Dynamics for Phytoplankton-Zooplankton System with Time Delays

By

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Abstract. In this paper, a system consisting of two harmful phytoplanktons and one zooplankton with two time delays is investigated. Firstly, the global existence, nonnegativity and boundedness of the solutions of the system are discussed. Secondly, using time delays as bifurcating parameters, the existence of local Hopf bifurcations at the positive equilibrium of the system is investigated in details. The phenomenon of stability switches is confirmed under some certain conditions. It is shown by numerical simulations under some suitable parameters that the system can exhibit complicated dynamic properties, and undergoes changes from stable periodic solution or equilibrium to chaos or from chaos to stable periodic solution or equilibrium. At last, some conclusions are given. The direction of the Hopf bifurcations and the stability of the bifurcation periodic solutions are given in Appendix by using the center manifold and normal form theory.

Key Words and Phrases. Phytoplankton-Zooplankton system, Time delay, Stability, Hopf bifurcation, Chaos.

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1. Introduction

Plankton is the basis of all aquatic food chains, especially, phytoplankton occupies the first trophic level. Phytoplanktons do huge contributions to our earth: food for marine life, oxygen for human life and also they absorb half of the carbon dioxide which may be contributing to global warming [1]. However there has been a global increase in harmful plankton blooms in the last three decades [2–4]. The negative effects of harmful plankton species on human health, ecosystem and environment are well established, but the control of such a problem is under investigation.

In recent years, there has been increasing interest in Harmful Algal Bloom (HAB) and its control (for example, see [5–9]). Generally high nutrient levels and favorable conditions for algae play a key role in rapid or massive growth of algae, high predation pressure as well as other unfavorable conditions for algae may limit their growth, but it may lead to oscillations or recurring blooms in the plankton system. A broad classification of HAB species is distinguished

into two groups: the toxin producers, which can contaminate seafood or kill fish, and the high-biomass producers, which can cause anoxia and indiscriminate mortalities of marine life after reaching dense concentrations. Phytoplankton blooms may be dispersed by physical factors or removed from the water column due to sinking, of which mortality of individual cell within blooms may be affected by autolysis, viruses, predatory bacteria, or grazing zooplankton [10–12]. Microzooplakton feeding on HAB species is important in two ways: first, grazing may serve to prevent blooms or lessen their magnitude; second, for toxin producing species, grazers may accumulate and subsequently transfer toxins. Hence it is necessary to study about the pattern of HAB and its control by microzooplankton.

Recent studies reveal that some times bloom of certain harmful species leads to release of both toxins and allelopathic substances. Allelopathic substances may physiologically impair, stun, repel or induce unavoidable reactions, and kill grazers. Among marine algae, allelopathy has been observed [13], but the chemical nature and the role of allelopathic compounds are still not known. The current studies have been originated from the theoretical as well as experimental results on the interaction of HAB and different types of phytoplankton-zooplankton interactions [7–9, 14].

Motivated from the literature and the field observations [7, 8, 14], the authors propose a dynamic model [6] consisting of two harmful phytoplanktons and zooplankton, and the role of harmful phytoplanktons in the termination of plankton bloom has been observed. In [7, 8, 14, 15], the authors conclude that the presence of two harmful phytoplanktons in the system reduces the high abundance of harmful phytoplankton and the zooplankton population. Furthermore, the biomass distribution observed in the field study demonstrates that introduction of two harmful phytoplankton leads to the stable co-existence of all the species through the termination of bloom and can be used as a controlling agent for the stability of marine system. The authors in [6] modify the model proposed by [7, 8], assuming the mortality process of the predator due to toxin liberation by harmful phytoplankton as a break-even point by discrete time delays, and investigate the effects of time delays to control blooms/oscillations. The authors in [6] observe that when there exists a single time delay in the mortality of zooplankton due to toxin liberation by one harmful phytoplankton, for certain critical value of the time delay, recurrent bloom occurs and similar phenomenon is observed for the other harmful phytoplankton. This phenomenon can be interpreted as a “paradox” in marine ecology. It is interesting because competitive exclusion principle plays major role and the co-existence of several prey-predator population is possible. But presence of two time delays in the mortality of zooplankton due to toxin liberation by two harmful phytoplanktons reduces the oscillations in the system and further stable

co-existence is possible. This resolves the plankton “paradox”. The above findings clearly demonstrate the role of the time delays in the mortality of zooplankton due to toxin liberation by two harmful phytoplanktons and also in the termination of plankton bloom.

In [6, 15], the authors use the linear function representing the distribution of toxin substances and the predation response function. As liberation of toxin reduces the growth of zooplankton and in this period toxin-producing plankton population is not easily accessible, a more common and intuitively obvious choice is the nonlinear functional form to describe the grazing phenomena. Moreover, saturation of grazing function allows the toxin-producing phytoplankton population to escape from grazing pressure of zooplankton and forms a tide. The main object for considering nonlinear functional form is to understand mechanisms for excitable nature of planktonic blooms and its possible control. In [8], the authors consider the distribution of toxin substances as Holling II type functional form as follows:

$$(1.1) \quad \begin{cases} \dot{p}_1(t) = r_1 p_1(t) \left(1 - \frac{p_1(t)}{K}\right) - \alpha p_1(t) p_2(t) - m p_1(t) z(t), \\ \dot{p}_2(t) = r_2 p_2(t) \left(1 - \frac{p_2(t)}{L}\right) - \beta p_1(t) p_2(t) - n p_2(t) z(t), \\ \dot{z}(t) = (m_1 p_1(t) + n_1 p_2(t)) z(t) - \mu z(t) - \frac{\theta_1 p_1(t) z(t)}{\gamma_1 + p_1(t)} - \frac{\theta_2 p_2(t) z(t)}{\gamma_2 + p_2(t)}, \end{cases}$$

where $p_1(t)$ and $p_2(t)$ are the concentrations of two harmful phytoplanktons at time t , $z(t)$ is the concentration of zooplankton at time t . All parameters are positive constants and their biological meanings are as follows. r_1 and r_2 represent the growth rates of the harmful phytoplanktons, respectively. K and L represent the environmental carrying capacity of the two harmful phytoplanktons, respectively. m and n represent the maximum zooplankton ingestion rates for both the harmful phytoplankton species and m_1 and n_1 represent the maximum zooplankton conversion rates, respectively. μ represents the natural death rate of zooplankton. α and β represent the inhibitory effects among the two competitive harmful phytoplanktons, respectively. θ_1 and θ_2 represent the rates of toxin liberation by the harmful phytoplanktons, respectively, which reduces the growth of zooplankton. γ_1 and γ_2 represent the half-saturation constants for the two toxin-producing phytoplanktons, respectively. From [19], it is known that the system (1.1) has seven equilibria denoted by $E_0(0, 0, 0)$, $E_1(K, 0, 0)$, $E_2(0, L, 0)$, $E_3(\tilde{p}_1, \tilde{p}_2, 0)$, $E_4(\bar{p}_1, 0, \bar{z})$, $E_5(0, \hat{p}_2, \hat{z})$, $E_6(p_1^*, p_2^*, z^*)$ under some certain conditions. The authors [19] give the stability conditions of the equilibria E_i ($i = 0, 1, 2, 3, 4, 5, 6$) in details and the persistence conditions of three species are also given.

The effect of toxic phytoplankton is not instantaneous but is mediated by some time delay. Now, to explain the periodic nature of bloom phenomena, we introduce discrete time delays τ_1 and τ_2 in the mortality of zooplankton due

to liberation of toxic substance by two harmful phytoplanktons p_1 and p_2 , respectively. Hence we add the two time delays in the system (1.1):

$$(1.2) \quad \begin{cases} \dot{p}_1(t) = r_1 p_1(t) \left(1 - \frac{p_1(t)}{K}\right) - \alpha p_1(t) p_2(t) - m p_1(t) z(t), \\ \dot{p}_2(t) = r_2 p_2(t) \left(1 - \frac{p_2(t)}{L}\right) - \beta p_1(t) p_2(t) - n p_2(t) z(t), \\ \dot{z}(t) = (m_1 p_1(t) + n_1 p_2(t)) z(t) - \mu z(t) - \frac{\theta_1 p_1(t-\tau_1) z(t)}{\gamma_1 + p_1(t-\tau_1)} - \frac{\theta_2 p_2(t-\tau_2) z(t)}{\gamma_2 + p_2(t-\tau_2)}. \end{cases}$$

On the basis of the biological meaning, the initial conditions of the system (1.2) are taken as follows,

$$(1.3) \quad \begin{aligned} p_1(\theta) = \varphi_1(\theta) &\geq 0, & p_2(\theta) = \varphi_2(\theta) &\geq 0, \\ z(\theta) = \varphi_3(\theta) &\geq 0, & \theta \in [-\tau, 0], & \varphi_i(0) > 0, \end{aligned}$$

where $\varphi_i(\theta) \in C$, $\tau = \max\{\tau_1, \tau_2\}$, $i = 1, 2, 3$, and C denotes the Banach space $C([-\tau, 0], \mathbf{R}_+^3)$ of continuous functions mapping the interval $[-\tau, 0]$ into $\mathbf{R}_+^3$ with supremum norm. It is easy to show that the system (1.2) has the same equilibria as the system (1.1). About the equilibria E_i ($i = 0, 1, 2, 3, 4, 5$), various dynamic properties, such as instability, locally asymptotical stability, globally asymptotical stability, bistability, Hopf bifurcation, and so on. These properties have been discussed in [16]. Hence in this paper, only the dynamic properties of the positive equilibrium $E_6 := E^*$ are considered.

