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Minimal Model of Plankton Systems Revisited with Spatial Diffusion and Maturation Delay

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Abstract This study revisits the minimal model for a plankton ecosystem proposed by Scheffer with spatial diffusion of plankton and the delay of the maturation period of herbivorous zooplankton. It deepens our understanding of effects of the nutrients and the predation of fish upon zooplankton on the dynamical patterns of the plankton system and also presents new phenomena induced by the delay with spatial diffusion. When the nutrient level is sufficient low, the zooplankton population collapses and the phytoplankton population reaches its carrying capacity. Mathematically, the global stability of the boundary equilibrium is proved. As the nutrient level increases, the system switches to coexistent equilibria or oscillations depending on the maturation period of zooplankton and the predation rate of fish on herbivorous zooplankton. Under an eutrophic condition, there is a unique coexistent homogeneous equilibrium, and the equilibrium density of phytoplankton increases, while the equilibrium density of herbivorous zooplankton decreases as the fish predation rate on herbivorous zooplankton is increasing. The study shows that the system will never collapses under the eutrophic condition unless the fish predation rate approaches infinite. The study also finds a functional bifurcation relation between the delay parameter of the maturation period of herbivorous zooplankton and the fish predation rate on herbivorous zooplankton that, above a critical value of the fish predation rate, the system stays at the coexistent equilibrium, and below that value, the system switches its dynam-

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ical patterns among stable and unstable equilibria and oscillations. The oscillations emerge from Hopf bifurcations, and a detailed mathematical analysis about the Hopf bifurcations is carried out to give relevant ecological predications.

Keywords Diffusive plankton ecosystem · Hopf bifurcation · Stability · Delay

1 Introduction

Plankton are floating organisms living in the pelagic of the sea, in large rivers, and in freshwater lakes. According to trophic relations, plankton can be mainly grouped into phytoplankton and zooplankton. Phytoplankton are microscopic plants that generate half of the oxygen and absorb half of the carbon dioxide of the world by photosynthesis (Williamson and Gribbin 1991; Duinker and Wefer 1994). Zooplankton are small animals that have two classes, herbivorous and non-herbivorous zooplankton. Herbivorous zooplankton graze on phytoplankton. Phytoplankton and herbivorous zooplankton constitute the basis for all food chains in the sea and for the maintenance of the world's climate (Anderson 1997). It is evidently important to understand the dynamics of plankton ecosystems.

The dynamics of plankton systems has been under investigation for many years. The first mathematical model related to plankton systems appeared in 1939 (Fleming 1939). Since then, many mathematical models have been built for variety of aspects of plankton ecosystems, for example, applications of predator–prey relations to describe phytoplankton–zooplankton interactions (Freedman and Ruan 1994; Levin and Segel 1976; Mimura and Murray 1978; Malchow et al. 2004; Ruan 1995a). About the nutrients in plankton systems, there have been several models with nutrient recycling (Beretta et al. 1990; He and Ruan 1998; Ruan 1993, 1995b, 2001; Ruan and Wolkowicz 1995; Yuan 2012). In particular, literature (Ruan 1995b) deals with a model with a discrete delay in the response term. Some models consider the combined effect of light and nutrients on the growth of phytoplankton (Du and Hsu 2010; Du and Mei 2011; Hsu and Lou 2010; Huisman and Weissing 1994, 1995), while recently some field and modeling studies have conducted on the reduction of zooplankton due to toxin production of phytoplankton (Chattopadhyay et al. 2002; Chattopadhyay and Sarkar 2002; Hallegraeff 1993). For a review, the reader is referred to Medvinsky et al. (2002). In this study, we will revisit a minimal model for a plankton ecosystem with two extensions, the spatial diffusion and delays of the zooplankton maturation period.

Considering three trophic levels, nutrients, phytoplankton and zooplankton, and fish, Scheffer proposed a nutrient-phytoplankton–zooplankton–fish model for a plankton ecosystem (Scheffer 1991). This model was originally formulated as a system of ordinary differential equations, which has since been extended spatially as reaction–diffusion system models (Malchow 2000; Malchow et al. 2000, 2002, 2004; Tikhonova et al. 2003; Sherratt et al. 1997). This model is called a minimal model in the sense that only a few important interactions are taken into account. For example, the model only counts the phytoplankton–zooplankton interaction as a predator–prey relation, the growth rate of phytoplankton as a Monod function of nutrients, and the

fish predation on zooplankton as a Holling type function, while the positive effect of fish on the sediment nutrients is omitted. Nevertheless, such a minimal model of the predator–prey system with external nutrients and fish predation built in displays a wide range of ecologically relevant behaviors, for example, spiral and target waves (Sherratt et al. 1997), diffusion-induced instability (Malchow et al. 2004; Dubey et al. 2009), and Chaos (Medvinsky et al. 2002; Pascual 1993). We recommend a relevant literature (Ruan 1998) which considers a plankton model with both diffusion and distributed delays and studies traveling waves and Turing patterns in plankton models. For a historical overview of modeling of plankton dynamical systems and pattern formations, the reader is referred to Medvinsky et al. (2002), Malchow et al. (2001).

Within this minimal model framework, we observe that the plankton life cycle is one of important factors that may affect the dynamics of plankton ecosystems. Each individual of phytoplankton or zooplankton takes time to mature and then produces new individuals to contribute its population. The life cycle varies. For example, some phytoplankton have a life cycle of 6 days, and some zooplankton have a life cycle of 200 days (Larsson 1978; Allan 1976; Dasson and Montresor 2011; Meadows and Campbell 1988). In this article, we will only consider the maturation period of zooplankton as a delay parameter, since the maturation period of phytoplankton is much shorter than that of zooplankton. The delay is incorporated into the reaction–diffusion model extended from the minimal model.

