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DYNAMICS OF HARMFUL ALGAE WITH SEASONAL TEMPERATURE VARIATIONS IN THE COVE-MAIN LAKE

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Abstract. In this paper, we investigate two-vessel gradostat models describing the dynamics of harmful algae with seasonal temperature variations, in which one vessel represents a small cove connected to a larger lake. We first define the basic reproduction number for the model system, and then show that the trivial periodic state is globally asymptotically stable, and algae is washed out eventually if the basic reproduction number is less than unity, while there exists at least one positive periodic state and algal blooms occur when it is greater than unity. There are several types of productions for dissolved toxins, related to the algal growth rate, and nutrient limitation, respectively. For the system with a specific toxin production, the global attractivity of positive periodic steady-state solution can be established. Numerical simulations from the basic reproduction number show that the factor of seasonality plays an important role in the persistence of harmful algae.

1. **Introduction.** Harmful algal blooms emerged as an important water quality issue in recent decades, and have apparently increased in frequency and intensity worldwide, in both coastal and inland waters. For example, blooms of the haptophyte algae *Prymnesium parvum* have become common in western Texas and other parts of the American Southwest, where it is referred to as golden algae [21, 24]. Blooms of this species were documented to cause large fish mortalities. However, it has been known that water flow in reservoirs can wash out the populations of planktonic algae, and their toxins [9]. This raises many ecological paradoxes [19]. Indeed, the shorelines and the bed can retard flow, producing slow-flowing regions

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which provide a hydraulic storage zone, so that the persistence of algae is enhanced (e.g., [7, Section 3.3]).

A recent study suggests a potential technique that is possible for managing and mitigating harmful algal blooms through flow manipulations in some river systems [17, 18, 20]. This fact motivates the theoretical exploration of harmful algal dynamics in riverine reservoirs considered in [9]. To understand longitudinal patterns arising along the axis of flow, advection-dispersion-reaction systems were proposed to incorporate the effects of spatial variations of harmful algae and its toxin production and decay, in riverine reservoirs [9]. The models are one-dimensional systems with simple habitat geometry and transport processes [9], and they were analyzed in [13].

In order to study differences between a single fringing cove and a main lake, the authors in [9] also proposed two-vessel gradostat models with constant volumes to represent the dynamics of harmful algae that can excrete a dissolved toxin. Indeed, fringing coves along the shoreline of riverine reservoirs also provide a storage zone that promotes the persistence of both algae and their toxins. In this paper, we shall give rigorous proofs in the two compartment gradostat models with the influences of seasonal temperature variations, that is, we incorporate the periodic time dependence in the parameters of the model system.

Following [9], we first describe model settings and assumptions. The limiting nutrient for algal growth enters the main lake and the single cove at a constant concentration $R_1^{\text{in}}(t)$ and $R_2^{\text{in}}(t)$, respectively. To simplify the model, constant volume is assumed and the system dilution rate is denoted by $D(t)$ and the system exchange rate between the main lake and the cove is denoted by $E(t)$. We assume that ψ represents the fraction of total volume in cove and ϕ represents the fraction of total inflow entering cove. In the following, we set

$$\begin{cases} R_1^{(0)}(t) = \frac{(1-\phi)D(t)}{1-\psi} R_1^{\text{in}}(t),\ R_2^{(0)}(t) = \frac{\phi D(t)}{\psi} R_2^{\text{in}}(t),\ \alpha_1(t) = \frac{D(t)+E(t)}{1-\psi}, \\ \alpha_2(t) = \frac{\phi D(t)+E(t)}{1-\psi},\ \beta_1(t) = \frac{E(t)}{\psi},\ \beta_2(t) = \frac{\phi D(t)+E(t)}{\psi}. \end{cases} \tag{1.1}$$

Note that the main purpose of the definitions of $R_i^{(0)}(t)$, $\alpha_i(t)$, and $\beta_i(t)$, $i = 1, 2$, is to save notations when we describe our governing systems (1.3) and (1.5) later.

The nutrient uptake function is assumed to be a Monod function of the limiting nutrient concentration (R) at a given location:

$$f(t, R) = \frac{\mu_{\max}(t)R}{K + R}. \tag{1.2}$$

Here, $\mu_{\max}(t)$ represents the maximal growth rate; K represents the half saturation constant; the mortality of algal is assumed to be a constant rate m. To simplify our model, we suppose that the nutrient content of algae that die is instantaneously and locally recycled [9]. Further, q_N represents nutrient quota of algae. To reflect temporal variations, we assume that there exists a $\tau > 0$ such that $R_1^{(0)}(t)$, $R_2^{(0)}(t)$, $\alpha_i(t)$, $\beta_i(t)$ and $\mu_{\max}(t)$ satisfy

$$\begin{cases} R_1^{(0)}(t) > 0,\ R_2^{(0)}(t) > 0,\ \alpha_i(t) > 0,\ \beta_i(t) > 0,\ \mu_{\max}(t) > 0, \\ R_1^{(0)}(t+\tau) = R_1^{(0)}(t),\ R_2^{(0)}(t+\tau) = R_2^{(0)}(t),\ \alpha_i(t+\tau) = \alpha_i(t), \\ \beta_i(t+\tau) = \beta_i(t),\ \mu_{\max}(t+\tau) = \mu_{\max}(t),\ i = 1, 2. \end{cases}$$

The following governing system represents the general form of two models, which is true for many flagellate toxins [9]:

$$\begin{cases} \frac{dR_1}{dt} = R_1^{(0)}(t) - \alpha_1(t)R_1 + \alpha_2(t)R_2 - q_N[f(t,R_1) - m]N_1, \\ \frac{dR_2}{dt} = R_2^{(0)}(t) + \beta_1(t)R_1 - \beta_2(t)R_2 - q_N[f(t,R_2) - m]N_2, \\ \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [f(t,R_1) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [f(t,R_2) - m]N_2, \\ \frac{dC_1}{dt} = -\alpha_1(t)C_1 + \alpha_2(t)C_2 + \epsilon p(t,R_1,N_1) - kC_1, \\ \frac{dC_2}{dt} = \beta_1(t)C_1 - \beta_2(t)C_2 + \epsilon p(t,R_2,N_2) - kC_2, \\ R_i(0) \geq 0,\ N_i(0) \geq 0,\ C_i(0) \geq 0,\ i = 1,2, \end{cases} \tag{1.3}$$

where $R_1(t)$, $N_1(t)$ and $C_1(t)$ denote dissolved nutrient concentration, algal abundance and dissolved toxin concentration at time t in the main lake, respectively; $R_2(t)$, $N_2(t)$ and $C_2(t)$ denote dissolved nutrient concentration, algal abundance and dissolved toxin concentration at time t in the cove, respectively. The terms kC_1 and kC_2 stand for toxin degradation. There are two types of productions for dissolved toxins. The first assumes that the algae produce toxin more rapidly when there is little nutrient in the system [9],

$$\epsilon p(t,R,N) = \epsilon[\mu_{\max}(t) - f(t,R)]N = \epsilon\frac{\mu_{\max}(t)K}{K+R}N, \tag{1.4}$$

where ϵ is a constant coefficient. It has been observed that toxins produced by *Prymnesium parvum* (toxic flagellates) are proportional to the degree of algal nutrient limitation ([3, 8, 15, 16]). The second type of toxin production assumes that the toxin is produced proportional to the algal productivity,

$$\epsilon p(t,R,N) = \epsilon f(t,R)N = \epsilon\frac{\mu_{\max}(t)R}{K+R}N.$$

This case assumes that toxin is produced in proportion to other cellular products and released into the water at a constant rate [9]. We refer to this as the case of cylindrospermopsin [6, 12], which is a cyanotoxin produced by a variety of freshwater cyanobacteria.

It was also known that cyanobacteria excrete some toxins that contain nitrogen, a potential limiting nutrient for algae. Hence, chemical decomposition of the toxin results in nutrient recycling [9]. We assume that ϵ represents a dimensionless coefficient that specifies the allocation to toxin production [9]. The nutrient content of the toxin is denoted by q_C and then the governing equations take the form [9]:

$$\begin{cases} \frac{dR_1}{dt} = R_1^{(0)}(t) - \alpha_1(t)R_1 + \alpha_2(t)R_2 - q_N[f(t,R_1) - m]N_1 + kq_CC_1, \\ \frac{dR_2}{dt} = R_2^{(0)}(t) + \beta_1(t)R_1 - \beta_2(t)R_2 - q_N[f(t,R_2) - m]N_2 + kq_CC_2, \\ \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [(1-\epsilon)f(t,R_1) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [(1-\epsilon)f(t,R_2) - m]N_2, \\ \frac{dC_1}{dt} = -\alpha_1(t)C_1 + \alpha_2(t)C_2 + \epsilon\frac{q_N}{q_C}f(t,R_1)N_1 - kC_1, \\ \frac{dC_2}{dt} = \beta_1(t)C_1 - \beta_2(t)C_2 + \epsilon\frac{q_N}{q_C}f(t,R_2)N_2 - kC_2, \\ R_i(0) \geq 0,\ N_i(0) \geq 0,\ C_i(0) \geq 0,\ i = 1,2. \end{cases} \tag{1.5}$$

The terms kq_CC_1 and kq_CC_2 in the first two equations of (1.5) reveal that the toxin can get recycled back into the system as available nutrient. From the third and fourth equations of (1.5), we realize that only a part, $(1-\epsilon)$, of the nutrient consumed is used for algal growth, which is discounted by the cost of toxin production.

The organization of the paper is as follows. The model analysis of systems (1.3) and (1.5) are presented in sections 2 and 3, respectively. The simulation results are presented in section 4. In section 5, we give some biological interpretations on the analysis of the models.

