Bifurcation analysis in a toxic-phytoplankton and zooplankton ecosystem with double delays and Monod-Haldane type functional response

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Abstract

In this paper, we structure a phytoplankton zooplankton interaction system with two delays and Monod-Haldane type functional response, and mainly discuss the affect of τ and τ_1 to the dynamic behavior of system. Firstly, we give the existence of equilibrium and property of solution. The sufficient conditions ensuring the globally asymptotical stability of the boundary equilibrium are given. The nonexistence of the positive equilibrium ensures the global stability of the boundary equilibrium. Secondly, let $\tau_1 = 0$ and dynamic behavior of system with one delay (τ) is investigated. The stability switches phenomenon can occur as τ varying. Then fixed τ in stable interval, using τ_1 as parameter, it can investigate the effect of τ_1 and find τ_1 can also cause the oscillation of system. Specially, when $\tau = \tau_1$, the system can also occur the stable switching phenomenon, and, under certain conditions, the periodic solution will exist with the wide range as delay away from critical value. Furthermore, using the crossing curve methods, it can obtain the stable changes of positive equilibrium in (τ, τ_1) plane. When choosing τ in the unstable interval, the system still can occur Hopf bifurcation as delays varying. Some numerical simulations are given to indicate the correction of the theoretical analyses. At last, some conclusions are given.

Keywords: Double delays; Monod-Haldane type functional response; Stability; Hopf bifurcation; Crossing curve;

1. Introduction

For decades, as plankton is the basis of all food chains and networks in the aquatic system and plays an important role in the Marine ecology, the dynamics of marine plankton has become an important research field. Phytoplankton, also known as microalgae, are similar to terrestrial plants because they contain chlorophyll and need sunlight to survive and grow. Most phytoplankton are buoyant, floating on top of the ocean where sunlight penetrates the water.In a balanced ecosystem, they feed a variety of Marine life, including whales, shrimp, snails and jellyfish. A striking characteristic associated with many phytoplankton populations is rapid and large-scale bloom formation. These events are characterized by a sharp increase in number, by several orders of magnitude, followed by a sudden decline in the phytoplankton population, which returns to its original low level as if nothing had happened. Zooplankton are animals that live in communities of plankton, both herbivores and carnivores, Herbivores feed on phytoplankton and are then eaten by carnivorous zooplankton.

However, a special class of phytoplankton common to most aquatic ecosystems has a special physiological characteristic of releasing "toxic" or "allelochemicals" that are harmful to the growth of other algae. Algal toxicity has an important effect on the distribution of phytoplankton and zooplankton populations. The human consequences of harmful algal blooms are high costs for fisheries and tourism.High mortality of fish and other Marine animals during the brown tide sometimes leads to a ban on trade in fish and shellfish for a considerable period thereafter. Further brown tides pose a problem for human health, as consumers may die from poisoning after exposure to toxic algae shellfish.Although human deaths are rare, cases of eye irritation, headaches or other diseases can be observed.The economic impact is severe, especially for communities that rely almost entirely on fishing.Tourism has also been affected, as tourists are not allowed to visit the affected areas. Zooplankton population is completely dependent on phytoplankton as the most favorable food source, and the change of phytoplankton density has a great influence on the growth of zooplankton.The effects of harmful phytoplankton blooms on zooplankton are well known.When these harmful species multiply in large Numbers, the cumulative effect of all the toxins may lead to a decrease in grazing pressure on zooplankton.

In 2002, Chattopadhyay et al.[1] proposed a mathematical model of the interaction between toxic phytoplankton (TPP) and zooplankton, and discussed the role of TPP in harmful algal blooms. The general form of the mathematical model they consider is the following nonlinear coupling of ordinary differential equations

$$\begin{cases} \frac{d\mathcal{P}(t)}{dt} = r\mathcal{P}(t)(1-\frac{\mathcal{P}(t)}{L}) - \alpha f(\mathcal{P}(t))\mathcal{Z}(t), \\ \frac{d\mathcal{Z}(t)}{dt} = \beta f(\mathcal{P}(t))\mathcal{Z}(t) - \mu\mathcal{Z}(t) - \theta g(\mathcal{P}(t))\mathcal{Z}(t), \end{cases} \tag{1.1}$$

where $\mathcal{P}(t)$ and $\mathcal{Z}(t)$ are the TPP population densities and zooplankton population densities at time t, respectively. $f(\mathcal{P}(t))$ indicates the functional response of zooplankton to phytoplankton and $g(\mathcal{P}(t))$ describes the distribution of toxic substance that eventually kill off zooplankton populations. Since the pioneering work of Chattopadhyay et al, a growing number of biological papers have been published on the TPP-zooplankton model, demonstrating the importance of this interaction [2, 3, 4, 5, 6, 7, 8, 9, 10].

Some researchers have shown that toxic substances released by certain phytoplankton species repel zooplankton, which try to leave areas of high phytoplankton density. This is similar to the phytoplankton group defense mechanism against zooplankton.The main purpose of this paper is to consider a plankton-zooplankton model that uses the monod-haldane type of functional response to simulate zooplankton grazing. The zooplankton ($\mathcal{Z}(t)$) can identify the TPP ($\mathcal{P}$(t)) because the latter consumes too much and thus kills too many zooplankton. The zooplankton reduces their consumption through a change in chemotactic sensitivity in a direction opposite to the TPP gradient. This is modeled with a simplified non-monotonic monod-haldane type of function response expressed by $\mathcal{P}/(m^2+\mathcal{P}^2)$ [4, 11, 12].

Hence, in this paper, we investigate the following system:

$$\begin{cases} \frac{d\mathcal{P}(t)}{dt} = r\mathcal{P}(t)\left(1-\frac{\mathcal{P}(t)}{L}\right) - \frac{\alpha\mathcal{P}(t)\mathcal{Z}(t)}{m^2+\mathcal{P}^2(t)}, \\ \frac{d\mathcal{Z}(t)}{dt} = \frac{\beta e^{-\mu\tau}\mathcal{P}(t-\tau)\mathcal{Z}(t-\tau)}{m^2+\mathcal{P}^2(t-\tau)} - \mu\mathcal{Z}(t) - \frac{\rho\mathcal{P}(t-\tau_1)\mathcal{Z}(t)}{m^2+\mathcal{P}^2(t-\tau_1)} \end{cases} \tag{1.2}$$

The function $\mathcal{P}(t-\tau_1)/(m^2+\mathcal{P}^2(t-\tau_1))$ represents the distribution of toxic substance that eventually kill off zooplankton populations.

The biological senses and units of these parameters are shown in Table 1.

The initial conditions are chosen as

$$\mathcal{P}(\theta) = \varphi_1(\theta) \geq 0, \mathcal{Z}(\theta) = \varphi_2(\theta) \geq 0, \varphi_i(0) > 0, i = 0, 1, \theta \in [-\tau_{max}, 0], \tag{1.3}$$

where $(\varphi_1(\theta), \varphi_2(\theta)) \in C([-\tau_{max}, 0], \mathbf{R}_+^2)$, $\tau_{max} = \max\{\tau, \tau_1\}$.

The paper is organized as follows. In Section 2, we give the existence of equilibrium and property of solution for system (1.2). In this paper, we mainly discuss the affect of τ and τ_1 to the dynamic behavior of system (1.2). Firstly, we give the sufficient conditions ensuring the globally asymptotical stability of the boundary equilibrium. It can find that the delay of maturity of TPP does not effect the stability of the boundary equilibrium while the delay of gestation of zooplankton can have the key influence. The nonexistence of the positive equilibrium ensures the global

Table 1: Descriptions and units of parameters of system (1.2)

Symbol	Parameter Definition	Unit
r	Intrinsic growth rate of phytoplankton population	day^{-1}
L	Environmental carrying capacity	gCm^{-3}
α	Grazing efficiency of zooplankton population	day$^{-1}gCm^{-3}$
β	Growth efficiency of zooplankton population	day$^{-1}gCm^{-3}$
μ	Natural death rate of zooplankton population	day^{-1}
m	The half-saturation constant	$[gCm^{-3}]^2$
ρ	Toxin-producing rate	gCm^{-3} day^{-1}
τ	Gestation delay of the zooplankton	day^{-1}
τ_1	Delay required for the maturity of TPP	day^{-1}

stability of the boundary equilibrium. Secondly, let $\tau_1 = 0$ and dynamic behavior of system with one delay (τ) is investigated. The stability switches phenomenon can occur as τ varying. Then fixed τ in stable interval, using τ_1 as parameter, it can investigate the effect of τ_1 and find τ_1 can also cause the oscillation of system, that is, τ_1 can lead to the existence of periodic solution. Specially, when $\tau = \tau_1$, the system can also occur the stable switching phenomenon, and, under certain conditions, the periodic solution will exist with the wide range as delay away from critical value. These results are shown in Section 4. In Section 5, using the crossing curve methods, it can obtain the stable changes of positive equilibrium in (τ, τ_1) plane. When choosing τ in the unstable interval, the system still can occur Hopf bifurcation as delays varying. Some numerical simulation examples are given to indicate the correction of the theoretical analyses when the delays change in Section 6. At last, some conclusions are given.

2. Equilibrium and Property of solutions

The system (1.2) always exists two boundary equilibira $E_0(0,0)$ and $E_1(L,0)$. The positive equilibrium is $E^*(\mathcal{P}^*, \mathcal{Z}^*)$, where $\mathcal{P}^*$ satisfies the equation $f(\mathcal{P}^*) := \mu\mathcal{P}^{*2} - (\beta e^{-\mu\tau} - \rho)\mathcal{P}^* + \mu m^2 = 0$ and $\mathcal{Z}^* = \frac{r}{\alpha L}(m^2 + \mathcal{P}^{*2})(L - \mathcal{P}^*)$.

Define $R_\tau = \frac{\beta e^{-\mu\tau} - \rho}{2\mu m}$, some conditions ensuring the existence of E^* are given as follows.

Lemma 2.1. *The number of positive equilibrium for system (1.2) is given as follows.*

(i) If $m \geq L$ and $R_\tau > \frac{L^2+m^2}{2mL}$, then system (1.2) exists a uniquely positive equilibrium $E^*_-(\mathcal{P}^*_-, \mathcal{Z}^*_-)$;
(ii) If $m < L$, then the following results hold.

(a) When $R_\tau \geq \frac{L^2+m^2}{2mL}$, system (1.2) exists a uniquely positive equilibrium $E^*_-(\mathcal{P}^*_-, \mathcal{Z}^*_-)$;

(b) When $1 < R_\tau < \frac{L^2+m^2}{2mL}$, system (1.2) exists two positive equilibria $E^*_\pm(\mathcal{P}^*_\pm, \mathcal{Z}^*_\pm)$;

(c) When $R_\tau = 1$, system (1.2) exists a uniquely positive equilibrium $E^*(\mathcal{P}^*_-, \mathcal{Z}^*_-) = E^*(\mathcal{P}^*_+, \mathcal{Z}^*_+)$;

(d) When $R_\tau < 1$, system (1.2) does not exist any positive equilibrium, where

$$\begin{cases} \mathcal{P}^*_\pm &= \frac{(\beta e^{-\mu\tau}-\rho)\pm\sqrt{(\beta e^{-\mu\tau}-\rho)^2-4\mu^2m^2}}{2\mu} = m\Big[R_\tau \pm \sqrt{R_\tau^2-1}\Big], \\ \mathcal{Z}^*_\pm &= \frac{r}{\alpha L}(m^2+\mathcal{P}^{*2}_\pm)(L-\mathcal{P}^*_\pm). \end{cases}$$

or

Lemma 2.2. *The number of positive equilibrium for system (1.2) is given as follows.*

(i) If $R_\tau > \frac{L^2+m^2}{2mL}$, then system (1.2) exists a uniquely positive equilibrium $E^*_-(\mathcal{P}^*_-, \mathcal{Z}^*_-)$;

(ii) When $1 < R_\tau < \frac{L^2+m^2}{2mL}$ and $m < L$, system (1.2) exists two positive equilibria $E^*_\pm(\mathcal{P}^*_\pm, \mathcal{Z}^*_\pm)$;

(iii) When $R_\tau = 1$ and $m < L$, system (1.2) exists a uniquely positive equilibrium $E^*(\mathcal{P}^*_-, \mathcal{Z}^*_-) = E^*(\mathcal{P}^*_+, \mathcal{Z}^*_+)$;

(iv) When $R_\tau = \frac{L^2+m^2}{2mL}$ and $m < L$, system (1.2) exists a uniquely positive equilibrium $E^*_-(\mathcal{P}^*_-, \mathcal{Z}^*_-)$;

(v) Under the other situations, system (1.2) does not exist any positive equilibrium, where

$$\begin{cases} \mathcal{P}^*_\pm &= \frac{(\beta e^{-\mu\tau}-\rho)\pm\sqrt{(\beta e^{-\mu\tau}-\rho)^2-4\mu^2m^2}}{2\mu} = m\Big[R_\tau \pm \sqrt{R_\tau^2-1}\Big], \\ \mathcal{Z}^*_\pm &= \frac{r}{\alpha L}(m^2+\mathcal{P}^{*2}_\pm)(L-\mathcal{P}^*_\pm), \end{cases}$$

and $\mathcal{P}^*_+\mathcal{P}^*_- = m$.

For convenience, when the positive equilibrium exists, we always assume that Lemma 2.1 (i) holds, that is, $m \geq L$ and $R_\tau > \frac{L^2+m^2}{2mL}$. Furthermore, when $(\beta-\rho)L > \mu(L^2+m^2)$ and $\tau \in [0, \bar{\tau})$, system (1.2) exists a uniquely positive equilibrium $E^*(\mathcal{P}^*, \mathcal{Z}^*)$, where

$$\mathcal{P}^* = \mathcal{P}^*_-,\ \mathcal{Z}^* = \mathcal{Z}^*_-,\ \bar{\tau} = \frac{1}{\mu}\ln\frac{\beta L}{\rho L+\mu(L^2+m^2)}.$$

Lemma 2.3. *Let $\varphi_i(0) > 0$ $(i = 1, 2)$ and there exists some constant $\sigma > 0$, for $t \in [0, \sigma)$, then* *(a) all solutions of system (1.2) with initial conditions (1.3) uniquely exist and are positive;*

(b) $\limsup_{t\to\infty} \mathcal{P}(t) \le L$ *and* $\limsup_{t\to\infty} \mathcal{Z}(t) \le M$, *where* $M = \frac{L(r+\mu)^2}{4r\mu}$;

(c) if $r > \frac{\alpha M}{m^2}$, *then* $\liminf_{t\to\infty} \mathcal{P}(t) \ge m_0$, *where* $m_0 = \frac{L}{r}\Big(r - \frac{\alpha M}{m^2}\Big)$.