The functional reaction–diffusion system we consider is given as follows:

$$
\begin{cases}
\dfrac{\partial P(x,t)}{\partial t} = D_p \Delta P(x,t) + \dfrac{\alpha N P(x,t)}{H_n + N} - \beta P^2(x,t) - \dfrac{\gamma P(x,t) Z(x,t)}{H_p + P(x,t)}, \\
\dfrac{\partial Z(x,t)}{\partial t} = D_z \Delta Z(x,t) + \dfrac{e\gamma P(x,t-\hat{\tau}) Z(x,t)}{H_p + P(x,t-\hat{\tau})} - \delta Z(x,t) - \dfrac{F Z^2(x,t)}{H_z^2 + Z^2(x,t)},
\end{cases}
\tag{1}
$$

where

- P is the phytoplankton biomass density;
- Z is the herbivorous zooplankton biomass density;
- N is the nutrient level of the system, while H_n is half-saturation constant of nutrient limitation, and α is the possible maximal per capita growth rate of phytoplankton;
- β is the competition intensity of phytoplankton, and γ is the possible maximal grazing rate of herbivorous zooplankton on phytoplankton;
- e is the conversion coefficient from phytoplankton into herbivorous zooplankton;
- δ is the mortality rate of herbivorous zooplankton;
- $\hat{\tau}$ is the maturation period of herbivorous zooplankton;
- D_p and D_z are the diffusion coefficients of phytoplankton and zooplankton, respectively;
- H_p and H_z are half-saturation constants of phytoplankton and zooplankton density for Holling type II and III functional response, respectively;
- F is the possible maximal predation rate of fish on herbivorous zooplankton.

The phytoplankton diffuse within the considered habitat and follow the logistic growth formulation whose growth rate is a Monod function of nutrients. In the absence of zooplankton, phytoplankton growth will saturate at a carrying capacity $\frac{\alpha N}{\beta(H_n+N)}$, which

is a function of nutrients. When the nutrient level is given, the growth is limited by the nutrient level. The grazing of herbivorous zooplankton on phytoplankton is formulated as a Holling type II functional response which is a Monod function of phytoplankton density. The herbivorous zooplankton also diffuse within the habitat, will die out in the absence of phytoplankton. The maturation period of herbivorous zooplankton $\hat{\tau}$ is considered as a constant. The growth rate of herbivorous zooplankton is formulated to be $\frac{e\gamma P(x,t-\hat{\tau})}{H_p+P(x,t-\hat{\tau})}$. The predation of fish on zooplankton is modeled as a Holling type III functional response which is a sigmoidal Monod function of herbivorous zooplankton density. The spatial dimension of the habitat can be one, two, or three. Since our focus in this research is to understand the effect of the zooplankton maturation period on the dynamics of the plankton system, we only study the case of spatial dimension one. However, the results about delay effects should be valid for spatial dimension two or higher.

The aim of this paper is to undertake a rigorous mathematical analysis for the functional reaction–diffusion system (1) and to present biological implications of the mathematical results. To investigate how the nutrients affect the system we define a parameter

$$h = \frac{b}{a+1} - c = \frac{e\gamma/r}{H_p/w+1} - \frac{\delta}{r} = \frac{1}{r}\left(e\gamma\frac{w}{H_p+w} - \delta\right),$$

a scaled maximal net growth rate of herbivorous zooplankton. h is an creasing function of nutrients N. When the nutrient level is sufficient low so that $h < 0$, the herbivorous zooplankton population cannot grow anymore no matter how long their maturation period could be. In this situation, herbivorous zooplankton will collapse and then phytoplankton population will grow to its carrying capacity. Mathematically, we prove that the boundary equilibrium is globally stable. When the nutrient level increases so that $h > 0$, and other two conditions that nutrients are not too high and the half-saturation rate (defined in Sect. 2.3) is not too fast, forming an eutrophic condition $(\mathcal{H})$, are satisfied, the system has a unique homogeneous coexistent equilibrium E^*. The equilibrium density of phytoplankton increases while the equilibrium density of herbivorous zooplankton decreases as the fish predation rate is increasing. However, the system will never collapses under the eutrophic condition unless the fish predation rate approaches infinite. This is one of new phenomena we derived. For the fish predation rate on herbivorous zooplankton, we find a critical value F^*, the coexistent equilibrium is locally asymptotical stable when the fish predation rate is above F^*. When the fish predation rate is below this critical value, the coexistent equilibrium may stable or unstable or the system oscillates depending on the delay parameter of the zooplankton maturation period. We find a functional relation between the fish predation rate F and the maturation period of zooplankton τ, a bifurcation curve. That is, for each F which is smaller than F^*, there is a critical value τ^* of the maturation period of zooplankton at which the system undergoes Hopf bifurcations and oscillations appear, and the coexistent equilibrium E^* is still stable when τ is below τ^*. This functional relation of two biological significant parameters is also a new phenomenon we obtained, which ecologically implies that, under the eutrophic condition

and the fish predation rate is below the critical value, increasing the fish predation delays the occurrence of oscillations. However, the system will be in the coexistent equilibrium when the fish predation rate is above the critical value, which means that the fish predation damps oscillations. We will see that the nutrient, the predation of fish on zooplankton, the maturation period of zooplankton, and spatial diffusion all play important roles in the dynamical patterns of plankton ecosystems.

The rest of the article is organized as follows. Section 2 presents equilibrium analysis about the system, which has three subsections. Section 2.1 studies the global stability of the homogeneous boundary equilibrium state. Section 2.2 investigates the existence and stability of a unique coexistent homogeneous equilibrium state. Section 2.3 explores the biological implications of equilibrium analysis. Section 3 investigates the zooplankton maturation period delay induced Hopf bifurcations and oscillations, which also has three subsections. Section 3.1 studies the emergence of Hopf bifurcations and a bifurcation curve in the parameter space. Section 3.2 investigates the stability and directions of the Hopf bifurcations. Section 3.3 explains the biological implications of the Hopf bifurcations and periodical solutions. Section 4 gives two examples to numerically demonstrate analysis results. Section 5 concludes the article with our major conclusions, discussion of the original minimal model, and some ideas for further studies.

