (i) of the theorem.

For the case $\Lambda^0 < 0$, it follows from Lemma 2.6 and [38, Thm. 1.2.2] that either $\mathcal{I} = \{(0, 0)\}$ or $\mathcal{I} = \{(\hat{u}(x, 0), \hat{U}(x, 0))\}$. Since $\Lambda^0 < 0$, we can find a sufficiently small number $\tilde{\epsilon} > 0$ such that $\tilde{\Lambda} < 0$, where $\tilde{\Lambda}$ is the principal eigenvalue of

$$\begin{cases} \phi_t = d\phi_{xx} + \mu\left(\frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x, t) + \Lambda\phi(x, t), & x \in (0, 1),\ t > 0, \\ \varphi_t = d\varphi_{xx} + [f\left(z^*(x, t), \frac{\varphi(x,t)}{\phi(x,t)}\right) - \tilde{\epsilon}]\phi(x, t) + \Lambda\varphi(x, t), & x \in (0, 1),\ t > 0, \\ w_x(0, t) = 0,\ w_x(1, t) + \gamma w(1, t) = 0, & w = \phi, \varphi,\ t > 0, \\ \phi, \varphi \text{ are } T\text{-periodic in } t. \end{cases} \tag{46}$$

Claim 2.5. $\mathcal{I} = \{(\hat{u}(\cdot, 0), \hat{U}(\cdot, 0))\}$.

Assume, by contradiction, that $\mathcal{I} = \{(0, 0)\}$, and hence, $\tilde{\omega} = \{0\}\times\mathcal{I} = \{(0, 0, 0)\}$. This implies that for any $(W^0, u^0, U^0) \in \tilde{\mathbf{Y}}_0$,

$$\tilde{\mathbf{P}}^n(W^0, u^0, U^0) = (W(\cdot, nT), u(\cdot, nT), U(\cdot, nT)) \to (0, 0, 0),\ \text{as } n \to \infty.$$

Equivalently,

$$\lim_{t\to\infty} ||(W(\cdot, t), u(\cdot, t), U(\cdot, t)) - (0, 0, 0)|| = 0.$$

From this, we have that

$$\lim_{t\to\infty} ||\,(z^*(\cdot, t) - U(\cdot, t) - W(\cdot, t)) - z^*(\cdot, t)|| = \lim_{t\to\infty} ||(U(\cdot, t) + W(\cdot, t)|| = 0,$$

which implies that there exists $t_1 > 0$ such that

$$f\left(z^*(x, t) - U(x, t) - W(x, t), \frac{U(x, t)}{u(x, t)}\right) > f\left(z^*(x, t), \frac{U(x, t)}{u(x, t)}\right) - \tilde{\epsilon},\ \forall\, x \in [0, 1],\ t \ge t_1.$$

Then it follows from the second and third equations of (39) that

$$\begin{cases} u_t = du_{xx} + \mu\left(\frac{U}{u}\right)u, & x \in (0, 1),\ t \ge t_1, \\ U_t \ge dU_{xx} + [f\left(z^*(x, t), \frac{U(x,t)}{u(x,t)}\right) - \tilde{\epsilon}]u, & x \in (0, 1),\ t \ge t_1, \\ w_x(0, t) = 0, \quad w_x(1, t) + \gamma w(1, t) = 0, & w = u, U, t \ge t_1. \end{cases} \tag{47}$$

Since $u^0 \not\equiv 0$, we may apply maximum principle to system (39) to show that $u(x, t_1) > 0$ and $U(x, t_1) > 0$ for all $x \in [0, 1]$. Thus, one can choose $c > 0$ such that

$$(u(\cdot, t_1), U(\cdot, t_1)) \ge_D c(\phi^{\tilde{\epsilon}}(\cdot, t_1), \varphi^{\tilde{\epsilon}}(\cdot, t_1)),$$

where $(\phi^{\tilde{\epsilon}}(x, t), \varphi^{\tilde{\epsilon}}(x, t)$ is the eigenfunction of (46) associated with $\tilde{\Lambda}$. On the other hand,

$$(\tilde{u}(x, t), \tilde{U}(x, t)) := ce^{-\tilde{\Lambda}(t-t_1)}(\phi^{\tilde{\epsilon}}(x, t), \varphi^{\tilde{\epsilon}}(x, t)) \tag{48}$$

satisfies the following cooperative system:

$$
\begin{cases}
\tilde{u}_t = d\tilde{u}_{xx} + \mu\left(\frac{\tilde{U}}{\tilde{u}}\right)\tilde{u}, & x \in (0,1),\ t \geq t_1,\\
\tilde{U}_t = d\tilde{U}_{xx} + [f\left(z^*(x,t), \frac{\tilde{U}}{\tilde{u}}\right) - \tilde{\epsilon}]\tilde{u}, & x \in (0,1),\ t \geq t_1,\\
w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = \tilde{u}, \tilde{U}, t \geq t_1,
\end{cases}
\tag{49}
$$

and

$$(u(\cdot,t_1), U(\cdot,t_1)) \geq_D (\tilde{u}(\cdot,t_1), \tilde{U}(\cdot,t_1)).$$

Therefore by comparison principle, we have

$$(u(\cdot,t), U(\cdot,t)) \geq_D (\tilde{u}(\cdot,t), \tilde{U}(\cdot,t)),\ \forall t \geq t_1.$$

In view of (48) and the fact $\tilde{\Lambda} < 0$, it follows that $(u(\cdot,t), U(\cdot,t))$ is unbounded. This contradiction finishes the proof of Claim 2.5.