2. **Mathematical analysis of system (1.3).** This section is devoted to the study of the global attractivity of system (1.3). We first show that $\mathbb{R}^6_+$ is positively invariant for (1.3). For any $(R_1^0, R_2^0, N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{R}^6_+$, it follows from [23, Theorem 5.2.1] that system (1.3) has a unique local nonnegative solution

$$(R_1(t), R_2(t), N_1(t), N_2(t), C_1(t), C_2(t)) \in \mathbb{R}^6_+$$

through the initial value

$$(R_1(0), R_2(0), N_1(0), N_2(0), C_1(0), C_2(0)) = (R_1^0, R_2^0, N_1^0, N_2^0, C_1^0, C_2^0).$$

Let

$$W_i(t) = R_i(t) + q_N N_i(t),\ i = 1, 2. \tag{2.1}$$

Then $W_1(t)$ and $W_2(t)$ satisfy the following coupled differential equations

$$\begin{cases} \frac{dW_1}{dt} = R_1^{(0)}(t) - \alpha_1(t)W_1 + \alpha_2(t)W_2, \\ \frac{dW_2}{dt} = R_2^{(0)}(t) + \beta_1(t)W_1 - \beta_2(t)W_2, \\ W_i(0) = W_i^0,\ i = 1, 2. \end{cases} \tag{2.2}$$

We have the following results concerned with the global dynamics of (2.2):

Lemma 2.1. *The system (2.2) admits a unique positive τ-periodic solution $(W_1^*(t), W_2^*(t))$ which is globally attractive in $\mathbb{R}^2$, that is, for any $(W_1(0), W_2(0)) \in \mathbb{R}^2$, we have*

$$\lim_{t\to\infty} [(W_1(t), W_2(t)) - (W_1^*(t), W_2^*(t))] = 0.$$

Proof. We first consider the following system:

$$\begin{cases} \frac{d\hat{W}_1}{dt} = -\alpha_1(t)\hat{W}_1 + \alpha_2(t)\hat{W}_2, \\ \frac{d\hat{W}_2}{dt} = \beta_1(t)\hat{W}_1 - \beta_2(t)\hat{W}_2. \end{cases} \tag{2.3}$$

Let

$$H(t) = \begin{pmatrix} -\alpha_1(t) & \alpha_2(t) \\ \beta_1(t) & -\beta_2(t) \end{pmatrix}.$$

From (1.1), it is easy to see that $H(t)$ is irreducible, cooperative, and the sum of each row in $H(t)$ is negative, which imply that the Floquet multipliers of $H(t)$ are both less than 1 (see, e.g., [22, Lemma 1.0.]. Hence, the unique equilibrium $(0, 0)$ is locally asymptotically stable. Furthermore, the system (2.3) is cooperative. Thus, $(0, 0)$ is globally asymptotically stable for (2.3) in $\mathbb{R}^2$ (see [14, Theorem D]). That is, $\lim_{t\to\infty} (\hat{W}_1(t), \hat{W}_2(t)) = (0, 0)$.

The solution of (2.2) can be expressed as

$$\begin{pmatrix} W_1(t) \\ W_2(t) \end{pmatrix} = \mathcal{T}(t) \begin{pmatrix} W_1^0 \\ W_2^0 \end{pmatrix} + \int_0^t \mathcal{T}(t-s) \begin{pmatrix} R_1^{(0)}(s) \\ R_2^{(0)}(s) \end{pmatrix} ds,$$

where $\mathcal{T}(t)$ is the solution semigroup generated by (2.3). It is easy to see that $(W_1(t), W_2(t))$ is a τ-periodic solution of (2.2) if and only if

$$(I - \mathcal{T}(\tau)) \begin{pmatrix} W_1^0 \\ W_2^0 \end{pmatrix} = \int_0^\tau \mathcal{T}(\tau - s) \begin{pmatrix} R_1^{(0)}(s) \\ R_2^{(0)}(s) \end{pmatrix} ds. \tag{2.4}$$

From above discussions, it follows that $r(\mathcal{T}(\tau)) < 1$. This implies that $I - \mathcal{T}(\tau)$ is invertible, and hence, (2.2) admits a unique τ-periodic solution $(W_1^*(t), W_2^*(t))$. Let $\hat{W}_1(t) = W_1(t) - W_1^*(t)$ and $\hat{W}_2(t) = W_2(t) - W_2^*(t)$. Then $(\hat{W}_1(t), \hat{W}_2(t))$ satisfies (2.3), and hence, $\lim_{t\to\infty} (\hat{W}_1(t), \hat{W}_2(t)) = (0, 0)$. Thus, we complete the proof. □

It follows from Lemma 2.1 that $R_i(t)$ and $N_i(t)$ are ultimately bounded, $i = 1, 2$. From the last two equations of (1.3), it is easy to see $C_1(t)$ and $C_2(t)$ are also ultimately bounded. Thus, the solutions of system (1.3) exist globally on the interval $[0, \infty)$. Let $\mathcal{P} : \mathbb{R}_+^6 \to \mathbb{R}_+^6$ be the Poincaré map associated with system (1.3), that is,

$$\mathcal{P}(R_1(0), R_2(0), N_1(0), N_2(0), C_1(0), C_2(0)) = (R_1(\tau), R_2(\tau), N_1(\tau), N_2(\tau), C_1(\tau), C_2(\tau)),$$

for all $x := (R_1(0), R_2(0), N_1(0), N_2(0), C_1(0), C_2(0)) \in \mathbb{R}_+^6$, where

$$(R_1(t), R_2(t), N_1(t), N_2(t), C_1(t), C_2(t))$$

is the unique solution of system (1.3). Then $\mathcal{P}$ is point dissipative (i.e., ultimately bounded) in $\mathbb{R}_+^6$, and $\mathcal{P}$ is compact. By [11, Theorem 3.4.8], it follows that $\mathcal{P} : \mathbb{R}_+^6 \to \mathbb{R}_+^6$ has a global compact attractor in $\mathbb{R}_+^6$.

We summarize our discussions above:

Lemma 2.2. *$\mathbb{R}_+^6$ is positively invariant for (1.3) and system (1.3) has a unique and bounded solution with the initial value in $\mathbb{R}_+^6$. Further, the Poincaré map associated with system (1.3) admits a connected global attractor on $\mathbb{R}_+^6$ which attracts all positive orbits in $\mathbb{R}_+^6$.*

2.1. **The basic reproduction number of system (1.3).** In order to find the trivial solution of (1.3), we assume $N_1 = N_2 = 0$ in (1.3). Then R_1 and R_2 satisfy the system (2.2) and it follows from Lemma 2.1 that

$$\lim_{t\to\infty} [(R_1(t), R_2(t)) - (W_1^*(t), W_2^*(t))] = 0.$$

Furthermore, C_1 and C_2 satisfy the following system

$$\begin{cases} \frac{dC_1}{dt} = -(\alpha_1(t) + k)C_1 + \alpha_2(t)C_2, \\ \frac{dC_2}{dt} = \beta_1(t)C_1 - (\beta_2(t) + k)C_2, \\ C_i(0) \geq 0, \ i = 1, 2. \end{cases} \tag{2.5}$$

By the same arguments as those in the dynamics of the system (2.3), we are able to show that

$$\lim_{t\to\infty} (C_1(t), C_2(t)) = (0, 0).$$

Bacaër and Guernaoui [2] investigated a vector-borne disease model with seasonality, and proposed a general definition of the basic reproduction number in periodic habitats. Wang and Zhao [27] further gave a computational formula for periodic compartmental epidemic models and showed that it is a threshold parameter for

the local stability of the disease-free periodic solution. Here, we introduce the basic reproduction number R_0 for the periodic compartmental ecological model (1.3). Linearizing system (1.3) at the trivial solution

$$E_0(t) := (W_1^*(t), W_2^*(t), 0, 0, 0, 0),$$

we get the following cooperative system:

$$\begin{cases} \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [f(t, W_1^*(t)) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [f(t, W_2^*(t)) - m]N_2, \\ N_i(0) \geq 0, \ i = 1, 2. \end{cases} \tag{2.6}$$

Next, we review some basic results related to a monodromy matrix that is needed for our subsequent discussions. Let $\mathbf{A}(t)$ be a continuous, cooperative, irreducible, and τ-periodic $k \times k$ matrix function. Suppose $\Phi_{\mathbf{A}(\cdot)}(t)$ is the monodromy matrix of the linear ordinary differential system

$$\frac{dx(t)}{dt} = \mathbf{A}(t)x, \tag{2.7}$$

and $r(\Phi_{\mathbf{A}(\cdot)}(\tau))$ is the spectral radius of $\Phi_{\mathbf{A}(\cdot)}(\tau)$. From [1, Lemma 2] (see also [10, Theorem 1.1]), it follows that $\Phi_{\mathbf{A}(\cdot)}(t)$ is a matrix with all entries positive for each $t > 0$. By the Perron-Frobenius theorem, $r(\Phi_{\mathbf{A}(\cdot)}(\tau))$ is the principal eigenvalue of $\Phi_{\mathbf{A}(\cdot)}(\tau)$ in the sense that it is simple and admits a positive eigenvector. We further have the following results:

Lemma 2.3. *([28, Lemma 2.1]) Let $\mu = \frac{1}{\tau}\ln r(\Phi_{\mathbf{A}(\cdot)}(\tau))$. Then there exists a positive, τ-periodic function $v(t)$ such that $e^{\mu t}v(t)$ is a solution of (2.7).*

Motivated by (2.6), we define

$$\mathbf{F}(t) = \begin{pmatrix} f(t, W_1^*(t)) & 0 \\ 0 & f(t, W_2^*(t)) \end{pmatrix}, \ \mathbf{V}(t) = \begin{pmatrix} \alpha_1(t) + m & -\alpha_2(t) \\ -\beta_1(t) & \beta_2(t) + m \end{pmatrix}. \tag{2.8}$$

Suppose $\Phi_{\mathbf{V}(\cdot)}(t)$ is the monodromy matrix of the linear τ-periodic differential system $\frac{dz(t)}{dt} = \mathbf{V}(t)z$. Assume $Y(t, s), \ t \geq s$, is the evolution operator of the linear τ-periodic system

$$\frac{dy(t)}{dt} = -\mathbf{V}(t)y, \tag{2.9}$$

that is, for each $s \in \mathbb{R}$, the 2×2 matrix $Y(t, s)$ satisfies

$$\frac{d}{dt}Y(t, s) = -\mathbf{V}(t)Y(t, s), \ \forall \ t \geq s, \ Y(s, s) = I,$$

where I is the 2×2 matrix. Thus, the monodromy matrix $\Phi_{-\mathbf{V}(\cdot)}(t)$ of (2.9) is equal to $Y(t, 0), \ t \geq 0$.