The purpose of this paper is to study the system (1.2) from the point of bifurcation and investigate the role of the time delays. By analyzing the distribution of the roots of the characteristic equation associated with the system (1.2) in details, the phenomenon of the stability switches can be found.

In addition, in [17, 18], chaotic phenomenon has been found in the system (1.2) when $\theta_1 = \theta_2 = 0$ under some parameters. Hence in the end of this paper, some numerical simulation examples are given to show complicated dynamic properties of the system (1.2) such as the changes of the dynamical behaviors from periodic orbits to chaos or from chaos to periodic orbits.

This paper is organized as follows. In Section 2, the global existence, nonnegativity and boundedness of the solutions of the system (1.2) with the initial conditions (1.3) are discussed. In Section 3, by employing the similar methods in [15, 19, 20] to analyze the distribution of the roots of the characteristic equation associated with the system (1.2), the existence of the local Hopf bifurcation is obtained. The phenomenon of stability switches can be found as the time delays changes. In Section 4, some numerical simulations are given to confirm the theoretical analyses. In Section 5, by some numerical simulation examples, the existence of chaos and its control are investigated. In Section 6, some conclusions are given. The direction of the Hopf bifurcations

and the stability of the bifurcated periodic solutions are also determined by using the theory of normal form and center manifold [15] in the Appendix.

2. Global existence, nonnegativity and boundedness of solutions

In this section, a theorem is given about the global existence, nonnegativity and boundedness of solutions of the system (1.2) with the initial conditions (1.3).

Theorem 2.1. *The solution $(p_1(t), p_2(t), z(t))$ of the system (1.2) with the initial conditions (1.3) exists and is unique, positive and bounded on $[0, +\infty)$.*

Proof. From local existence and uniqueness theorem of solutions for functional differential equations [21], the solution $(p_1(t), p_2(t), z(t))$ exists and is unique on $[0, \sigma)$ for some constant $\sigma > 0$. Firstly, we show that the solution $(p_1(t), p_2(t), z(t))$ is positive on $[0, \sigma)$. In fact, from the system (1.2), for $t \in [0, \sigma)$, we have that

$$p_1(t) = p_1(0)e^{\int_0^t [r_1(1-p_1(u)/K) - \alpha p_2(u) - m z(u)] du} > 0,$$

$$p_2(t) = p_2(0)e^{\int_0^t [r_2(1-p_2(u)/L) - \beta p_1(u) - n z(u)] du} > 0,$$

$$z(t) = z(0)e^{\int_0^t [m_1 p_1(u) + n_1 p_2(u) - \mu - \theta_1 p_1(u - \tau_1)/(\gamma_1 + p_1(u - \tau_1)) - \theta_2 p_2(u - \tau_2)/(\gamma_2 + p_2(u - \tau_2))] du} > 0.$$

In the following, it further is shown that the solution $(p_1(t), p_2(t), z(t))$ of the system (1.2) is bounded on $t \in [0, \sigma)$. From the system (1.2) and the positivity of the solution on $t \in [0, \sigma)$, we have

$$(2.1) \quad \begin{cases} \dot{p}_1(t) \leq r_1 p_1(t) \left(1 - \frac{p_1(t)}{K}\right), \\ \dot{p}_2(t) \leq r_2 p_2(t) \left(1 - \frac{p_2(t)}{L}\right). \end{cases}$$

Hence, $p_1(t)$ and $p_2(t)$ are bounded on $t \in [0, \sigma)$.

Next we prove the boundedness of $z(t)$ for $t \in [0, \sigma)$. Let $y(t) = (m_1/m)p_1(t) + (n_1/n)p_2(t) + z(t)$, then

$$(2.2) \quad \begin{aligned} \dot{y}(t) &= \frac{m_1}{m} \dot{p}_1(t) + \frac{n_1}{n} \dot{p}_2(t) + \dot{z} \\ &\leq \frac{m_1}{m} r_1 p_1(t) \left(1 - \frac{p_1}{K}\right) + \frac{n_1}{n} r_2 p_2(t) \left(1 - \frac{p_2}{L}\right) \\ &\quad + \frac{m_1}{m} \mu p_1(t) + \frac{n_1}{n} \mu p_2(t) - \mu y(t). \end{aligned}$$

Since the boundness of $p_1(t)$ and $p_2(t)$, from (2.2) we have that $y(t)$ is bounded on $t \in [0, \sigma)$. Furthermore, $z(t)$ is bounded on $t \in [0, \sigma)$.

Therefore, from continuation theorem of solutions for functional differential equations [21] it has that the solution (p_1, p_2, z) of the system (1.2) is existent, unique, positive and bounded on $t \in [0, +\infty)$.

By comparison theorem [22], from (2.1), it can obtain that $\limsup_{t \rightarrow \infty} p_1(t) \leq K$ and $\limsup_{t \rightarrow \infty} p_2(t) \leq L$. Furthermore, from (2.2), it can yield

$$\dot{y}(t) \leq \frac{m_1}{m} r_1 \frac{K}{4} + \frac{n_1}{n} r_2 \frac{L}{4} + \frac{m_1}{m} \mu K + \frac{n_1}{n} \mu L - \mu y(t),$$

which shows that

$$\limsup_{t \rightarrow \infty} y(t) \leq \frac{m_1 n K (r_1 + 4\mu) + m n_1 L (r_2 + 4\mu)}{4 m n \mu}.$$

This completes the proof. $\square$

3. Stability of the positive equilibrium and local Hopf bifurcation

In this section, the local stability of the positive equilibrium and the existence of local Hopf bifurcations are investigated. Let $E^*(p_1^*, p_2^*, z^*)$ denote the positive equilibrium, where

$$p_2^* = L A p_1^* + L B, \quad z^* = \frac{r_2(1-B)}{n} - \frac{r_2 A + \beta}{n} p_1^*$$

and p_1^* satisfies the relation

$$C_1 p_1^{*3} + C_2 p_1^{*2} + C_3 p_1^* + C_4 = 0,$$

where

$$A = \frac{n r_1 - m \beta K}{K(m r_2 - n \alpha L)}, \quad B = \frac{m r_2 - n r_1}{m r_2 - n \alpha L}, \quad C_1 = L A (m_1 + n_1 L A),$$

$$C_2 = (\gamma_2 + L B)(m_1 + n_1 L A) + L A (m_1 \gamma_1 + n_1 \gamma_1 L A + n_1 L B - \mu - \theta_1 - \theta_2),$$

$$C_3 = (\gamma_2 + L B)(m_1 \gamma_1 + n_1 \gamma_1 L A + n_1 L B - \mu - \theta_1)$$

$$+ L A \gamma_1 (n_1 L B - \mu - \theta_2) - \theta_2 L B,$$

$$C_4 = \gamma_1 [(\gamma_2 + L B)(n_1 L B - \mu) - \theta_2 L B].$$

Hence the positive equilibrium E^* exists if the following inequalities hold [8]:

$$(H) \quad r_1 > \alpha L, \quad \frac{\alpha L}{r_2} < \frac{m}{n} < \frac{r_1}{\beta K}, \quad p_1^* < \frac{K r_2 (r_1 - \alpha L)}{r_1 r_2 - \alpha \beta K L}.$$

In the following, we always assume that (H) holds.

Let $u_1(t) = p_1(t) - p_1^*$, $u_2(t) = p_2(t) - p_2^*$, $u_3(t) = z(t) - z^*$, then the system (1.2) becomes:

$$(3.1) \quad \begin{cases} \dot{u}_1(t) = -\frac{r_1 p_1^*}{K} u_1(t) - \alpha p_1^* u_2(t) - m p_1^* u_3(t) - \frac{r_1}{K} u_1^2(t) \\ \quad - \alpha u_1(t) u_2(t) - m u_1(t) u_3(t), \\ \dot{u}_2(t) = -\beta p_2^* u_1(t) - \frac{r_2 p_2^*}{L} u_2(t) - n p_2^* u_3(t) - \frac{r_2}{L} u_2^2(t) \\ \quad - \beta u_1(t) u_2(t) - n u_2(t) u_3(t), \\ \dot{u}_3(t) = (m_1 u_1(t) + n_1 u_2(t)) z^* - \frac{\theta_1 \gamma_1 z^*}{(\gamma_1 + p_1^*)^2} u_1(t - \tau_1) \\ \quad - \frac{\theta_2 \gamma_2 z^*}{(\gamma_2 + p_2^*)^2} u_2(t - \tau_2) + \rho(u_{1t}, u_{2t}, u_{3t}), \end{cases}$$

where

$$\begin{aligned} \rho(u_{1t}, u_{2t}, u_{3t}) &= [m_1 u_1(t) + n_1 u_2(t)] u_3(t) \\ &\quad - \left[\frac{\theta_1 \gamma_1}{(\gamma_1 + p_1^*)^2} u_1(t - \tau_1) + \frac{\theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} u_2(t - \tau_2) \right] u_3(t) \\ &\quad + \frac{\theta_1 \gamma_1}{(\gamma_1 + p_1^*)^3} u_1^2(t - \tau_1) u_3(t) - \frac{\theta_1 \gamma_1 z^*}{(\gamma_1 + p_1^*)^4} u_1^3(t - \tau_1) \\ &\quad + \frac{\theta_2 \gamma_2}{(\gamma_2 + p_2^*)^3} u_2^2(t - \tau_2) u_3(t) - \frac{\theta_2 \gamma_2 z^*}{(\gamma_2 + p_2^*)^4} u_2^3(t - \tau_2) + O(4). \end{aligned}$$