Thus, $\mathcal{I} = \{(\hat{u}(\cdot,0), \hat{U}(\cdot,0))\}$, and hence, $\tilde{\omega} = \{0\} \times \mathcal{I} = \{(0, \hat{u}(\cdot,0), \hat{U}(\cdot,0))\}$. This implies that $(0, \hat{u}(\cdot,0), \hat{U}(\cdot,0))$ is globally attractive for $\tilde{\mathbf{P}}$ in $\tilde{\mathbf{Y}}_0$. Corresponding to the fixed point $(\hat{u}(\cdot,0), \hat{U}(\cdot,0))$ of the period map $\tilde{\mathbf{P}}$, the system (39) has a globally attractive positive T-periodic solution $(0, \hat{u}(\cdot,t), \hat{U}(\cdot,t))$ in $\tilde{\mathbf{Y}}_0$. Let $\hat{S}(x,t) = z^*(x,t) - \hat{U}(x,t)$, it follows from (38) and (43) that Part (ii) of the theorem holds. □

2.3. **Effects of diffusion rate on single species model.** In this subsection, we study the role of diffusion rate on the extinction/persistence of system (27). Let

$$\overline{z}(t) := \max_{x\in[0,1]} z^*(x,t) \quad \text{and} \quad \underline{z}(t) := \min_{x\in[0,1]} z^*(x,t).$$

Then we consider the following two ODEs:

$$
\begin{cases}
\frac{dQ}{dt} = f(\overline{z}(t), Q) - \mu(Q)Q,\\
Q(0) \geq Q_{\min},
\end{cases}
\tag{50}
$$

and

$$
\begin{cases}
\frac{dQ}{dt} = f(\underline{z}(t), Q) - \mu(Q)Q,\\
Q(0) \geq Q_{\min}.
\end{cases}
\tag{51}
$$

From [32, Proposition 1.1], we have the following result:

Lemma 2.8. *System (50) (resp. (51)) admits a unique T-periodic solution $\overline{Q}(t)$ (resp. $\underline{Q}(t)$) to which all solutions are attracted. Moreover, $\overline{Q}(t) > \underline{Q}(t) > Q_{\min}$ for all t.*

Consider the following periodic eigenvalue problem

$$
\begin{cases}
\phi_t(x,t) = d\phi_{xx}(x,t) + h(t)\phi + \lambda\phi, & x \in (0,1), t > 0,\\
\phi_x(0,t) = 0,\ \phi_x(1,t) + \gamma\phi(1,t) = 0, & t > 0,\\
\phi(x,t) \text{ is } T\text{-periodic in } t,
\end{cases}
\tag{52}
$$

where $h(t)$ is a T-periodic continuous function in $\mathbb{R}$. By the Krein-Rutman Theorem (see [13, Chapter II.14]), it follows that (52) has a principal eigenvalue, denoted by $\lambda_1 = \lambda_1(d,h)$, with an associated T-periodic eigenfunction $\phi_1(x,t) > 0$ on $(x,t) \in [0,1] \times [0,T]$. It is easy to see that the elliptic eigenvalue problem

$$
\begin{cases}
d\psi_{xx}(x) + \eta\psi(x) = 0, & x \in (0,1),\\
\psi_x(0) = \psi_x(1) + \gamma\psi(1) = 0,
\end{cases}
$$

has a principal eigenvalue $\eta_1(d) = k_0^2 d > 0$ with the corresponding positive eigenfunction $\psi_1(x) = \cos(k_0 x)$ uniquely determined by the normalization $\max_{x\in[0,1]} \psi_1(x) = \psi_1(0) = 1$, where $k_0 \in (0, \pi/2)$ is the smallest root of the equation $\tan(k) = \gamma/k$. It follows from [13] that

$$\lambda_1(d,h) = dk_0^2 - \frac{1}{T}\int_0^T h(t)\,dt \text{ and } \phi_1(x,t) = e^{\int_0^t [h(s) - \frac{1}{T}\int_0^T h(\tau)\,d\tau]ds}\psi_1(x). \tag{53}$$

Define

$$\bar{d} := \frac{1}{Tk_0^2}\int_0^T \mu(\bar{Q}(t))\,dt \quad \text{and} \quad \underline{d} := \frac{1}{Tk_0^2}\int_0^T \mu(\underline{Q}(t))\,dt, \tag{54}$$

where $\bar{Q}(t)$ and $\underline{Q}(t)$ are given in Lemma 2.8. It is easy to see that $0 < \underline{d} < \bar{d}$. Furthermore, we have the following results:

Lemma 2.9. *Assume that $\Lambda^0(d)$ is the principal eigenvalue of (26). Then the following statements are valid:*

(i) If $d > \bar{d}$, then $\Lambda^0(d) > 0$.
(ii) If $0 < d < \underline{d}$, then $\Lambda^0(d) < 0$.

Proof. Recall that system (25) generates solution maps $\Pi(t)$ on C. Furthermore, $\Pi(t) : C \to C$ is D-strongly-order-preserving, for all $t > 0$.

We first prove Part (i) of the theorem. It follows from (53) and (54) that

$$\bar{\lambda} := \lambda_1(d, \mu(\bar{Q}(t))) > 0 \text{ if } d > \bar{d}.$$

Motivated by [20], for each $d > \bar{d}$, we define

$$(\bar{u}(x,t),\, \bar{U}(x,t)) := (\rho e^{-\bar{\lambda}t}\bar{\phi}(x,t), \rho e^{-\bar{\lambda}t}\bar{\phi}(x,t)\bar{Q}(t)),$$

where $\rho > 0$ is a positive constant and $\bar{\phi}$ is the positive eigenfunction corresponding to $\bar{\lambda}$ normalized such that $\max_{(x,t)\in[0,1]\times[0,T]} \bar{\phi}(x,t) = 1$. We claim that $(\bar{u}, \bar{U})$ is a strict upper solution of (25) in the sense that $(\bar{u}, \bar{U})$ satisfies the following relations:

$$\begin{cases} \overline{u}_t \geq d\overline{u}_{xx} + \mu\left(\frac{\overline{U}}{\overline{u}}\right)\overline{u}, & x \in (0,1),\ t > 0, \\ \overline{U}_t \geq d\overline{U}_{xx} + f\left(z^*(x,t), \frac{\overline{U}}{\overline{u}}\right)\overline{u}, & x \in (0,1),\ t > 0, \\ -w_x(0,t) \geq 0,\ w_x(1,t) + \gamma w(1,t) \geq 0, & w = \overline{u}, \overline{U}, t > 0, \\ (\bar{u}(\cdot,0),\, \bar{U}(\cdot,0)) \gg (\bar{u}(\cdot,T),\, \bar{U}(\cdot,T)). \end{cases} \tag{55}$$