Proof Theorems 2.1 and 2.3 in [13], solutions of system (1.2) with initial conditions (1.3) exist on $t \in [0,\sigma)$ for some $\sigma > 0$ and are unique. Suppose $(\mathcal{P}(t), \mathcal{Z}(t))$ is a solution of system (1.2) for $t \in [0,\sigma)$. Without loss of generality, it assumes that $t \in [0,\sigma)$ is the maximum internal of the solution and $\sigma = \infty$ if the solution exists for any $t > 0$. Integrating the first equation of system (1.2) gives

$$\mathcal{P}(t) = \varphi_1(0)e^{\int_0^t [r(1-\mathcal{P}(u)/L) - \frac{\alpha\mathcal{Z}(u)}{m^2+\mathcal{P}^2(u)}]du} > 0,\ t \in [0,\sigma).$$

To prove the $\mathcal{Z}(t) > 0$ for any $t \in [0,\sigma)$, it uses the method of contradiction. Suppose that there exists a $t^* \in [0,\sigma)$ such that $\mathcal{Z}(t^*) = 0, \mathcal{Z}'(t^*) \le 0$ and $\mathcal{Z}(t) > 0$ for any $t \in [0,t^*)$. From the second equation of system (1.2), we have

$$\begin{array}{rcl} \dot{\mathcal{Z}}(t^*) = & \frac{\beta e^{-d\tau}\mathcal{P}(t^*-\tau)\mathcal{Z}(t^*-\tau)}{m^2+\mathcal{P}^2(t^*-\tau)} - \mu\mathcal{Z}(t^*) - \frac{\rho\mathcal{P}(t^*-\tau_1)\mathcal{Z}(t^*)}{m^2+\mathcal{P}^2(t^*-\tau_1)} \\ = & \frac{\beta e^{-d\tau}\mathcal{P}(t^*-\tau)Z(t^*-\tau)}{m^2+\mathcal{P}^2(t^*-\tau)} > 0, \end{array} \tag{2.1}$$

which is a contradiction with $\mathcal{Z}'(t^*) \le 0$. Hence $\mathcal{Z}(t) > 0$ for all $t \in [0,\sigma)$. This completes the proof of (a).

It follows from the first equation of system (1.2) that $\mathcal{P}' \le r\mathcal{P}(1-\mathcal{P}/L)$, which implies that $\limsup_{t\to\infty} \mathcal{P}(t) \le L$. Define

$$W(t) = \mathcal{P}(t) + \tfrac{\alpha e^{d\tau}}{\beta}\mathcal{Z}(t+\tau),\ t \ge 0.$$

Then from system (1.2), we obtain

$$\begin{array}{rl} \dot{W}(t) = & r\mathcal{P}(t)\Big(1 - \frac{\mathcal{P}(t)}{L}\Big) - \frac{\mu\alpha e^{d\tau}}{\beta}\mathcal{Z}(t+\tau) - \frac{\rho\alpha e^{d\tau}}{\beta}\frac{\mathcal{P}(t+\tau-\tau_1)\mathcal{Z}(t+\tau)}{m^2+\mathcal{P}^2(t+\tau-\tau_1)} \\ \le & r\mathcal{P}(t)\Big(1 - \frac{\mathcal{P}(t)}{L}\Big) - \frac{\mu\alpha e^{d\tau}}{\beta}\mathcal{Z}(t+\tau) \\ = & -\mu W(t) + (r+\mu)\mathcal{P}(t) - \frac{r}{L}\mathcal{P}^2(t) \\ \le & -\mu W(t) + \frac{L(r+\mu)^2}{4r}. \end{array}$$

Applying the theorem of differential inequality, we obtain that

$$0 < W(t) \le \tfrac{L(r+\mu)^2}{4r\mu}(1 - e^{-\mu t}) + W(0)e^{-\mu t}.$$

Therefore, $\limsup_{t\to\infty} \mathcal{Z}(t) \le \frac{L(r+\mu)^2}{4r\mu} = M$. This completes the proof of (b).

From the first equation of system (1.2), we get

$$\begin{aligned}\dot{\mathcal{P}}(t) = &\ r\mathcal{P}(t)\Big(1-\frac{\mathcal{P}(t)}{L}\Big)-\frac{\alpha\mathcal{P}(t)\mathcal{Z}(t)}{M^2+\mathcal{P}^2(t)}\\ \geq &\ r\mathcal{P}(t)\Big(1-\frac{\mathcal{P}(t)}{L}\Big)-\frac{\alpha M}{m^2}\mathcal{P}(t)\\ = &\ \mathcal{P}(t)\Big[r-\frac{\alpha M}{m^2}-\frac{r}{L}\mathcal{P}(t)\Big]\end{aligned}$$

which implies that $\lim_{t\to\infty}\inf\mathcal{P}(t)\geq\frac{L}{r}(r-\frac{\alpha M}{m^2})=m_0$ if $r>\frac{\alpha M}{m^2}$. This completes the proof of (c).

Therefore, from the continuation theorem of solutions for functional differential equations [13] and using the same methods as Lemma 2.2, it has the following theorem.

Theorem 2.1. *The solution of system (1.2) with the initial condition (1.3) is existent, unique, positive and bounded on* $[0,+\infty)$ *and* $\Gamma=\{(\varphi_1(\theta),\varphi_2(\theta))\in C|m_0\leq\varphi_1(\theta)\leq L,0\leq\varphi_2(\theta)\leq M\}$ *is positively invariant set for system (1.2).*

3. Stability of boundary equilibrium

That's clear that E_0 is always an unstable saddle point. For E_1, the following global stability result holds.

Theorem 3.1. *If* $0\leq\tau<\bar{\tau}$, *then* E_1 *is unstable; If* $\tau>\hat{\tau}:=\frac{1}{\mu}\ln\frac{\beta L}{\mu m^2}$, *then* E_1 *is globally asymptotically stable (GAS), where* $\bar{\tau}<\hat{\tau}$.

Proof The characteristic equation of system (1.2) at E_1 is

$$(\lambda+r)\Big[\lambda+\mu+\frac{\rho L}{m^2+L^2}-e^{-(\lambda+\mu)\tau}\frac{\beta L}{m^2+L^2}\Big]=0. \tag{3.1}$$

Equation (3.1) has one root $\lambda=-r<0$, and the other roots satisfy

$$\Big[\lambda+\mu+\frac{\rho L}{m^2+L^2}\Big]e^{(\lambda+\mu)\tau}=\frac{\beta L}{m^2+L^2}. \tag{3.2}$$

Define $H(\lambda):=[\lambda+\mu+\frac{\rho L}{m^2+L^2}]e^{(\lambda+\mu)\tau}$, we have $H(0)=(\mu+\frac{\rho L}{m^2+L^2})e^{\mu\tau}>0, H'(\lambda)>0, H(+\infty)=+\infty$. Since $\tau<\bar{\tau}$, by intermediate value theorem, (4) has a unique positive root $\lambda(\tau)$, then (3.1) has at least one positive root. Hence E_1 is unstable when $\tau<\bar{\tau}$.

Next, it will prove E_1 is GAS. Let $i\omega$ $(\omega>0)$ be root of (3.2), then ω satisfies

$$\omega^2=\Big[\frac{(\beta e^{-\mu\tau}+\rho)L}{m^2+L^2}+\mu\Big]\Big[\frac{(\beta e^{-\mu\tau}-\rho)L}{m^2+L^2}-\mu\Big].$$

If $\tau_1>\bar{\tau}_1$, then the above equation has no positive roots, i.e., (3.2) has no purely imaginary roots. Hence E_1 is LAS if $\tau_1>\bar{\tau}_1$.

Furthermore, choosing

$$V(\mathcal{P},\mathcal{Z}) = \mathcal{P} - L - L\ln\frac{\mathcal{P}}{L} + \frac{\alpha}{\beta e^{-\mu\tau}}\mathcal{Z} + \alpha\int_{t-\tau}^{t}\frac{\mathcal{P}\mathcal{Z}}{m^2+\mathcal{P}^2}dt,$$

its derivative along solution of system (1.2) is

$$\begin{aligned}
\dot{V} = &\ \frac{\mathcal{P}-L}{\mathcal{P}}\dot{\mathcal{P}} + \frac{\alpha}{\beta e^{-\mu\tau}}\dot{\mathcal{Z}} + \alpha\frac{\mathcal{P}\mathcal{Z}}{m^2+\mathcal{P}^2} - \alpha\frac{\mathcal{P}(t-\tau)\mathcal{Z}(t-\tau)}{m^2+\mathcal{P}^2(t-\tau)}\\
= &\ \frac{\mathcal{P}-L}{\mathcal{P}}\Big[r\mathcal{P}(1-\frac{\mathcal{P}}{L}) - \alpha\frac{\mathcal{P}\mathcal{Z}}{m^2+\mathcal{P}^2}\Big] + \frac{\alpha}{\beta e^{-\mu\tau}}\Big[\frac{\beta e^{-\mu\tau}\mathcal{P}(t-\tau)Z(t-\tau)}{m^2+\mathcal{P}^2(t-\tau)} - \mu\mathcal{Z}(t)\\
&-\frac{\rho\mathcal{P}(t-\tau_1)Z(t)}{m^2+\mathcal{P}^2(t-\tau_1)}\Big] + \alpha\frac{\mathcal{P}\mathcal{Z}}{m^2+\mathcal{P}^2} - \alpha\frac{\mathcal{P}(t-\tau)\mathcal{Z}(t-\tau)}{m^2+\mathcal{P}^2(t-\tau)}\\
= &\ -\frac{r}{L}(\mathcal{P}-L)^2 + \frac{\alpha L\mathcal{Z}}{m^2+\mathcal{P}^2} - \frac{\mu\alpha\mathcal{Z}}{\beta e^{-\mu\tau}} - \frac{\alpha\mathcal{P}(t-\tau)\mathcal{Z}(t-\tau)}{m^2+\mathcal{P}^2(t-\tau)} - \frac{\alpha\rho\mathcal{P}(t-\tau_1)\mathcal{Z}(t)}{\beta e^{-\mu\tau}(m^2+\mathcal{P}^2(t-\tau_1))}\\
\le &\ -\frac{r}{L}(\mathcal{P}-L)^2 + \alpha\Big[\frac{L}{m^2} - \frac{\mu}{\beta e^{-\mu\tau}}\Big]\mathcal{Z}.
\end{aligned}$$

If $\tau_1 > \hat{\tau}_1$, then $\frac{L}{m^2} - \frac{\mu}{\beta e^{-\mu\tau}} < 0$ and $\dot{V} \le 0$. Furthermore, it has $\dot{V} = 0$ iff $\mathcal{P} = L, \mathcal{Z} = 0$. Let Φ be largest invariant subset of $\dot{V} = 0$, then for each element in Φ, it has $\mathcal{P}(t) = L$ and $\mathcal{Z}(t) = 0$. By Lasalle invariance principle, E_1 is globally attractive. Adding to the local stability, E_1 is GAS. This completes the proof.

Remark 3.1. *From the above results, it has that the maturity delay of TPP has no affect to the stability of E_1. For the small gestation delay τ of zooplankton, E_1 is unstable and the positive equilibrium exists. For the large gestation delay τ and exceeding some value, E_1 is globally asymptotically stable. That is, the large gestation delay of zooplankton contributes zooplankton to die out and the small gestation delay may contribute to persistent existence of two populations.*

4. Stability of positive equilibrium

In this section, we always assume that $m \ge L$ and $R_\tau > \frac{m^2+L^2}{2mL}$. Let $x(t) = P(t) - P^*, y(t) = Z(t) - Z^*$, then system (1.2) becomes

$$\begin{cases}
\frac{dx(t)}{dt} = & A_1x(t) - \alpha A_2y(t) + O(2),\\
\frac{dy(t)}{dt} = & \beta e^{-\mu\tau}A_3\mathcal{Z}^*x(t-\tau) + \beta e^{-\mu\tau}A_2y(t-\tau)\\
& -\rho A_3\mathcal{Z}^*x(t-\tau_1) - (\mu+\rho A_2)y(t) + O(2),
\end{cases} \tag{4.1}$$

where

$$A_1 = -\frac{r\mathcal{P}^*}{L} + 2\alpha A_2^2\mathcal{Z}^*,\ A_2 = \frac{\mathcal{P}^*}{m^2+\mathcal{P}^{*2}} > 0,\ A_3 = \frac{m^2-\mathcal{P}^{*2}}{(m^2+\mathcal{P}^{*2})^2} > 0.$$

whose characteristic equation is

$$\begin{aligned}
\mathbf{D}(\lambda,\tau,\tau_1) := &\ \lambda^2 + (\mu+\rho A_2 - A_1)\lambda - A_1(\mu+\rho A_2)\\
&+[\beta e^{-\mu\tau}A_2(\alpha A_3\mathcal{Z}^* + A_1 - \lambda)]e^{-\lambda\tau} - \alpha\rho A_2A_3\mathcal{Z}^*e^{-\lambda\tau_1} = 0.
\end{aligned} \tag{4.2}$$

$$\begin{aligned}
\mathbf{D}(\lambda,0,0) := &\ \lambda^2 + (\mu+\rho A_2 - A_1 - \beta A_2)\lambda - A_1(\mu+\rho A_2 - \beta A_2)\\
&+\alpha(\beta-\rho)A_2A_3\mathcal{Z}^* = 0.
\end{aligned} \tag{4.3}$$