We assume that $\phi(s)$, τ-periodic in s, is the initial distribution of algae individuals. Then $\mathbf{F}(s)\phi(s)$ is the rate of new population generated by initial fertile algae individuals who were introduced at time s. Given $t \geq s$, then $Y(t, s)\mathbf{F}(s)\phi(s)$ gives the distribution of those fertile individuals who were newly produced at time s and remain in the fertile compartments at time t. It follows that

$$\psi(t) := \int_{-\infty}^{t} Y(t, s)\mathbf{F}(s)\phi(s)ds = \int_{0}^{\infty} Y(t, t-a)\mathbf{F}(t-a)\phi(t-a)da$$

is the distribution of accumulative new individuals at time t produced by all those fertile individuals $\phi(s)$ introduced at time previous to t.

Let C_τ be the ordered Banach space of all τ-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, which is equipped with the maximum norm $\|\cdot\|$ and the positive cone $C_\tau^+ := \{\phi \in C_\tau : \phi(t) \geq 0,\ \forall\, t \in \mathbb{R}\}$. Then we define a linear operator $L : C_\tau \to C_\tau$ by

$$(L\phi)(t) = \int_0^\infty Y(t, t-a)\mathbf{F}(t-a)\phi(t-a)da,\ \forall\, t \in \mathbb{R},\ \phi \in C_\tau. \tag{2.10}$$

Then we call L the next generation operator [27], and define the basic reproduction number as

$$\mathcal{R}_0 := r(L), \tag{2.11}$$

the spectral radius of L.

We present the following result, which will be used in the proof of our main result.

Lemma 2.4. [27, Theorem 2.2] *The following statements hold.*

(i) $\mathcal{R}_0 = 1$ *if and only if* $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\tau)) = 1$*;*
(ii) $\mathcal{R}_0 > 1$ *if and only if* $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\tau)) > 1$*;*
(iii) $\mathcal{R}_0 < 1$ *if and only if* $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\tau)) < 1$*.*

It follows from Lemma 2.4 that the trivial solution

$$E_0(t) := (W_1^*(t), W_2^*(t), 0, 0, 0, 0),$$

is locally asymptotically stable for (1.3) if $\mathcal{R}_0 < 1$, and unstable if $\mathcal{R}_0 > 1$.

In the following, we shall discuss a special case where $\mu_{\max}(t) \equiv \mu_{\max}$ and all the parameters in (1.1) are positive constants. Then it is easy to see that

$$(W_1^*(t), W_2^*(t)) \equiv (A_1^{(0)}, A_2^{(0)}) := \left(\frac{\alpha_2 R_2^{(0)} - \beta_2 R_1^{(0)}}{\alpha_2\beta_1 - \alpha_1\beta_2}, \frac{\alpha_1 R_2^{(0)} - \beta_1 R_1^{(0)}}{\alpha_2\beta_1 - \alpha_1\beta_2}\right)$$

is the unique equilibrium for (2.2). Hence,

$$\mathbf{F} = \begin{pmatrix} f(A_1^{(0)}) & 0 \\ 0 & f(A_2^{(0)}) \end{pmatrix},\ \mathbf{V} = \begin{pmatrix} \alpha_1 + m & -\alpha_2 \\ -\beta_1 & \beta_2 + m \end{pmatrix}, \tag{2.12}$$

where we may choose $f(R) = \frac{\mu_{\max} R}{K+R}$ as a classical example. Then the basic reproduction number corresponds to the spectral radius of $\mathbf{F}\mathbf{V}^{-1}$ (see [4, 5]), that is,

$$\mathcal{R}_0 = r(\mathbf{F}\mathbf{V}^{-1}). \tag{2.13}$$

By computations, it follows that

$$\mathbf{F}\mathbf{V}^{-1} = \frac{1}{\det \mathbf{V}} \begin{pmatrix} (\beta_2 + m) f(A_1^{(0)}) & \alpha_2 f(A_1^{(0)}) \\ \beta_1 f(A_2^{(0)}) & (\alpha_1 + m) f(A_2^{(0)}) \end{pmatrix}, \tag{2.14}$$

where $\det \mathbf{V} := (\alpha_1 + m)(\beta_2 + m) - \alpha_2\beta_1 > 0$ (using (1.1)).

2.2. **Global attractivity of system (1.3).** We first study the following systems:

$$\begin{cases} \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [f(t, W_1^*(t) - q_N N_1) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [f(t, W_2^*(t) - q_N N_2) - m]N_2, \\ N_i(0) \geq 0,\ i = 1, 2. \end{cases} \tag{2.15}$$

If we linearize the system (2.15) at the trivial solution $(0, 0)$, we get the linear system (2.6). This means the trivial solution $(0, 0)$ is locally asymptotically stable

for (2.15) if $\mathcal{R}_0 < 1$, and unstable if $\mathcal{R}_0 > 1$. From the biological view of point, the feasible domain $\Lambda(t)$ for (2.15) should be

$$\Lambda(t) = \{(N_1, N_2) \in \mathbb{R}_+^2 : q_N N_1 \le W_1^*(t),\ q_N N_2 \le W_2^*(t)\}. \tag{2.16}$$

It is not hard to see that for any $(N_1^0, N_2^0) \in \Lambda(0)$, system (2.15) has a unique solution $(N_1(t), N_2(t))$ with $(N_1(0), N_2(0)) = (N_1^0, N_2^0)$ and $(N_1(t), N_2(t)) \in \Lambda(t),\ \forall\, t \ge 0$.

Lemma 2.5. *Let $X := \Lambda(0)$. The following statements hold.*

(i) *If $\mathcal{R}_0 \le 1$, then the trivial solution $(0,0)$ is globally attractive in X for (2.15);*
(ii) *If $\mathcal{R}_0 > 1$, then every solution $(N_1(t), N_2(t))$ of (2.15) with $(N_1(0), N_2(0)) \in X\backslash\{(0,0)\}$ satisfies*

$$\lim_{t\to\infty} [(N_1(t), N_2(t)) - (N_1^*(t), N_2^*(t))] = (0,0),$$

where $(N_1^*(t), N_2^*(t))$ is the unique positive τ-periodic solution of (2.15).

Proof. Let $P : X \to X$ be the Poincaré map associated with system (2.15), that is,

$$P(N_1(0), N_2(0)) = (N_1(\tau), N_2(\tau)),\ \forall\, x := (N_1(0), N_2(0)) \in X,$$

where $(N_1(t), N_2(t))$ is the unique solution of system (2.15). It is easy to see that $P : X \to X$ is strongly monotone, and strongly subhomogeneous in the sense that $P(\theta x) \gg \theta P(x)$, $\forall\, x \in X$, $\theta \in (0,1)$ (see [30, section 2.3]). Further, it is not hard to see that $P(0,0) = (0,0)$ and $DP(0,0) = \Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\tau)$, where $DP(0,0)$ denotes the Fréchet derivative of P at $(0,0)$, and $\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(t)$ denotes the monodromy matrix of the linear ordinary differential system (2.6) (see [30, section 3.1.2]). From Lemma 2.4 and [30, Theorem 2.3.4], it follows that

(i) If $\mathcal{R}_0 \le 1$, then every positive orbit of P in X converges to $(0,0)$;
(ii) If $\mathcal{R}_0 > 1$, then there exists a unique fixed point $\mathcal{E} \gg 0$ in X such that every positive orbit of P in $X\backslash\{(0,0)\}$ converges to $\mathcal{E}$.

Corresponding to the fixed point of the period map P, the conclusions in the Lemma are true. □

Since the equations of R_i and N_i, $i = 1,2$ in (1.3) are independent of the equations of C_1 and C_2, we first study the following subsystem:

$$\begin{cases} \frac{dR_1}{dt} = R_1^{(0)}(t) - \alpha_1(t)R_1 + \alpha_2(t)R_2 - q_N[f(t,R_1) - m]N_1, \\ \frac{dR_2}{dt} = R_2^{(0)}(t) + \beta_1(t)R_1 - \beta_2(t)R_2 - q_N[f(t,R_2) - m]N_2, \\ \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [f(t,R_1) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [f(t,R_2) - m]N_2, \\ R_i(0) \ge 0,\ N_i(0) \ge 0,\ i = 1,2. \end{cases} \tag{2.17}$$

We are now in the position to address the dynamics of system (2.17) in the sense of the following theorem.

Theorem 2.1. *Let $(W_1^*(t), W_2^*(t))$ be a unique positive τ-periodic solution of the system (2.2). Then the following statements hold.*

(i) *If $\mathcal{R}_0 \le 1$, then the trivial solution $(W_1^*(t), W_2^*(t), 0, 0)$ is globally attractive in $\mathbb{R}_+^4$ for (2.17);*
(ii) *If $\mathcal{R}_0 > 1$, then every solution $(R_1(t), R_2(t), N_1(t), N_2(t))$ of (2.17) with $(R_1(0), R_2(0), N_1(0), N_2(0)) \in \mathbb{R}_+^4\backslash\{(a,b,0,0) : a,b \in \mathbb{R}_+\}$ satisfies*

$$\lim_{t\to\infty} ((R_1(t), R_2(t), N_1(t), N_2(t)) - (R_1^*(t), R_2^*(t), N_1^*(t), N_2^*(t))) = (0,0,0,0),$$

where $R_i^*(t) := W_i^*(t) - q_N N_i^*(t),\ i = 1, 2,$ *and* $(N_1^*(t), N_2^*(t))$ *is the unique positive* τ*-periodic solution of* (2.15).

Proof. We rewrite the system (2.17) as follows:

$$\begin{cases} \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [f(t, W_1 - q_N N_1) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [f(t, W_1 - q_N N_2) - m]N_2, \\ \frac{dW_1}{dt} = R_1^{(0)}(t) - \alpha_1(t)W_1 + \alpha_2(t)W_2, \\ \frac{dW_2}{dt} = R_2^{(0)}(t) + \beta_1(t)W_1 - \beta_2(t)W_2, \\ W_i(0) = W_i^0,\ N_i(0) \geq 0,\ i = 1, 2, \end{cases} \tag{2.18}$$

where W_1 and W_2 are defined in (2.1). Let

$$\tilde{X} = \{(N_1, N_2, W_1, W_2) \in \mathbb{R}_+^4 : q_N N_1 \leq W_1,\ q_N N_2 \leq W_2\},$$

$\tilde{X}_0 := \{(N_1, N_2, W_1, W_2) \in \tilde{X} : (N_1, N_2) \neq (0, 0)\}$, and $\partial\tilde{X}_0 = \tilde{X} \backslash \tilde{X}_0$.