Obviously, the third inequality in (55) is true. Since $\bar{\lambda} > 0$, the last inequality also holds. Thus, it suffices to show that the first two inequalities in (55) holds. For the first equality of (55),

$$\begin{aligned} \overline{u}_t &= \rho\left[-\overline{\lambda}e^{-\overline{\lambda}t}\overline{\phi}(x,t) + e^{-\overline{\lambda}t}\overline{\phi}_t(x,t)\right] \\ &= \rho e^{-\overline{\lambda}t}\left[-\overline{\lambda}\,\overline{\phi}(x,t) + \overline{\phi}_t(x,t)\right] \\ &= \rho e^{-\overline{\lambda}t}\left[d\overline{\phi}_{xx}(x,t) + \mu\left(\overline{Q}(t)\right)\overline{\phi}\right] \\ &= d\overline{u}_{xx} + \mu\left(\frac{\overline{U}}{\overline{u}}\right)\overline{u}. \end{aligned}$$

For the second inequality of (55),

$$\begin{aligned}\overline{U}_t &= \rho\left[-\overline{\lambda}e^{-\overline{\lambda}t}\overline{\phi}(x,t)+e^{-\overline{\lambda}t}\overline{\phi}_t(x,t)\right]\overline{Q}(t)+\rho e^{-\overline{\lambda}t}\overline{\phi}(x,t)\frac{d\overline{Q}(t)}{dt}\\ &= \rho e^{-\overline{\lambda}t}\left[d\overline{\phi}_{xx}(x,t)+\mu\left(\overline{Q}(t)\right)\overline{\phi}\right]\overline{Q}(t)+\rho e^{-\overline{\lambda}t}\overline{\phi}\left[f(\overline{z}(t),\overline{Q}(t))-\mu(\overline{Q}(t))\overline{Q}(t)\right]\\ &= \rho e^{-\overline{\lambda}t}d\overline{\phi}_{xx}(x,t)\overline{Q}(t)+\rho e^{-\overline{\lambda}t}\overline{\phi}f(\overline{z}(t),\overline{Q}(t))\\ &= d\overline{U}_{xx}+f\left(\overline{z}(t),\frac{\overline{U}}{\overline{u}}\right)\overline{u}\geq d\overline{U}_{xx}+f\left(z^*(x,t),\frac{\overline{U}}{\overline{u}}\right)\overline{u},\end{aligned}$$

where we have used the facts that $\overline{z}(t)\geq z^*(x,t)$ and $\frac{\overline{U}}{\overline{u}}=\overline{Q}(t)$.

By strong-order-preserving property, it follows that

$$\Pi(T)(\bar{u}(x,0),\,\bar{U}(x,0))\ll_D(\bar{u}(x,0),\,\bar{U}(x,0)).$$

We claim that the Bonsall cone spectral radius $\tilde{r}$ of $\Pi(T)$ is strictly less than 1. By the proof of Lemma 2.4, there exists $(\phi(x),\varphi(x))\in C\cap\operatorname{Int}D$ such that $\Pi(T)(\phi(x),\varphi(x))=\tilde{r}(\phi(x),\varphi(x))$, where $\tilde{r}$ is the Bonsall cone spectral radius of $\Pi(T):C\to C$. Since $(\overline{u}(x,0),\overline{U}(x,0))\in\operatorname{Int}D$, we may scale $(\phi(x),\varphi(x))$ such that $(\phi(x),\varphi(x))\leq_D(\overline{u}(x,0),\overline{U}(x,0))$, but $k(\phi(x),\varphi(x))\not\leq_D(\overline{u}(x,0),\overline{U}(x,0))$ for all $k>1$. Then

$$\tilde{r}(\phi(x),\varphi(x))=\Pi(T)(\phi(x),\varphi(x))\leq_D\Pi(T)(\overline{u}(x,0),\overline{U}(x,0))\ll_D(\overline{u}(x,0),\overline{U}(x,0)),$$

and hence, $\tilde{k}\tilde{r}(\phi(x),\varphi(x))\leq_D(\overline{u}(x,0),\overline{U}(x,0))$ for some $\tilde{k}>1$. Thus, $\tilde{k}\tilde{r}\leq 1$. Therefore $\tilde{r}\leq 1/\tilde{k}<1$, which implies that $\Lambda^0(d)=-\frac{\log\tilde{r}}{T}>0$. This finishes the proof of Part (i).

We now prove Part (ii). It follows from (53) that

$$\text{if } d<\underline{d}, \text{then } \underline{\lambda}:=\lambda_1(d,\mu(\underline{Q}(t)))<0.$$

Motivated by [20], for each $d<\underline{d}$, we define

$$(\underline{u}(x,t),\,\underline{U}(x,t)):=(\delta\underline{\phi}(x,t),\delta\underline{\phi}(x,t)\underline{Q}(t)),$$

where $\underline{\phi}(x,t)$ is the positive eigenfunction corresponding to $\underline{\lambda}$ normalized such that

$$\max_{(x,t)\in[0,1]\times[0,T]}\underline{\phi}(x,t)=1.$$

We claim that $(\underline{u},\,\underline{U})$ is a strict lower solution of (25) in the sense that $(\underline{u},\,\underline{U})$ satisfies the following relations:

$$\begin{cases}\underline{u}_t<\underline{u}_{xx}+\mu\left(\frac{\underline{U}}{\underline{u}}\right)\underline{u}, & x\in(0,1),\ t>0,\\ \underline{U}_t<d\underline{U}_{xx}+f\left(z^*(x,t),\frac{\underline{U}}{\underline{u}}\right)\underline{u}, & x\in(0,1),\ t>0,\\ -w_x(0,t)=0,\ w_x(1,t)+\gamma w(1,t)=0, & w=\underline{u},\underline{U},t>0,\\ (\underline{u}(\cdot,0),\,\underline{U}(\cdot,0))=(\underline{u}(\cdot,T),\,\underline{U}(\cdot,T)).\end{cases}\tag{56}$$

Obviously, the boundary conditions for $\underline{u}$ and $\underline{U}$ hold. The last equality also holds due the periodicity of $\underline{\phi}(x,t)$ and $\underline{Q}(t)$ in t. Thus, it suffices to show that the first two inequalities in (56) holds.