4.1. Case 1: $\tau_1 = 0, \tau > 0$

Firstly, we let $\tau \geq 0, \tau_1 = 0$, then system (4.1) becomes

$$\left\{\begin{array}{rl} \frac{dx(t)}{dt} = & A_1 x(t) - \alpha A_2 y(t) + O(2), \\ \frac{dy(t)}{dt} = & -\rho A_3 \mathcal{Z}^* x(t) - (\mu + \rho A_2) y(t) + \beta e^{-\mu\tau} A_3 \mathcal{Z}^* x(t-\tau) \\ & +\beta e^{-\mu\tau} A_2 y(t-\tau) + O(2), \end{array}\right. \tag{4.4}$$

and (4.3) becomes

$$\begin{array}{rl} \Delta(\lambda, \tau, 0) = & \lambda^2 + (\mu + \rho A_2 - A_1)\lambda - A_1(\mu + \rho A_2) - \alpha\rho A_2 A_3 \mathcal{Z}^* \\ & +[\beta e^{-\mu\tau} A_2(\alpha A_3 \mathcal{Z}^* + A_1 - \lambda)] e^{-\lambda\tau} = 0. \end{array} \tag{4.5}$$

Rewrite (4.5) as the following form

$$\Delta_1(\lambda, \tau) + \Delta_2(\lambda, \tau) e^{-\lambda\tau} = 0, \tag{4.6}$$

where

$$\begin{array}{rl} \Delta_1(\lambda, \tau) = & \lambda^2 + p\lambda + q, \ \Delta_2(\lambda, \tau) = r_1 + s\lambda, \\ p = & \mu + \rho A_2 - A_1, \ q = -A_1(\mu + \rho A_2) - \alpha\rho A_2 A_3 \mathcal{Z}^*, \\ r_1 = & -s(\alpha A_3 \mathcal{Z}^* + A_1), \ s = -\beta e^{-\mu\tau} A_2. \end{array}$$

Next, it investigates the existence of purely imaginary roots $\lambda = i\varpi$ ($\varpi = \varpi(\tau) > 0$). Equation (4.5) is exponential polynomial about λ with coefficients depending on delay τ. Beretta and Kuang [14] established a geometrical method to decide the existence of purely imaginary roots when the coefficients contained delay. It easily can verify the following relations:

(i) $\Delta_1(0, \tau) + \Delta_2(0, \tau) \neq 0$;

(ii) $\Delta_1(i\varpi, \tau) + \Delta_2(i\varpi, \tau) \neq 0$;

(iii) $\limsup \left\{ \left| \frac{\Delta_2(\lambda, \tau_1)}{\Delta_1(\lambda, \tau_1)} \right| : |\lambda| \to \infty, \mathbf{Re}\lambda \geq 0 \right\} < 1$;

(iv) Let $\mathbf{F}(\varpi, \tau) = |\Delta_1(i\varpi, \tau)|^2 - |\Delta_2(i\varpi, \tau)|^2$, then it has finite roots;

(v) If $\varpi > 0$ exists satisfying $\mathbf{F}(\varpi, \tau) = 0$, then it is continuous and differentiable in τ.

Substitute $\lambda = i\varpi$ into (4.6), it can yield

$$\left\{\begin{array}{l} r_1 \cos\varpi\tau + s\varpi \sin\varpi\tau = \varpi^2 - q, \\ s\varpi \cos\varpi\tau - r_1 \sin\varpi\tau = -p\varpi. \end{array}\right. \tag{4.7}$$

From (4.7), it has

$$\left\{\begin{array}{l} \sin\varpi\tau = \frac{(\varpi^2 - q)s\varpi + \varpi p r_1}{\varpi^2 s^2 + r_1^2}, \\ \cos\varpi\tau = -\frac{(q - \varpi^2) r_1 + \varpi^2 p s}{\varpi^2 s^2 + r_1^2}. \end{array}\right. \tag{4.8}$$

Using (4.6) and the property (i), (4.21) is equivalent to

$$\begin{cases} \sin\varpi\tau = \mathbf{Im}\left(\frac{\Delta_1(i\varpi,\tau)}{\Delta_2(i\varpi,\tau)}\right), \\ \cos\varpi\tau = -\mathbf{Re}\left(\frac{\Delta_1(i\varpi,\tau)}{\Delta_2(i\varpi,\tau)}\right), \end{cases} \tag{4.9}$$

which yields

$$\mathbf{F}(\varpi,\tau) = \varpi^4 + \Im_1(\tau)\varpi^2 + \Im_2(\tau) = 0, \tag{4.10}$$

whose roots are given by

$$\varpi_\pm^2 = \tfrac{1}{2}\left[-\Im_1(\tau) \pm \sqrt{\mathbf{\Delta}})\right], \tag{4.11}$$

where

$$\Im_1(\tau) = p^2 - 2q - s^2,\ \Im_2(\tau) = q^2 - r_1^2,\ \mathbf{\Delta} = \Im_1^2(\tau) - 4\Im_2(\tau).$$

Since $\Im_1(\tau) = 2\alpha\rho A_2 A_3 \mathcal{Z}^* > 0$ and $q + r_1 = \mu\alpha A_3 \mathcal{Z}^* > 0$, (4.10) has a uniquely positive real root ϖ_+ iff $q < r_1$.

Let

$$I_\tau = \Big\{\tau \in [0,\bar{\tau}) : q < r_1\Big\}.$$

Then for all $\tau \in I_\tau$, ϖ satisfies (4.11) and ϖ is not definited if $\tau \notin I_\tau$.

For $\tau \in I_\tau$, let $\theta_+(\tau) \in [0, 2\pi)$ be defined by

$$\begin{cases} \sin\theta_+(\tau) = \frac{(\varpi_+^2 - q)s\varpi_+ + \varpi_+ p r_1}{\varpi_+^2 s^2 + r_1^2}, \\ \cos\theta_+(\tau) = -\frac{(q-\varpi_+^2)r_1 + \varpi_+^2 ps}{\varpi_+^2 s^2 + r_1^2}, \end{cases}$$

and the maps $\tau_n(\tau) : I_\tau \longrightarrow \mathbf{R}_+$ defined by

$$\tau_n(\tau) := \tfrac{\theta_+(\tau) + 2n\pi}{\varpi_+(\tau)},\ n \in \mathbf{N}.$$

Furthermore, it can introduce the continuous and differentiable functions $\mathcal{S}_n(\tau)$ in τ:

$$\mathcal{S}_n(\tau) := \tau - \tau_n(\tau),\ \tau \in I_\tau,\ n \in \mathbf{N}.$$

Theorem 4.1. *The equation (4.6) has a pair of simply imaginary roots $\lambda = \pm i\varpi_+$, ϖ_+ is real for $\tau \in I_\tau$, and at some $\tau^* \in I_\tau$,*

$$\mathcal{S}_n(\tau^*) = 0 \quad for \quad some \quad n \in \mathbf{N}.$$

This pair roots cross the imaginary axis from left (right) to right (left) if $\delta_+(\tau^*) > 0$ (< 0), where

$$\delta_+(\tau^*) := \quad \mathbf{Sign}\Big\{\tfrac{\mathbf{dRe}\lambda}{\mathbf{d}\tau}\Big|_{\lambda = i\varpi_+}\Big\} = \mathbf{Sign}\Big\{\tfrac{\mathbf{d}\mathcal{S}_n(\tau)}{\mathbf{d}\tau}\Big|_{\tau=\tau^*}\Big\}.$$

Hence, the following theorem holds for system (4.4).

Theorem 4.2. *Assume that $0 < \tau < \bar{\tau}$. System (4.4), has the following dynamic properties.*
(i) If I_τ is empty or not empty set, but $\mathcal{S}_n(\tau) = 0$ has no positive root in I_τ, then E^* is LAS for all $\tau \in [0, \bar{\tau})$;
(ii) If I_τ is non-empty, $\mathcal{S}_n(\tau) = 0$ has positive roots in I_τ and $\delta_+(\tau^*) \neq 0$, for some $n \in \mathbf{N}$, let $\tau^0 = \min\{\tau : \mathcal{S}_n(\tau) = 0\}$ and $\tau^1 = \max\{\tau : \mathcal{S}_n(\tau) = 0\}$, then E^* is LAS for $\tau \in [0, \tau^0) \bigcup (\tau^1, \bar{\tau})$ and unstable for $\tau \in (\tau^0, \tau^1)$. Here τ^0 and τ^1 are the Hopf bifurcation values.

4.2. Case 2: $\tau > 0$, $\tau_1 > 0$

In the following, fixed $\tau = \tau^*$ in its stable interval $\mathbf{U}$ and using τ_1 as the bifurcation parameter. We rewrite (4.3) as

$$\begin{aligned} \mathbf{D}(\lambda, \tau^*, \tau_1) = \;& \lambda^2 + (\mu + \rho A_2 - A_1)\lambda - A_1(\mu + \rho A_2) \\ & + [\beta e^{-\mu\tau} A_2(\alpha A_3 \mathcal{Z}^* + A_1 - \lambda)] e^{-\lambda\tau^*} - \alpha\rho A_2 A_3 \mathcal{Z}^* e^{-\lambda\tau_1} \\ := \;& \lambda^2 + p\lambda + q_1 + (r_1 + s\lambda) e^{-\lambda\tau^*} + q_2 e^{-\lambda\tau_1} = 0, \end{aligned} \tag{4.12}$$

where

$$q_1 = -A_1(\mu + \rho A_2), \;\; q_2 = -\alpha\rho A_2 A_3 \mathcal{Z}^*.$$

By computing, it has

$$\begin{cases} q_1 - q_2 + r_1 & = \alpha A_2 A_3 \mathcal{Z}^* (\beta e^{-\mu\tau} + \rho) > 0, \\ q_1 + q_2 + r_1 & = \alpha A_2 A_3 \mathcal{Z}^* (\beta e^{-\mu\tau} - \rho) > 0. \end{cases}$$

Let iw $(w > 0)$ be the root of (4.12), separating the real part from the imaginary part, it has

$$\begin{cases} q_2 \cos w\tau_1 = w^2 - q_1 - r_1 \cos w\tau^* - \omega s \sin w\tau^*, \\ q_2 \sin w\tau_1 = wp + \omega s \cos w\tau^* - r_1 \sin w\tau^*. \end{cases} \tag{4.13}$$

Furthermore,

$$\begin{aligned} \breve{F}(w) := \;& \left[w^2 - q_1 - r_1 \cos w\tau^* - ws \sin w\tau^*\right]^2 \\ & + \left[wp + ws \cos w\tau^* - r_1 \sin w\tau^*\right]^2 - q_2^2 = 0, \end{aligned} \tag{4.14}$$

with $\breve{F}(0) = (q_1 + r_1)^2 - q_2^2 > 0$ and $\breve{F}(+\infty) = +\infty$. If (4.14) has roots, then (4.14) has at most finite roots denoted by $\{w_\kappa\}_{\kappa=1}^n$. Substituting $\{w_\kappa\}_{\kappa=1}^n$ into (4.14), we can get

$$\tau_1^{\kappa,j} = \frac{1}{w_\kappa}\left\{ \arccos\left(\frac{1}{q_2}\left[w_\kappa^2 - q_1 - r_1 \cos w_\kappa\tau^* - w_\kappa s \sin w_\kappa\tau^* \right] \right) + 2j\pi \right\}, j = 0, 1, 2, ...$$

Let $\tau_1^0 = \min\{\tau_1^{\kappa,j}\}$ and $\pm iw_0$ are the roots of (4.12) for $\tau_1 = \tau_1^0$.

Lemma 4.1. *If (4.14) has roots, for $\tau = \tau^* \in \mathbf{U}$, then it has the following conclusions.*
(i) If (4.14) has no positively real roots, then all roots of (4.12) have negative real parts for any $\tau_1 \geq 0$;
(ii) If (4.14) has finite real roots denoted by $\{w_\kappa\}_{\kappa=1}^n$, then the roots of (4.12) have negative real parts for $\tau_1 \in [0, \tau_1^0)$.

Let $\lambda(\tau_1) = \alpha_1(\tau_1) + i\alpha_2(\tau_1)$ be the root of (4.12) satisfying $\alpha_1(\tau_1^0) = 0$ and $\alpha_2(\tau_1^0) = w_0$. Derivating to τ_1 at τ_1^0 in two sides of (4.12), it has

Lemma 4.2. $\mathbf{Sign}\{\alpha_1'(\tau_1^0)\} = \mathbf{Sign}\{\breve{A}_1\breve{A}_3 + \breve{A}_2\breve{A}_4\}$, *where*

$$\breve{A}_1 = q_2 w_0 \sin w_0\tau_1^0, \breve{A}_2 = q_2 w_0 \cos w_0\tau_1^0,$$

$$\begin{aligned}\breve{A}_3 = \; & p - \tau^*(sw_0 \sin w_0\tau^* + r_1 \cos w_0\tau^*) \\ & + s\cos w_0\tau^* - \tau_1^0 q_2 \cos w_0\tau_1^0,\end{aligned}$$

$$\begin{aligned}\breve{A}_4 = \; & 2w_0 - \tau^*(sw_0 \cos w_0\tau^* - r_1 \sin w_0\tau^*) \\ & - s\sin w_0\tau^* + \tau_1^0 q_2 \sin w_0\tau_1^0.\end{aligned}$$

Theorem 4.3. *Suppose that $\tau = \tau^* \in \mathbf{U}$ is satisfied.*
(i) If (4.14) has no positive roots, then E^* is LAS for any $\tau_1 \geq 0$;
(ii) If (4.14) has positive roots denoted by $\{\omega_k\}_{k=1}^n$ and $\mathbf{Sign}\{\alpha_1'(\tau_1^0)\} \neq 0$, then E^* is LAS for $\tau_1 \in [0, \tau_1^0)$. τ_1^0 are Hopf bifurcation values.