Claim. *If* $\tilde{x} := (N_1^0, N_2^0, W_1^0, W_2^0) \in \tilde{X}$*, then the solution of* (2.18) *through* $\tilde{x}$ *satisfies*

$$(N_1(t), N_2(t), W_1(t), W_2(t)) \in \tilde{X},\ \forall\ t \geq 0.$$

For this, we let $R_1(t) = W_1(t) - q_N N_1(t)$ *and* $R_2(t) = W_2(t) - q_N N_2(t)$*. Then* $(R_1(t), R_2(t), N_1(t), N_2(t))$ *satisfies* (2.17) *and* $R_1(0) \geq 0,\ R_2(0) \geq 0,\ N_1(0) \geq 0,\ N_2(0) \geq 0$*. It is not hard to see that*

$$(R_1(t), R_2(t), N_1(t), N_2(x, t)) \geq 0,\ \forall\ t \geq 0.$$

Thus, our claim is true.

Let $\tilde{P} : \tilde{X} \to \tilde{X}$ be the Poincaré map associated with system (2.18) and $\tilde{\omega}(\tilde{x})$ be the omega-limit set of the orbit of $\tilde{P}$ with initial values $\tilde{x} \in \tilde{X}$. From the third and fourth equations of (2.18) and Lemma 2.1, it follows that

$$\lim_{t\to\infty} [(W_1(t), W_2(t)) - (W_1^*(t), W_2^*(t))] = 0.$$

Thus, there exists a set $\mathcal{I} \subset \mathbb{R}_+^2$ such that $\tilde{\omega}(\tilde{x}) = \mathcal{I} \times \{(W_1^*(0), W_2^*(0))\}$. For any given $(N_1^0, N_2^0) \in \mathcal{I}$, we have $(N_1^0, N_2^0, W_1^*(0), W_2^*(0)) \in \tilde{\omega}(\tilde{x}) \subset \tilde{X}$. By the definition of $\tilde{X}$, it follows that $(N_1^0, N_2^0) \subset X$. Thus, $\mathcal{I} \subset X$, where $X := \Lambda(0)$ is defined in (2.16).

By [30, Lemma 1.2.1′], $\tilde{\omega}(\tilde{x})$ is a compact, invariant and internal chain transitive set for $\tilde{P}$. Moreover, if $x^0 \in \mathbb{R}_+^2$ with $(x^0, W_1^*(0), W_2^*(0)) \in \tilde{\omega}(\tilde{x})$, there holds

$$\tilde{P}\mid_{\tilde{\omega}(\tilde{x})} (x^0, W_1^*(0), W_2^*(0)) = (P(x^0), W_1^*(\tau), W_2^*(\tau)),$$

where $P : X \to X$ is the Poincaré map associated with system (2.15). It then follows that $\mathcal{I}$ is a compact, invariant and internal chain transitive set for $P : X \to X$.

In the case where $\mathcal{R}_0 \leq 1$, it follows from Lemma 2.5 (i) that (2.15) has a globally attractive positive τ-periodic solution $(0, 0)$ in X. This implies that the unique fixed point $(0, 0)$ is an isolated invariant set in X and no cycle connecting $(0, 0)$ to itself in X. Since $\mathcal{I}$ is a compact, invariant and internal chain transitive set for $P : X \to X$, it follows from a convergence theorem (see, e.g., [30, Theorem 1.2.2]) that $\mathcal{I}$ is a fixed point of P. That is, $\mathcal{I} = \{(0, 0)\}$, and hence, $\tilde{\omega}(\tilde{x}) = \mathcal{I} \times \{(W_1^*(0), W_2^*(0))\} = \{(0, 0, W_1^*(0), W_2^*(0))\}$. This implies that $(0, 0, W_1^*(0), W_2^*(0))$ is globally attractive for $\tilde{P}$ in $\tilde{X}$. Corresponding to the fixed point of the period map $\tilde{P}$, system (2.18) has a globally attractive positive τ-periodic solution $(0, 0, W_1^*(t), W_2^*(t))$ in $\tilde{X}$. In view of (2.1), we see that statement (i) is true.

In the case where $\mathcal{R}_0 > 1$, that is, $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\tau)) > 1$. Thus, we may choose $\zeta_0 > 0$ small enough such that $r(\Phi_{\mathbf{F}_{\zeta_0}(\cdot)-\mathbf{V}(\cdot)}(\tau)) > 1$, where

$$\mathbf{F}_{\zeta_0}(t) = \begin{pmatrix} f(t, W_1^*(t)) - \zeta_0 & 0 \\ 0 & f(t, W_2^*(t)) - \zeta_0 \end{pmatrix}.$$

Since $\mathcal{R}_0 > 1$, it follows from Lemma 2.5 (ii) that (2.15) has a globally attractive positive τ-periodic solution $(N_1^*(t), N_2^*(t))$ in $X_0 := X\backslash\{(0,0)\}$. Note that $(0,0)$ is also a τ-periodic solution of (2.15). This implies that the possible fixed points $(0,0)$ and $(N_1^*(0), N_2^*(0))$ are isolated invariant sets in X and no subset of $\{(0,0)\} \cup \{(N_1^*(0), N_2^*(0))\}$ forms a cycle in X. Since $\mathcal{I}$ is a compact, invariant and internal chain transitive set for $P : X \to X$, it follows from a convergence theorem (see, e.g., [30, Theorem 1.2.2]) that either $\mathcal{I} = \{(0,0)\}$ or $\mathcal{I} = \{(N_1^*(0), N_2^*(0))\}$.

Suppose, by contradiction, that $\mathcal{I} = \{(0,0)\}$. This implies that

$$\begin{aligned} \tilde{P}^n(N_1(0), N_2(0), W_1(0), W_2(0)) &:= (N_1(n\tau), N_2(n\tau), W_1(n\tau), W_2(n\tau)) \\ &\to (0, 0, W_1^*(0), W_2^*(0)) \text{ as } n \to \infty. \end{aligned}$$

Equivalently,

$$\lim_{t\to\infty} |(N_1(t), N_2(t), W_1(t), W_2(t)) - (0, 0, W_1^*(t), W_2^*(t))| = 0,$$

and hence, $\lim_{t\to\infty} |(W_i(t) - q_N N_i(t)) - W_i^*(t))| = 0$, $i = 1, 2$. By the continuity of f, it follows that there exists $t_1 > 0$ such that

$$f(t, W_i(t) - q_N N_i) > f(t, W_i^*(t)) - \zeta_0, \ \forall\, t \geq t_1, \ i = 1, 2.$$

From the first two equations (2.18), it follows that

$$\begin{cases} \frac{dN_1}{dt} \geq -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [f(t, W_1^*(t)) - m - \zeta_0]N_1, \ \forall\, t \geq t_1, \\ \frac{dN_2}{dt} \geq \beta_1(t)N_1 - \beta_2(t)N_2 + [f(t, W_2^*(t)) - m - \zeta_0]N_2, \ \forall\, t \geq t_1, \end{cases}$$

From $(N_1^0, N_2^0) > (0,0)$ and the version for nonautonomous systems in [23, Theorem 4.1.1], it follows that the irreducibility of the cooperative matrix

$$\begin{pmatrix} -\alpha_1(t) + [f(t, W_1 - q_N N_1) - m] & \alpha_2(t) \\ \beta_1(t) & -\beta_2(t) + [f(t, W_2 - q_N N_2) - m] \end{pmatrix}$$

and the first two equations of system (2.18) imply that $(N_1(t), N_2(t))^T \gg (0,0)$, $\forall\, t > 0$, and hence, $(N_1(t_1), N_2(t_1))^T \gg (0,0)$.

By Lemma 2.3, it follows that there exists a positive, τ-periodic function $\mathfrak{J}(t)$ and $\hat{\mu} = \frac{1}{\tau}\ln r(\Phi_{\mathbf{F}_{\zeta_0}(\cdot)-\mathbf{V}(\cdot)}(\tau))$ such that $\bar{\mathfrak{J}}(t) := \bar{c}e^{\hat{\mu}(t-t_1)}\mathfrak{J}(t)$ is a solution of

$$\frac{dx(t)}{dt} = (\mathbf{F}_{\zeta_0}(t) - \mathbf{V}(t))\, x(t),$$

where $\bar{c}$ satisfies $\bar{\mathfrak{J}}(t_1) := \bar{c}\mathfrak{J}(t_1) \leq (N_1(t_1), N_2(t_1))$. The standard comparison theorem (see, e.g., [25, Theorem B.1]) implies that

$$(N_1(t), N_2(t)) \geq \bar{\mathfrak{J}}(t), \ \forall\, t \geq t_1.$$

In particular, there exists n_1 such that

$$(N_1(n\tau), N_2(n\tau)) \geq \bar{\mathfrak{J}}(n\tau), \ \forall\, n \geq n_1.$$

Since $\hat{\mu} > 0$, it follows that $\bar{\mathfrak{J}}(n\tau) \to \infty$ as $n \to \infty$. Thus, $(N_1(n\tau), N_2(n\tau)) \to \infty$ as $n \to \infty$. This contradiction proves that $\mathcal{I} = \{(N_1^*(0), N_2^*(0))\}$, and hence,

$$\tilde{\omega}(\tilde{x}) = \mathcal{I} \times \{(W_1^*(0), W_2^*(0))\} = \{(N_1^*(0), N_2^*(0), W_1^*(0), W_2^*(0))\}.$$

This implies that $(N_1^*(0), N_2^*(0), W_1^*(0), W_2^*(0))$ is globally attractive for $\tilde{P}$ in $\tilde{X}$. Corresponding to the fixed point of the period map $\tilde{P}$, system (2.18) has a globally attractive positive τ-periodic solution $(N_1^*(t), N_2^*(t), W_1^*(t), W_2^*(t))$ in $\tilde{X}$. By virtue of (2.1), we complete the proof of (ii). □

By Theorem 2.1 and the theory of asymptotically periodic semiflows (see, e.g., [29] or [30, section 3.2]), it is easy to obtain the following results:

Theorem 2.2. *The following statements hold.*

(i) *If $\mathcal{R}_0 \le 1$, then the trivial solution $(W_1^*(t), W_2^*(t), 0, 0, 0, 0)$ is globally attractive in $\mathbb{R}_+^6$ for (1.3);*