The characteristic equation of the system (3.1) at $(0, 0, 0)$ is

$$(3.2) \quad \lambda^3 + b_2 \lambda^2 + b_1 \lambda + b_0 + (q_1 \lambda + q_0) e^{-\lambda \tau_1} + (h_1 \lambda + h_0) e^{-\lambda \tau_2} = 0,$$

where

$$\begin{aligned} b_0 &= \left[n_1 \left(\frac{nr_1}{K} - m\beta \right) + m_1 \left(\frac{mr_2}{L} - \alpha n \right) \right] p_1^* p_2^* z^*, \\ b_1 &= \left[\frac{r_1 r_2}{KL} - \alpha \beta \right] p_1^* p_2^* + (mm_1 p_1^* + nn_1 p_2^*) z^*, \quad b_2 = \frac{r_1 p_1^*}{K} + \frac{r_2 p_2^*}{L}, \\ q_0 &= -\frac{\theta_1 \gamma_1}{(\gamma_1 + p_1^*)^2} \left[\frac{mr_2}{L} - \alpha n \right] p_1^* p_2^* z^*, \quad q_1 = -\frac{\theta_1 m \gamma_1 p_1^* z^*}{(\gamma_1 + p_1^*)^2}, \\ h_0 &= -\frac{\theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} \left[\frac{nr_1}{K} - m\beta \right] p_1^* p_2^* z^*, \quad h_1 = -\frac{n \theta_2 \gamma_2 p_2^* z^*}{(\gamma_2 + p_2^*)^2}. \end{aligned}$$

Now the similar methods in [20, 23, 24] are applied to investigate the distribution of roots of (3.2). When $\tau_1 = \tau_2 = 0$, (3.2) becomes

$$(3.3) \quad \lambda^3 + b_2 \lambda^2 + (b_1 + q_1 + h_1) \lambda + b_0 + q_0 + h_0 = 0.$$

By Routh-Hurwitz criterion, if

$$(3.4) \quad b_0 + q_0 + h_0 > 0 \quad \text{and} \quad b_2(b_1 + q_1 + h_1) > b_0 + q_0 + h_0$$

hold, then all roots of (3.3) have negative real parts and $\lambda = 0$ is not the root of (3.2).

In the following, the case $\tau_2 = 0$ and $\tau_1 > 0$ is considered. Obviously, $i\zeta$ ($\zeta > 0$) is a root of (3.2) with $\tau_2 = 0$ if and only if

$$-\zeta^3 i - b_2 \zeta^2 + (b_1 + h_1)\zeta i + b_0 + h_0 + (iq_1 \zeta + q_0)(\cos \zeta \tau_1 - i \sin \zeta \tau_1) = 0.$$

Separating the real and imaginary parts gives

$$(3.5) \quad \begin{cases} -\zeta^3 + (b_1 + h_1)\zeta = q_0 \sin \zeta \tau_1 - q_1 \zeta \cos \zeta \tau_1, \\ b_2 \zeta^2 - (b_0 + h_0) = q_0 \cos \zeta \tau_1 + q_1 \zeta \sin \zeta \tau_1, \end{cases}$$

which leads to

$$(3.6) \quad \zeta^6 + p\zeta^4 + q\zeta^2 + r = 0,$$

where

$$p = b_2^2 - 2(b_1 + h_1), \quad q = (b_1 + h_1)^2 - 2b_2(b_0 + h_0) - q_1^2, \quad r = (b_0 + h_0)^2 - q_0^2.$$

Let $v = \zeta^2$, then (3.6) becomes

$$(3.7) \quad h(v) := v^3 + pv^2 + qv + r = 0.$$

From [19], the following lemma is obtained.

Lemma 3.1. *Let $\Delta = p^2 - 3q$, $v^* = (-p + \sqrt{\Delta})/3$, then, the following conclusions hold.*

- (i) *If $r < 0$, then (3.7) has at least one positive root.*
- (ii) *If $r \geq 0$ and $\Delta < 0$, then (3.7) has no positive roots.*
- (iii) *If $r \geq 0$, then (3.7) has positive roots if and only if $v^* > 0$ and $h(v^*) \leq 0$.*

Suppose that (3.7) has positive roots. (3.7) has at most three positive roots, denoted by v_k ($k = 1, 2, 3$), respectively. Then (3.6) has three positive roots $\zeta_k = \sqrt{v_k}$ ($k = 1, 2, 3$). By (3.5), we have

$$\cos \zeta_k \tau_1 = \frac{(b_2 \zeta_k^2 - b_0 - h_0)q_0 + [\zeta_k^3 - (b_1 + h_1)\zeta_k]q_1 \zeta_k}{q_0^2 + q_1^2 \zeta_k^2}.$$

Denote

$$(3.8) \quad \tau_{1k}^j = \frac{1}{\zeta_k} \left[\arccos \frac{(b_2 \zeta_k^2 - b_0 - h_0)q_0 + [\zeta_k^3 - (b_1 + h_1)\zeta_k]q_1 \zeta_k}{q_0^2 + q_1^2 \zeta_k^2} + 2j\pi \right],$$

where $k = 1, 2, 3$, $j = 0, 1, 2, \dots$. Then $\pm i\xi_k$ is a pair of purely imaginary roots of (3.2) with $\tau_1 = \tau_{1k}^j$ and $\tau_2 = 0$.

When $\tau_2 = 0$, let $\lambda(\tau_1) = \alpha(\tau_1) + i\xi(\tau_1)$ be the root of (3.2) satisfying $\alpha(\tau_{1k}^j) = 0$, $\xi(\tau_{1k}^j) = \xi_k$. Then the following transverse condition holds [19, 20, 23].

Lemma 3.2. *If $v_k = \xi_k^2$, then $\text{Sign}\{\alpha'(\tau_{1k}^j)\} = \text{Sign}\{h'(v_k)\}$.*

Proof. Let $\lambda(\tau_1)$ be the root of (3.2). Substituting $\lambda(\tau_1) \equiv \lambda$ into (3.2) and differentiating the both sides of (3.2) with respect to τ_1 , yields that

$$\{3\lambda^2 + 2b_2\lambda + b_1 + h_1 + [q_1 - \tau_1(q_1\lambda + q_0)]e^{-\lambda\tau_1}\} \frac{d\lambda}{d\tau_1} = \lambda(q_1\lambda + q_0)e^{-\lambda\tau_1}.$$

Thus,

$$\left(\frac{d\lambda}{d\tau_1}\right)^{-1} = \frac{(3\lambda^2 + 2b_2\lambda + b_1 + h_1)e^{\lambda\tau_1}}{\lambda(q_1\lambda + q_0)} + \frac{q_1}{\lambda(q_1\lambda + q_0)} - \frac{\tau_1}{\lambda}.$$

From (3.5)–(3.7), we have

$$\begin{aligned} \left[\frac{d\lambda}{d\tau_1}(\tau_{1k}^j)\right]^{-1} &= \frac{b_1 + h_1 - 3\xi_k^2 + i2b_2\xi_k}{-\xi_k^4 + (b_1 + h_1)\xi_k^2 + i[b_2\xi_k^3 - (b_0 + h_0)\xi_k]} \\ &\quad + \frac{q_1}{q_1\xi_k^2 + iq_0\xi_k} + \frac{i\tau_1}{\xi_k}, \\ \text{Re}\left\{\left[\frac{d\lambda}{d\tau_1}(\tau_{1k}^j)\right]^{-1}\right\} &= \frac{(b_1 + h_1 - 3\xi_k^2)[- \xi_k^4 + (b_1 + h_1)\xi_k^2] + 2b_2\xi_k^2[b_2\xi_k^2 - (b_0 + h_0)]}{[- \xi_k^4 + (b_1 + h_1)\xi_k^2]^2 + [b_2\xi_k^3 - (b_0 + h_0)\xi_k]^2} \\ &\quad - \frac{q_1^2}{q_1^2\xi_k^2 + q_0^2} \\ &= \frac{1}{A[q_1^2\xi_k^2 + q_0^2]} \{3\xi_k^4 + 2p\xi_k^2 + q + q_1^2\}[q_1^2\xi_k^2 + q_0^2] \\ &\quad - q_1^2\{\xi_k^2[(b_1 + h_1)^2 - 2(b_1 + h_1)\xi_k^2 + \xi_k^4] + b_2^2\xi_k^4 \\ &\quad - 2b_2(b_0 + h_0)\xi_k^2 + (b_0 + h_0)^2\} \\ &= \frac{1}{A[q_1^2\xi_k^2 + q_0^2]} \{[h'(v_k) + q_1^2][q_1^2\xi_k^2 + q_0^2] \\ &\quad - q_1^2[\xi_k^6 + p\xi_k^4 + q\xi_k^2 + r] - q_1^2[q_1^2\xi_k^2 + q_0^2]\} \\ &= \frac{1}{A}h'(v_k). \end{aligned}$$