For the first inequality of (56),

$$\begin{aligned}\underline{u}_t &= \delta\left[d\underline{\phi}_{xx}(x,t)+\mu\left(\underline{Q}(t)\right)\underline{\phi}+\underline{\lambda}\underline{\phi}\right]\\ &= d\underline{u}_{xx}+\mu\left(\frac{\underline{U}}{\underline{u}}\right)\underline{u}+\underline{\lambda}\delta\underline{\phi}\\ &< d\underline{u}_{xx}+\mu\left(\frac{\underline{U}}{\underline{u}}\right)\underline{u},\end{aligned}$$

where we have used the fact $\underline{\lambda}<0$.

For the second inequality of (56),

$$\begin{aligned}\underline{U}_t &= \delta\underline{\phi}_t(x,t)\underline{Q}(t)+\delta\underline{\phi}(x,t)\frac{d\underline{Q}(t)}{dt}\\ &= \delta\left[d\underline{\phi}_{xx}(x,t)+\mu\left(\underline{Q}(t)\right)\underline{\phi}+\underline{\lambda}\underline{\phi}\right]\underline{Q}(t)+\delta\underline{\phi}(x,t)\left[f(\underline{z}(t),\underline{Q}(t))-\mu(\underline{Q}(t))\underline{Q}(t)\right]\\ &= \delta d\underline{\phi}_{xx}(x,t)\underline{Q}(t)+\delta\underline{\phi}(x,t)f(\underline{z}(t),\underline{Q}(t))+\delta\underline{\lambda}\ \underline{\phi}\ \underline{Q}(t)\\ &= d\underline{U}_{xx}+\delta\underline{\phi}(x,t)\left[f\left(\underline{z}(t),\underline{Q}(t)\right)+\underline{\lambda}\ \underline{Q}(t)\right]\\ &< d\underline{U}_{xx}+f\left(z^*(x,t),\frac{\underline{U}}{\underline{u}}\right)\underline{u}.\end{aligned}$$

Thus the strongly order preserving property of $\Pi(t)$ implies that

$$\Pi(T)(\underline{u}(x,0),\,\underline{U}(x,0))\gg_D(\underline{u}(x,0),\,\underline{U}(x,0)).$$

This means $\Pi(T)(\underline{u}(x,0),\,\underline{U}(x,0))\geq_D k(\underline{u}(x,0),\,\underline{U}(x,0))$ for some $k>1$, whence the Bonsall cone spectral radius $\tilde{r}$ must be strictly greater than 1, and by definition, $\Lambda^0=-\frac{\log\tilde{r}}{T}<0$. □

From a biological point of view, roughly speaking, a smaller diffusion rate d and a smaller washout constant γ would be more advantageous for the survival of the species. Moreover, as pointed out in [18] that for a system defined on interval $[0,L]$, the parameter d is equivalent to L^{-2} and γ is equivalent to L^{-1}. Hence, for a fixed diffusion rate and washout constant, a larger patch size of the domain would be more beneficial for the survival of the species. These are consistent with the results obtained for the constant input of nutrient rate considered in [16, 18].

3. **The two-species competition model.**

Now we consider the two-species model (6)-(8). Introduce the new variable $\Gamma=S+U_1+U_2$. By similar arguments as in Lemma 2.1, we can show that

$$\lim_{t\to\infty}(\Gamma(x,t)-z^*(x,t))=0 \text{ uniformly on } [0,1],$$

where $z^*(x,t)$ is defined as in Lemma 2.1.

Let

$$\begin{aligned}\mathbf{X}=\{(S^0,u_1^0,U_1^0,u_2^0,U_2^0)\in C([0,1];\mathbb{R}_+^5):\exists\tilde{Q}>0 \text{ s.t.}\\ Q_{\min,i}u_i^0(x)\leq U_i^0(x)\leq\tilde{Q}u_i^0(x)\text{for all } x\in[0,1] \text{ and } i=1,2\}.\end{aligned}\tag{57}$$

By similar arguments as in the proof of Proposition 1, we can show the following result:

Proposition 3. *Suppose* (H1) *and* (H2) *hold. Then for each initial condition in* $\mathbf{X}$, *system* (6)-(8) *has a unique classical solution* (S,u_1,U_1,u_2,U_2) *that exists for all* $t>0$. *Moreover, the solution satisfies* $(S(\cdot,t),u_1(\cdot,t),U_1(\cdot,t),u_2(\cdot,t),U_2(\cdot,t))\in\mathbf{X}$

for all $t > 0$. There exists a constant $C > 0$ independent of initial conditions in $\mathbf{X}$ *such that for any solution (S, u_1, U_1, u_2, U_2) of system (6)-(8), we have*

$$\limsup_{t\to\infty} \|(S(\cdot,t), u_1(\cdot,t), U_1(\cdot,t), u_2(\cdot,t), U_2(\cdot,t))\| \le C. \tag{58}$$

3.1. **Coexistence for the full system.** Since Theorem 2.7 can be applied to either of the two systems obtained from (6)-(8) by setting $(u_1, U_1) = (0, 0)$ or $(u_2, U_2) = (0, 0)$, we see that T-periodic solutions of the system (6)-(8) take the following forms:

(i) Trivial solution $E_0(x,t) := (z^*(x,t), 0, 0, 0, 0)$ always exists;
(ii) Semi-trivial solution $E_1(x,t) := (\hat{S}_1(x,t), \hat{u}_1(x,t), \hat{U}_1(x,t), 0, 0)$ exists provided that $\Lambda_1^0 < 0$;
(iii) Semi-trivial solution $E_2(x,t) := (\hat{S}_2(x,t), 0, 0, \hat{u}_2(x,t), \hat{U}_2(x,t))$ exists provided that $\Lambda_2^0 < 0$;
(iv) There may be additional T-periodic solutions as well and these must be positive.