(ii) *If $\mathcal{R}_0 > 1$, then every solution $(R_1(t), R_2(t), N_1(t), N_2(t), C_1(t), C_2(t))$ of (1.3) with $(R_1(0), R_2(0), N_1(0), N_2(0), C_1(0), C_2(0)) \in \mathbb{R}_+^6 \backslash \{(a, b, 0, 0, 0, 0) : a, b \in \mathbb{R}_+\}$ satisfies*

$$\lim_{t\to\infty} ((R_1(t), R_2(t), N_1(t), N_2(t), C_1(t), C_2(t)) - E^*(t)) = (0, 0, 0, 0, 0, 0),$$

where $E^*(t) := (R_1^*(t), R_2^*(t), N_1^*(t), N_2^*(t), C_1^*(t), C_2^*(t))$. Here, $R_i^*(t) := W_i^*(t) - q_N N_i^*(t)$, $i = 1, 2$, $(N_1^*(t), N_2^*(t))$ is the unique positive τ-periodic solution of (2.15) and $(C_1^*(t), C_2^*(t))$ is the unique positive τ-periodic solution of the following system

$$\begin{cases} \frac{dC_1}{dt} = -\alpha_1(t)C_1 + \alpha_2(t)C_2 + \epsilon p(t, R_1^*(t), N_1^*(t)) - kC_1, \\ \frac{dC_2}{dt} = \beta_1(t)C_1 - \beta_2(t)C_2 + \epsilon p(t, R_2^*(t), N_2^*(t)) - kC_2, \\ C_i(0) \ge 0, \ i = 1, 2. \end{cases} \tag{2.19}$$

3. **Threshold dynamics of system (1.5).** This section is devoted to the study of threshold dynamics of system (1.5). From [23, Theorem 5.2.1], it follows that for any $(R_1^0, R_2^0, N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{R}_+^6$, system (1.5) has a unique local nonnegative solution

$$(R_1(t), R_2(t), N_1(t), N_2(t), C_1(t), C_2(t)) \in \mathbb{R}_+^6$$

through the initial value

$$(R_1(0), R_2(0), N_1(0), N_2(0), C_1(0), C_2(0)) = (R_1^0, R_2^0, N_1^0, N_2^0, C_1^0, C_2^0).$$

In the following, we will demonstrate that mass conservation for (1.5). Let

$$V_i(t) = R_i(t) + q_N N_i(t) + q_C C_i(t), \ i = 1, 2. \tag{3.1}$$

Then $V_i(t)$, $i = 1, 2$, satisfy the differential equations (2.2). From Lemma 2.1, it follows that there exists a unique positive τ-periodic solution $(W_1^*(t), W_2^*(t))$ such that for any $(V_1(0), V_2(0)) \in \mathbb{R}^2$, we have

$$\lim_{t\to\infty} [(V_1(t), V_2(t)) - (W_1^*(t), W_2^*(t))] = 0. \tag{3.2}$$

This implies that $R_i(t)$, $N_i(t)$ and $C_i(t)$ are ultimately bounded, $i = 1, 2$. Thus, the solutions of system (1.5) exist globally on the interval $[0, \infty)$.

By our discussions above and the similar arguments in Lemma 2.2, we have the following results:

Lemma 3.1. *$\mathbb{R}_+^6$ is positively invariant for (1.5) and system (1.5) has a unique and bounded solution with the initial value in $\mathbb{R}_+^6$. Further, the Poincaré map associated with system (1.5) admits a connected global attractor on $\mathbb{R}_+^6$ which attracts all positive orbits in $\mathbb{R}_+^6$.*

From (3.2), we conclude that the limiting systems of (1.5) take the forms

$$\begin{cases} \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [(1-\epsilon)f(t, W_1^*(t) - q_N N_1 - q_C C_1) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [(1-\epsilon)f(t, W_2^*(t) - q_N N_2 - q_C C_2) - m]N_2, \\ \frac{dC_1}{dt} = -\alpha_1(t)C_1 + \alpha_2(t)C_2 + \epsilon\frac{q_N}{q_C}f(t, W_1^*(t) - q_N N_1 - q_C C_1)N_1 - kC_1, \\ \frac{dC_2}{dt} = \beta_1(t)C_1 - \beta_2(t)C_2 + \epsilon\frac{q_N}{q_C}f(t, W_2^*(t) - q_N N_2 - q_C C_2)N_2 - kC_2, \\ N_i(0) \geq 0,\ C_i(0) \geq 0,\ i = 1, 2. \end{cases} \tag{3.3}$$

Clearly, reasonable region for (3.3) is

$$\Sigma(t) = \{(N_1, N_2, C_1, C_2) \in \mathbb{R}_+^4 : q_N N_1 + q_C C_1 \leq W_1^*(t),\ q_N N_2 + q_C C_2 \leq W_2^*(t)\},$$

where $\mathbb{R}_+ := [0, \infty)$. It is easy to see that for any $(N_1^0, N_2^0, C_1^0, C_2^0) \in \Sigma(0)$, system (3.3) has a unique mild solution $(N_1(t), N_2(t), C_1(t), C_2(t))$ with

$$(N_1(0), N_2(0), C_1(0), C_2(0)) = (N_1^0, N_2^0, C_1^0, C_2^0)$$

and $(N_1(t), N_2(t), C_1(t), C_2(t)) \in \Sigma(t),\ \forall\ t \geq 0$. We will always restrict the initial values of (3.3) in this region $\Sigma(0)$. The solutions of the system (3.3) are in the following forms:

(i) Trivial solution $\hat{0} := (0, 0, 0, 0)$ always exists;
(ii) There may be additional solutions as well and these must be positive.

Next, we shall discuss the stability of the trivial solution $\hat{0} := (0, 0, 0, 0)$ of (3.3). Linearizing system (3.3) at the trivial solution $\hat{0} := (0, 0, 0, 0)$, we get the following cooperative system for (N_1, N_2) compartments:

$$\begin{cases} \frac{dN_1}{dt} = -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [(1-\epsilon)f(t, W_1^*(t)) - m]N_1, \\ \frac{dN_2}{dt} = \beta_1(t)N_1 - \beta_2(t)N_2 + [(1-\epsilon)f(t, W_2^*(t)) - m]N_2, \\ N_i(0) \geq 0,\ i = 1, 2. \end{cases} \tag{3.4}$$

Then we define

$$\mathbf{F}^\epsilon(t) = \begin{pmatrix} (1-\epsilon)f(t, W_1^*(t)) & 0 \\ 0 & (1-\epsilon)f(t, W_2^*(t)) \end{pmatrix}, \tag{3.5}$$

and a linear operator $L^\epsilon : C_\tau \to C_\tau$ by

$$(L^\epsilon\phi)(t) = \int_0^\infty Y(t, t-a)\mathbf{F}^\epsilon(t-a)\phi(t-a)da,\ \forall\ t \in \mathbb{R},\ \phi \in C_\tau. \tag{3.6}$$

Then we call L^ϵ the next generation operator [27], and define the basic reproduction number as

$$\mathcal{R}_0^\epsilon := r(L^\epsilon), \tag{3.7}$$

the spectral radius of L^ϵ. Furthermore, $\mathcal{R}_0^\epsilon - 1$ and $r(\Phi_{\mathbf{F}^\epsilon(\cdot) - \mathbf{V}(\cdot)}(\tau)) - 1$ have the same sign.

In order to present our results, we introduce the following notations: $\mathbb{X} := \Sigma(0)$, $\mathbb{X}_0 := \{(N_1, N_2, C_1, C_2) \in \mathbb{X} : (N_1, N_2) \neq (0, 0)\}$ and $\partial\mathbb{X}_0 = \mathbb{X}\backslash\mathbb{X}_0$. Suppose $S : \mathbb{X} \to \mathbb{X}$ is the Poincaré map associated with system (3.3), that is,

$$S(x^0) = u(\tau, x^0),\ \forall\ x^0 := (N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X},$$

where $u(t, x^0)$ is the unique solution of system (3.3) with $u(0, x^0) = x^0$. It is easy to see that

$$S^n(x^0) = u(n\tau, x^0),\ \forall\ n \geq 0.$$

Lemma 3.2. *Let $\mathcal{R}_0^\epsilon > 1$. Then there exists $\sigma > 0$ such that for any $(N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X}_0$ with*

$$\|(N_1^0, N_2^0, C_1^0, C_2^0) - \hat{0}\| \le \sigma,$$

we have $\limsup_{n\to\infty} \mathrm{dist}(S^n(N_1^0, N_2^0, C_1^0, C_2^0), \hat{0}) \ge \sigma$.

Proof. Since $\mathcal{R}_0^\epsilon > 1$, it follows that $r(\Phi_{\mathbf{F}^\epsilon(\cdot)-\mathbf{V}(\cdot)}(\tau)) > 1$. Thus, we may choose $\xi_0 > 0$ small enough such that $r(\Phi_{\mathbf{F}^\epsilon_{\xi_0}(\cdot)-\mathbf{V}(\cdot)}(\tau)) > 1$, where

$$\mathbf{F}^\epsilon_{\xi_0}(t) = \begin{pmatrix} (1-\epsilon)f(t, W_1^*(t)) - \xi_0 & 0 \\ 0 & (1-\epsilon)f(t, W_2^*(t)) - \xi_0 \end{pmatrix}.$$

By the continuity of f, it is easy to see that

$$\lim_{(N_i, C_i)\to(0,0)} f(t, W_i^*(t) - q_N N_i - q_C C_i) = f(t, W_i^*(t)),\ i = 1, 2.$$

Thus, we can choose $\rho > 0$ such that

$$f(t, W_i^*(t) - q_N N_i - q_C C_i) > f(t, W_i^*(t)) - \frac{\xi_0}{1-\epsilon},\ \forall\ \|(N_i(\cdot), C_i(\cdot))\| < \rho. \tag{3.8}$$

By the continuity of the solutions with respect to the initial values, there exists a $\sigma > 0$ such that for all $(N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X}_0$ with

$$\|(N_1^0, N_2^0, C_1^0, C_2^0) - \hat{0}\| \le \sigma,$$

there holds $\|u(t, (N_1^0, N_2^0, C_1^0, C_2^0)) - u(t, \hat{0})\| < \rho$, $\forall\ t \in [0, \tau]$.