Remark 4.1. *If (4.3) has two pairs of purely imaginary roots for some τ and τ_1, say $\pm iw_1$ and $\pm iw_2$, and all the other roots have non-zero real parts, then system (1.2) undergoes a double-Hopf bifurcation with a ratio $k_1 : k_2$, where $w_1 : w_2 = k_1 : k_2$. When $k_1, k_2 \in \mathbf{Z}^+$, it is called $k_1 : k_2$ resonant double-Hopf bifurcation, otherwise, it is called a non-resonant double Hopf bifurcation. More specially, since there are multiple parameters in system (1.2) except for τ and τ_1, tne bifurcation with codimension greater than 1 can be considered. The interesting researches on this topic can be found in [15, 16, 17, 18], and so on.*

4.3. Case 3: $\tau_1 = \tau := \nu > 0$

In this part, it will investigate local Hopf bifurcation when $\tau_1 = \tau = \nu$. In this situation, system (4.1) becomes

$$\left\{\begin{aligned} \frac{dx(t)}{dt} = \; & A_1x(t) - \alpha A_2 y(t) + O(2), \\ \frac{dy(t)}{dt} = \; & \Big[\beta e^{-\mu\nu} A_3 \mathcal{Z}^* - \rho A_3 \mathcal{Z}^*\Big] x(t-\nu) + \beta e^{-\mu\nu} A_2 y(t-\nu) \\ & -(\mu + \rho A_2) y(t) + O(2), \end{aligned}\right. \tag{4.15}$$

The system (4.15) has the same equilibria as system (1.2) when $\tau_1 = \tau$, $E_0(0,0)$, $E_1(L,0)$ and $E^*(\mathcal{P}(\nu), \mathcal{Z}(\nu))$. E^* exists when $0 \leq \nu < \bar{\nu} := \frac{1}{\mu} \ln \frac{\beta L}{\rho L + \mu(L^2 + m^2)}$.

As for E_1, the characteristic equation at E_1 of system (4.1) is given by

$$(\lambda + r)\Big[\lambda + \mu + \tfrac{\rho L}{m^2+L^2} - e^{-(\lambda+\mu)\nu}\tfrac{\beta L}{m^2+L^2}\Big] = 0. \tag{4.16}$$

Using the same method as Theorem 4.1, it has

Theorem 4.4. *If* $0 \le \nu < \bar{\nu}$, *then* E_1 *is unstable; If* $\nu > \hat{\nu} := \frac{1}{\mu}\ln\frac{\beta L}{\mu m^2}$, *then* E_1 *is GAS, where* $\bar{\nu} < \hat{\nu}$.

Equation (4.3) has one root $\lambda = -r < 0$, while the other roots satisfy the following equation

$$\mathcal{P}_1(\lambda,\nu) + \mathcal{Q}_1(\lambda,\nu)e^{-\lambda\nu} = 0, \tag{4.17}$$

where

$$\mathcal{P}_1(\lambda,\nu) = \lambda + \mu + \tfrac{\rho L}{m^2+L^2},\ \ \mathcal{Q}_1(\lambda,\nu) = -e^{-\mu\nu}\tfrac{\beta L}{m^2+L^2}.$$

It's obvious that

$$\mathcal{P}_1(0,\nu) + \mathcal{Q}_1(0,\nu) \neq 0,\ \ \mathcal{P}_1(i\omega,\nu) + \mathcal{Q}_1(i\omega,\nu) \neq 0.$$

Let $\lambda = \pm i\omega^0(\nu)$ ($\omega^0(\nu) > 0$) be the roots of (4.17), then stability switches may occur at $\nu_n^+(\nu)$ values:

$$\nu_n^+(\nu) = \tfrac{\theta_+^0(\nu)+2n\pi}{\omega_+^0(\nu)},\ \ n \in \mathbf{N},$$

where

$$\omega_+^0(\nu) = \sqrt{\tfrac{\beta^2L^2e^{-2\mu\nu}}{(m^2+L^2)^2} - (\mu + \tfrac{\rho L}{m^2+L^2})^2}$$

and $\theta_+^0(\nu) \in [0, 2\pi)$ satisfies

$$\begin{cases} \sin\theta_+^0(\nu) = -\frac{\omega_+^0(\nu)(m^2+L^2)e^{\mu\nu}}{\beta L}, \\ \cos\theta_+^0(\nu) = \frac{[\mu(m^2+L^2)+\rho L]e^{\mu\nu}}{\beta L}. \end{cases}$$

Hence,

$$\nu_n^+(\nu) = \tfrac{1}{\omega_+^0(\nu)}\Big\{\text{arcos}\tfrac{[\mu(m^2+L^2)+\rho k]e^{\mu\nu}}{\beta L} + 2n\pi\Big\}.$$

Define

$$\mathrm{Z}_n(\tau) := \nu - \nu_n^+(\nu),\ \ n \in \mathbf{N}$$

and

$$J^0 = \Big\{\nu_j :\ \nu_j \in [0, \bar{\nu}) \text{ and } \mathrm{Z}_n(\nu_j) = 0\Big\}.$$

Theorem 4.5. *If* $0 \le \nu < \bar{\nu}$, *then* $\pm i\omega_+^0(\nu)$ *are the roots of (4.4). For some* $\nu_* \in [0, \bar{\nu})$ *and* $n \in \mathbf{N}$, $\mathrm{Z}_n(\nu_*) = 0$. *This pair of roots traverse the axis of imaginaries from left (right) to right (left) if* $\delta_+^0(\nu_*) > 0$ (< 0), *where*

$$\delta_+^0(\nu_*) := \mathbf{Sign}\Big\{\frac{\mathbf{dRe}\lambda}{\mathbf{d}\nu}\Big|_{\lambda = i\omega_+^0(\nu_*)}\Big\} = \mathbf{Sign}\Big\{\frac{\mathbf{d}\mathrm{Z}_n(\nu)}{\mathbf{d}\nu}\Big|_{\nu=\nu_*}\Big\}.$$

If J^0 *is not empty. For all* $\nu_j \in J^0$, *if* $\mathrm{Z}_n'(\nu_j) \neq 0$ *holds, then system (4.15) undergoes Hopf bifurcations at* E_1 *when* $\nu = \nu_j$.

In the following, it investigates the existence of local Hopf bifurcation at E^*. When $\tau_1 = \tau = \nu$, the characteristic equation (4.3) becomes

$$\Delta^1(\lambda, \nu) + \Delta^2(\lambda, \nu)e^{-\lambda\nu} = 0, \tag{4.18}$$

where

$$\Delta^1(\lambda, \nu) = \lambda^2 + p\lambda + q_1,\ \Delta^2(\lambda, \nu) = r_1 + q_2 + s\lambda.$$

Let $\lambda = i\omega$ $(\omega = \omega(\nu) > 0)$ be the root of (4.18) and use the same methods as Section 3. The following relations hold.

(i) $\Delta^1(0, \nu) + \Delta^2(0, \nu) \neq 0$;

(ii) $\Delta^1(i\omega, \nu) + \Delta^2(i\omega, \nu) \neq 0$;

(iii) $\limsup \Big\{\Big|\frac{\Delta^2(\lambda,\nu)}{\Delta^1(\lambda,\nu)}\Big| : |\lambda| \to \infty, \mathbf{Re}\lambda \ge 0\Big\} < 1$;

(iv) Define $\mathcal{F}(\omega, \nu) = |\Delta^1(i\omega, \nu)|^2 - |\Delta^2(i\omega, \nu)|^2$, then it has finite roots;

(v) If there exists $\omega > 0$ satisfying $\mathcal{F}(\omega, \nu) = 0$, then it is continuous and differentiable in ν.

Substituting $\lambda = i\omega$ $(\omega = \omega(\nu) > 0)$ into (4.18), it has

$$\begin{cases} \omega^2 - q_1 &= (r_1 + q_2)\cos\omega\nu + s\omega\sin\omega\nu, \\ p\omega &= -s\omega\cos\omega\nu + (r_1 + q_2)\sin\omega\nu, \end{cases}$$

furthermore,

$$\begin{cases} \sin\omega\nu = \frac{(\omega^2 - q_1)s\omega + \omega p(r_1+q_2)}{\omega^2 s^2 + (r_1+q_2)^2}, \\ \cos\omega\nu = -\frac{(q_1 - \omega^2)(r_1+q_2) + \omega^2 ps}{\omega^2 s^2 + (r_1+q_2)^2}. \end{cases} \tag{4.19}$$

From the definitions of Δ^1 and Δ^2, (4.19) can be written:

$$\sin\omega\nu = \mathbf{Im}\Big(\frac{\Delta^1(i\omega,\nu)}{\Delta^2(i\omega,\nu)}\Big),\ \cos\omega\nu = -\mathbf{Re}(\frac{\Delta^1(i\omega,\nu)}{\Delta^2(i\omega,\nu)}),$$

which yields

$$\mathcal{F}(\omega, \nu) := \omega^4 + \Xi_1(\nu)\omega^2 + \Xi_2(\nu) = 0, \tag{4.20}$$

and its roots are given by

$$\omega_{\pm}^2 = \tfrac{1}{2}\Big[-\Xi_1(\nu) \pm \sqrt{\Delta}\Big], \tag{4.21}$$

where

$$\Xi_1(\nu) = p^2 - 2q_1 - s^2,\ \Xi_2(\nu) = q_1^2 - (r_1 + q_2)^2,\ \Delta = \Xi_1^2(\tau) - 4\Xi_2(\tau).$$

We have $\Xi_1(\nu) = A_1^2 > 0$ and $q_1 + r_1 + q_2 = \mu\alpha A_3 \mathcal{Z}^* > 0$, then (4.20) has a uniquely positive real root ω_+ iff $q_1 < r_1 + q_2$.

Let

$$I_\nu = \{\tau \in [0, \bar{\nu}) : q_1 < r_1 + q_2\}.$$

Then, for $\nu \in I_\nu$, $\Theta(\nu) \in [0, 2\pi)$ satisfies

$$\begin{cases} \sin\Theta(\nu) = \frac{(\omega^2 - q_1)s\omega + \omega p(r_1+q_2)}{\omega^2 s^2 + (r_1+q_2)^2}, \\ \cos\Theta(\nu) = -\frac{(q_1-\omega^2)(r_1+q_2) + \omega^2 ps}{\omega^2 s^2 + (r_1+q_2)^2}, \end{cases}$$

with $\mathcal{F}(\omega, \nu) = 0$ for $\tau \in I_\nu$. Hence, the maps $\nu_n(\nu) : I_\nu \to \mathbf{R}_+$ are defined by

$$\nu_n(\nu) := \tfrac{\Theta(\nu) + 2n\pi}{\omega(\nu)},\ n \in \mathbf{N}.$$

Furthermore, define the continuous and differentiable functions in ν:

$$\mathbf{T}_n(\nu) := \nu - \nu_n(\nu),\ \nu \in I_\nu,\ n \in \mathbf{N}.$$

Theorem 4.6. *The equation (4.18) has the roots $\lambda = \pm i\omega(\nu^*)$, and at some $\nu^* \in I_\nu$,*

$$\mathbf{T}_n(\nu^*) = 0 \quad for \quad some \quad n \in \mathbf{N}.$$

This pair of roots cross the imaginary axis from left (right) to right (left) if $\delta_+(\nu^*) > 0$ (< 0), where

$$\delta_+(\nu^*) := \mathbf{Sign}\Big\{\tfrac{\mathbf{dRe}\lambda}{\mathbf{d}\nu}\Big|_{\lambda = i\omega_+}\Big\} = \mathbf{Sign}\Big\{\tfrac{\mathbf{dT}_n(\nu)}{\mathbf{d}\nu}\Big|_{\nu=\nu^*}\Big\}.$$

Remark 4.2. *For $\nu \in I_\nu$, then it has the following one sequence of functions:*

$$\mathbf{T}_n(\nu) = \nu - \tfrac{\theta_+(\nu) + 2n\pi}{\omega_+(\nu)}.$$

Theorem 4.7. *For system (4.15), it assumes that $0 < \nu < \bar{\nu}$.*
(i) If I_ν is empty set or not empty set, but $\mathbf{T}_n(\nu) = 0$ has no positive root in I_ν, then E^* is LAS for any $\tau \in [0, \bar{\nu})$;
(ii) If I_ν is non-empty set, $\mathbf{T}_n(\nu) = 0$ exists positive roots at I_ν and $\delta_+(\nu^*) \neq 0$, for $n \in \mathbf{N}$, and rearrange these roots as the set $J := \{\nu^0, \nu^1, ..., \nu^{\mathbf{m}}\}$ with $\nu^j < \nu^{j+1}, j = 0, ..., \mathbf{m} - 1$. Then E^* is LAS for $\nu \in [0, \nu^0) \cup (\nu^{\mathbf{m}}, \bar{\nu})$ and unstable for $\nu \in (\nu^0, \nu^{\mathbf{m}})$. Hopf bifurcations occur at E^* when $\nu = \nu^j$.

4.4. Global Hopf bifurcation of system (4.15)

In Section 4.2, it has known that system (4.15) undergoes local Hopf bifurcations at E^* when ν near ν^j, $\nu^j \in J$. In this section, using the methods in [19, 20, 21], it investigates the existence of globally periodic solutions.

The following notations from [21] are given. Denote

$$J_0 = \Big\{\nu \in J : \mathbf{T}_0(\nu) = 0\Big\},\ J_+ := J - J_0,$$

$$A_j = \begin{cases} \max\{\nu_j :\ \nu_j \in J^0, \nu_j < \nu^j\}, & J^0 \neq \emptyset, \\ 0, & \text{else}, \end{cases}$$

$$B_j = \begin{cases} \min\{\nu_j :\ \nu_j \in J^0, \nu_j > \nu^j\}, & J^0 \neq \emptyset, \\ \sup I_\nu, & \text{else}, \end{cases}$$

$$\begin{aligned} A^j &= \max\{\nu^i :\ \nu^i \in J_+ \cup J^0,\ \tau^i < \nu^j \in J_+\}, \\ B^j &= \min\{\nu^i :\ \nu^i \in J_+ \cup J^0,\ \nu^i > \nu^j \in J_+\}. \end{aligned}$$

Next, it assumes that $J_+ \neq \emptyset$, using global Hopf bifurcation theorem [19], it will investigat the global existence of periodic solutions bifurcating from $(E^*, \nu^j, \frac{2\pi}{\omega_+^j})$ for system (4.15), where $\nu^j \in J^+$ and $\omega_+^j = \omega_+(\nu^j)$, and $\pm i\omega_+^j$ is the roots of (4.18) when $\nu = \nu^j$.