2 Equilibrium Analysis

In this section, we conduct equilibrium analysis for the system (1) and describe some biological implications. We find a biologically significant parameter h and condition $(\mathcal{H})$. h actually is a scaled maximal net growth rate of herbivorous zooplankton that is limited by nutrient levels. $(\mathcal{H})$ is an eutrophic condition that, the herbivorous zooplankton population is under growth, the nutrient level for the growth is not too high (upper-bounded), and the half-saturation rate (defined in Sect. 2.3) of fish predation is not too fast such that the herbivorous zooplankton population can be established. When $h < 0$, the system has a boundary homogeneous equilibrium state (the phytoplankton population reaches its carrying capacity while the herbivorous zooplankton population collapses) which is globally asymptotical stable. When the condition $(\mathcal{H})$ is satisfied, the system has a unique coexistent homogeneous equilibrium state which is locally asymptotical stable for the delay parameter $\tau = 0$. We also find that how the fish predation on zooplankton affects the dynamics of the system under the eutrophic condition. That is, increasing predation rate F of fish on herbivorous zooplankton, the equilibrium density of phytoplankton will increase while the equilibrium density of herbivorous zooplankton will decrease. However, under the condition $(\mathcal{H})$ the system will never come back to the boundary equilibrium state, unless the predation rate F of fish on herbivorous zooplankton approaches infinite. There are three subsections in this section, global stability of the boundary equilibrium, stability of coexistent equilibria, and biological implications of equilibrium analysis.

To reduce the difficulty of analysis, we re-scale the system to nondimensional form. We define combined parameters as follows, and some of them will be of biological significance:

$$r = \frac{\alpha N}{H_n + N}, \quad w = \frac{r}{\beta}, \quad \tilde{x} = x \left(\frac{r}{D_P} \right)^{\frac{1}{2}}, \quad \tilde{t} = rt, \quad \tau = r\hat{\tau},$$

$$D = \frac{D_z}{D_p}, \quad u(\tilde{x}, \tilde{t}) = \frac{P(x, t)}{w}, \quad v(\tilde{x}, \tilde{t}) = \frac{\gamma Z(x, t)}{wr} \quad a = \frac{H_p}{w},$$

$$b = \frac{e\gamma}{r}, \quad c = \frac{\delta}{r}, \quad d = \frac{\gamma H_Z}{rw}, \quad f = \frac{\gamma F}{wr^2}.$$

For example, r is the per capita growth rate of phytoplankton, and w is the carrying capacity of phytoplankton at a nutrient level in a concerned habitat. It is obvious that a, b, c, d, f, D are nonnegative constants.

Dropping the bars for simplification, specifying the spatial location as an interval $x \in [0, \pi]$ and Neumann boundary conditions, the system (1) takes the form

$$
\begin{cases}
\dfrac{\partial u(x, t)}{\partial t} = \Delta u(x, t) + u(x, t)(1 - u(x, t)) - \dfrac{u(x, t)v(x, t)}{a + u(x, t)}, \\[2mm]
\dfrac{\partial v(x, t)}{\partial t} = D\Delta v(x, t) + \dfrac{bu(x, t - \tau)v(x, t)}{a + u(x, t - \tau)} - cv(x, t) - \dfrac{fv^2(x, t)}{d^2 + v^2(x, t)}, \\[2mm]
\hspace{5cm} t > 0, x \in (0, \pi), \\[2mm]
\dfrac{\partial u(x, t)}{\partial \nu} = \dfrac{\partial v(x, t)}{\partial \nu} = 0, \quad t \geq 0, \quad x = 0 \ or \ \pi, \\[2mm]
u(x, t) = u_0(x, t) \geq 0, \quad v(x, t) = v_0(x, t) \geq 0, \quad t \in [-\tau, 0], \ x \in [0, \pi].
\end{cases}
\tag{2}
$$

2.1 Global Stability of the Boundary Equilibrium

The system (2) always has a trivial equilibrium $E_0(0, 0)$ and a boundary equilibrium $E_1(1, 0)$. It is easy to see that the trivial equilibrium E_0 is an unstable saddle point. In this subsection, we use the method proposed in Pao (2002) to analyze the stability of the boundary equilibrium E_1.

Define a parameter $h \stackrel{def}{=} b/(a + 1) - c$, and we will explain some biological significance of this parameter in Sect. 2.3. Consider the case $h < 0$ first.

Denote

$$g_1(\varphi, \psi) = \varphi_1(1 - \varphi_1) - \frac{\varphi_1 \varphi_2}{a + \varphi_1}, \quad g_2(\varphi, \psi) = \frac{b\psi_1 \varphi_2}{a + \psi_1} - c\varphi_2 - \frac{f\varphi_2^2}{d^2 + \varphi_2^2},$$

where $\varphi = (\varphi_1, \varphi_2)^T$, $\psi = (\psi_1, \psi_2)^T$. It is easy to see that $g = (g_1, g_2)$ is mixed quasi-monotone in $\overline{\mathbb{R}}_+^2 \times \overline{\mathbb{R}}_+^2$. Let $(\hat{u}, \hat{v}) = (0, 0)$ and $(\tilde{u}, \tilde{v}) = (M_1, M_2)$, where $M_1 \geq 1$ and $M_2 \geq \frac{bM_1}{a + M_1}$. Then $(\tilde{u}, \tilde{v})$ and $(\hat{u}, \hat{v})$ are coupled upper and lower solutions of the system (2), since

$$\tilde{u}(1 - \tilde{u}) - \frac{\tilde{u}\hat{v}}{a + \tilde{u}} \leq 0, \quad \frac{b\tilde{u}\tilde{v}}{a + \tilde{u}} - c\tilde{v} - \frac{f\tilde{v}^2}{d^2 + \tilde{v}^2} \leq 0,$$

$$\hat{u}(1 - \hat{u}) - \frac{\hat{u}\tilde{v}}{a + \hat{u}} \geq 0, \quad \frac{b\hat{u}\hat{v}}{a + \hat{u}} - c\hat{v} - \frac{f\hat{v}^2}{d^2 + \hat{v}^2} \geq 0.$$

Because M_1 and M_2 can be chosen sufficiently large, from Theorem 2.1 in Pao (2002), we see that there exists a unique global nonnegative solution (u, v) to the system (2) with nonnegative initial value

$$(u_0(x, t), v_0(x, t)), \; (x, t) \in [0, \pi] \times [-\tau, 0]$$

and $u_0(x, t) \not\equiv 0, \; v_0(x, t) \not\equiv 0$. Furthermore, the maximum principe implies that $u(x, t), \; v(x, t) > 0$ for $t > 0$.