Claim.

$$\limsup_{n\to\infty} dist(S^n(N_1^0, N_2^0, C_1^0, C_2^0), \hat{0}) \ge \sigma.$$

Assume, by contradiction, that the above conclusion does not hold. Then we have

$$\limsup_{n\to\infty} dist(S^n(N_1^0, N_2^0, C_1^0, C_2^0), \hat{0}) < \sigma,$$

for some $(N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X}_0$. Without loss of generality, we assume that

$$dist(S^n(N_1^0, N_2^0, C_1^0, C_2^0), \hat{0}) < \sigma,\ \forall\ n \ge 0.$$

It follows that

$$\|u(t, S^n(N_1^0, N_2^0, C_1^0, C_2^0)) - u(t, \hat{0})\| < \rho,\ \forall\ t \in [0, \tau],\ n \ge 0.$$

For any $t \ge 0$, let $t = m\tau + t'$, where $t' \in [0, \tau)$, and m is the largest integer less than or equal to $\frac{t}{\tau}$. Therefore, we have $\|u(t, (N_1^0, N_2^0, C_1^0, C_2^0)) - u(t, \hat{0})\| = \|u(t', S^m(N_1^0, N_2^0, C_1^0, C_2^0)) - u(t', \hat{0})\| < \rho$. Note that $(N_1(t), N_2(t), C_1(t), C_2(t)) = u(t, (N_1^0, N_2^0, C_1^0, C_2^0))$ and $u(t, \hat{0}) = \hat{0}$, $\forall\ t \ge 0$. It then follows that $\|(N_i(t), C_i(t))\| < \rho$, $\forall\ t \ge 0$ and $i = 1, 2$. Thus, (3.8) implies that

$$f(t, W_i^*(t) - q_N N_i - q_C C_i) > f(t, W_i^*(t)) - \frac{\xi_0}{1-\epsilon},\ t \ge 0,\ i = 1, 2. \tag{3.9}$$

From the first two equations (3.3), it follows that

$$\begin{cases} \frac{dN_1}{dt} \ge -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [(1-\epsilon)f(t, W_1^*(t)) - m - \xi_0]N_1,\ \forall\ t \ge 0, \\ \frac{dN_2}{dt} \ge \beta_1(t)N_1 - \beta_2(t)N_2 + [(1-\epsilon)f(t, W_2^*(t)) - m - \xi_0]N_2,\ \forall\ t \ge 0, \end{cases} \tag{3.10}$$

Since $(N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X}_0$ and regarding [23, Theorem 4.1.1] *as generalized to nonautonomous systems, the irreducibility of the cooperative matrix*

$$\begin{pmatrix} -\alpha_1(t) + [(1-\epsilon)f(t, \mathcal{W}_1^*(t)) - m] & \alpha_2(t) \\ \beta_1(t) & -\beta_2(t) + [(1-\epsilon)f(t, \mathcal{W}_2^*(t)) - m] \end{pmatrix} \tag{3.11}$$

and the first two equations of system (3.3) *imply that* $(N_1(t), N_2(t))^T \gg (0,0)$, $\forall\, t > 0$. *Here,* $\mathcal{W}_i^*(t) = W_i^*(t) - q_N N_i - q_C C_i$, $i = 1,2$. *Fix* $t_0 > 0$, *it follows that* $(N_1(t_0), N_2(t_0))^T \gg (0,0)$.

By Lemma 2.3, it follows that there exists a positive, τ-periodic function $J(t)$ and $\tilde{\mu} = \frac{1}{\tau}\ln r(\Phi_{\mathbf{F}^\epsilon_{\xi_0}(\cdot)-\mathbf{V}(\cdot)}(\tau))$ such that $\bar{J}(t) := \bar{b}e^{\hat{\mu}(t-t_0)}J(t)$ is a solution of

$$\frac{dx(t)}{dt} = \left(\mathbf{F}^\epsilon_{\xi_0}(t) - \mathbf{V}(t)\right)x(t),$$

where $\bar{b}$ satisfies $\bar{J}(t_0) := \bar{b}J(t_0) \le (N_1(t_0), N_2(t_0))$. The standard comparison theorem (see, e.g., [25, Theorem B.1]) implies that

$$(N_1(t), N_2(t)) \ge \bar{J}(t),\ \forall\, t \ge t_0.$$

In particular, there exists n_1 such that

$$(N_1(n\tau), N_2(n\tau)) \ge \bar{J}(n\tau),\ \forall\, n \ge n_1.$$

Since $\tilde{\mu} > 0$, it follows that $\bar{J}(n\tau) \to \infty$ as $n \to \infty$. Thus, $(N_1(n\tau), N_2(n\tau)) \to \infty$ as $n \to \infty$. This contradiction completes the proof. □

Now we are ready to state the main result of this section, which indicates that $\mathcal{R}_0^\epsilon$ is a threshold index for the persistence of algae.

Theorem 3.1. *The following statements hold.*

(i) *If* $\mathcal{R}_0^\epsilon < 1$, *then the trivial solution* $\hat{0} := (0,0,0,0)$ *is globally attractive for system* (3.3) *in* $\mathbb{X}$;

(ii) *If* $\mathcal{R}_0^\epsilon > 1$, *there exists* $\eta > 0$ *such that for any solution* $(N_1(t), N_2(t), C_1(t), C_2(t))$ *with initial value* $(N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X}_0$ *satisfies*

$$\liminf_{t\to\infty} N_i(t) \ge \eta,\ \textit{for some } i = 1,2.$$

Moreover, system (3.3) *admits at least one positive* τ*-periodic solution*

$$(\tilde{N}_1(t), \tilde{N}_2(t), \tilde{C}_1(t), \tilde{C}_2(t)).$$

Proof. Assume that $\mathcal{R}_0^\epsilon < 1$, that is, $r(\Phi_{\mathbf{F}^\epsilon(\cdot)-\mathbf{V}(\cdot)}(\tau)) < 1$. From the first two equations of (3.3), it follows that

$$\begin{cases} \frac{dN_1}{dt} \le -\alpha_1(t)N_1 + \alpha_2(t)N_2 + [(1-\epsilon)f(t, W_1^*(t)) - m]N_1,\ t > 0, \\ \frac{dN_2}{dt} \le \beta_1(t)N_1 - \beta_2(t)N_2 + [(1-\epsilon)f(t, W_2^*(t)) - m]N_2,\ t > 0, \\ N_i(0) = N_i^0 \ge 0,\ i = 1,2. \end{cases} \tag{3.12}$$

By Lemma 2.3, it follows that there exists a positive, τ-periodic function $v(t)$ and $\mu^\epsilon = \frac{1}{\tau}\ln[r(\Phi_{\mathbf{F}^\epsilon(\cdot)-\mathbf{V}(\cdot)}(\tau))]$ such that $\bar{v}(t) := \bar{a}e^{\mu^\epsilon t}v(t)$ is a solution of

$$\frac{dx(t)}{dt} = (\mathbf{F}^\epsilon(t) - \mathbf{V}(t))\,x(t),$$

where $\bar{a}$ satisfies $\bar{v}(0) := \bar{a}v(0) \ge (N_1(0), N_2(0), C_1(0), C_2(0))$. The standard comparison theorem (see, e.g., [25, Theorem B.1]) implies that

$$(N_1(t), N_2(t), C_1(t), C_2(t)) \le \bar{v}(t),\ \forall\, t \ge 0.$$

Since $\mu^\epsilon < 0$, it follows that $\bar{v}(t) \to 0$ as $t \to \infty$. Thus, $(N_1(t), N_2(t)) \to 0$ as $t \to \infty$. This implies that (C_1, C_2) is asymptotic to (2.5). By the theory of asymptotically periodic semiflows (see, e.g., [29] or [30, section 3.2]), it follows that $\lim_{t\to\infty}(C_1(t), C_2(t)) = (0,0)$. We complete the proof of Part (i).

Next, we consider the case where $\mathcal{R}_0^\epsilon > 1$. From (3.1) and (3.2), it follows that the discrete-time system $\{S^n\}_{n\geq 0}$ admits a global attractor in $\mathbb{X}$. Now we prove that $\{S^n\}_{n\geq 0}$ is uniformly persistent with respect to $(\mathbb{X}_0, \partial\mathbb{X}_0)$.

Given $(N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X}_0$. Then by [23, Theorem 4.1.1] as generalized to nonautonomous systems, the irreducibility of the cooperative matrix (3.11) and the first two equations of system (3.3) imply that $(N_1(t), N_2(t))^T \gg (0,0),\ \forall\ t > 0$. Hence, $\mathbb{X}$ and $\mathbb{X}_0$ are positively invariant. Clearly, $\partial\mathbb{X}_0$ is relatively closed in $\mathbb{X}$.

Let

$$M_\partial = \{(N_1^0, N_2^0, C_1^0, C_2^0) \in \partial\mathbb{X}_0 : S^n(N_1^0, N_2^0, C_1^0, C_2^0) \in \partial\mathbb{X}_0,\ \forall\ n \geq 0\}.$$

We are going to prove that

$$M_\partial := \{(0, 0, C_1^0, C_2^0) \in \partial\mathbb{X}_0 : C_1^0 \geq 0,\ C_2^0 \geq 0\}. \tag{3.13}$$

It suffices to prove that for any $(N_1^0, N_2^0, C_1^0, C_2^0) \in M_\partial$, we have $(N_1(m\tau), N_2(m\tau)) = (0,0),\ \forall\ m \geq 0$. If it is not true, then there exists $m_1 \geq 0$ such that $(N_1^0, N_2^0, C_1^0, C_2^0) \in M_\partial$ and $(N_1(m_1\tau), N_2(m_1\tau)) > (0,0)$. Hence, the irreducibility of the cooperative matrix (3.11) implies that $(N_1(m\tau), N_2(m\tau))^T \gg (0,0),\ \forall\ m > m_1$. This contradicts the definition of M_∂, and hence, (3.13) is true.

Note that every orbit in M_∂ approaches to $\{\hat{0}\}$, and $\{\hat{0}\}$ is acyclic in M_∂. By [30, Theorem 1.3.1], it follows that $\{S^n\}_{n\geq 0}$ is uniformly persistent with respect to $(\mathbb{X}_0, \partial\mathbb{X}_0)$. By [30, Theorem 3.1.1], the solutions of system (3.3) are uniformly persistent with respect to $(\mathbb{X}_0, \partial\mathbb{X}_0)$, that is, there exists a $\eta > 0$ such that for any solution $(N_1(t), N_2(t), C_1(t), C_2(t))$ with initial value $(N_1^0, N_2^0, C_1^0, C_2^0) \in \mathbb{X}_0$ satisfies $\liminf_{t\to\infty} N_i(t) \geq \eta,$ for some $i = 1, 2$.