Hence,

$$\text{Sign}\{\alpha'(\tau_{1k}^j)\} = \text{Sign}\left\{\text{Re}\left[\frac{d\lambda}{d\tau_1}(\tau_{1k}^j)\right]^{-1}\right\} = \text{Sign}\left\{\frac{1}{A}h'(v_k)\right\},$$

where $A = \xi_k^2[b_1 + h_1 - \xi_k^2]^2 + [b_2\xi_k^2 - (b_0 + h_0)]^2$. Notice that $A > 0$, it has $\text{Sign}\{\alpha'(\tau_{1k}^j)\} = \text{Sign}\{h'(v_k)\}$. This completes the proof. $\square$

Let I be the stability interval for τ_1 which ensures the stability of E^* . From Lemmas 3.1 and 3.2, if (3.7) has only one positive root, then $I = [0, \tau_{11}^0)$. If (3.7) has more than one positive roots, then I is the union of a finite number of finite intervals and the stability switches may exist (see the example in Section 4). Therefore, the following theorem is obtained.

Theorem 3.1. *Suppose that inequality (3.4) is satisfied and $\tau_2 = 0$. Then the following conclusions hold.*

(i) *If $r \geq 0$ and $\Delta < 0$, then, for $\tau_1 \geq 0$, all roots of (3.2) have negative real parts. Hence the positive equilibrium E^* is locally asymptotically stable for all $\tau_1 \geq 0$.*

(ii) *If either $r < 0$ or $r \geq 0$, $\Delta > 0$, $v^* > 0$ and $h(v^*) \leq 0$ hold, then $h(v) = 0$ has at least one positive root v_k , the stability switches may exist, all roots of (3.2) have negative real parts for $\tau_1 \in I$. Hence the positive equilibrium E^* is asymptotically stable for $\tau_1 \in I$.*

(iii) *If all conditions as stated in (ii) and $h'(v_k) \neq 0$ hold, then system (1.2) undergoes Hopf bifurcations at E^* when $\tau_1 = \tau_{1k}^j$ ($j = 0, 1, 2, \dots$), where τ_{1k}^j is defined as (3.8).*

Now fix $\tau_1 = \tau_1^* \in I$, $\tau_2 > 0$ and $\lambda = i\omega$ ($\omega > 0$) be a root of (3.2). Then we have

$$(3.9) \quad \begin{cases} -\omega^3 + b_1\omega + q_1\omega \cos \omega\tau_1^* - q_0 \sin \omega\tau_1^* = h_0 \sin \omega\tau_2 - h_1\omega \cos \omega\tau_2, \\ b_2\omega^2 - b_0 - q_0 \cos \omega\tau_1^* - q_1\omega \sin \omega\tau_1^* = h_1\omega \sin \omega\tau_2 + h_0 \cos \omega\tau_2. \end{cases}$$

Furthermore, it can obtain that

$$(3.10) \quad \begin{aligned} &\omega^6 + (b_2^2 - 2b_1)\omega^4 + (b_1^2 - 2b_0b_2 + q_1^2 - h_1^2)\omega^2 + b_0^2 + q_0^2 - h_0^2 \\ &\quad + 2[q_0(\omega^3 - b_1\omega) - q_1\omega(b_2\omega^2 - b_0)] \sin \omega\tau_1^* \\ &\quad + 2[q_1\omega(b_1\omega - \omega^3) - q_0(b_2\omega^2 - b_0)] \cos \omega\tau_1^* = 0. \end{aligned}$$

Note that (3.10) has at most finite positive roots. If (3.10) has positive roots, without loss of generality, we assume that the number of the roots is N and

denote them by ω_i ($i = 1, 2, \dots, N$). From (3.9), we get

$$\tau_{2i}^j = \frac{1}{\omega_i} \left[\arccos \frac{\Gamma}{h_0^2 + h_1^2 \omega_i^2} + 2j\pi \right],$$

where

$$\begin{aligned} \Gamma = & h_1 \omega_i^4 + [h_0 b_2 - h_1 b_1 - h_1 q_1 \cos \omega_i \tau_1^*] \omega_i^2 + [h_1 q_0 \sin \omega_i \tau_1^* - h_0 q_1 \sin \omega_i \tau_1^*] \omega_i \\ & - h_0 b_0 - h_0 q_0 \cos \omega_i \tau_1^*, \quad i = 1, 2, \dots, N; j = 0, 1, 2, \dots \end{aligned}$$

Define $\tau_2^0 = \tau_{2i_0}^0 = \min\{\tau_{2i}^0\}$, $\omega_0 = \omega_{i_0}$. Let $\lambda(\tau_2) = \alpha(\tau_2) + i\omega(\tau_2)$ be the root of (3.2) satisfying $\alpha(\tau_2^0) = 0$, $\omega(\tau_2^0) = \omega_0$. Simple computations, gives

$$\begin{aligned} \alpha'(\tau_2^0) = & A_1^{-1} \{ (q_1 h_1 \tau_1^* \omega_0^3 - q_0 h_0 \tau_1^* \omega_0 + q_1 h_0 \omega_0) \sin \omega_0 (\tau_1^* + \tau_2^0) \\ & + (q_0 h_1 \tau_1^* + q_1 h_0 \tau_1^* - q_1 h_1) \omega_0^2 \cos \omega_0 (\tau_1^* + \tau_2^0) \\ & + [h_0 (b_1 \omega_0 + 3\omega_0^3) + 2b_2 q_1 \omega_0^3] \sin \omega_0 \tau_2^0 - h_1 \omega_0^2 \\ & + [2b_2 h_0 \omega_0^2 - q_1 \omega_0 (b_1 \omega_0 + 3\omega_0^3)] \cos \omega_0 \tau_2^0 \}, \end{aligned}$$

where $A_1 = h_1^2 \omega_0^4 + h_0^2 \omega_0^2$.

Hence, the following conclusions are obtained.

Theorem 3.2. *Let us fix $\tau_1 = \tau_1^* \in I$. Suppose that inequality (3.4) is satisfied.*

(i) *If (3.10) has no positive roots, then, for all $\tau_2 \geq 0$, all roots of (3.2) have negative real parts and the positive equilibrium E^* of the system (1.2) is locally asymptotically stable.*

(ii) *If (3.10) has positive roots, then the following conclusions hold.*

(a) *For $\tau_2 \in [0, \tau_2^0)$, all roots of (3.2) have negative real parts and the positive equilibrium E^* of the system (1.2) is locally asymptotically stable.*

(b) *If $\alpha'(\tau_2^0) \neq 0$, then the system (1.2) undergoes Hopf bifurcation at E^* when $\tau_2 = \tau_2^0$.*

Furthermore, one can compute the properties of Hopf bifurcations as shown in Appendix to determine the direction of Hopf bifurcation and the stability of the bifurcating periodic solutions by using the center manifold theorem and normal form theory [25].

4. Numerical simulations

In this section, we use Matlab program to perform some numerical simulations on the system (1.2). The following parameter values are taken from [6, 15]:

$$\begin{aligned}
r_1 &= 2.5 \text{ day}^{-1}, K = L = 20 \text{ nos.ml}^{-1}, \alpha = 0.01 \text{ ml nos}^{-1} \text{ day}^{-1}, \mu = 0.1 \text{ day}^{-1}, \\
r_2 &= 2.3 \text{ day}^{-1}, \beta = 0.02 \text{ ml nos}^{-1} \text{ day}^{-1}, m = 0.6 \text{ ml nos}^{-1} \text{ day}^{-1}, \\
m_1 &= 0.4 \text{ ml nos}^{-1} \text{ day}^{-1}, n = 0.55 \text{ ml nos}^{-1} \text{ day}^{-1}, n_1 = 0.3 \text{ ml nos}^{-1} \text{ day}^{-1}, \\
\theta_1 &= 0.06 \text{ ml day}^{-1}, \theta_2 = 0.07 \text{ ml day}^{-1}, \gamma_1 = 0.2 \text{ nos.ml}^{-1}, \gamma_2 = 0.25 \text{ nos.ml}^{-1}.
\end{aligned}$$

For this set of parameter values, there exist the following equilibria,

$$E_0(0, 0, 0), E_1(20, 0, 0), E_2(0, 20, 0), E_3(18.6596, 16.7549, 0),$$

$$E_4(0.3449, 0, 4.0948), E_5(0, 0.9276, 4.1173), E^*(0.2152, 0, 2711, 4.0154).$$

The above digits show the termination of plankton bloom through reduction of equilibrium sizes due to presence of two harmful phytoplanktons. In the following, we will try to find the effect of time delays on the dynamic properties of the system (1.2).