Here, Λ_i^0, $i = 1, 2$, is the principal eigenvalue of the periodic-parabolic eigenvalue problem (26) with $\mu \equiv \mu_i$ and $f \equiv f_i$; $(\hat{S}_i(x,t), \hat{u}_i(x,t), \hat{U}_i(x,t))$, $i = 1, 2$, denotes the unique positive T-periodic solution of (11) resulting from putting $\mu \equiv \mu_i$ and $f \equiv f_i$. The two species can coexist if a positive T-periodic solution exists. Furthermore, it is not hard to see that

$$\hat{S}_i(x,t) = z^*(x,t) - \hat{U}_i(x,t),\ \forall\, x \in [0,1],\ t \in [0,T],\ i = 1, 2. \tag{59}$$

In order to discuss the instability of $E_1(x,t)$, we consider the following system:

$$\begin{cases} (u_2)_t = d(u_2)_{xx} + \mu_2\left(\frac{U_2}{u_2}\right)u_2, & x \in (0,1),\ t > 0,\\ (U_2)_t = d(U_2)_{xx} + f_2\left(\hat{S}_1(x,t), \frac{U_2}{u_2}\right)u_2, & x \in (0,1),\ t > 0,\\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u_2, U_2, t > 0,\\ w(x,0) = w^0(x) \ge (\not\equiv) 0, & w = u_2, U_2, x \in (0,1). \end{cases} \tag{60}$$

The following periodic parabolic nonlinear eigenvalue problem is associated with (60) ([17]):

$$\begin{cases} \phi_t = d\phi_{xx} + \mu_2\left(\frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x,t) + \Lambda\phi(x,t), & x \in (0,1),\ t > 0,\\ \varphi_t = d\varphi_{xx} + f_2\left(\hat{S}_1(x,t), \frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x,t) + \Lambda\varphi(x,t), & x \in (0,1),\ t > 0,\\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = \phi, \varphi, t > 0,\\ \phi, \varphi \text{ are } T\text{-periodic in } t. \end{cases} \tag{61}$$

By the same arguments in Lemma 2.4 (see also [17]), the eigenvalue problem (61) admits a unique principal eigenvalue $\hat{\Lambda}_1$ corresponding to which there is a strongly positive eigenfunction $(\hat{\phi}_1(x,t), \hat{\varphi}_1(x,t))$.

Similarly, the following system is related to the instability of $E_2(x,t)$:

$$\begin{cases} (u_1)_t = d(u_1)_{xx} + \mu_1\left(\frac{U_1}{u_1}\right)u_1, & x \in (0,1),\ t > 0,\\ (U_1)_t = d(U_1)_{xx} + f_1\left(\hat{S}_2(x,t), \frac{U_1}{u_1}\right)u_1, & x \in (0,1),\ t > 0,\\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u_1, U_1, t > 0,\\ w(x,0) = w^0(x) \ge (\not\equiv) 0, & w = u_1, U_1, x \in (0,1). \end{cases} \tag{62}$$

We also have the following periodic parabolic nonlinear eigenvalue problem associated with (62) ([17]):

$$
\begin{cases}
\phi_t = d\phi_{xx} + \mu_1 \left(\frac{\varphi(x,t)}{\phi(x,t)}\right) \phi(x,t) + \Lambda \phi(x,t), & x \in (0,1),\ t > 0, \\
\varphi_t = d\varphi_{xx} + f_1 \left(\hat{S}_2(x,t), \frac{\varphi(x,t)}{\phi(x,t)}\right) \phi(x,t) + \Lambda \varphi(x,t), & x \in (0,1),\ t > 0, \\
w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = \phi, \varphi, t > 0, \\
\phi, \varphi \text{ are } T\text{-periodic in } t.
\end{cases}
\tag{63}
$$

The eigenvalue problem (63) admits a unique principal eigenvalue $\hat{\Lambda}_2$ corresponding to which there is a strongly positive eigenfunction $(\hat{\phi}_2(x,t), \hat{\varphi}_2(x,t))$.

Let $\Psi_t : \mathbf{X} \to \mathbf{X}$ be the solution map associated with (6)-(8). We denote the Poincaré map

$$
\mathbb{P} : \mathbf{X} \ \to \ \mathbf{X} \text{ by } \mathbb{P} = \Psi_T. \tag{64}
$$

Then

$$
\mathbb{P}^n(S^0(\cdot), u_1^0(\cdot), U_1^0(\cdot), u_2^0(\cdot), U_2^0(\cdot)) = \Psi_{nT}(S^0(\cdot), u_1^0(\cdot), U_1^0(\cdot), u_2^0(\cdot), U_2^0(\cdot)),
$$

for all $(S^0(\cdot), u_1^0(\cdot), U_1^0(\cdot), u_2^0(\cdot), U_2^0(\cdot)) \in \mathbf{X},\ n \in \mathbb{Z}_+$. Set

$$
\begin{aligned}
&\mathbf{X}_0 := \{(S^0(\cdot), u_1^0(\cdot), U_1^0(\cdot), u_2^0(\cdot), U_2^0(\cdot)) \in \mathbf{X} : u_1^0(\cdot) \not\equiv 0 \text{ and } u_2^0(\cdot) \not\equiv 0\} \text{ and} \\
&\partial \mathbf{X}_0 := \mathbf{X} \backslash \mathbf{X}_0.
\end{aligned}
$$