In this part, $\nu \in [0, \bar{\nu})$ always holds. Setting $z_t = (\mathcal{P}_t, \mathcal{Z}_t)$, it rewrites system (4.15) as:

$$\dot{z}(t) = \Upsilon(z_t, \nu, p), \tag{4.22}$$

where $z_t(\theta) = z(t + \theta)$. System (4.22) has three equilibria $\bar{z}_1 = (0, 0)$, $\bar{z}_2 = (L, 0)$ and $z^* = E^*$.

Define

$$\begin{aligned} &\mathbf{X} = \mathcal{C}([-\nu, 0], \mathbf{R}^2_+), \\ &\Sigma = \mathbf{Cl}\{(z_t, \nu, p) \in \mathcal{X} \times \mathbf{R} \times \mathbf{R}^+ : z_{t+p} = z_t\}, \\ &\mathbf{N} = \{(\bar{z}, \nu, p) : \Upsilon(\bar{z}, \nu, p) = 0\}, \end{aligned}$$

and let $\ell_{(z^*, \nu^j, \frac{2\pi}{\omega_+^j})}$ which is nonempty be the connected component of $(z^*, \nu^j, \frac{2\pi}{\omega_+^j})$ in Σ, and $\mathrm{Proj}_\nu\ (z^*, \nu^j, \frac{2\pi}{\omega_+^j})$ be its projection on ν. By Theorem 3.1, it has the following results.

Lemma 4.3. *All periodic solutions of system (4.22) are uniformly bounded in* $\mathbf{R}^2_+$.

Lemma 4.4. *If $m \geq L$, then system (4.22) does not exist nonconstant τ-periodic solution.*

Proof Because the orbits of system (4.22) don't intersect and $\mathcal{P}$-$\mathcal{Z}$ axis are the invariable manifold, which implies that, in the first quadrant, if there exists any periodic solutions, then there must be E^* in its interior. It will prove by contradiction. It assumes that system (4.22) has nonconstant τ-periodic solution, then it definitely obtain that the following systems have nontrivial periodic solutions:

$$\begin{cases} \frac{d\mathcal{P}(t)}{dt} = r\mathcal{P}(t)(1-\frac{\mathcal{P}(t)}{L}) - \frac{\alpha\mathcal{P}(t)\mathcal{Z}(t)}{m^2+\mathcal{P}^2(t)} := \mathbf{M}, \\ \frac{d\mathcal{Z}(t)}{dt} = \frac{\beta e^{-\mu\tau}\mathcal{P}(t)\mathcal{Z}(t)}{m^2+\mathcal{P}^2(t)} - \mu\mathcal{Z}(t) - \frac{\rho\mathcal{P}(t)\mathcal{Z}(t)}{m^2+\mathcal{P}^2(t)} := \mathbf{N}, \end{cases} \tag{4.23}$$

Define Dulac function $\mathbf{Q} = \frac{m^2+\mathcal{Z}^2}{\mathcal{P}\mathcal{Z}}$, then

$$\begin{aligned} \frac{\partial(\mathbf{MQ})}{\partial\mathcal{P}} + \frac{\partial(\mathbf{NQ})}{\partial\mathcal{Z}} &= \frac{1}{\mathcal{Z}}\Big[-\frac{r}{L}(m^2+\mathcal{P}^2) + 2\mathcal{P}r(1-\frac{\mathcal{P}}{L})\Big] \\ &= -\frac{r}{L\mathcal{Z}}\Big[m^2 + 2\mathcal{P}^2 + (\mathcal{P}-L)^2 - L^2\Big]. \end{aligned}$$

If $m \geq L$, then $\frac{\partial(\mathbf{MQ})}{\partial\mathcal{P}} + \frac{\partial(\mathbf{NQ})}{\partial\mathcal{Z}} < 0$. By Dulac theorem, system (4.23) has no periodic solution in the first quadrant, which is a contradiction. This completes the proof.

Theorem 4.8. *Assume that the conditions $J_+ \neq \emptyset$, $\tau \in [0,\bar{\nu})$ and $(\beta-\rho)L > \mu(L^2+m^2)$ hold. Then for any $\nu^j \in J_+$, there exists $\nu^i \in J^0 \cup J_+ - \{\nu^j\}$, so that system (4.22) has at least one positive periodic solution for ν varies between ν^i and ν^j.*

Proof The characteristic equation of system (4.22) at an equilibrium $\bar{z}$ are expressed as:

$$\Delta(\bar{z},\nu,p)(\lambda) = \lambda Id - \mathbf{D}\Upsilon(\bar{z},\nu,p)(e^{\lambda\cdot}Id) = 0.$$

The system (4.22) has three equilibria $\bar{z}_1, \bar{z}_2$ and z^*. From Section 4, it knows that $(\bar{z}_1,\nu,p)$ is not a center, while $(\bar{z}_2,\nu,p)$ and (z^*,ν,p) are isolated centers. By Theorem 4.7 and $\dot{T}_n(\nu^j) \neq 0$, there exist $\varepsilon > 0,\ \delta > 0$ and $\lambda : (\nu^j-\delta, \nu^j+\delta) \to C$, such that $\det(\triangle(\lambda(\nu^j))) = 0, |\lambda(\nu^j) - i\omega_+^j| < \varepsilon$ for all $\nu \in [\nu^j-\delta,\nu^j+\delta]$ and $\lambda(\nu^j) = i\omega_+^j$, $\mathbf{dRe}\lambda(\nu^j)/\mathbf{d}\nu \neq 0$.

Let $\Omega_{\epsilon,\frac{2\pi}{\omega_+^j}} = \{(\eta,p) : 0 < \eta < \varepsilon, |p - \frac{2\pi}{\omega_+^j}| < \varepsilon\}$. It can verify that on $[\nu^j-\delta,\nu^j+\delta] \times \partial\Omega_{\varepsilon,\frac{2\pi}{\omega_+^j}}$, $\Delta(z^*,\nu,p)(\eta+\frac{2\pi}{p}i) = 0$ iff $\eta = 0, \nu = \nu^j, p = \frac{2\pi}{\omega_+^j}$. Furthermore, define

$$R^{\pm}\Big(z^*,\nu^j,\frac{2\pi}{\omega_+^j}\Big)(\eta,p) = \Delta(z^*,\nu^j\pm\delta,p)(\eta+\frac{2\pi}{p}i),$$

then the crossing number of $(z^*,\nu^j,\frac{2\pi}{\omega_j^+})$ is given by

$$\begin{aligned} \chi\Big(z^*,\nu^j,\frac{2\pi}{\omega_+^j}\Big) &= \deg_{\mathbf{B}}\Big(R^-(z^*,\nu^j,\frac{2\pi}{\omega_+^j}),\Omega_{\epsilon,\frac{2\pi}{\omega_+^j}}\Big) - \deg_{\mathbf{B}}\Big(R^+(z^*,\nu^j,\frac{2\pi}{\omega_+^j}),\Omega_{\epsilon,\frac{2\pi}{\omega_+^j}}\Big) \\ &= \begin{cases} -1, & \dot{\mathbf{T}}_n(\nu^j) > 0, \\ 1, & \dot{\mathbf{T}}_n(\nu^j) < 0. \end{cases} \end{aligned}$$

Furthermore,

$$\Sigma_{(\bar{z},\nu,p)\in\ell_{(z^*,\nu^j,\frac{2\pi}{\omega_+^j})}}\ \chi(\bar{z},\nu,p)\neq 0,$$

where $\bar{z}$ is either z^* or $\bar{z}_2$. Hence, the connected component $\ell_{(z^*,\nu^j,\frac{2\pi}{\omega_+^j})}$ through $(z^*,\nu^j,\frac{2\pi}{\omega_+^j})$ in Σ is unbounded.

By the definition of ν^j, there exists an integer $j>0$ such that

$$2\pi<\nu^j\omega_+^j<2(j+1)\pi,\quad \nu^j\in J_+,$$

which implies that

$$\tfrac{\nu^j}{j+1}<\tfrac{2\pi}{\omega_+^j}<\nu^j.$$

Therefore, $\frac{\nu}{j+1}<T<\nu$ if $(\bar{z},\nu,T)\in\ell_{(z^*,\nu^j,\frac{2\pi}{\omega_+^j})}$. This fact combining with Lemma 4.4 show that $\mathrm{Proj}_\nu\ \ell_{(z^*,\nu^j,\frac{2\pi}{\omega_+^j})}$ is bounded. In addition , Lemmas 4.3 and 4.4 imply that the projection of $\ell_{(z^*,\nu^j,\frac{2\pi}{\omega_+^j})}$ onto the z-space is uniformly bounded for $\nu\in\mathrm{Proj}_\tau(z^*,\nu^j,\frac{2\pi}{\omega_+^j})\cap(A_j,B_j)$. Therefore, either $[A^j,\nu^j]\subset\mathrm{Proj}_\tau(z^*,\nu^j,\frac{2\pi}{\omega_+^j})\cap(A_j,B^j)$ or $[\nu^j,B^j]\subset\mathrm{Proj}_\nu(z^*,\nu^j,\frac{2\pi}{\omega_+^j})\cap(A_j,B_j)$ holds. Otherwise, $\ell_{(z^*,\nu^j,\frac{2\pi}{\omega_+^j})}$ is unbounded and $\mathrm{Proj}_\nu(z^*,\nu^j,\frac{2\pi}{\omega_+^j})\subset(A_j,B_j)$, which is a contradicts.This completes the proof.

5. Crossing curve methods

The result of theorem 4.3 clearly shows the stability of the equilibrium $E^*$when τ and τ_1 change. Clearly, there is a Hopf bifurcation at τ_1^0 and there may be multiple stable switches. If you leave τ in an unstable region, τ_1^0 may not exist such that E^* is unstable in $\tau_1\in[0,\tau_1^0)$, it is stable in $\tau_1>\tau_1^0$. However, this is not entirely satisfactory because it does not allow for a bifurcated analysis of (τ,τ_1). That is, no information is given about (τ,τ_1) that generates stable or unstable stable states. For this purpose, Gu et al. [22] provided crossing curve method which are defined as the curves that separate the stable and unstable regions in the (τ,τ_1) plane. However, the system referenced in Gu2005 does not depend on the delay in the coefficients, so these results cannot be used directly (4.1). Recently, An et al. [23] improve these results in [22] to the system with the coefficients depending on the delay. In the following, we will use the methods in [23] to give the couples (τ,τ_1) that generate a stable or an unstable equilbrium.

We rewrite (4.1) as

$$\begin{cases} \frac{dx(t)}{dt} = & A_1x(t) - \alpha A_2 y(t) + O(2), \\ \frac{dy(t)}{dt} = & \beta e^{-\mu\tau} A_3 Z^* x(t-\tau) + \beta e^{-\mu\tau} A_2 y(t-\tau) \\ & -\rho A_3 Z^* x(t-\tau_1) - (\mu + \rho A_2) y(t) + O(2), \end{cases} \tag{5.1}$$

whose characteristic equation is

$$\mathbf{D}(\lambda, \tau, \tau_1) := \Sigma_0(\lambda, \tau) + \Sigma_1(\lambda, \tau) e^{-\lambda\tau} + \Sigma_2(\lambda, \tau) e^{-\lambda\tau_1} = 0, \tag{5.2}$$

where

$$\Sigma_0(\lambda, \tau) = \lambda^2 + (\mu + \rho A_2 - A_1)\lambda - A_1(\mu + \rho A_2),$$
$$\Sigma_1(\lambda, \tau) = \beta e^{-\mu\tau} A_2(\alpha A_3 Z^* + A_1 - \lambda),\ \Sigma_2(\lambda, \tau) = -\alpha\rho A_2 A_3 Z^*.$$

It is easily to verify $\Sigma_s(\lambda, \tau), s = 0, 1, 2$ satisfying the following conditions [23]:
(C1) $\Sigma_0(0, \tau) + \Sigma_1(0, \tau) + \Sigma_2(0, \tau) \neq 0$;
(C2) $\lim\limits_{\mathbf{Re}\lambda \geq 0, |\lambda| \to \infty} \sup\limits_{\tau \in \mathbf{I}} \left(\left| \frac{\Sigma_1(\lambda,\tau)}{\Sigma_0(\lambda,\tau)} \right| + \left| \frac{\Sigma_2(\lambda,\tau)}{\Sigma_0(\lambda,\tau)} \right| \right) < 1$;
(C3) $\Sigma_s(\lambda, \tau) \neq 0$, $s = 0, 1, 2$, for any $\tau \in [0, \bar{\tau})$ and $\omega \in \mathbf{R}_+$;
(C4) For any $\omega \in \mathbf{R}_+$, at least one of $|\Sigma_s(i\omega, \tau)|$ $(s = 0, 1, 2)$ tends to infinity as τ tending $-\infty$.

5.1. Crossing curve

Next, we will determine the feasible values of $(\tau, \tau_1) \in [0, \bar{\tau}) \times \mathbf{R}_+$ so that $\lambda = i\omega$ $(\omega > 0)$ is a root of (6.2). The curve formed by all these points is called "crossing curve". Let

$$\begin{cases} \beta_1(\omega, \tau) = \frac{\Sigma_1(i\omega,\tau)}{\Sigma_0(i\omega,\tau)}, \\ \beta_2(\omega, \tau) = \frac{\Sigma_2(i\omega,\tau)}{\Sigma_0(i\omega,\tau)}, \end{cases} \tag{5.3}$$

where

$$\Sigma_0(i\omega, \tau) = -\omega^2 - A_1(\mu + \rho A_2) + i\omega(\mu + \rho A_2 - A_1),$$
$$\Sigma_1(i\omega, \tau) = \beta e^{-\mu\tau} A_2(\alpha A_3 Z^* + A_1 - i\omega),\ \Sigma_2(i\omega, \tau) = -\alpha\rho A_2 A_3 Z^*.$$

Hence, $(i\omega, \tau, \tau_1)$ is the zeros of (6.2) iff

$$\mathcal{D}(\omega, \tau, \tau_1) := 1 + \beta_1(\omega, \tau) e^{-i\omega\tau} + \beta_2(\omega, \tau) e^{-i\omega\tau_1} = 0. \tag{5.4}$$

It assumes that $(i\omega, \tau, \tau_1)$ is the zero of (6.2), then the left side of (5.4) must form a triangle on the complex plane. Since $|\Sigma_0(i\omega, \tau)| + |\Sigma_1(i\omega, \tau)| \geq |\Sigma_2(i\omega, \tau)|$ is always true, therefore, the feasible region Ω can be obtained.