At first, let us consider the effect of the single time delay $\tau_1 \geq 0$ ($\tau_2 = 0$). By computations, we can obtain that (3.6) has two positive roots $\xi_1 = 0.6229$ and $\xi_2 = 0.5705$. Substituting these parameters into (3.8), gives

$$\tau_{11}^{(j)} = 5.9827 + 10.0819j, \quad \tau_{12}^{(j)} = 10.0601 + 11.0079j.$$

(3.2) has pure imaginary roots when $\tau_1 = \tau_{11}^{(j)}$ or $\tau_1 = \tau_{12}^{(j)}$. Furthermore, $\alpha'(\tau_{11}^{(j)}) = 0.0250 > 0$ and $\alpha'(\tau_{12}^{(j)}) = -0.0209 < 0$. By Theorem 3.1, the stability switches exist and E^* is asymptotically stable when $\tau_1 \in I$, where

$$\begin{aligned}
I &= [0, 5.9827) \cup (10.0601, 16.0646) \cup (21.0680, 26.1465) \\
&\cup (32.0759, 36.2248) \cup (43.0838, 46.3103) \cup (54.0917, 56.3922) \\
&\cup (65.0996, 66.4741) \cup (76.1075, 76.550).
\end{aligned}$$

Figure 1 (A) shows the stability of the positive equilibrium for the three populations for $\tau_1 = 3$. Figure 1 (B) shows stable limit cycles for all the three populations for $\tau_1 = 8$.

Next, let us consider the case that both time delays τ_1 and τ_2 are present. Fix $\tau_1 = 14.5 \in (10.0601, 16.0646)$. Then $\tau_2^0 \doteq 8.1472$ is the first Hopf bifurcation value and that E^* is asymptotically stable for $\tau_2 \in [0, \tau_2^0)$. Furthermore, by the algorithm in Appendix, we have that $C_1(0) = -0.8762 - 0.9831i$. Hence, it follows from Theorem A.1 that, for $\tau_2 = \tau_2^0$, a periodic solution caused by Hopf bifurcation is orbitally asymptotically stable, and the direction of Hopf bifurcation is supercritical. The results are illustrated by Figures 2(A) and 2(B).

Fix $\tau_1 = 8$, it can notice that $\tau_1 \notin I$ and E^* is unstable when $\tau_2 = 0$. As τ_2 increases, the oscillations representing recurrent bloom situation can be observed. Figure 3 (A) shows the stability of the positive equilibrium for

Fig. 1. The phase plots for two harmful phytoplanktons and one zooplankton population with single time delay. Figure (A) shows stable dynamics of all three populations for $\tau_1 = 3$. Figure (B) shows stable limit cycles for $\tau_1 = 8$. The initial conditions are chosen as $\varphi_1 \equiv 1$, $\varphi_2 \equiv 1$ and $\varphi_3 \equiv 4$.

Fig. 2. The phase plots for two harmful phytoplanktons and one zooplankton population with two time delays. Figure (A) shows stable dynamics of all three populations for $\tau_1 = 14.5$ and $\tau_2 = 2$. Figure (B) shows stable limit cycle for $\tau_1 = 14.5$ and $\tau_2 = 8.2$. The initial conditions are chosen as $\varphi_1 \equiv 1$, $\varphi_2 \equiv 1$ and $\varphi_3 \equiv 4$.

Fig. 3. The phase plots for two harmful phytoplanktons and one zooplankton population with two time delays. Figure (A) shows stable dynamics of all three populations for $\tau_1 = 8$ and $\tau_2 = 4$. Figure (B) shows stable limit cycle for $\tau_1 = 8$ and $\tau_2 = 5$. The initial conditions are chosen as $\varphi_1 \equiv 1$, $\varphi_2 \equiv 1$ and $\varphi_3 \equiv 4$.

$\tau_2 = 4$ and Figure 3 (B) shows the existence of stable limit cycle for $\tau_2 = 5$. These show that τ_2 can make the system tend to a stable equilibrium or a periodic solution when the system (1.2) loses its stability for τ_1 , which also explain that liberating toxin in two kind of phytoplanktons can have the positive effects for stabilizing ecological systems and controlling the occurrence of planktonic blooms.

5. Chaotic behavior and control strategies

In this section, some numerical simulation examples are given to show the occurrence of chaotic behavior in the system (1.2) and its control strategies. We mainly investigate the effect of the following parameters: the rates of toxin liberation θ_1 (or/and θ_2), the maximum zooplankton conversion rate m_1 and the time delays τ_1 (or/and τ_2).

Firstly, let us investigate the effect of the rates of toxin liberation θ_1 (or/and θ_2) by the harmful phytoplanktons under the conditions $\tau_1 = \tau_2 = 0$. The other parameters are the same as the literature [17, 18]:

$$(6.1) \quad r_1 = 1, K = 1, \alpha = 1, m = 10, r_2 = 1, L = 1, \beta = 1.5, n = 1, \\ m_1 = 5, n_1 = 0.5, \mu = 1, \gamma_1 = 0.2, \gamma_2 = 0.25.$$

With these parameters, one can find that there exists a unique positive equilibrium $E^*(0.1549, 0.7590, 0.0086)$ and that the system (1.2) can exhibit chaotic behavior for $\theta_1 = \theta_2 = 0$ (see Figure 4 (A)). By choosing (i) $\theta_1 = 1.2$, $\theta_2 = 0$, (ii) $\theta_1 = 0$, $\theta_2 = 0.8$, (iii) $\theta_1 = 0.4$, $\theta_2 = 0.8$, respectively, the chaotic behaviors disappear (see Figure 4 (B–D)). These results show that the rates of toxin liberation θ_1 (or/and θ_2) can make chaotic behavior disappear for the system (1.2).

In the following, the effects of the delays τ_1 and τ_2 are investigated. Firstly, let $\theta_1 = 0$ and $\theta_2 \neq 0$, that is, investigate the effect of the time delay τ_2 to the system of one toxin-producing phytoplankton. Let us choose $\theta_1 = 0$, $\theta_2 = 0.05$. The other parameters are chosen as in (6.1). When $\tau_2 = 0$, the system (1.2) exhibits chaotic behavior (see Figure 5 (A)). If we increase τ_2 to a sufficiently large value, the solutions for the system (1.2) tend always the boundary equilibrium E_2 (see Figure 5 (B)). These show that the time delay τ_2 can make chaotic behavior disappear though the zooplankton becomes extinct. Next, let us investigate the effects of the delays τ_1 and τ_2 with $\theta_1 = 0.08$ and $\theta_2 = 0.05$, that is, the effect of the time delay τ_1 and τ_2 to the system (1.2) with two toxin-producing phytoplanktons. When $\tau_1 = \tau_2 = 0$, the system (1.2) shows chaotic behavior (see Figure 6 (A)). When $\tau_1 = 0.001$ and $\tau_2 = 0.005$, chaotic behavior disappears and the solution of the system (1.2) tends to the boundary

Fig. 4. Figure (A) shows that the positive equilibrium is unstable and chaos exists for the system (1.2) with the data (6.1) and $\theta_1 = \theta_2 = 0$. Figure (B) shows that the equilibrium is stable and chaos vanishes when $\theta_1 = 1.2$, $\theta_2 = 0$. Figure (C) shows that the equilibrium is unstable and there exists a stable periodic solution and chaos vanishes when $\theta_1 = 0$, $\theta_2 = 0.8$. Figure (D) shows that the equilibrium is stable and chaos vanishes when $\theta_1 = 0.4$, $\theta_2 = 0.8$. The initial conditions are chosen as $\varphi_1 \equiv 0.1$, $\varphi_2 \equiv 0.4$ and $\varphi_3 \equiv 0.12$.

Fig. 5. Figure (A) shows that the system (1.2) exhibits chaos phenomenon when $\theta_1 = 0$, $\theta_2 = 0.05$ and $\tau_2 = 0$. Figure (B) shows that the solution of the system (1.2) tends to boundary equilibrium $(0, 1, 0)$ when $\theta_1 = 0$, $\theta_2 = 0.05$ and $\tau_2 = 0.2$ and chaos disappears. The initial conditions are chosen as $\varphi_1 \equiv 0.8$, $\varphi_2 \equiv 1.5$ and $\varphi_3 \equiv 0.1$.

Fig. 6. Figure (A) shows that the system (1.2) exhibits chaos when $\tau_1 = \tau_2 = 0$. Figure (B) shows that the solution of the system (1.2) tends to a stable boundary equilibrium $(0,1,0)$ when $\tau_1 = 0.001$ and $\tau_2 = 0.005$ and chaos disappears. The initial conditions are chosen as $\varphi_1 \equiv 0.6$, $\varphi_2 \equiv 0.8$ and $\varphi_3 \equiv 0.2$.

equilibrium (see Figure 6 (B)). Furthermore, with the increases of the delays τ_1 and τ_2 , we can find that chaotic behavior does not reappear. These situations show that the time delays τ_1 and τ_2 can make the system to have a change from chaotic behavior to order.