Theorem 3.1. *Assume that $\Lambda_i^0 < 0$ and $\hat{\Lambda}_i < 0$, for all $i = 1, 2$. Then system (6)-(8) admits at least one positive T-periodic solution and there exists a positive constant $\zeta > 0$ such that any solution $(S(\cdot,t), u_1(\cdot,t), U_1(\cdot,t), u_2(\cdot,t), U_2(\cdot,t))$ of (6)-(8) with the initial data in $\mathbf{X}_0$ satisfies that*

$$
\liminf_{t \to \infty} u_i(\cdot, t) \geq \zeta,\ \ i = 1, 2. \tag{65}
$$

Proof. By Proposition 3 and the maximum principle, it follows that $\mathbf{X}$ and $\mathbf{X}_0$ are positively invariant for the solution maps Ψ_t. Moreover, $\mathbb{P} : \mathbf{X} \ \to \ \mathbf{X}$ is point dissipative. Obviously, $\mathbb{P}^n : \mathbf{X} \ \to \ \mathbf{X}$ is compact, $\forall\ n \in \mathbb{Z}_+$. By [12, Theorem 2.4.7], it follows that $\mathbb{P}$ admits a connected global attractor in $\mathbf{X}$, i.e., a compact, invariant set which attracts every bounded set in $\mathbf{X}$.

We are ready to show that $\mathbb{P} : \mathbf{X} \ \to \ \mathbf{X}$ is uniformly persistent with respect to $(\mathbf{X}_0, \partial \mathbf{X}_0)$. Let

$$
M_\partial := \{\mathbf{u}^0 \in \partial \mathbf{X}_0 : \mathbb{P}^n \mathbf{u}^0 \in \partial \mathbf{X}_0, \forall\ n \geq 0\},
$$

and $\omega(\mathbf{u}^0)$ be the omega limit set of the orbit $O^+(\mathbf{u}^0) := \{\mathbb{P}^n \mathbf{u}^0 : n \geq 0\}$. Then we have the following result.

Claim 3.1. $\omega(\mathbf{u}^0) = \{E_0(\cdot, 0)\} \cup \{E_1(\cdot, 0)\} \cup \{E_2(\cdot, 0)\},\ \forall\ \mathbf{u}^0 \in M_\partial$.

To see this, for any $\mathbf{u}^0 \in M_\partial$, it follows that

$$
u_1(\cdot, t, \mathbf{u}^0) \equiv 0 \text{ or } u_2(\cdot, t, \mathbf{u}^0) \equiv 0,\ \forall\ t \geq 0. \tag{66}
$$

In case where $u_1(\cdot, t, \mathbf{u}^0) \equiv 0,\ \forall\ t \geq 0$, we must have $U_1(\cdot, t, \mathbf{u}^0) \equiv 0,\ \forall\ t \geq 0$. Then it follows that $(S(x,t), u_2(x,t), U_2(x,t))$ satisfies system (11) with the substitutions $\mu \equiv \mu_2$ and $f \equiv f_2$. By Theorem 2.7, it follows that either

$$
\lim_{t \to \infty} [(S(\cdot,t), u_2(\cdot,t), U_2(\cdot,t)) - (z^*(\cdot,t), 0, 0)] = (0, 0, 0)
$$

or

$$
\lim_{t \to \infty} [(S(\cdot,t), u_2(\cdot,t), U_2(\cdot,t)) - (\hat{S}_2(\cdot,t), \hat{u}_2(\cdot,t), \hat{U}_2(\cdot,t))] = (0, 0, 0).
$$

In case where $u_1(\cdot, t_0, \mathbf{u}^0) \not\equiv 0$, for some $t_0 \geq 0$. Then one can further show that $u_1(\cdot, t, \mathbf{u}^0) > 0,\ \forall\ t \geq t_0$. This implies that $u_2(\cdot, t, \mathbf{u}^0) \equiv 0,\ \forall\ t \geq t_0$. The proof for this case is similar to previous discussions. Thus, the proof of Claim 3.1 can be finished.

Recall that $\hat{\Lambda}_1$ is the principal eigenvalue of system (61). Since $\hat{\Lambda}_1 < 0$, it follows that there exists $\epsilon_1 > 0$ such that $\hat{\Lambda}_1^{\epsilon_1} < 0$, where $\hat{\Lambda}_1^{\epsilon_1}$ is the principal eigenvalue of the periodic-parabolic eigenvalue problem

$$\begin{cases} \phi_t = d\phi_{xx} + \mu_2\left(\frac{\varphi(x,t)}{\phi(x,t)}\right)\phi(x,t) + \Lambda\phi(x,t), & x \in (0,1),\ t > 0, \\ \varphi_t = d\varphi_{xx} + [f_2\left(\hat{S}_1(x,t), \frac{\varphi(x,t)}{\phi(x,t)}\right) - \epsilon_1]\phi(x,t) + \Lambda\varphi(x,t), & x \in (0,1),\ t > 0, \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = \phi, \varphi,\ t > 0, \\ \phi, \varphi \text{ are } T\text{-periodic in } t. \end{cases} \tag{67}$$

By the continuity of $f_2\left(S, \frac{U_2}{u_2}\right)$, it is easy to see that there exists some $\sigma_1 > 0$ such that $f_2\left(S, \frac{U_2}{u_2}\right) > f_2\left(\hat{S}_1(x,t), \frac{U_2}{u_2}\right) - \epsilon_1$ whenever $|S - \hat{S}_1(x,t)| < \sigma_1$. Note that $\Psi_t : \mathbf{X} \to \mathbf{X}$ is a continuous map and $\Psi_t(E_1(\cdot,0)) = E_1(\cdot,t)$, for all $t \geq 0$. It then follows that there exists some $\varrho_1 > 0$ such that

$$\parallel \Psi_t(S^0(\cdot), u_1^0(\cdot), U_1^0(\cdot), u_2^0(\cdot), U_2^0(\cdot)) - E_1(\cdot,t) \parallel < \frac{\sigma_1}{2},\ \forall\ t \in [0,T]$$

whenever

$$\parallel (S^0(\cdot), u_1^0(\cdot), U_1^0(\cdot), u_2^0(\cdot), U_2^0(\cdot)) - E_1(\cdot,0) \parallel < \varrho_1.$$

Claim 3.2. $\limsup_{k\to\infty} \|\Psi_{kT}(\Theta) - E_1(\cdot,0)\| \geq \varrho_1,\ \forall\ \Theta := (S^0(\cdot), u_1^0(\cdot), U_1^0(\cdot), u_2^0(\cdot), U_2^0(\cdot)) \in \mathbf{X}_0$.