Let $(\hat{u}, \hat{v}) = (\varepsilon, 0)$ and $(\tilde{u}, \tilde{v}) = (1, \delta(\varepsilon))$, where ε is a small positive number and $\delta(\varepsilon) = (1 - \varepsilon)(a + \varepsilon)$. It is easy to verify that $(\varepsilon, 0)$ and $(1, \delta(\varepsilon))$ are also coupled upper and lower solutions of the system (2). When

$$\varepsilon \leq \varphi_1, \; \psi_1 \leq 1, \; 0 \leq \varphi_2, \; \psi_2 \leq \delta(\varepsilon),$$

from the boundedness of the partial derivative of $g_i (i = 1, 2)$ with respect to $\varphi, \; \psi$, we know that g_i satisfy the Lipschitz condition. We denote the Lipschitz constants by $K_i, \; i = 1, 2$. From Theorem 2.1 in Pao (2002), we see that there exists a unique global solution (u, v) to the system (2) and it satisfies $(\varepsilon, 0) \leq (u, v) \leq (1, \delta(\varepsilon))$ whenever $(\varepsilon, 0) \leq (u_0(x, t), v_0(x, t)) \leq (1, \delta(\varepsilon))$.

We define two sequences $\{\overline{u}_{(m)}, \overline{v}_{(m)}\}$ and $\{\underline{u}_{(m)}, \underline{v}_{(m)}\}$ as follows,

$$\overline{u}_{(m)} = \overline{u}_{(m-1)} + \frac{1}{K_1}\left[\overline{u}_{(m-1)}(1 - \overline{u}_{(m-1)}) - \frac{\overline{u}_{(m-1)}\underline{v}_{(m-1)}}{a + \overline{u}_{(m-1)}}\right],$$

$$\underline{u}_{(m)} = \underline{u}_{(m-1)} + \frac{1}{K_1}\left[\underline{u}_{(m-1)}(1 - \underline{u}_{(m-1)}) - \frac{\underline{u}_{(m-1)}\overline{v}_{(m-1)}}{a + \underline{u}_{(m-1)}}\right],$$

$$\overline{v}_{(m)} = \overline{v}_{(m-1)} + \frac{1}{K_2}\left[\frac{b\overline{u}_{(m-1)}\overline{v}_{(m-1)}}{a + \overline{u}_{(m-1)}} - c\overline{v}_{(m-1)} - \frac{f\overline{v}_{(m-1)}^2}{d^2 + \overline{v}_{(m-1)}^2}\right],$$

$$\underline{v}_{(m)} = \underline{v}_{(m-1)} + \frac{1}{K_2}\left[\frac{b\underline{u}_{(m-1)}\underline{v}_{(m-1)}}{a + \underline{u}_{(m-1)}} - c\underline{v}_{(m-1)} - \frac{f\underline{v}_{(m-1)}^2}{d^2 + \underline{v}_{(m-1)}^2}\right],$$

$$\text{for } m = 1, 2, \ldots \tag{3}$$

where $(\overline{u}_{(0)}, \overline{v}_{(0)}) = (1, \delta(\varepsilon))$, $(\underline{u}_{(0)}, \underline{v}_{(0)}) = (\varepsilon, 0)$. From Lemma 2.1 in Pao (2002), we know that $\{\overline{u}_{(m)}, \overline{v}_{(m)}\}$ and $\{\underline{u}_{(m)}, \underline{v}_{(m)}\}$ converge monotonically to some limits $\{\overline{u}, \overline{v}\}$ and $\{\underline{u}, \underline{v}\}$, respectively, and

$$\varepsilon \leq \underline{u} \leq \overline{u} \leq 1, \quad 0 \leq \underline{v} \leq \overline{v} \leq (1 - \varepsilon)(a + \varepsilon).$$

Since $\underline{v}_{(0)} = 0$, we have $\underline{v}_{(m)} = 0$, for $m = 1, 2, \ldots$. This implies $\underline{v} = 0$. From (3), we obtain that $\overline{u}, \; \overline{v}$ and $\underline{u}$ satisfy

$$\bar{u}(1 - \bar{u}) = 0, \ \underline{u}(1 - \underline{u}) - \frac{\underline{u}\,\bar{v}}{a + \underline{u}} = 0, \ \frac{b\,\underline{u}\,\bar{v}}{a + \bar{u}} - c\bar{v} - \frac{f\,\bar{v}^2}{d^2 + \bar{v}^2} = 0.$$

Notice that $0 < \varepsilon \le \underline{u} \le \bar{u} \le 1$ and $h < 0$, we have $\bar{u} = \underline{u} = 1$, $\bar{v} = \underline{v} = 0$. Since ε can be sufficiently small, from Theorem 2.2 in Pao (2002), we know that the solution $((u, t), v(x, t))$ of (2) converges to $(1, 0)$ as $t \to \infty$ when $0 < u_0(x, t) \le 1$ and $0 \le v_0(x, t) \le \delta(\varepsilon)$ in $[0, \pi] \times [-\tau, 0]$.

From a comparison theorem for parabolic boundary-value problems, we have $u(x, t) < U(x, t)$ in $\overline{\Omega} \times [0, \infty)$, where $U(x, t)$ is the positive solution of the problem

$$\begin{cases} \dfrac{\partial U}{\partial t} = \Delta U + U(1 - U), & x \in (0, \pi), \ t > 0, \\ \dfrac{\partial U}{\partial \nu} = 0, & x = 0 \text{ or } \pi, \ t > 0, \\ U(x, 0) = u_0(x, 0) \ge 0 (\not\equiv 0), & x \in [0, \pi]. \end{cases}$$

It is well known that $U(x, t) \to 1$ as $t \to \infty$. So we see that there exists $T_1 > 0$ such that $u(x, t) < 1 + \varepsilon$ in $[0, \pi] \times [T_1, \infty)$. Since ε can be sufficiently small, $u(x, t) \le 1$ in $[0, \pi] \times [T_1, \infty)$. Furthermore, the comparison theorem for parabolic boundary-value problems implies that $v(x, t) < V(x, t)$ when $t > T_1$, where $V(x, t)$ is the solution of the problem

$$\begin{cases} \dfrac{\partial V}{\partial t} = D\Delta V + hV, & x \in (0, \pi), \ t > T_1, \\ \dfrac{\partial V}{\partial \nu} = 0, & x = 0 \text{ or } \pi, \ t > T_1, \\ V(x, T_1) = v(x, T_1) > 0, & x \in [0, \pi]. \end{cases}$$

Because $h < 0$, $V(x, t) \to 0$ when $t \to \infty$. There exists $T_2 > T_1$ such that $v(x, t) < \delta(\varepsilon)$ in $[0, \pi] \times [T_2, \infty)$. From the discussions above and Corollary 2.1 in Pao (2002), we have the following conclusion.