Lemma 5.1. *$\tau \in [0, \bar{\tau})$, the feasible region Ω for (ω, τ) satisfies*

$$\Omega = \Big\{(\omega, \tau) \in \mathbf{R}_+ \times \mathbf{I} : f_1(\omega, \tau) \geq 0,\ \ f_2(\omega, \tau) \geq 0\ \Big\},$$

where $f_1(\omega, \tau) = |\Sigma_1(i\omega, \tau)| + |\Sigma_2(i\omega, \tau)| - |\Sigma_0(i\omega, \tau)|$ and $f_2(\omega, \tau) = |\Sigma_0(i\omega, \tau)| + |\Sigma_2(i\omega, \tau)| - |\Sigma_1(i\omega, \tau)|$.

Therefore, the feasible region is surrounded by the line $\tau = \bar{\tau}$, τ-axis and ω-axis, the curves $f_1(\omega, \tau) = 0$ and $f_2(\omega, \tau) = 0$. For every connected region Ω_k, the feasible range for ω is denoted by $I_k = [\omega_k^l, \omega_k^r]$, $k = 1, 2, ..., N$. Furthermore, for each $\omega \in I_k$, there exists the intervals $I_\omega^k = [\tau_\omega^{k,l}, \tau_\omega^{k,r}] \subseteq \mathbf{I}$, on which two inequalities hold in Ω.

Let the angles formed by 1 and $\beta_1(\omega, \tau)e^{-i\omega\tau}$ be $\theta_1(\omega, \tau)$, and the angles formed by 1 and $\beta_2(\omega, \tau)e^{-i\omega\tau_1}$ be $\theta_2(\omega, \tau)$, by the law of cosine, it has

$$\begin{cases} \theta_1(\omega, \tau) = \mathbf{arcos}\left[\frac{1+|\beta_1(\omega,\tau)|^2-|\beta_2(\omega,\tau)|^2}{2|\beta_1(\omega,\tau)|}\right], \\ \theta_2(\omega, \tau) = \mathbf{arcos}\left[\frac{1+|\beta_2(\omega,\tau)|^2-|\beta_1(\omega,\tau)|^2}{2|\beta_2(\omega,\tau)|}\right], \end{cases}$$

where

$$|\beta_1(\omega, \tau)| = \Big|\frac{\Sigma_1(i\omega, \tau)}{\Sigma_0(i\omega, \tau)}\Big| \text{ and } |\beta_2(\omega, \tau)| = \Big|\frac{\Sigma_2(i\omega, \tau)}{\Sigma_0(i\omega, \tau)}\Big|.$$

For each fixed $\omega \in I_k$, it can note that $\mathbf{Im}(\beta_1(\omega, \tau)e^{-i\omega\tau}) = 0$ iff $\theta_1(\omega, \tau) = 0$ or π, which is equivalent to $\tau = \tau_\omega^{k,l}$ or $\tau = \tau_\omega^{k,r}$. Therefore, $\mathbf{Im}(\beta_1(\omega, \tau)e^{-i\omega\tau})$ cannot change sign for $\tau \in \mathbf{Int}I_\omega^k$.

In the following, two feasible cases are considered:

(i) $\mathbf{Im}(\beta_1(\omega, \tau)e^{-i\omega\tau}) > 0$:
From the triangle, it can obtain

$$\mathbf{arg}(\beta_1(\omega, \tau)e^{-i\omega\tau}) = \pi - \theta_1(\omega, \tau),\ \mathbf{arg}(\beta_2(\omega, \tau_1)e^{-i\omega\tau_1}) = \theta_2(\omega, \tau) - \pi.$$

Then there exists an $n \in \mathbf{Z}$ such that

$$\mathbf{arg}(\beta_1(\omega, \tau)) + \theta_1(\omega, \tau) + (2n - 1)\pi = \omega\tau, \tag{5.5}$$

and

$$\tau_1 = \tfrac{1}{\omega}\Big[\mathbf{arg}(\beta_2(\omega, \tau)) - \theta_2(\omega, \tau) + (2k + 1)\pi\Big],\ \ \textit{for some } k \in \mathbf{Z}, \tag{5.6}$$

where $k \geq k_0^+$ and k_0^+ is the smallest integer such that the right side of (5.6) is positive.

(ii) $\mathbf{Im}(\beta_1(\omega,\tau)e^{-i\omega\tau})<0$:
In this case, the triangle formed is the mirror image of the case (i) about the real axis. We have

$$\mathbf{arg}(\beta_1(\omega,\tau))-\theta_1(\omega,\tau)+(2n-1)\pi=\omega\tau,\ \ for\ some\ n\in\mathbf{Z}, \tag{5.7}$$

and

$$\tau_1=\frac{1}{\omega}\Big[\mathbf{arg}(\beta_2(\omega,\tau))+\theta_2(\omega,\tau)+(2j+1)\pi\Big],\ \ for\ some\ j\in\mathbf{Z}, \tag{5.8}$$

where $j\geq j_0^-$ and j_0^- is the smallest integer such that the right side of (5.8) is positive.

Now it can define $\mathbf{I}^\omega$ as the interval of ω and $\mathbf{I}_\tau^\omega$ the feasible values of τ for every fixed $\omega\in\mathbf{I}^\omega$. Fixed $\omega\in\mathbf{I}^\omega$, it can define the following functions:

$$\mathbf{S}_n^{\pm}(\omega,\tau)=\ \ \tau-\frac{1}{\omega}\Big[\mathbf{arg}(\beta_1(\omega,\tau))\pm\theta_1(\omega,\tau)+(2n-1)\pi\Big],\ \ fro\ some\ n\in\mathbf{Z}. \tag{5.9}$$

If (5.9) has zeros written as $\hat{\tau}^{i^\pm}(\omega), i=1,2,\cdots$. Furthermore, it can obtain τ_1 values as follows:

$$\hat{\tau}_1^{i^\pm,j^\pm}(\omega)=\frac{1}{\omega}\Big[\mathbf{arg}(\beta_2(\omega,\hat{\tau}^{i^\pm}))\mp\theta_2(\omega,\hat{\tau}^{i^\pm})+(2j^\pm+1)\pi\Big], \tag{5.10}$$

where $j^\pm\geq j_0^\pm$ and $j_0^\pm$ is the smallest integer such that $\hat{\tau}_1^{i^\pm,j^\pm}(\omega)>0$.

If ω takes all the values in the whole interval $\mathbf{I}^\omega$, then it can obtain the following curve on Ω

$$\mathbf{C}:=\Big\{(\omega,\hat{\tau}^{i^\pm}(\omega)):\omega\in\mathbf{I}^\omega,\mathbf{S}_n(\omega,\hat{\tau}^{i^\pm}(\omega))=0\Big\}, \tag{5.11}$$

and the crossing curves on (τ,τ_1) plane

$$\mathbf{T}:=\{(\hat{\tau}^{i^\pm}(\omega),\hat{\tau}_1^{i^\pm,j^\pm}(\omega))\in[0,\bar{\tau})\times\mathbf{R}_+:\omega\in\mathbf{I}^\omega,\mathbf{S}_n(\omega,\hat{\tau}^{i^\pm}(\omega))=0\}. \tag{5.12}$$

Note that $\tau_\omega=\tau_\omega^{k,l}\neq 0$ or $\tau_\omega=\tau_\omega^{k,r}\neq\infty$ must satisfying one of the following equations:

$$\begin{cases}|\beta_1(\omega,\tau_\omega)|+|\beta_2(\omega,\tau_\omega)|=1, & (5.13a)\\ |\beta_1(\omega,\tau_\omega)|-|\beta_2(\omega,\tau_\omega)|=1, & (5.13b)\\ |\beta_1(\omega,\tau_\omega)|-|\beta_2(\omega,\tau_\omega)|=-1. & (5.13c)\end{cases}$$

Lemma 5.2. *(i) If (5.13a) or (5.13b) holds for $\tau_\omega=\tau_\omega^{k,l}\neq 0$ or $\tau_\omega=\tau_\omega^{k,r}\neq+\infty$, then $\theta_1(\omega,\tau_\omega)=0$ and $\mathbf{S}_n^+(\omega,\tau_\omega)=\mathbf{S}_n^-(\omega,\tau_\omega)$;*
(ii) If (5.13c) holds for $\tau_\omega=\tau_\omega^{k,l}\neq 0$ or $\tau_\omega=\tau_\omega^{k,r}\neq+\infty$, then $\theta_1(\omega,\tau_\omega)=\pi$ and $\mathbf{S}_n^+(\omega,\tau_\omega)=\mathbf{S}_{n+1}^-(\omega,\tau_\omega)$.

For each fixed $\omega \in I_k$, it can classify the interval I_ω^k into 4 types: Type 1: $\theta_1(\omega, \tau_\omega^{k,l}) = \theta_1(\omega, \tau_\omega^{k,r})$; Type 2: $\theta_1(\omega, \tau_\omega^{k,l}) \neq \theta_1(\omega, \tau_\omega^{k,r})$; Type 3: $\tau_\omega^{k,l} = 0$ and $\tau_\omega^{k,r} \neq +\infty$; Type 4: $\tau_\omega^{k,r} = +\infty$. On each Type, the plots of $\mathbf{S}_n^{\pm}(\omega, \tau)$ are different.

Furthermore, it assumes that

$$(C5) \qquad \partial \mathbf{S}_n^{\pm}(\omega, \tau)/\partial \tau \neq 0 \ \textit{for any} \ (\omega, \tau) \in \mathbf{C}.$$

By (C5), the endpoints $(\omega_e, \hat{\tau}^{i^{\pm}}(\omega_e))$ of every component of $\mathbf{C}$ must locate the boundary of Ω and can be divided into 3 types:

Type A: (5.13a) holds for $(\omega, \tau_\omega) = (\omega_e, \hat{\tau}^{i^{\pm}}(\omega_e))$.

Type B: (5.13b) holds for $(\omega, \tau_\omega) = (\omega_e, \hat{\tau}^{i^{\pm}}(\omega_e))$.

Type C: (5.13c) holds for $(\omega, \tau_\omega) = (\omega_e, \hat{\tau}^{i^{\pm}}(\omega_e))$.

For convenience, Type AA indicates that both end points of the component are Type A. Depending on the type of endpoint, each component of the curve $\mathbf{C}$ falls into the following six categories: AA, BB, CC, AB, AC, and BC.

Lemma 5.3. *If the condition $(C5)$ holds, then any two components of $\mathbf{C}$ will not intersect in* $\mathbf{Int}\Omega$.

Theorem 5.1. *Under the conditions (C1)-(C5) the crossing curve on (τ, τ_1)-plane consists of one or several curves in the following types:*
(a) A series of open-ended curves along τ_1-axis;
(b) A series of closed curves along τ_1-axis;
(c) A series of spiral-like curves along τ_1-axis; and each of these curves approaching ∞ in the direction of τ_1-axis;
(d) Truncated curves of one of the above 3 cases.

5.2. Crossing directions

Assume that $(\tau^*, \tau_1^*) \in \mathbf{T}$, then there is an $\omega^* > 0$ such that $(i\omega^*, \tau^*, \tau_1^*)$ is the zero of (6.2). If $\partial \mathbf{D}/\partial \lambda \neq 0$, then $\lambda(\tau, \tau_1) = \gamma_1(\tau, \tau_1) + i\gamma_2(\tau, \tau_1)$ is the simple root of (6.2), which satisfies $\gamma_1(\tau^*, \tau_1^*) = 0$ and $\gamma_2(\tau^*, \tau_1^*) = \omega^*$ in the neighborhood of (τ^*, τ_1^*). In this section, we can calculate the crossing direction of the crossing curve (5.12). Define

$$\begin{aligned} R(\tau, \tau_1) &= \mathbf{Re}\Big\{\tfrac{\partial \mathbf{D}(\lambda, \tau, \tau_1)}{\partial \tau}\Big\}, \ I(\tau, \tau_1) = \mathbf{Im}\Big\{\tfrac{\partial \mathbf{D}(\lambda, \tau, \tau_1)}{\partial \tau}\Big\}, \\ R_1(\tau, \tau_1) &= \mathbf{Re}\Big\{\tfrac{\partial \mathbf{D}(\lambda, \tau, \tau_1)}{\partial \tau_1}\Big\}, \ I_1(\tau, \tau_1) = \mathbf{Im}\Big\{\tfrac{\partial \mathbf{D}(\lambda, \tau, \tau_1)}{\partial \tau_1}\Big\}. \end{aligned}$$

Furthermore, it can calculate $RI_1 - R_1 I = -\mathbf{Im}\{\frac{\partial \mathbf{D}}{\partial \tau} \cdot \overline{\frac{\partial \mathbf{D}}{\partial \tau_1}}\}$.