Finally, the effect of the maximum zooplankton conversion rate m_1 is investigated. For convenience, let $\tau_1 = \tau_2 = 0$ in the system (1.2). We fix $\theta_1 = 0.2$, $\theta_2 = 0.08$, and choose $m_1 = 3, 3.5, 5, 8$, respectively, and other parameters are the same as (6.1). When $m_1 = 3$, the system (1.2) has a stable positive equilibrium (see Figure 7 (A)). Increasing m_1 , the system (1.2) will have a 1-periodic solution, 2-periodic solution and finally exhibits chaotic behavior (see Figure 7 (B–D)). These show that the maximum zooplankton conversion rate m_1 makes the system (1.2) to have a change from order to chaos. In fact, period doubling bifurcations seem to be responsible for this kind of dynamical behavior. These results are analogical to that of [17] though $\theta_1, \theta_2 \neq 0$.

In short, the above numerical simulations show that the system (1.2) can exhibit complicated dynamic behaviors. With the changes of the parameters, the system (1.2) can have a change from chaos to order or order to chaos. Both the toxin liberation rate θ_i ($i = 1, 2$) and the time delays τ_1 and τ_2 can be used to control of the chaos.

6. Conclusion

In this paper, the dynamic properties of the system (1.2) at the positive equilibrium E^* are investigated. Firstly, in the case of $\tau_2 = 0$, by analyzing the distribution of the roots of the corresponding characteristic equation, there are

Fig. 7. Figure (A) shows that the system (1.2) has a stable equilibrium when $m_1 = 3$. Figure (B) shows that the system (1.2) has a stable 1-periodic solution when $m_1 = 3.5$. Figure (C) shows that the system (1.2) has a 2-periodic solution when $m_1 = 5$. Figure (D) shows that the system (1.2) exhibits chaos when $m_1 = 8$. The initial conditions are chosen as $\varphi_1 \equiv 0.6$, $\varphi_2 \equiv 0.4$ and $\varphi_3 \equiv 0.12$.

stability switches phenomena at E^* when the time delay τ_1 varies. Furthermore, fixing τ_1 in an interval ensuring the stability for E^* and regarding the delay τ_2 as parameter, there exists a first critical value of τ_2 at which the positive equilibrium loses its stability and the Hopf bifurcation occurs. The direction of Hopf bifurcation and the stability of the bifurcating periodic solutions are also given. Furthermore, by choosing some suitable parameters, the system (1.2) can exhibit complicated dynamic properties, and undergo changes from stable periodic solution or equilibrium to chaos or from chaos to stable periodic solution or equilibrium.

The factors affecting plankton dynamics have been the subject of intensive research recently. From the previous studies, the positive impact of toxin-producing phytoplankton for the control of algal bloom is known. In this paper the same conclusions are obtained. Thus it may finally conclude that harmful phytoplankton may be used as a bio-control agent for the HAB problems. The role of time delay in the two harmful phytoplankton-zooplankton system may give some interesting results and needs further

investigation. The reasons for the occurrence of planktonic blooms and their possible control mechanism are still in its infancy, hence, the progress of such important areas urgently requires special attention both from experimental and mathematical ecologists.

Appendix

Property of Hopf bifurcation at E^*

In the Section 3, it has already obtained some sufficient conditions ensuring for the system (1.2) to undergo a Hopf bifurcation at E^* when $\tau_2 = \tau_2^0$. In this Appendix, the aim is to consider the case given in Theorem 3.2 (ii) and establish the explicit formula determining the direction, stability and period of periodic solutions bifurcating from E^* at the critical value $\tau_2 = \tau_2^0$, by using the normal form theory and the center manifold arguments developed by Hassard et al. [25].

For convenience, let us assume $\tau_1^* > \tau_2^0$ and let $\bar{\tau}_2 = \tau_2^0 + \mu$, $\mu \in \mathbf{R}$, and dropping the bar for simplification of notations. Then $\mu = 0$ is the Hopf bifurcation value for the system (1.2). Since $\tau_1^* > \tau_2^0$, by choosing the phase space as $C = C([- \tau_1^*, 0], \mathbf{R}^3)$, the system (1.2) is transformed into the following functional differential equation in C ,

$$(A.1) \quad \dot{u}_t = L_\mu(u_t) + f(\mu, u_t),$$

where $u_t(\theta) = u(t + \theta) \in C$, $u_t(\theta) = (p_1(t + \theta), p_2(t + \theta), z(t + \theta))^T$ and $L_\mu : C \rightarrow \mathbf{R}^3$, $f : \mathbf{R} \times C \rightarrow \mathbf{R}^3$ are given, respectively, by

$$L_\mu \varphi = A_1 \varphi(0) + B_1 \varphi(-\tau_1^*) + B_2 \varphi(-\tau_2^0),$$

where $\varphi = (\varphi_1, \varphi_2, \varphi_3)^T$ and

$$A_1 = \begin{pmatrix} -\frac{r_1 p_1^*}{K} & -\alpha p_1^* & -m p_1^* \\ -\beta p_2^* & -\frac{r_2 p_2^*}{L} & -n p_2^* \\ m_1 z^* & n_1 z^* & 0 \end{pmatrix},$$

$$B_1 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ -\frac{\theta_1 \gamma_1 z^*}{(\gamma_1 + p_1^*)^2} & 0 & 0 \end{pmatrix}, \quad B_2 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & -\frac{\theta_2 \gamma_2 z^*}{(\gamma_2 + p_2^*)^2} & 0 \end{pmatrix},$$

$$f(\mu, \varphi) = \begin{pmatrix} -\frac{r_1}{K} \varphi_1^2(0) - \alpha_1 \varphi_1(0) \varphi_2(0) - m \varphi_1(0) \varphi_3(0) \\ -\beta \varphi_1(0) \varphi_2(0) - \frac{r_2}{L} \varphi_1^2(0) - n \varphi_2(0) \varphi_3(0) \\ G \end{pmatrix},$$

$$\begin{aligned}
G &= m_1 \varphi_1(0) \varphi_3(0) + n_1 \varphi_2(0) \varphi_3(0) \\
&\quad - \left[\frac{\theta_1 \gamma_1}{(\gamma_1 + p_1^*)^2} \varphi_1(-\tau_1^*) + \frac{\theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} \varphi_2(-\tau_2^0) \right] \varphi_3(0) \\
&\quad + \left[\frac{\theta_1 \gamma_1}{(\gamma_1 + p_1^*)^3} \varphi_1^2(-\tau_1^*) \varphi_3(0) - \frac{\theta_1 \gamma_1 z^*}{(\gamma_1 + p_1^*)^4} \varphi_1^3(-\tau_1^*) \right] \\
&\quad + \left[\frac{\theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} \varphi_2^2(-\tau_2^0) \varphi_3(0) - \frac{\theta_2 \gamma_2 z^*}{(\gamma_2 + p_2^*)^4} \varphi_2^3(-\tau_2^0) \right] + O(4).
\end{aligned}$$

By the Riesz representation theorem, there exists a function $\eta(\theta, \mu)$ of bounded variation for $\theta \in [-\tau_1^*, 0]$, such that for $\varphi \in C$

$$L_\mu \varphi = \int_{-\tau_1^*}^0 d\eta(\theta, \mu) \varphi(\theta).$$

In fact, we can choose

$$\eta(\theta, \mu) = \begin{cases} A_1 + B_2, & \theta = 0, \\ B_2, & \theta \in [-\tau_2^0, 0), \\ 0, & \theta \in (-\tau_1^*, -\tau_2^0), \\ -B_1, & \theta = -\tau_1^*. \end{cases}$$

For $\varphi \in C^1([-\tau_1^*, 0], \mathbf{R}^3)$, define

$$A(\mu) \varphi = \begin{cases} \dot{\varphi}(\theta), & \theta \in [-\tau_1^*, 0), \\ \int_{-\tau_1^*}^0 d\eta(s, \mu) \varphi(s), & \theta = 0, \end{cases}$$

and

$$(A.2) \quad R\varphi = \begin{cases} 0, & \theta \in [-\tau_1^*, 0), \\ f(\mu, \varphi), & \theta = 0. \end{cases}$$

For $u_t(\theta) = u(t + \theta) \in C^1$, we have $du_t/d\theta = du_t/dt$. Then the system (A.1) can be rewritten as

$$(A.3) \quad \dot{u}_t = A(\mu)u_t + R(\mu)u_t.$$

For $\psi \in C^1([0, \tau_1^*], \mathbf{R}^{3*})$ and $\varphi \in C([-\tau_1^*, 0], \mathbf{R}^3)$, define

$$A^* \psi(s) = \begin{cases} -\dot{\psi}(s), & s \in (0, \tau_1^*], \\ \int_{-\tau_1^*}^0 d\eta^T(t, 0) \psi(-t), & s = 0, \end{cases}$$

and a bilinear inner product

$$\langle \psi, \varphi \rangle = \bar{\psi}(0) \varphi(0) - \int_{-\tau_1^*}^0 \int_{\xi=0}^{\theta} \bar{\psi}^T(\xi - \theta) d\eta(\theta) \varphi(\xi) d\xi,$$

where $\eta(\theta) = \eta(\theta, 0)$. It has that A^* and $A = A(0)$ are adjoint operators. By the above discussion, $\pm i\omega_0$ are eigenvalues of $A(0)$ when $\tau_2 = \tau_2^0$. Then they are also eigenvalues of A^* . By computations, it can obtain $q(\theta) = q(0)e^{i\omega_0\theta}$ is an eigenvector of A corresponding to the eigenvalue $i\omega_0$, and $q^*(s) = \bar{D}q_1^*(0)e^{i\omega_0 s}$ is an eigenvector of A^* corresponding to the eigenvalue $-i\omega_0$.