We now prove Claim 3.2. Suppose that Claim 3.2 is not true for contradiction. Then there exists some $\Theta_0 \in \mathbf{X}_0$ such that

$$\limsup_{k\to\infty} \|\Psi_{kT}(\Theta_0) - E_1(\cdot,0)\| < \varrho_1.$$

Thus, there exists an integer $k_1 \geq 1$ such that $\|\Psi_{kT}(\Theta_0) - E_1(\cdot,0)\| < \varrho_1,\ \forall\ k \geq k_1$. For each $t \geq k_1 T$, we can choose $t_1' \in [0,T)$ such that $t = kT + t_1'$ with $k \geq k_1$. It follows from the continuity of Ψ_t that

$$\|\Psi_t(\Theta_0) - E_1(\cdot,t)\| = \|\Psi_{t_1'}\Psi_{kT}(\Theta_0) - E_1(\cdot,t_1')\| < \frac{\sigma_1}{2},\ \forall\ t \geq k_1 T.$$

This implies that $S(\cdot,t,\Theta_0) > \hat{S}_1(\cdot,t) - \sigma_1/2$, $\forall\ t \geq k_1 T$. It then follows that

$$f_2\left(S, \frac{U_2}{u_2}\right) > f_2\left(\hat{S}_1(\cdot,t) - \frac{\sigma_1}{2}, \frac{U_2}{u_2}\right) > f_2\left(\hat{S}_1(x,t), \frac{U_2}{u_2}\right) - \epsilon_1,\ \forall\ t \geq k_1 T.$$

Consequently, it follows from the fourth and fifth equations in (6) that

$$\begin{cases} (u_2)_t = d(u_2)_{xx} + \mu_2\left(\frac{U_2}{u_2}\right)u_2, & x \in (0,1),\ t \geq k_1 T, \\ (U_2)_t > d(U_2)_{xx} + [f_2\left(\hat{S}_1(x,t), \frac{U_2}{u_2}\right) - \epsilon_1]u_2, & x \in (0,1),\ t \geq k_1 T, \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u_2, U_2,\ t \geq k_1 T. \end{cases} \tag{68}$$

Since $\Psi_t(\Theta_0) \in \mathbf{X}_0$ for all $t > 0$, there exists a real number $\hat{a} > 0$ such that

$$(u_2(\cdot, k_1 T, \Theta_0), U_2(\cdot, k_1 T, \Theta_0)) > \hat{a}(\hat{\phi}_1^{\epsilon_1}(x, k_1 T), \hat{\varphi}_1^{\epsilon_1}(x, k_1 T)),$$

where $(\hat{\phi}_1^{\epsilon_1}(x,t), \hat{\varphi}_1^{\epsilon_1}(x,t))$ is the strongly positive eigenfunction of (67) associated with $\hat{\Lambda}_1^{\epsilon_1}$. On the other hand,

$$(\hat{u}_2(x,t), \hat{U}_2(x,t)) := \hat{a}e^{-\hat{\Lambda}_1^{\epsilon_1}(t-k_1T)}(\hat{\phi}_1^{\epsilon_1}(x,t), \hat{\varphi}_1^{\epsilon_1}(x,t)) \tag{69}$$

satisfies the following cooperative system:

$$\begin{cases} (u_2)_t = d(u_2)_{xx} + \mu_2\left(\frac{U_2}{u_2}\right)u_2, & x \in (0,1), t \geq k_1T, \\ (U_2)_t = d(U_2)_{xx} + [f_2\left(\hat{S}_1(x,t), \frac{U_2}{u_2}\right) - \epsilon_1]u_2, & x \in (0,1), t \geq k_1T, \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u_2, U_2, t \geq k_1T. \end{cases} \tag{70}$$

By the standard comparison theorem, it follows that

$$(u_2(\cdot,t,\Theta_0), U_2(\cdot,t,\Theta_0)) > \hat{a}e^{-\hat{\Lambda}_1^{\epsilon_1}(t-k_1T)}(\hat{\phi}_1^{\epsilon_1}(\cdot,t), \hat{\varphi}_1^{\epsilon_1}(\cdot,t)), \forall\ t \geq k_1T.$$

Then we see that $\lim_{t\to\infty}(u_2(x,t,\Theta_0), U_2(x,t,\Theta_0))$ is unbounded, due to the fact $\hat{\Lambda}_1^{\epsilon_1} < 0$. This is a contradiction and hence Claim 3.2 is proved.