If $RI_1 - R_1 I > 0$, then the pair characteristic roots $\gamma_1(\tau, \tau_1) \pm \gamma_2(\tau, \tau_1)$ of (6.2) cross the imaginary axis to the right half plane when (τ, τ_1) crosses the crossing curve to the right region. If the inequality is reversed, the crossing direction is opposite. From (6.2), it has

$$\begin{aligned}&\tfrac{\partial \mathbf{D}}{\partial \tau}(i\omega^*,\tau^*,\tau_1^*)=\Sigma_{0\tau}^*+\Sigma_{1\tau}^*e^{-i\omega^*\tau^*}+\Sigma_{2\tau}^*e^{-i\omega^*\tau_1^*}+i\omega^*\Sigma_1^*e^{-i\omega^*\tau^*},\\&\tfrac{\partial \mathbf{D}}{\partial \tau_1}(i\omega^*,\tau^*,\tau_1^*)=\Sigma_{0\tau_1}^*-i\omega^*\Sigma_2^*e^{-i\omega^*\tau_1^*},\end{aligned}$$

where $\Sigma_s^*=\Sigma_s(\omega^*,\tau^*)$ and $\Sigma_{s\tau}^*=\partial\Sigma_s(\omega^*,\tau^*)/\partial\tau,\ s=0,1,2.$

Furthermore,

$$-\mathbf{Im}\Big\{\tfrac{\partial \mathbf{D}}{\partial \tau}\cdot\overline{\tfrac{\partial \mathbf{D}}{\partial \tau_1}}\Big\}=\ -\omega^*\mathbf{Re}\Big\{\Big[\Sigma_{0\tau}^*e^{i\omega^*\tau_1^*}+(\Sigma_{1\tau}^*-i\omega^*\Sigma_1^*)e^{i\omega^*(\tau_1^*-\tau^*)}+\Sigma_{2\tau}^*\Big]\overline{\Sigma_2^*}\Big\}.$$

Hence it has the following theorem.

Theorem 5.2. *If $\delta(\tau^*,\tau_1^*)>0$ (<0), then the pair imaginary roots crosses the imaginary axis from left to right, as (τ,τ_1) passes through the crossing curve to the right (left) region , where*

$$\delta(\tau^*,\tau_1^*)=\ -\mathbf{Re}\Big\{\Big[\Sigma_{0\tau}^*e^{i\omega^*\tau_1^*}+(\Sigma_{1\tau}^*-i\omega^*\Sigma_1^*)e^{i\omega^*(\tau_1^*-\tau^*)}+\Sigma_{2\tau}^*\Big]\overline{\Sigma_2^*}\Big\}.$$

6. Numerical simulations

In this part, firstly, choosing the following parameters in system (1.2):

$$r=5,\ L=8,\ m=10,\ \mu=0.005,\ \alpha=0.8,\ \beta=0.6,\ \rho=0.02. \qquad (6.1)$$

When $\tau_1=0$, $\bar{\tau}$ can obtained as 317.7637. Under the parameters in (6.1), it can obtain the plots of $(\tau,\mathcal{S}_n(\tau))$ (see Figure 1). From the plots, it knows that $\mathcal{S}_n(\tau)=0$ $(n=0,1)$ has two roots $\tau^0=54.4$ and $\tau^1=165.247$. Therefore, choosing $\tau=30<\tau^0,\tau=54.4\doteq\tau^0,\tau=200>\tau^1$, respectively, the results are shown in Figures 2-4 and it can verify the correction of theoretical analysis.

Furthermore, fixed $\tau=30\in[0,\tau^0)$ and choosing τ_1 as parameter, it can obtain $\tau_1^0=100.29$. Let $\tau_1=5<\tau_1^0$, the results of the numerical simulations are sown in Figure 5.

Specially, when $\tau=\tau_1=\nu$, the following parameters are chosen

$$r=5,\ L=8,\ m=6,\ \mu=0.005,\ \alpha=0.8,\ \beta=0.7,\ \rho=0.01. \qquad (6.2)$$

It can obtain $\bar{\nu}=453.4988$ under the parameters (6.2). The plots of $(\nu,T_n(\nu))$ can be obtained (see Figure 6). From the plots, it knows that $T_n(\nu)=0$ $(n=0,1,2)$ has four roots $\nu^0=7.5,\nu^1=73.5,\nu^2=381.26$ and $\nu^3=425.266$. Therefore, choosing

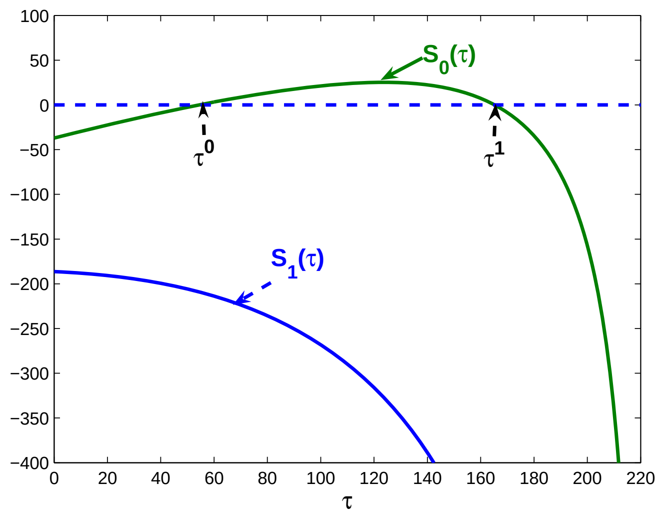
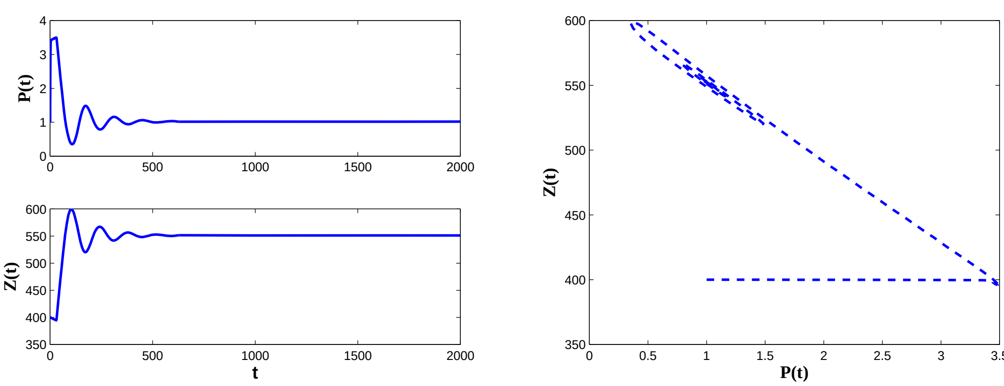
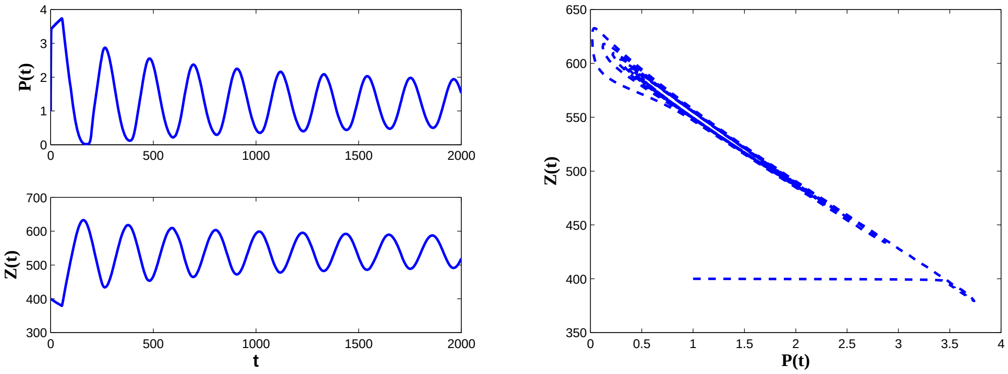


Figure 1: $(\tau, \mathcal{S}_n(\tau))$ $(n = 0, 1)$ plots



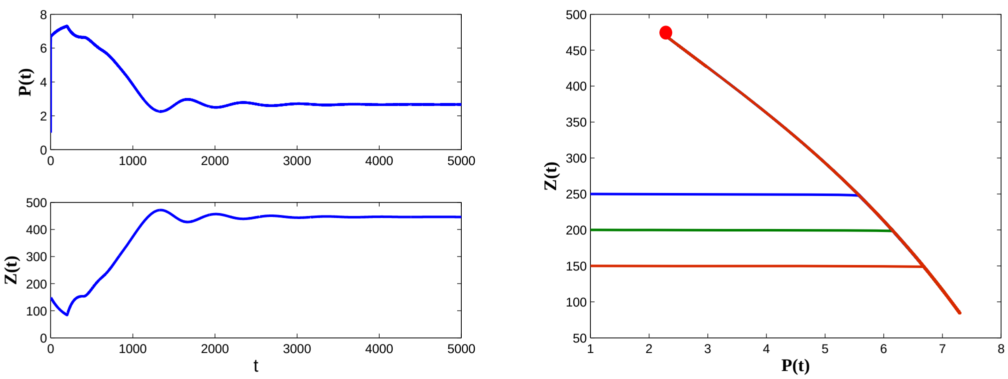
(A) Wave plot. (B) Phase plot.

Figure 2: E^* is stable when $\tau = 30$.



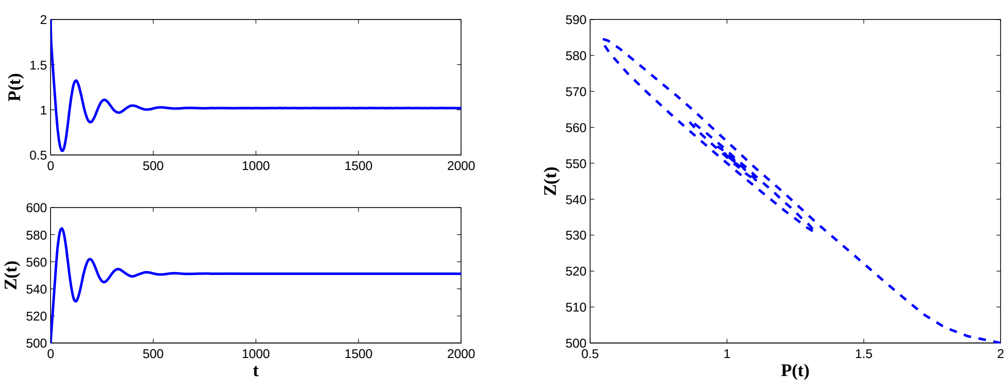
(A) Wave plot. (B) Phase plot.

Figure 3: E^* is unstable when $\tau = 54.4$ and there exists a stable periodic solution.



(A) Wave plot. (B) Phase plot.

Figure 4: E^* is still stable when $\tau = 200$.



(A) Wave plot. (B) Phase plot.

Figure 5: E^* is stable when $\tau = 30$ and $\tau_1 = 5$.

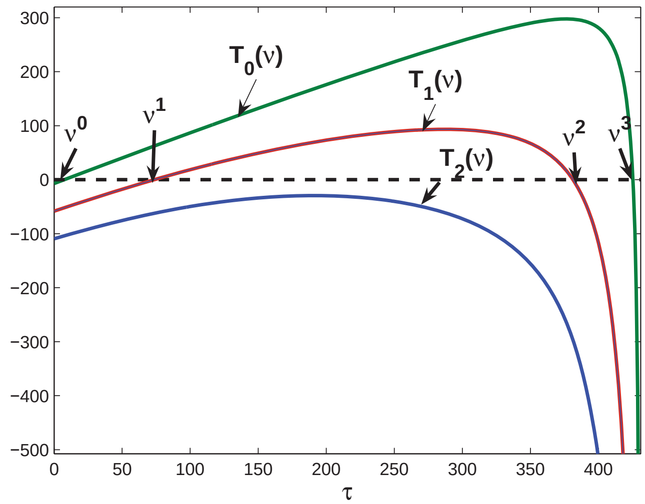


Figure 6: $(\nu, T_n(\nu))$ plots $(n = 0, 1, 2)$.

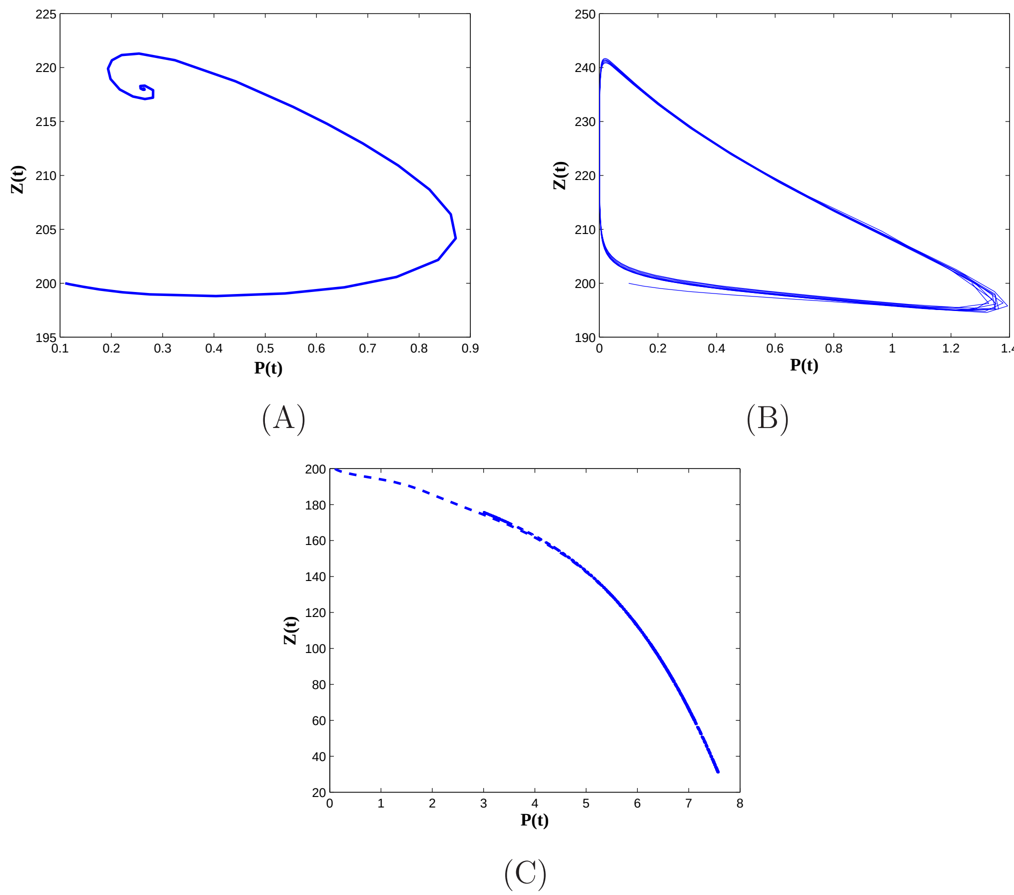


Figure 7: (A) When $\nu = 1$, E^* is stable. (B) When $\nu = 7.5$, E^* is unstable and the re exists a stable periodic solution. (C) When $\nu = 430$, E^* is still stable.