Theorem 2.1 *If* $h = b/(a + 1) - c < 0$, *then the system* (2) *with* $u_0(x, t) \not\equiv 0$ *and* $v_0(x, t) \not\equiv 0$ *has a unique global positive solution* $(u(x, t), v(x, t))$ *which satisfies*

$$\lim_{t \to \infty} (u(x, t), v(x, t)) = (1, 0), \quad x \in [0, \pi].$$

The linearization of the system (2) at the boundary equilibrium $E_1(1, 0)$ is

$$\begin{cases} \dfrac{\partial u(x, t)}{\partial t} = \Delta u(x, t) - u(x, t), & t > 0, x \in (0, \pi), \\ \dfrac{\partial v(x, t)}{\partial t} = D\Delta v(x, t) + hv, & t > 0, x \in (0, \pi), \\ \dfrac{\partial u(x, t)}{\partial \nu} = \dfrac{\partial v(x, t)}{\partial \nu} = 0, & t \ge 0, \ x = 0 \text{ or } \pi, \\ u(x, t) = u_0(x, t) \ge 0, \ v(x, t) = v_0(x, t) \ge 0, & t \in [-\tau, 0], \ x \in [0, \pi]. \end{cases} \quad (4)$$

From Wu (1996), the characteristic equation of (4) is

$$\left(\lambda + n^2 + 1\right)\left(\lambda + Dn^2 - h\right) = 0, \ n \in \mathbb{N}_0 = \{0, 1, 2, \ldots\}. \tag{5}$$

So the eigenvalues are

$$\lambda_{1,n} = -n^2 - 1 < 0, \ \lambda_{2,n} = -Dn^2 + h, \ n \in \mathbb{N}_0.$$

Since $h < 0$, we have $\lambda_{2,n} < 0$ for $n \in \mathbb{N}_0$. This implies that the boundary equilibrium $E_1(1, 0)$ is asymptotically stable. Combining Theorem 2.1, we obtain the following theorem.

Theorem 2.2 *If $h = b/(a + 1) - c < 0$, the boundary equilibrium $E_1(1, 0)$ of the system* (2) *is globally asymptotically stable on* $\{(u, v)|u > 0, v \geq 0\}$.

2.2 Stability of Coexistent Equilibria

In this subsection, the sufficient conditions for the existence and uniqueness of a coexistent homogeneous equilibrium state $E^*(u^*, v^*)$ of the system (2) are given. The stability of the coexistent equilibrium state E^* is also studied for the delay parameter $\tau = 0$. The influence of the delay on the stability of the coexistent equilibrium will be studied in the next section.

If a positive coexistent equilibrium state $E^*(u^*, v^*)$ exists, then u^* and v^* should satisfy the following algebraic equations:

$$v = (1 - u)(a + u), \tag{6}$$

$$\frac{fv}{d^2 + v^2} = \frac{bu}{a + u} - c. \tag{7}$$
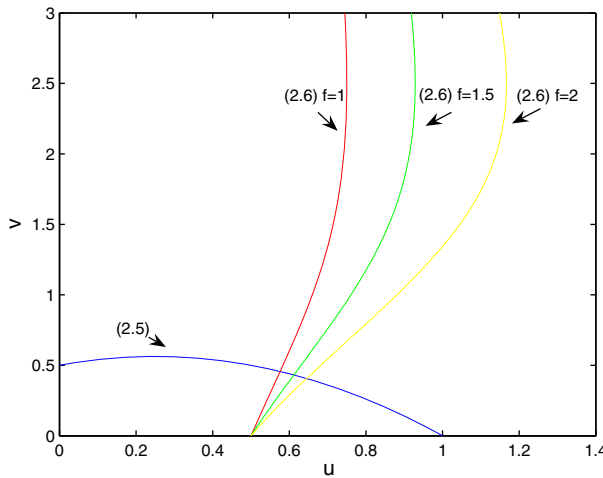
From (6), we have

$$\begin{aligned}
&\text{when } v = 0, \ \text{then } u = 1, \ \text{as } a + u > 0, \\
&\text{when } u = 0, \ \text{then } v = a, \\
&\frac{dv}{du} = 1 - a - 2u \text{ is } \begin{cases} > 0, \text{ if } u < (1 - a)/2, \\ = 0, \text{ if } u = (1 - a)/2, \\ < 0, \text{ if } u > (1 - a)/2. \end{cases}
\end{aligned}$$

From (7), we have

$$\text{when } v = 0, \ \text{then } u = ac/(b - c) \text{ is } \begin{cases} < 1, \text{ if } h > 0, \\ = 1, \text{ if } h = 0, \\ > 1, \text{ if } h < 0. \end{cases}$$

Fig. 1 $a = 0.5$, $b = 2$, $c = 1$, $d = 2.5$, $f = 1$ (*red line*), $f = 1.5$ (*green line*) or $f = 2$ (*yellow line*). A positive equilibrium $E^*(u^*, v^*)$ is obtained at the intersection of two isoclines (6) and (7). We also observe that u^* increases and v^* decreases as f increases under certain parameter range (Color figure online)

$$\frac{\mathrm{d}u}{\mathrm{d}v} = \frac{f(d^2 - v^2)(a + u)^2}{ab(d^2 + v^2)^2} \text{ is } \begin{cases} > 0, & \text{if } 0 < v < d, \\ = 0, & \text{if } v = d, \\ < 0, & \text{if } v > d. \end{cases}$$

We summarize these information graphically in Fig. 1.