In fact, let $q_1^*(s) = q_1^*(0)e^{i\omega_0 s}$, then $q(0) = (1, a, b)^T$ and $q_1^*(0) = (1, a^*, b^*)$ satisfy the following equalities:

$$\begin{aligned}(i\omega_0 I)q(0) &= A_1 q(0) + B_1 q(0)e^{-i\omega_0 \tau_1^*} + B_2 q(0)e^{-i\omega_0 \tau_2^0}, \\ (-i\omega_0 I)q_1^*(0) &= A_1^T q_1^*(0) + B_1^T q_1^*(0)e^{i\omega_0 \tau_1^*} + B_2^T q_1^*(0)e^{i\omega_0 \tau_2^0}.\end{aligned}$$

Furthermore, it can get

$$\begin{aligned}a &= \frac{L[K\beta m p_1^* p_2^* - n p_2^*(i\omega_0 K + r_1 p_1^*)]}{K[L n \alpha p_1^* p_2^* - m p_1^*(i\omega_0 L + r_2 p_2^*)]}, \\ b &= \frac{KL\alpha\beta p_1^* p_2^* - r_1 r_2 p_1^* p_2^* + KL\omega_0^2 - i\omega_0(r_1 p_1^* L + r - 2p_2^* K)}{K m r_2 p_1^* p_2^* - K L n \alpha p_1^* p_2^* + i\omega_0 K L m p_1^*}, \\ a^* &= \frac{L[i\omega_0 \alpha p_1^*(\gamma_2 + p_2^*)^2 - m p_1^*(n_1 z^*(\gamma_2 + p_2^*)^2 - \theta_2 \gamma_2 z^* e^{i\omega_0 \tau_2^0})]}{i\omega_0(\gamma_2 + p_2^*)^2(i\omega_0 L - r_2 p_2^*) + n p_2^*[n_1 z^* L(\gamma_2 + p_2^*)^2 - L \theta_2 \gamma_2 z^* e^{i\omega_0 \tau_2^0}]}, \\ b^* &= \frac{L n \alpha p_1^* p_2^*(\gamma_2 + p_2^*)^2 + m p_1^*(\gamma_2 + p_2^*)^2(i\omega_0 L - r_2 p_2^*)}{i\omega_0(i\omega_0 L - r_2 p_2^*)(\gamma_2 + p_2^*)^2 + L n p_2^*[n_1 z^*(\gamma_2 + p_2^*)^2 - \theta_2 \gamma_2 z^* e^{i\omega_0 \tau_2^0}]}.\end{aligned}$$

For $\langle q^*(s), q(\theta) \rangle = 1$, it may compute D using the above bilinear inner product by $\langle q^*(s), q(\theta) \rangle = \langle \bar{D}q_1^*(s), q(\theta) \rangle = 1$. At the same time, it also has $\langle q^*(s), \bar{q}(\theta) \rangle = 0$. By the above computation, the expression of D is as follows

$$D = \left\{ 1 + a^* \bar{a}^* + b^* \bar{b}^* - \bar{b}^* \left[\frac{\tau_1^* \theta_1 \gamma_1 z^* e^{-i\omega_0 \tau_1^*}}{(\gamma_1 + p_1^*)^2} + \frac{a \tau_2^0 \theta_2 \gamma_2 z^* e^{-i\omega_0 \tau_2^0}}{(\gamma_2 + p_2^*)^2} \right] \right\}^{-1}.$$

Now, let us use the same notations as in Hassard et al. [25]. Let u_t be the solution of the system (A.1) when $\mu = 0$. Define $Z(t) = \langle q^*, u_t \rangle$, then

$$(A.4) \quad \dot{Z} = \langle q^*, \dot{u}_t \rangle = i\omega_0 Z + \bar{q}^*(0) \hat{f}(Z, \bar{Z}),$$

where

$$\hat{f} = f(0, W(Z, \bar{Z}) + 2 \operatorname{Re}\{Zq\}), \quad W(Z, \bar{Z}) = u_t - 2 \operatorname{Re}\{Zq\},$$

$$W(Z, \bar{Z}) = W_{20} \frac{Z^2}{2} + W_{11} Z \bar{Z} + W_{02} \frac{\bar{Z}^2}{2} + \dots$$

Notice that W is real if u_t is real. Only real solutions are considered. Rewriting (A.4) as

$$\dot{u}_t = i\omega_0 Z + g(Z, \bar{Z}),$$

where

$$g(Z, \bar{Z}) = g_{20} \frac{Z^2}{2} + g_{11} Z \bar{Z} + g_{02} \frac{\bar{Z}^2}{2} + g_{21} \frac{Z^2 \bar{Z}}{2} \dots$$

Substituting (A.3) and (A.4) into $\dot{W} = \dot{u}_t - \dot{Z}q - \dot{\bar{Z}}\bar{q}$, gives

$$\dot{W} = \begin{cases} AW - 2 \operatorname{Re}\{\bar{q}^*(0)\hat{f}q(\theta)\}, & \theta \in [-\tau, 0) \\ AW - 2 \operatorname{Re}\{\bar{q}^*(0)\hat{f}q(\theta)\} + \hat{f}, & \theta = 0 \end{cases} \stackrel{\text{def}}{=} AW + H(Z, \bar{Z}, \theta),$$

where

$$H(Z, \bar{Z}, \theta) = H_{20}(\theta) \frac{Z^2}{2} + H_{11}(\theta) Z \bar{Z} + H_{02}(\theta) \frac{\bar{Z}^2}{2} + \dots$$

Expanding the above series and comparing the coefficients, gives

$$(A - 2i\omega_0 I)W_{20}(\theta) = -H_{20}(\theta), \quad AW_{11} = -H_{11}(\theta).$$

For

$$u_t = u(t + \theta) = W(Z, \bar{Z}, \theta) + Zq(\theta) + \bar{Z}\bar{q}(\theta),$$

then

$$g(Z, \bar{Z}) = g_{20} \frac{Z^2}{2} + g_{11} Z \bar{Z} + g_{02} \frac{\bar{Z}^2}{2} + \dots = \bar{q}^*(0)\hat{f}(Z, \bar{Z}).$$

Notice that

$$u_{1t}(0) = Z + \bar{Z} + W_{20}^{(1)}(0) \frac{Z^2}{2} + W_{11}^{(1)}(0) Z \bar{Z} + \dots,$$

$$u_{2t}(0) = aZ + \bar{a}\bar{Z} + W_{20}^{(2)}(0) \frac{Z^2}{2} + W_{11}^{(2)}(0) Z \bar{Z} + W_{02}^{(2)}(0) \frac{\bar{Z}^2}{2} + \dots,$$

$$u_{3t}(0) = bZ + \bar{b}\bar{Z} + W_{20}^{(3)}(0) \frac{Z^2}{2} + W_{11}^{(3)}(0) Z \bar{Z} + W_{02}^{(3)}(0) \frac{\bar{Z}^2}{2} + \dots,$$

$$u_{1t}(-\tau_1^*) = e^{-i\omega_0\tau_1^*} Z + e^{i\omega_0\tau_1^*} \bar{Z} + W_{20}^{(1)}(-\tau_1^*) \frac{Z^2}{2} + W_{11}^{(1)}(-\tau_1^*) Z \bar{Z} + \dots,$$

$$u_{2t}(-\tau_1^*) = ae^{-i\omega_0\tau_1^*} Z + \bar{a}e^{i\omega_0\tau_1^*} \bar{Z} + W_{20}^{(2)}(-\tau_1^*) \frac{Z^2}{2} + W_{11}^{(2)}(-\tau_1^*) Z \bar{Z} + \dots,$$

$$u_{1t}(-\tau_2^0) = e^{-i\omega_0\tau_2^0} Z + e^{i\omega_0\tau_2^0} \bar{Z} + W_{20}^{(1)}(-\tau_2^0) \frac{Z^2}{2} + W_{11}^{(1)}(-\tau_2^0) Z \bar{Z} + \dots,$$

$$u_{2t}(-\tau_2^0) = ae^{-i\omega_0\tau_2^0} Z + \bar{a}e^{i\omega_0\tau_2^0} \bar{Z} + W_{20}^{(2)}(-\tau_2^0) \frac{Z^2}{2} + W_{11}^{(2)}(-\tau_2^0) Z \bar{Z} + \dots$$