By similar arguments as above, we can also show that there exist $\varrho_0 > 0$ and $\varrho_2 > 0$ such that

$$\limsup_{k\to\infty} \|\Psi_{kT}(\Theta) - E_0(\cdot,0)\| \geq \varrho_0 \text{ and } \limsup_{k\to\infty} \|\Psi_{kT}(\Theta) - E_2(\cdot,0)\| \geq \varrho_2,\ \forall\ \Theta \in \mathbf{X}_0.$$

It follows from the above discussions that any forward orbit of $\mathbb{P} = \Psi_T : \mathbf{X} \to \mathbf{X}$ in M_∂ converges to either $\{E_0(\cdot,0)\}$ or $\{E_1(\cdot,0)\}$ or $\{E_2(\cdot,0)\}$. It is easy to see that $\{E_0(\cdot,0)\}$, $\{E_1(\cdot,0)\}$ and $\{E_2(\cdot,0)\}$ are isolated in $\partial\mathbf{X}_0$ and $W^s(\{E_i(\cdot,0)\}) \cap \mathbf{X}_0 = \emptyset$, $\forall\ i = 0,1,2$, where $W^s(\{E_i(\cdot,0)\})$ is the stable set of $\{E_i(\cdot,0)\}$ (see [38]). Further, no subsets of $\{\{E_0(\cdot,0)\}, \{E_1(\cdot,0)\}, \{E_2(\cdot,0)\}\}$ forms a cycle in $\partial\mathbf{X}_0$. By [38, Theorem 1.3.1 and Remark 1.3.1], we see that $\mathbb{P}$ is uniformly persistent with respect to $(\mathbf{X}_0, \partial\mathbf{X}_0)$.

Furthermore, [38, Theorem 1.3.6] implies that $\mathbb{P}$ has a fixed point $\bar{\Theta} \in \mathbf{X}_0$, and hence, system (6)-(8) admits a T-periodic solution $\Psi_t(\bar{\Theta}) \in \mathbf{X}_0$. Since $\mathbb{P}$ is compact, point dissipative and uniformly persistent with respect to $(\mathbf{X}_0, \partial\mathbf{X}_0)$, it follows from [25, Theorem 3.8] that $\mathbb{P} = \Psi_T : \mathbf{X}_0 \to \mathbf{X}_0$ admits a global attractor A_0. Obviously, $\bar{\Theta} \in A_0$. Let $B_0 = \cup_{t\in[0,T]}\Psi_t A_0$. Then it follows from [38, Theorem 3.1.1] that $B_0 \subset \mathbf{X}_0$ is a compact set, and B_0 attracts every point in $\mathbf{X}_0$ for Ψ_t in the sense that

$$\lim_{t\to\infty} dist(\Psi_t\Theta, B_0) = 0,\ \forall\ \Theta \in \mathbf{X}_0. \tag{71}$$

Since $A_0 \subset \mathbf{X}_0$ and $A_0 = \Psi_T(A_0)$, we further have $A_0 \subset \mathrm{Int}(C([0,1], \mathbb{R}_+^5))$, and hence $B_0 \subset \mathrm{Int}(C([0,1], \mathbb{R}_+^5))$. Since $\Psi_t\bar{\Theta}$ is a T-periodic solution of (6)-(8), it is easy to see that $\Psi_t\bar{\Theta} \in B_0$. By virtue of the property in (71), the proof of this theorem is complete.

□

3.2. **Effects of diffusion rates on coexistence.** For $i = 1,2$, we consider

$$\begin{cases} \frac{dQ_i}{dt} = f_i(\underline{z}(t), Q_i) - \mu_i(Q_i)Q_i, \\ Q_i(0) \geq Q_{\mathrm{min,i}}, \end{cases} \tag{72}$$

and

$$\begin{cases} \frac{dQ_i}{dt} = f_i(\overline{z}(t), Q_i) - \mu_i(Q_i)Q_i, \\ Q_i(0) \geq Q_{\mathrm{min,i}}. \end{cases} \tag{73}$$

As shown in Lemma 2.8, system (72) (resp. (73)) has a unique T-periodic solution $\underline{Q}_i(t)$ (resp. $\overline{Q}_i(t)$) to which all solutions are attracted. Define

$$\bar{d}_i := \frac{1}{Tk_0^2}\int_0^T \mu_i(\overline{Q}_i(t))\,dt \quad \text{and} \quad \underline{d}_i := \frac{1}{Tk_0^2}\int_0^T \mu_i(\underline{Q}_i(t))\,dt, \quad i=1,2. \tag{74}$$

Next, we set

$$S_2^{\min}(t) = \min_{x\in[0,1]} \hat{S}_2(x,t) = \min_{x\in[0,1]}[z^*(x,t) - U_2^*(x,t)],$$

and

$$S_1^{\min}(t) = \min_{x\in[0,1]} \hat{S}_1(x,t) = \min_{x\in[0,1]}[z^*(x,t) - U_1^*(x,t)].$$

Then we consider

$$\begin{cases} \frac{dQ_1}{dt} = f_1(S_2^{\min}(t), Q_1) - \mu_1(Q_1)Q_1, \\ Q_1(0) \geq Q_{\min,1}, \end{cases} \tag{75}$$

and

$$\begin{cases} \frac{dQ_2}{dt} = f_2(S_1^{\min}(t), Q_2) - \mu_2(Q_2)Q_2, \\ Q_2(0) \geq Q_{\min,2}. \end{cases} \tag{76}$$

It follows form [32, Proposition 1.1] that system (75) (resp. (76)) has a unique T-periodic solution $Q_1^{\min}(t)$ (resp. $Q_2^{\min}(t)$) to which all solutions are attracted. Define

$$d_1^{\min} := \frac{1}{Tk_0^2}\int_0^T \mu_1(Q_1^{\min}(t))\,dt \quad \text{and} \quad d_2^{\min} := \frac{1}{Tk_0^2}\int_0^T \mu_2(Q_2^{\min}(t))\,dt. \tag{77}$$

It is obvious that $d_i^{\min} < \underline{d}_i$, for $i = 1,2$. Hence, $\min\{d_1^{\min}, d_2^{\min}\} < \min\{\underline{d}_1, \underline{d}_2\}$.

Using the same arguments in Lemma 2.9, we can show that:

Corollary 1. *If $d < \min\{d_1^{\min}, d_2^{\min}\}$, then $\Lambda_i^0 < 0$ and $\hat{\Lambda}_i < 0$ for all $i = 1,2$. Thus, there is a coexistence periodic solution for system (6)-(8) for $d < \min\{d_1^{\min}, d_2^{\min}\}$.*

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