Eliminate variable v from the Eqs. (6) and (7), and suppose (u^*, v^*) is an intersection of two curves in Fig. 1, we obtain the following fifth-order algebraic equation that u^* must be satisfied:

$$p_5 u^5 + p_4 u^4 + p_3 u^3 + p_2 u^2 + p_1 u + p_0 = 0, \tag{8}$$

where

$$
\begin{aligned}
p_0 &= -(a^2 + d^2)ac - fa^2, \\
p_1 &= (a^2 + d^2)(b - c) - 2ca^2(1 - a) - 2fa + fa^2, \\
p_2 &= 2a(1 - a)(b - c) - (1 - 4a + a^2)ac - f + 2fa, \\
p_3 &= (1 - 4a + a^2)(b - c) + 2ac(1 - a) + f, \\
p_4 &= -2(1 - a)(b - c) - ac, \\
p_5 &= b - c.
\end{aligned}
$$

Since all parameters are nonnegative, $p_0 = -(a^2 + d^2)ac - fa^2 < 0$. If $h \geq 0$, then $p_5 = b - c > 0$, and so, (8) exists at least one positive solution. Under other conditions specified in the following theorem, the system of the Eqs. (6) and (7) has a unique intersection. Therefore, the system (2) exists the unique positive equilibrium point under these conditions. It is summarized as a theorem.

Theorem 2.3 *If*

$$(\mathcal{H}): \quad h > 0, \quad \frac{1-a}{2} \le \frac{ac}{b-c}, \quad d \ge \frac{(1+a)^2}{4},$$

then the system (2) *has a unique positive equilibrium* $E^*(u^*, v^*)$, *where* $v^* = (1 - u^*)(a + u^*)$, u^* *is the unique positive solution of* (8) *and* $u^* < 1$.

Notice that

$$1 - u^* - \frac{v^*}{a + u^*} = 0, \quad \frac{bu^*}{a + u^*} - c - \frac{fv^*}{d^2 + v^{*2}} = 0,$$

the linearization of the system (2) at the positive equilibrium $E^*(u^*, v^*)$ is

$$\begin{pmatrix} \frac{\partial u(x, t)}{\partial t} \\ \frac{\partial v(x, t)}{\partial t} \end{pmatrix} = \begin{pmatrix} \Delta u(x, t) \\ D\Delta v(x, t) \end{pmatrix} + L_1 \begin{pmatrix} u(x, t) \\ v(x, t) \end{pmatrix} + L_2 \begin{pmatrix} u(x, t - \tau) \\ v(x, t - \tau) \end{pmatrix}, \quad (9)$$

where

$$L_1 = \begin{pmatrix} -u^* + \dfrac{u^* v^*}{(a + u^*)^2} & -\dfrac{u^*}{a + u^*} \\ 0 & \dfrac{fv^*(v^{*2} - d^2)}{(d^2 + v^{*2})^2} \end{pmatrix}, \quad L_2 = \begin{pmatrix} 0 & 0 \\ \dfrac{abv^*}{(a + u^*)^2} & 0 \end{pmatrix}.$$

The characteristic equation of the Eq. (9) is

$$\det(\lambda I_2 - M_n - L_1 - L_2 e^{-\lambda \tau}) = 0, \quad n \in \mathbb{N}_0, \quad (10)$$

where I_2 is the 2×2 identity matrix and $M_n = -n^2 \mathrm{diag}(1, D)$. That is, each eigenvalue λ is a root of an equation

$$\lambda^2 + T_n \lambda + D_n + B e^{-\lambda \tau} = 0, \quad n \in \mathbb{N}_0, \quad (11)$$

where

$$T_n = (1 + D)n^2 + u^* - \frac{u^* v^*}{(a + u^*)^2} - \frac{fv^*(v^{*2} - d^2)}{(d^2 + v^{*2})^2},$$

$$D_n = \left[n^2 + u^* - \frac{u^* v^*}{(a + u^*)^2} \right]\left[Dn^2 - \frac{fv^*(v^{*2} - d^2)}{(d^2 + v^{*2})^2} \right],$$

$$B = \frac{abu^* v^*}{(a + u^*)^3} > 0.$$

When $\tau = 0$, the characteristic equation (11) becomes the following sequence of equations

$$\lambda^2 + T_n\lambda + D_n + B = 0, \ n \in \mathbb{N}_0. \tag{12}$$

If $T_n > 0, \ D_n + B > 0$ for $n \in \mathbb{N}_0$, then all roots of the Eq. (12) have negative real parts.

In the following we give some sufficient conditions to ensure the stability of the positive equilibrium state $E^*(u^*, v^*)$.

Theorem 2.4 *Assume that* $(\mathcal{H})$ *holds, then all roots of the characteristic equation* (11) *have negative real parts for* $\tau = 0$. *Furthermore, the equilibrium state* $E^*(u^*, v^*)$ *of the system* (2) *is locally asymptotically stable when* $\tau = 0$.

Proof If the condition $(\mathcal{H})$ holds, then $u^* > (1 - a)/2$ and $v^* \leq d$. Now, we only need to show $T_n > 0, \ D_n + B > 0$ when $u^* > (1 - a)/2$ and $v^* \leq d$.

$$u^* > (1 - a)/2 \Leftrightarrow a + u^* > 1 - u^* \Leftrightarrow (a + u^*)^2 > (1 - u^*)(a + u^*).$$

From $v^* = (1 - u^*)(a + u^*)$, we have $(a + u^*)^2 > v^*$, i.e. $u^* - u^*v^*/(a + u^*)^2 > 0$. Notice that $v^* \leq d$, we get

$$T_n > T_{n-1} > \cdots > T_0 > 0, \ D_n + B > D_{n-1} + B > \cdots > D_0 + B > 0 \ \text{for} \ n \in \mathbb{N}.$$

The proof is complete. □

2.3 Biological Implications of Equilibrium Analysis

We defined a combined parameter $h = b/(a + 1) - c$, and according to the sign of this parameter the system will display different dynamical behaviors. When $h < 0$, the system will reach the equilibrium $E_1(1, 0)$ no matter where it starts as stated in Theorem 2.1 and Theorem 2.2. When $h > 0$, the system will reach the positive coexistent homogeneous equilibrium $E^*(u^*, v^*)$ under other extra conditions as stated in Theorem 2.3, or will have more complicated dynamical behaviors which will be explored in the next section. In this subsection, we explore the possible biological implications of this parameter, the extra conditions, and related statements about equilibrium analysis.