Furthermore, [30, Theorem 1.3.6] implies that S has a fixed point

$$(\tilde{N}_1(0), \tilde{N}_2(0), \tilde{C}_1(0), \tilde{C}_2(0)) \in \mathbb{X}_0.$$

The irreducibility of the cooperative matrix (3.11) implies

$$(\tilde{N}_1(t), \tilde{N}_2(t)) \gg 0,\ \forall\ t > 0.$$

From the third equation of (3.3), we have

$$\tilde{C}_1(t) = e^{-\int_0^t [\alpha_1(s_1)+k]ds_1}\left[\int_0^t e^{\int_0^{s_2}[\alpha_1(s_1)+k]ds_1}\Lambda(s_2)ds_2 + \tilde{C}_1(0)\right], \tag{3.14}$$

where

$$\Lambda(t) := \alpha_2(t)\tilde{C}_2(t) + \epsilon\frac{q_N}{q_C}f(t, W_1^*(t) - q_N\tilde{N}_1(t) - q_C\tilde{C}_1(t))\tilde{N}_1(t). \tag{3.15}$$

From (3.14) and (3.15), it is easy to see that $\tilde{C}_1(t) > 0,\ \forall\ t > 0$. Similarly, we can show that $\tilde{C}_2(t) > 0,\ \forall\ t > 0$. We complete the proof. □

By Theorem 3.1, [30, Theorem 1.3.1] and the similar arguments as in Theorem 2.1, we can obtain the dynamics of the full system (1.5).

Theorem 3.2. *The following statements hold.*

(i) *If $\mathcal{R}_0^\epsilon < 1$, then the trivial solution $(W_1^*(t), W_2^*(t), 0, 0, 0, 0)$ is globally attractive in $\mathbb{R}_+^6$ for (1.5);*

(ii) *If $\mathcal{R}_0^\epsilon > 1$, then there exists $\eta > 0$ such that every solution*

$$(R_1(t), R_2(t), N_1(t), N_2(t), C_1(t), C_2(t))$$

of (1.5) *with* $(R_1(0), R_2(0), N_1(0), N_2(0), C_1(0), C_2(0)) \in \mathbb{R}^6_+ \setminus \{(a, b, 0, 0, c, d) : a, b, c, d \in \mathbb{R}_+\}$ *satisfies*

$$\liminf_{t\to\infty} N_i(t) \geq \eta, \text{ for some } i = 1, 2.$$

Moreover, system (1.5) *admits at least one positive* τ*-periodic solution*

$$(\tilde{R}_1(t), \tilde{R}_2(t), \tilde{N}_1(t), \tilde{N}_2(t), \tilde{C}_1(t), \tilde{C}_2(t)),$$

where $(\tilde{N}_1(t), \tilde{N}_2(t), \tilde{C}_1(t), \tilde{C}_2(t))$ *is a positive* τ*-periodic solution of system* (3.3).

4. **Numerical simulations.** We first explore influences of seasonality on algae growth/bloom by numerical simulations of system (1.3). We choose the basal parameters by

$$D = 0.01, E = 0.3, \psi = 0.2, \phi = 0.1, m = 0.1, \tag{4.1}$$

and $\epsilon p(t, R, N) = \epsilon \frac{\mu_{\max}(t)K}{K+R} N$. Then we select $K = 1$ and let

$$\begin{aligned} R_1^{\text{in}}(t) &= 0.5[u\cos(2\pi t/365) + 1.01], \\ R_2^{\text{in}}(t) &= u\cos(2\pi t/365) + 1.01, \\ \mu_{\max}(t) &= 0.3131. \end{aligned} \tag{4.2}$$

As u varies in $[0.4, 0.9]$, numerical calculations indicate that the algae growth/bloom threshold $\mathcal{R}_0$ is a decreasing function of u (see Figure 4.1). Since the the time

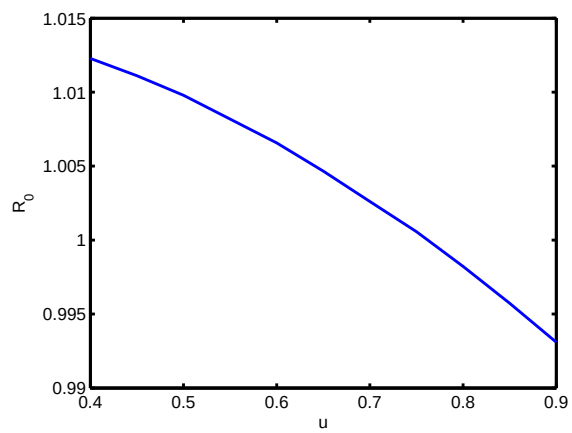

FIGURE 4.1. $\mathcal{R}_0$ decreases as the heterogenous coefficient u increases.

averages of R_1^{in} and R_2^{in} in (4.2) are given at $u = 0$, it suggests that the more time heterogeneity of resource inputs, the lower of the basic reproduction number. One more interesting thing from the simulation is that suitable heterogenous resource inputs can reduce the algae growth/bloom threshold below unity under the condition that the time averages are fixed.

Now, we select $K = 0.2$, take

$$\begin{aligned} R_1^{\text{in}}(t) &= 0.5[\cos(2\pi t/365) + 1.01], \\ R_2^{\text{in}}(t) &= \cos(2\pi t/365) + 1.01, \\ \mu_{\max}(t) &= 0.15[1.01 + u\cos(2\pi t/365)] \end{aligned} \tag{4.3}$$

and fix the other parameters as in (4.1). Through the synthetic effects of heterogenous resource inputs and heterogenous nutrient conversions, the algae growth/bloom threshold becomes an increasing function of u (see Figure 4.2). This means that the higher heterogenous conversion rate, the more risk algae blooming. In contrast,

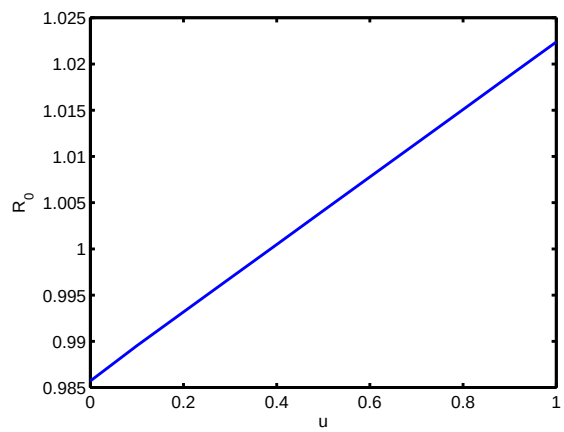

FIGURE 4.2. $\mathcal{R}_0$ increases as the heterogenous coefficient u increases.

if we replace the fluctuation functions of resource inputs by their time averages and let only $\mu_{\max}(t)$ fluctuate by (4.3). Then numerical calculations show that $\mathcal{R}_0$ is a decreasing function of u. Therefore, the combined-effects of resource oscillations and conversion oscillations result in the monotonic increase of $\mathcal{R}_0$ in u. Further numerical computations for model (1.3) support the above results for the persistence and extinction of algae according to algae growth/bloom threshold $\mathcal{R}_0$. Let $u = 0$ in (4.3), which corresponds to $\mathcal{R}_0 < 1$ (see Figure 4.2). Then algae die out (see the left panel of Figure 4.3). If $u = 1$ in (4.3), which corresponds to $\mathcal{R}_0 > 1$ (see Figure

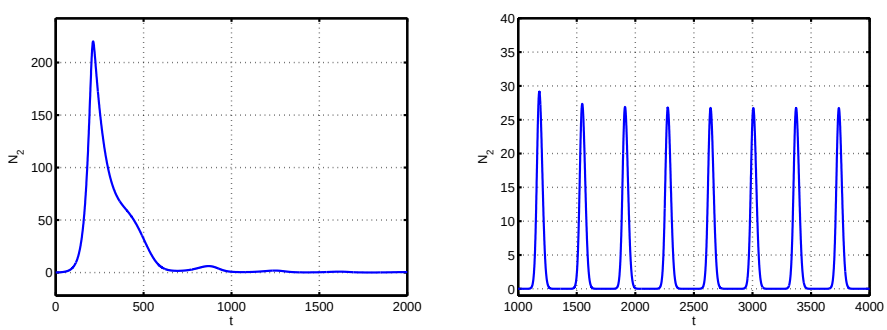

FIGURE 4.3. The left panel shows that algae die out where u takes zero in (4.3). The right panel indicates that algae invade periodically where u takes 1 in (4.3).

4.2), then algae populations invade seasonally (see the right panel of Figure 4.3).

Inspired by practical management of algae blooming, we introduce a term $-k_1(t)N_1$ in the third equation of (1.3) and a term $-k_2(t)N_2$ in the fourth equation of

(1.3) to simulate the removal of algae by mechanical or chemical approaches. Then we select $K = 0.2$, take

$$\begin{aligned} k_1(t) &= 0.04u[\cos(2\pi t/365) + 1.01], \\ k_2(t) &= 0.08u[\cos(2\pi t/365) + 1.01], \\ \mu_{\max}(t) &= 0.15[1.01 + \cos(2\pi t/365)], \end{aligned} \tag{4.4}$$

and fix $R_i^{\text{in}}(t)$ by (4.3). Simulations indicate that $\mathcal{R}_0$ is below 1 when $u > 0.5$ (see Figure 4.4).

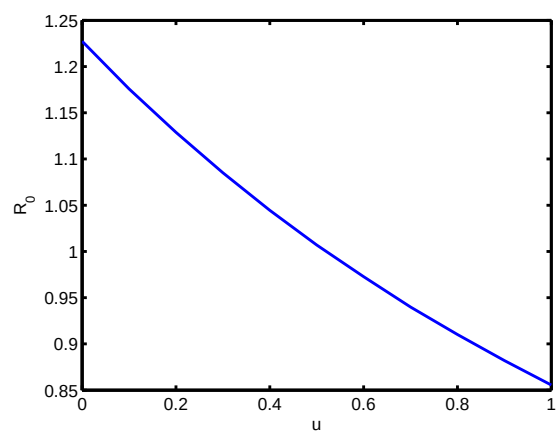

FIGURE 4.4. $\mathcal{R}_0$ decreases as the heterogenous coefficient u increases and is below 1 when $u > 0.5$.