Hence the following important quantities can be obtained by coefficient comparison method

$$\begin{aligned}
g_{20} &= 2D \left\{ -\frac{r_1}{K} - a(\alpha_1 + \beta \bar{a}^*) - b(m - \bar{b}^* m_1) - \frac{\bar{a}^* r_2}{L} a^2 - ab(n\bar{a}^* - n_1 \bar{b}^*) \right. \\
&\quad \left. - b\bar{b}^* \frac{\theta_1 \gamma_1 e^{-i\omega_0 \tau_1^*}}{(\gamma_1 + p_1^*)^2} - ab\bar{b}^* \frac{\theta_2 \gamma_2 e^{-i\omega_0 \tau_2^0}}{(\gamma_2 + p_2^*)^2} \right\}, \\
g_{11} &= D \left\{ -\frac{2r_1}{K} - (\alpha_1 + \beta \bar{a}^*)(a + \bar{a}) - (m - \bar{b}^* m_1)(b + \bar{b}) - \frac{2\bar{a}^* r_2 a \bar{a}}{L} \right. \\
&\quad - (n\bar{a}^* - n_1 \bar{b}^*)(a\bar{b} + \bar{a}b) - \frac{\bar{b}^* \theta_1 \gamma_1}{(\gamma_1 + p_1^*)^2} (\bar{b} e^{-i\omega_0 \tau_1^*} + b e^{i\omega_0 \tau_1^*}) \\
&\quad \left. - \frac{\bar{b}^* \theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} (a\bar{b} e^{-i\omega_0 \tau_2^0} + \bar{a} b e^{i\omega_0 \tau_2^0}) \right\}, \\
g_{02} &= 2D \left\{ -\frac{r_1}{K} - \bar{a}(\alpha_1 + \beta \bar{a}^*) - \bar{b}(m - \bar{b}^* m_1) - \frac{\bar{a}^* r_2}{L} \bar{a}^2 - \bar{a}\bar{b}(n\bar{a}^* - n_1 \bar{b}^*) \right. \\
&\quad \left. - \bar{b}\bar{b}^* \frac{\theta_1 \gamma_1 e^{-i\omega_0 \tau_1^*}}{(\gamma_1 + p_1^*)^2} - \bar{a}\bar{b}\bar{b}^* \frac{\theta_2 \gamma_2 e^{i\omega_0 \tau_2^0}}{(\gamma_2 + p_2^*)^2} \right\}, \\
g_{21} &= 2D \left\{ -\frac{r_1}{K} [W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)] \right. \\
&\quad - (\alpha_1 + \beta \bar{a}^*) \left[W_{11}^{(2)}(0) + \frac{1}{2} W_{20}^{(2)}(0) + \frac{1}{2} \bar{a} W_{20}^{(1)}(0) + a W_{11}^{(1)}(0) \right] \\
&\quad - (m - \bar{b}^* m_1) \left[W_{11}^{(3)}(0) + \frac{1}{2} W_{20}^{(3)}(0) + \frac{1}{2} \bar{b} W_{20}^{(1)}(0) + b W_{11}^{(1)}(0) \right] \\
&\quad - \frac{\bar{a}^* r_2}{L} [\bar{a} W_{20}^{(2)}(0) + 2a W_{11}^{(2)}(0)] \\
&\quad - (n\bar{a}^* - n_1 \bar{b}^*) \left[a W_{11}^{(3)}(0) + \frac{1}{2} \bar{a} W_{20}^{(3)}(0) + \frac{1}{2} \bar{b} W_{20}^{(2)}(0) + b W_{11}^{(2)}(0) \right] \\
&\quad - \frac{\bar{b}^* \theta_1 \gamma_1}{(\gamma_1 + p_1^*)^2} \left[W_{11}^{(3)}(0) e^{-i\omega_0 \tau_1^*} + \frac{1}{2} q W_{20}^{(3)}(0) e^{i\omega_0 \tau_1^*} \right. \\
&\quad \left. + \frac{1}{2} \bar{b} W_{20}^{(1)}(-\tau_1^*) + b W_{11}^{(1)}(-\tau_1^*) \right]
\end{aligned}$$

$$\begin{aligned}
& -\frac{\bar{b}^* \theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} \left[a W_{11}^{(3)}(0) e^{-i\omega_0 \tau_2^0} + \frac{1}{2} W_{20}^{(3)}(0) \bar{a} e^{i\omega_0 \tau_2^0} \right. \\
& \quad \left. + \frac{1}{2} \bar{b} W_{20}^{(2)}(-\tau_2^0) + b W_{11}^{(2)}(-\tau_2^0) \right] \\
& + \frac{\bar{b}^* \theta_1 \gamma_1}{(\gamma_1 + p_1^*)^3} [e^{-2i\omega_0 \tau_1^*} \bar{b} + 2b] - \frac{3\bar{b}^* \theta_1 \gamma_1 z^* e^{-i\omega_0 \tau_1^*}}{(\gamma_1 + p_1^*)^4} \\
& + \frac{\bar{b}^* \theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} [a^2 \bar{b} e^{-2i\omega_0 \tau_2^0} + 2ab\bar{b}] - \frac{3a^2 \bar{a} \bar{b}^* \theta_2 \gamma_2 z^* e^{-i\omega_0 \tau_2^0}}{(\gamma_2 + p_2^*)^4} \Big\},
\end{aligned}$$

where

$$\begin{aligned}
W_{20}(\theta) &= \frac{ig_{20}}{\omega_0} q(0) e^{i\omega_0 \theta} + \frac{i\bar{g}_{02}}{3\omega_0} \bar{q}(0) e^{-i\omega_0 \theta} + E_1 e^{2i\omega_0 \theta}, \\
W_{11}(\theta) &= -\frac{ig_{11}}{\omega_0} q(0) e^{i\omega_0 \theta} + \frac{i\bar{g}_{11}}{\omega_0} \bar{q}(0) e^{-i\omega_0 \theta} + E_2, \\
E_1 &= \begin{pmatrix} 2i\omega_0 + \frac{r_1 p_1^*}{K} & \alpha p_1^* & m p_1^* \\ \beta p_2^* & 2i\omega_0 + \frac{r_2 p_2^*}{L} & n p_2^* \\ -m_1 z^* + \frac{\theta_1 \gamma_1 z^* e^{-2i\omega_0 \tau_1^*}}{(\gamma_1 + p_1^*)^2} & -n_1 z^* + \frac{\theta_2 \gamma_2 z^* e^{-2i\omega_0 \tau_2^0}}{(\gamma_2 + p_2^*)^2} & 2i\omega_0 \end{pmatrix}^{-1} \\
&\quad \times \begin{pmatrix} -\frac{r_1}{K} - \alpha_1 a - mb \\ -\beta a - \frac{r_2}{L} a^2 - nab \\ m_1 b + n_1 ab - \frac{\theta_1 \gamma_1 b}{(\gamma_1 + p_1^*)^2} e^{-i\omega_0 \tau_1^*} - \frac{\theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} a b e^{-i\omega_0 \tau_2^0} \end{pmatrix}, \\
E_2 &= \begin{pmatrix} \frac{r_1 p_1^*}{K} & \alpha p_1^* & m p_1^* \\ \beta p_2^* & \frac{r_2 p_2^*}{L} & n p_2^* \\ \frac{\theta_1 \gamma_1 z^*}{(\gamma_1 + p_1^*)^2} - m_1 z^* & \frac{\theta_2 \gamma_2 z^*}{(\gamma_2 + p_2^*)^2} - n_1 z^* & 0 \end{pmatrix}^{-1} \\
&\quad \times \begin{pmatrix} -\frac{2r_1}{K} - \alpha_1(a + \bar{a}) - m(b + (\bar{b})) \\ -\beta(a + \bar{a}) - \frac{2a\bar{a}r_2}{L} - n(a\bar{b} + \bar{a}b) \\ m_1(b + \bar{b}) + n_1(a\bar{b} + \bar{a}b) \\ -\frac{\theta_1 \gamma_1}{(\gamma_1 + p_1^*)^2} (\bar{b} e^{-i\omega_0 \tau_1^*} + b e^{i\omega_0 \tau_1^*}) - \frac{\theta_2 \gamma_2}{(\gamma_2 + p_2^*)^2} (\bar{a} b e^{-i\omega_0 \tau_2^0} + \bar{a} b e^{i\omega_0 \tau_2^0}) \end{pmatrix}.
\end{aligned}$$

By substituting E_1 and E_2 into $W_{20}(\theta)$ and $W_{11}(\theta)$, respectively, g_{21} can be expressed by the parameters. Based on the above analysis, each g_{ij} can be determined by the parameters. Thus we can compute the following quantities:

$$C_1(0) = \frac{i}{2\omega_0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2 \right) + \frac{g_{21}}{2}, \quad \mu_2 = -\frac{\operatorname{Re}\{C_1(0)\}}{\operatorname{Re}\lambda'(\tau_2^0)},$$

$$T_2 = -\frac{\operatorname{Im}\{C_1(0)\} + \mu_2 \operatorname{Im}\lambda'(\tau_2^0)}{\omega_0}, \quad \beta_2 = 2 \operatorname{Re}\{C_1(0)\}.$$

Hence, we have from [25] that

- Theorem A.1.** (i) μ_2 determines the direction of Hopf bifurcation. If $\mu_2 > 0$ (< 0), Hopf bifurcation is supercritical (subcritical).
(ii) β_2 determines the stability of the bifurcated periodic solutions. If $\beta_2 < 0$ (> 0), the bifurcated periodic solutions are orbitally stable (unstable).
(iii) T_2 determines the period of the bifurcated periodic solutions. If $T_2 > 0$ (< 0), the period increase (decrease).

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