We notice that $h = \frac{b}{a+1} - c = \frac{e\gamma/r}{H_p/w+1} - \frac{\delta}{r} = \frac{1}{r}(e\gamma \frac{w}{H_p+w} - \delta)$. At a fixed nutrient level, $\gamma \frac{w}{H_p+w}$ is the maximal grazing rate of herbivorous zooplankton on phytoplankton since w is the carrying capacity of phytoplankton. So $e\gamma \frac{w}{H_p+w}$ is the maximal per capita growth rate of herbivorous zooplankton. Since δ is the mortality rate of herbivorous zooplankton, $e\gamma \frac{w}{H_p+w} - \delta$ is the maximal net growth rate of herbivorous zooplankton. Therefore, h is a scaled maximal net growth rate of herbivorous zooplankton (scaled by the per capita growth rate of phytoplankton r). If $h < 0$, the herbivorous zooplankton population cannot grow anymore no matter how long their maturation period could be. In this situation, the herbivorous zooplankton will collapse and then phytoplankton population will grow into its carrying capacity. The fish population plays no role in this situation.

To understand how the parameter h changes as the nutrient level changes, we should consider h as a function of the nutrient parameter N. However, since the per capita growth rate r of phytoplankton is an increasing function of N, and to simplify calculation, we consider $h(r)$ is a function of r. Then

$$\frac{dh}{dr} = -\frac{1}{r^2}\left(e\gamma \frac{w}{H_p + w} - \delta\right) + \frac{1}{r}\frac{e\gamma H_p}{(H_p + w)^2 \beta}.$$

It is easy to see that, when $r \geq (e\gamma \frac{w}{H_p+w} - \delta)\frac{(H_p+w)^2\beta}{e\gamma H_p}$, we have $\frac{dh}{dr} \geq 0$. When the maximal net growth rate of herbivorous zooplankton is negative ($e\gamma \frac{w}{H_p+w} - \delta < 0$), if the nutrient level is increased, $h(r)$ will increase. At the critical point of nutrient level where $h(r) = 0$, but the derivative $\frac{dh}{dr} > 0$. Therefore, the system shifts its behavior from the collapsing of herbivorous zooplankton population to coexistence stages.

We know that only the condition $h > 0$, that is, the system has a positive maximal net growth rate of herbivorous zooplankton, will ensure the system has at least one positive equilibrium state. In general, the system may have four equilibria. To ensure the system has a unique positive equilibrium state, we need some extra conditions. It turns out that these conditions have some biological significance. We first define a half-saturation rate for Holling type functional responses. Let $g_2(x) = \frac{ax}{b+x}$ and $g_3(x) = \frac{ax^2}{b^2+x^2}$ be Holling type II and III function, respectively, we define the half-saturation rate to be the average of rate of change:

$$\frac{g_i(b) - g_i(0)}{b - 0} = \frac{a}{2b}, \quad i = 2, 3.$$

When the maximal value of the function is given, the half-saturation rate measures how fast the function reaches its half-saturation value.

We look into the details of the condition $(\mathcal{H})$ in Theorem 2.3 or Theorem 2.4. We know that w is the carrying capacity of phytoplankton, H_p is the half-saturation of phytoplankton as predation of herbivorous zooplankton on phytoplankton, and so $H_p \leq w$. Thus, $1 - a \geq 0$, and then $\frac{1-a}{2} \leq \frac{ac}{b-c}$ implies $b - c > 0$. But, $b - c = \frac{1}{r}(e\gamma - \delta) > 0$. $e\gamma$ is the theoretical maximum of per capita growth rate of herbivorous zooplankton, and $e\gamma \frac{w}{H_p+w}$ is the maximum of per capita growth rate. Therefore, $h = \frac{1}{r}(e\gamma \frac{w}{H_p+w} - \delta) > 0$ implies $b - c > 0$. Thus, we do not need the extra condition $b - c > 0$. Now, from the condition $\frac{1-a}{2} \leq \frac{ac}{b-c}$, we can easily derive $w \leq \frac{e\gamma+\delta}{e\gamma-\delta}H_p$. Then, we have $\frac{1}{\beta}\frac{\alpha N}{H_n+N} \leq \frac{e\gamma+\delta}{e\gamma-\delta}H_p$. If we are concerned with the nutrient level, we have

$$\frac{N}{H_n + N} \leq \frac{\beta(e\gamma + \delta)}{\alpha(e\gamma - \delta)}H_p.$$

This relation means that the nutrient level cannot be too high to ensure that the system has a unique positive stable equilibrium state. This is consistent with some early studies (Scheffer 1991; Dubey et al. 2009). The nutrient level changes the dynamics of the system. From the condition $d \geq \frac{(1+a)^2}{4}$, we easily get $\frac{\beta(H_p+w)^2}{4\gamma} \leq H_z$, or

$$\frac{1}{H_z} \leq \frac{4\gamma}{\beta(H_p + w)^2}.$$

This relation means that the half-saturation rate cannot exceed a limitation to ensure that the system has a unique positive stable equilibrium state when the predation rate of fish on herbivorous zooplankton is fixed. The system needs time to establish the herbivorous zooplankton population.

Putting together, the condition $(\mathcal{H})$ says that, to have the system stays at a coexistence equilibrium state, the herbivorous zooplankton population must grow (that is, the maximal net growth rate of herbivorous zooplankton must be positive), the growth needs nutrient but the nutrient level cannot be too high and the half-saturation rate of predation of fish also cannot be too fast such that it ensures the establishment of the herbivorous zooplankton population. We may call the condition $(\mathcal{H})$ an eutrophic condition.