$\nu = 1 < \nu^0, \tau = 7.5 = \nu^0, \tau = 430 > \nu^3$, respectively, the results are shown in Figure 7 and it is consistent with theoretical results.

In the following, it also obtain the crossing curves in (τ, τ_1) plane using the parameters in (6.1). Under the parameters (6.1), it can obtain $I_1 = [0.04, 0.044]$ and $I_2 = [0, 0.04]$, furthermore, $I_\omega^1 = [0, 15.0495]$ and $I_\omega^2 = [0, 222.425]$. It can know that both $I_\omega^1 = [0, 15.0495]$ and $I_\omega^2 = [0, 222.425]$ belong to Type 1. The C curves and crossing curves are shown in Figures 8-9. It can obtain the feasible region Ω that is surrounded by τ-axis, ω-axis and the blue curves in Figure 8. The curve C, which is composed by the feasible values of (τ, ω) (see the color loops between the two blue curves in Figure 8). Furthermore, we can see that the two closed loop curves C on Ω with Type AB lead to two series of spiral-like crossing curves on (τ, τ_1) plane along τ_1-axis shown in Figure 9. Finally, according to theorem 5.2, the crossing direction is calculated and the final result is given in Figure 9, that is, when (τ, τ_1) changes along the arrow direction, the feature root passes through the imaginary axis from left to right. Fixed $\tau_1 = 10$ and choosing $\tau = 20, 80, 180$, it can obtain the stable switches phenomena (see Figures 10-12). It shows that Hopf bifurcation can still occur when τ locates the unstable interval.

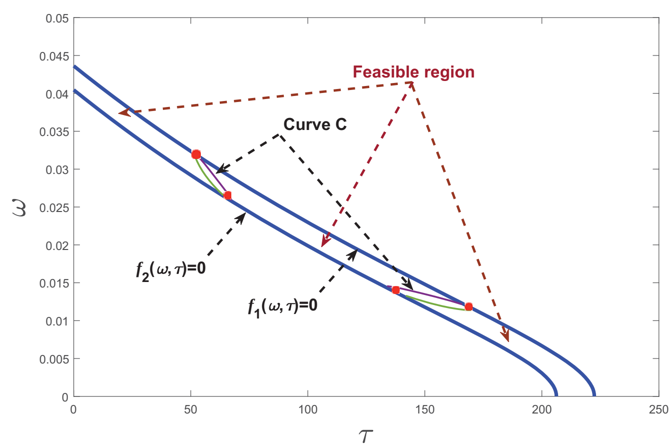


Figure 8: Feasible region and C curves, which composed by the admissible values (ω, τ).

7. Conclusion

In this paper, we study a planktonic ecosystem (1.2) with two delays and Monod-Haldane type functional response. We focus on the effects of two delays on the system. In Theorem 2.1, we obtain the positively invariant set for system (1.2).

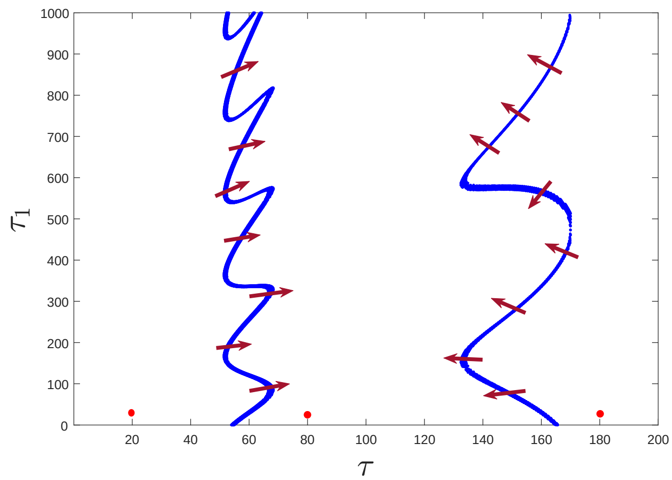
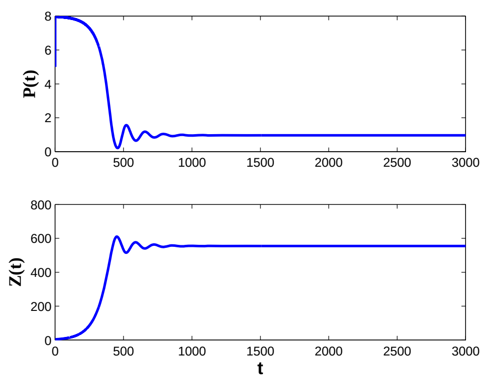
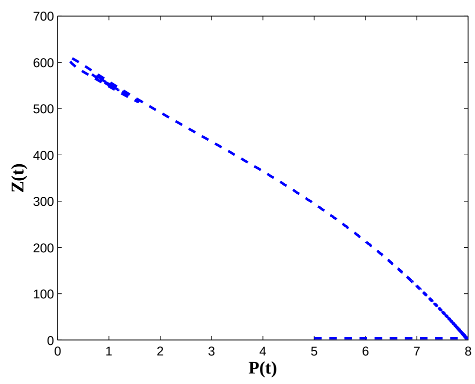


Figure 9: Crossing curves (spiral-like curves) and crossing direction.

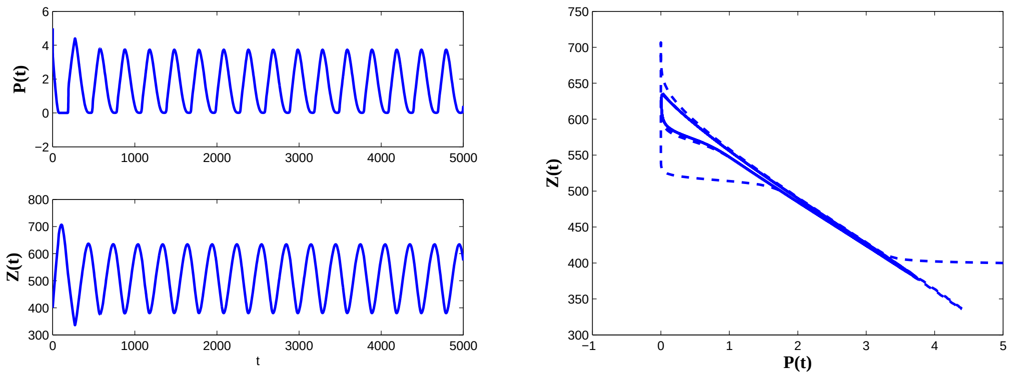


(A) Wave plot.



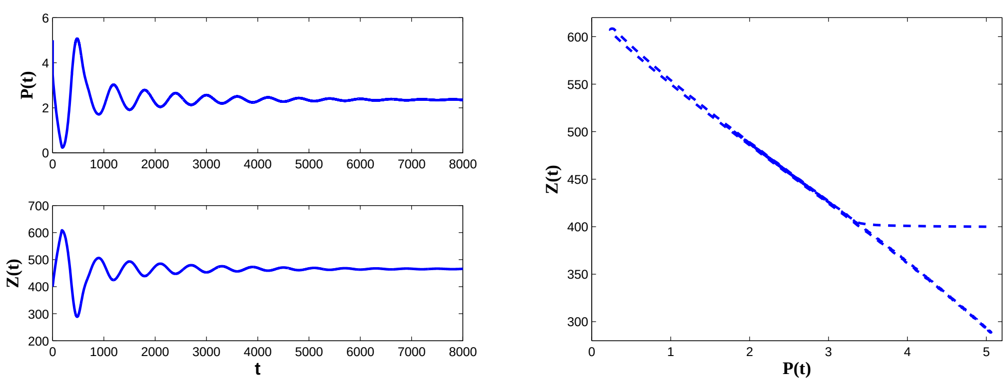
(B) Phase plot.

Figure 10: E^* is stable when $\tau = 20$ and $\tau_1 = 10$.



(A) Wave plot. (B) Phase plot.

Figure 11: E^* is unstable and there exists a stable periodic solution when $\tau = 80$ and $\tau_1 = 10$.



(A) Wave plot. (B) Phase plot.

Figure 12: E^* is still stable when $\tau = 180$ and $\tau_1 = 10$.

The system (1.2) always exists two boundary equilibria $E_0(0,0)$ and $E_1(K,0)$ while $E_0(0,0)$ is unstable and the stability of $E_1(K,0)$ is shown in Theorem 3.1.

When the maturation rate τ of zooplankton is more than some value, zooplankton population will dies out in the end. When the maturation rate of zooplankton τ are restricted to a certain interval, the system (1.2) exists a uniquely positive equilibrium $E^*(P^*, Z^*)$. When the toxin delay τ_1 does not exist, Theorem 4.2 shows the stability of E^* and system (1.2) may occur the stability switches when the maturation rate τ of zooplankton changes which depends on the set I_τ and the roots of $\mathcal{S}_n^+(\tau) = 0$. When $\tau_1 > 0$, it still can obtain the conditions which the system occurs Hopf bifurcation. Furthermore, using the method in [23], the purpose is to find stability crossing curve. When τ is chosen in unstable interval it also can obtain the stability of E^*. By these researches, it can know the important effect of two delays and the correction of theory analyses is verified in Section 6 for some numerical examples.

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References

[1] Chattopadhyay J, Sarkar R R, Mandal S. Toxin producing plankton may act as a biological control for planktonic blooms: A field study and mathematical modelling. *J. Theor. Biol.* 2002; 215: 333-344.

[2] Chattopadhyay J, Sarkar R R, Abdllaoui AE. [2002b]. A delay differential equation model on harmful algal blooms in the presence of toxic substances. *IMA J. Appl. Math.* 2002b; 19: 137-161.

[3] Roy S, Bhattacharya S, Das P, Chattopadhyay J. Interaction among non-toxic phytoplankton, toxic phytoplankton and zooplankton: Inferences from field observations. *J. Biol. Phys.* 2007; 33: 1-17.

[4] Pal R, Basu D, Banerjee M. Modelling of phytoplankton allelopathy with MonodCHaldanetype functional response–A mathematical study. *Biosystems.* 2009; 95: 243-253.

[5] Khare S, Misra OP, Dhar J. Role of toxin producing phytoplankton on a plankton ecosystem. *Nonlin. Anal.: Hybrid Syst.* 2010; 4: 496-502.

[6] Wang Y, Jiang W, Wang H. Stability and global Hopf bifurcation in toxic phytoplankton-zooplankton model with delay and selective harvesting. *Nonlin. Dyn.* 2013; 73: 881-896.

[7] Jiang Z, Ma W, Li D. Dynamical behavior of a delay differential equation system on toxin producing phytoplankton and zooplankton interaction. *Japan J. Indust. Appl. Math.* 2014; 31: 583-609.

[8] Jiang Z, Zhang T. Dynamical analysis of a reaction-diffusion phytoplankton-zooplankton system with delay. *Chaos, Solitons Fractals.* 2017; 104: 693-704.

[9] Jiang Z, Ma W, Takeuchi Y. Complicated dynamics for two toxin-producing phytoplankton-zooplankton system with time delays. *Funkcialaj Ekvacioj.* 2017; 60: 279-304.

[10] Jiang Z, Zhang W, Zhang J, Zhang T. [2018]. Dynamical Analysis of a Phytoplankton-Zooplankton System with Harvesting Term and Holling III Functional Response. *Internat. J. Bifur. Chaos.* 2018; 28: 1850162, 23 pages.

[11] Banerjee M, Venturino E. A phytoplankton-toxic phytoplankton-zooplankton model. *Ecol. Complex.* 2011; 8: 239-248.

[12] Han R, Dai B. Cross-diffusion induced Turing instability and amplitude equation for a toxic-phytoplankton-zooplankton model with nonmonotonic functional response. *Internat. J. Bifur. Chaos.* 2017; 27: 1750088 (24 pages).

[13] Hale J, Lunel S. *Introduction to Functional Differential Equations.* New York: Springer-Verlag, 1993.

[14] Beretta E, Kuang Y. Geometric, stability switch criteria in delay differential systems with delay dependent parameters. *SIAM J. Math. Anal.* 2002; 33: 1144-1165.

[15] Ma S, Lu Q, Feng Z. Double Hopf bifurcation for van der Pol-Duffing oscillator with parametric delay feedback control. *J. Math. Anal. Appl.* 2008; 338: 993-1007.

[16] Bi P,Ruan S. Bifurcations in Delay Differential Equations and Applications to Tumor and Immune System Interaction Models. *SIAM J. Applied Dynamical Systems.* 2013; 12: 1847-1888.

[17] Ding Y, Jiang W, Yu P. Double Hopf bifurcation in delayed vander pol-duffing equation. *International Journal of Bifurcation and Chaos.* 2013; 23: 1350014 (15 pages).

[18] Jiang H, Song Y. Normal forms of non-resonance and weak resonance double Hopf bifurcation in the retarded functional differential equations and applications. *Appl. Math. Comput.* 2015; 266: 1102-1126.

[19] Wu J. Symmetric functional differential equations and neural networks with memory. *Trans. Amer. Math. Soc.* 1998; 35: 4799-4838.

[20] Jiang Z, Wang L. Global Hopf bifurcation for a predator-prey system with three delays. *Internat. J. Bifur. Chaos.* 2017; 27: 1750108, 15pages.

[21] Qu Y, Wei J, Ruan S. Stability and bifurcation analysis in hematopoietic stem cell dynamics with multiple delays. *Physica D.* 2010; 239: 2011-2024.

[22] Gu K, Niculescu S, Chen J. On stability crossing curves for general systems with two delays. *J. Math. Anal. Appl.* 2005; 311: 231-253.

[23] An Q, Beretta E, Kuang Y, Wang C, Wang H. Geometric stability switch criteria in delay differential equations with two delays and delay dependent parameters. *J. Differential Equations.* 2019; 266: 7073-7100.