In the rest of this section, we focus on the numerical simulations of system (1.5) to demonstrate influences of allocation coefficient ϵ and recycling coefficient q_C on the dynamics of (1.5). For illustration purpose, we take $K = 0.2, q_N = 0.0139, k = 0.1$, and use the parameter values in (4.1) and the time-dependent coefficients:

$$\begin{aligned} R_1^{\text{in}}(t) &= 0.0056(1.01 + \cos(2\pi t/365)), \\ R_2^{\text{in}}(t) &= 0.005(1.01 + \cos(2\pi t/365)), \\ \mu_{\max}(t) &= 0.15(1.01 + \cos(2\pi t/365)). \end{aligned} \tag{4.5}$$

In the first step, we fix $k = 0.1$ and then take $\epsilon = 0.012, 0.022, 0.032$ respectively. Numerical simulations indicate that algae concentrations decreases as ϵ increases, which results in the decrease of toxin (see Figure 4.5). Further simulations indicate that C_2 increases as ϵ increases in the left of $\epsilon = 0.012$ and approximates the maximum at $\epsilon = 0.012$ (see Figure 4.6). It should be noted that the enhance of allocation coefficient ϵ adds more production coefficient of toxin, but lowers the production of algae. Since algae are the main pool to produce toxin in the former case, the concentration of toxin is reduced. However, the production coefficient of toxin plays the major role in the latter, thus giving more toxin concentrations when ϵ increases in the left of $\epsilon = 0.012$.

In the second step, we fix $\epsilon = 0.01$ and take $q_C = 0.01, 0.02, 0.03$ respectively. Numerical calculations show that toxin concentrations are reduced due to larger inhibition coefficient q_C in the production rates of toxins, but this coefficient gives little effect on the concentrations of resources for large time (see Figure 4.7).

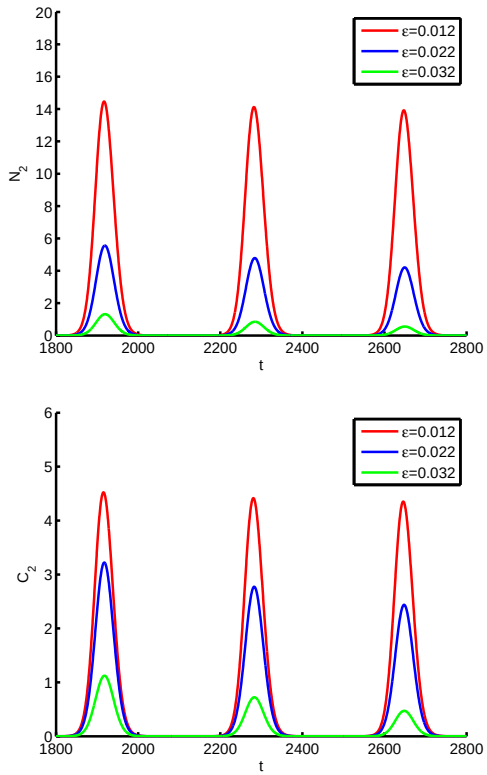

FIGURE 4.5. The left panel shows that algae decrease as ϵ increases. The right panel indicates that toxin decreases as a result of algae decrease.

5. **Discussion.** In this paper, we analyze two mathematical models which were established to represent the growth of populations of toxic flagellates or cyanobacteria in the cove-main lake. Large lakes often have a number of smaller adjoining coves, and that previous models either treat these as an ensemble, or focus on a single cove [9]. For the approach where an ensemble of fringing coves is represented as a hydraulic storage zone, the authors in [9] proposed an advection-dispersion-reaction system to model the interactions of nutrient, algae and their toxins in a riverine reservoir. Those mathematical analyses of this model are given in [13]. Here, we concentrate on the study of another approach, that is, we focus on the investigation of the dynamics of nutrient, algae and their toxins with exchange between a single cove and a large lake. To incorporate the influence of seasonal temperature variations on non-steady dynamics, the coefficients in the model systems are time-dependent.

For many flagellate toxins, the toxin contains little or none of the limiting nutrient and the model (1.3) is more appropriate. Since the first four equations of (1.3) are independent of the equations of C_1 and C_2, this makes the analyses easier and the results more complete. We first define the basic reproduction number, $\mathcal{R}_0$, for the system (1.3) in (2.11). Then, we are able to prove that the washout periodic state is globally stable if $\mathcal{R}_0 < 1$, and there exists a globally stable coexistence

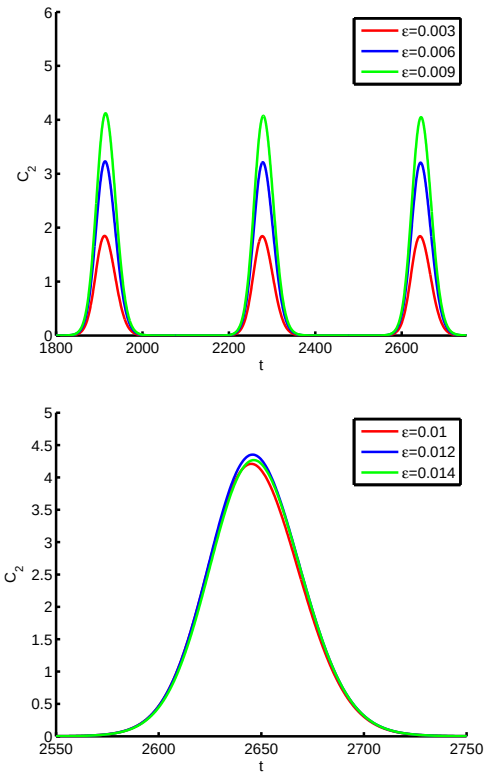

FIGURE 4.6. The left panel shows that toxin concentration C_2 increase as ϵ increases in the left of $\epsilon = 0.012$. The right panel indicates that C_2 attains the maximum at $\epsilon = 0.012$.

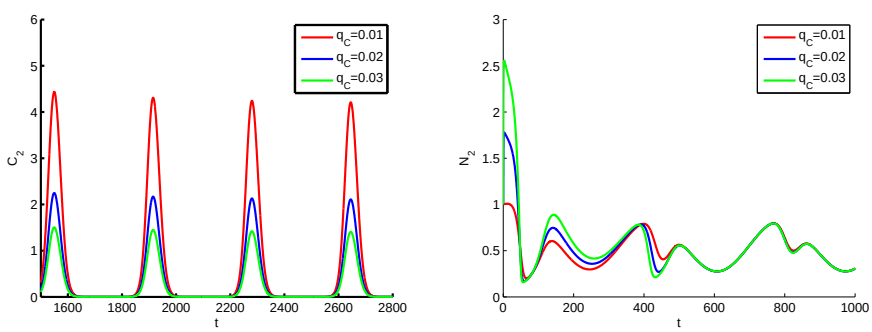

FIGURE 4.7. The left panel shows that toxin concentration decreases as q_C increases. The right panel indicates that the nutrient recycling coefficient contributes little to the nutrient concentration in the long run.

periodic state if $\mathcal{R}_0 > 1$ (see Theorem 2.1 and Theorem 2.2) by appealing to the theory of monotone dynamical systems and chain transitive sets (see, e.g., [23, 26]). Although $\mathcal{R}_0$ is abstractly given in (2.11), we can calculate it numerically (see our numerical simulations). For the special where the coefficients of (1.3) are all positive constants (i.e., the system (1.3) is temporally homogenous), $\mathcal{R}_0$ is reduced into the one defined in (2.13). For this homogenous case, it follows that $\mathcal{R}_0$ is the largest real eigenvalue of $\mathbf{F}\mathbf{V}^{-1}$ by (2.13) and the Perron-Frobenius Theorem (see, e.g., [23, Theorem 4.3.1]), where $\mathbf{F}\mathbf{V}^{-1}$ is given in (2.14).

The toxin production of cyanobacteria (cylindrospermopsin case) is assumed to be proportional to the product of growth rate and abundance, and the governing system is (1.5). In (3.7), we also define the basic reproduction number, $\mathcal{R}_0^\epsilon$, for the system (1.5). Then we determine the threshold dynamics of system (1.5), namely, the trivial periodic state is globally asymptotically stable, and the algae will be washed out eventually if $\mathcal{R}_0^\epsilon < 1$, while there exists at least one positive periodic state and the algae can persist continuously when $\mathcal{R}_0^\epsilon > 1$ (see Theorem 3.1 and Theorem 3.2). In general, the uniqueness and stability of this positive periodic state remain open. However, we point out that we are able to prove the positive periodic state is unique and globally stable for system (1.5) under the additional assumption:

$$m \text{ (algal mortality) } = k \text{ (toxin decay)}.$$

Mathematically, (1.5) is more tractable if we further impose this extra assumption (mathematical proofs not shown). When the coefficients of (1.5) are all positive constants, we can also show that $\mathcal{R}_0^\epsilon$ is the largest real eigenvalue of $\mathbf{F}^\epsilon\mathbf{V}^{-1} := (1-\epsilon)\mathbf{F}\mathbf{V}^{-1}$, where $\mathbf{F}\mathbf{V}^{-1}$ is given in (2.14).

There might be opportunities to mitigate algal blooms in some reservoirs where toxic blooms have occurred. It was recognized that mathematical modeling can provide assistance in management of harmful algae within coves through flow manipulations. Here, we rigorously determine a threshold index, the basic reproduction number for the algae, and show that it can predict the algal persistence or extinction for the two-compartment model of algal dynamics with temporal variations proposed by the authors in [9]. The basic reproduction number for the algae involves: the main-cove characteristics (i.e. $D(t)$ and $E(t)$); the inflowing nutrient concentration ($R_1^{\text{in}}(t)$ and $R_2^{\text{in}}(t)$); a value of the nutrient uptake rate (or growth rate) $f(t, R)$; and the value of period τ. We numerically compute the basic reproduction number and show the influences of seasonality on algae growth in Section 4. This study provides a computable formula that predicts the algal dynamics with temporal variations.

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