To understand how the fish population affects the system, particularly, the coexistence equilibrium state $E^*(u^*, v^*)$, we look at how u^* and v^* change as the predation rate F of fish on herbivorous zooplankton changes, or the combined parameter f changes. From the condition $(\mathcal{H})$, we know that $(1 - a)/2 < u^* < 1$, and $v^* \leq (1 + a)^2/4 \leq d$. With respect to f, differentiating

$$\begin{cases} v^* = (1 - u^*)(a + u^*), \\ \dfrac{fv^*}{d^2 + v^{*2}} = \dfrac{bu^*}{a + u^*} - c, \end{cases}$$

we get

$$\frac{\partial v^*}{\partial f} = (1 - a - 2u^*)\frac{\partial u^*}{\partial f},$$

and

$$\frac{v^*}{d^2 + v^{*2}} + \frac{f(d^2 - v^{*2})}{(d^2 + v^{*2})^2}\frac{\partial v^*}{\partial f} = \frac{ab}{(a + u^*)^2}\frac{\partial u^*}{\partial f}.$$

After a little bit changes, we have

$$\frac{\partial u^*}{\partial f} = \frac{v^*}{d^2 + v^{*2}}\left[\frac{ab}{(a + u^*)^2} - \frac{f(d^2 - v^{*2})}{(d^2 + v^{*2})^2}(1 - a - 2u^*)\right]^{-1}.$$

With the constraints $u^* > (1 - a)/2$ and $v^* \leq d$, we have

$$\begin{cases} \dfrac{\partial u^*}{\partial f} > 0, \\ \dfrac{\partial v^*}{\partial f} < 0. \end{cases} \tag{13}$$

We know $f = \frac{\gamma F}{wr^2}$, where the carrying capacity of phytoplankton population w and per capita growth rate r are constants when the nutrient level is fixed. Therefore, increas-

ing predation rate F of fish on herbivorous zooplankton, the equilibrium density of phytoplankton will increase while the equilibrium density of herbivorous zooplankton will decrease. We also see that, as long as the equilibrium density of phytoplankton is above certain level $u^* > (1 - a)/2$, the equilibrium density of herbivorous zooplankton cannot increase as predation of fish increases. This pattern seems to counter intuitive. However, it may explain why the equilibrium density of phytoplankton must be above certain limit, since there must be sufficient phytoplankton to establish herbivorous zooplankton population. Once the equilibrium is established, predation of fish on herbivorous zooplankton will naturally decrease herbivorous zooplankton while increase phytoplankton near the coexistence equilibrium.

The property (13) also gives some interesting consequence that seems to counter intuitive very much. u^* is a increasing function and v^* is a decreasing function of f while $u^* \leq 1$ and $v^* \geq 0$. We may think there should exist a value of f at which the herbivorous zooplankton population collapses ($v = 0$) or the phytoplankton population reaches its carrying capacity. However, under the condition $(\mathcal{H})$ (an eutrophic condition), the system will never come back to the boundary equilibrium state, that is, the herbivorous zooplankton population collapses, unless the predation rate f of fish on herbivorous zooplankton approaches infinite. Therefore, under the eutrophic condition, the system will not collapse no matter how predation of fish on herbivorous zooplankton could be. We also obtain a range for the predation rate of fish on herbivorous zooplankton

$$0 \leq f < \infty, \quad \text{or } 0 \leq F < \infty. \tag{14}$$

3 Delay Induced Hopf Bifurcations and Oscillations

In this section, we study how the maturation period of herbivorous zooplankton, considered as a parameter of delay τ, affects the dynamics of the system (1). Under the eutrophic condition $(\mathcal{H})$, we find that there exists a value of the predation rate of fish on herbivorous zooplankton, F^*. The coexistent equilibrium state E^* is locally asymptotical stable when $F \geq F^*$ no matter what the zooplankton maturation period is. However, when $0 < F < F^*$, the zooplankton maturation period comes to effect on the dynamics of the system. Corresponding to each $0 < F < F^*$, we obtain a critical value of the delay parameter at which the system undergoes Hopf bifurcations, above that value the system will display oscillating behavior, while below that value the coexistent equilibrium state is still stable. We actually obtain a bifurcation curve in the parameter space of the delay and the fish predation rate. We also study the stability and direction of the Hopf bifurcations and give some conditions under which the system has stable or unstable periodical solutions. In this section, there are three subsections, delay induced Hopf bifurcations, stability and directions of the Hopf bifurcations, and biological implications of oscillations induced by delay.

3.1 Delay Induced Hopf Bifurcations

In this subsection, we assume that the condition $(\mathcal{H})$ is satisfied. We see that, 0 is not the solution of (11). We need to seek critical values of the delay parameter τ such that

there exist a pair of simple purely imaginary eigenvalues. Suppose $\pm i\omega(\omega > 0)$ is solutions of the $(n + 1)$th equation (11). Then we have

$$-\omega^2 + T_n i\omega + D_n + Be^{-i\omega\tau} = 0.$$

Separating the real and imaginary parts, we get that ω and τ satisfy

$$\begin{cases} B\cos\omega\tau = \omega^2 - D_n, \\ B\sin\omega\tau = T_n\omega. \end{cases} \tag{15}$$

It follows from (15) that

$$\omega^4 + (T_n^2 - 2D_n)\omega^2 + D_n^2 - B^2 = 0. \tag{16}$$

Let $z = \omega^2$, then (16) can be rewritten as the following form

$$z^2 + (T_n^2 - 2D_n)z + D_n^2 - B^2 = 0. \tag{17}$$

Under the condition $(\mathcal{H})$, we have

$$T_n^2 - 2D_n = (1 + D)^2 n^4 + 2(l_{11} + Dl_{22})n^2 + l_{11}^2 + l_{22}^2 > 0, \text{ for } n \in \mathbb{N}_0,$$

where

$$l_{11} = u^* - \frac{u^*v^*}{(a + u^*)^2} > 0, \ l_{22} = -\frac{fv^*(v^{*2} - d^2)}{(d^2 + v^{*2})^2} > 0.$$

Therefore, if $D_n^2 - B^2 < 0$, the Eq. (17) has positive roots

$$Z_n = \frac{2D_n - T_n^2 + \sqrt{T_n^4 - 4T_n^2 D_n + 4B^2}}{2}.$$

However, when $D_n^2 - B^2 \geq 0$, the Eq. (17) has no positive roots. We see that, $D_n^2 - B^2$ is monotonically increasing in n, and tends to ∞ as $n \to \infty$. So, if $D_0^2 - B^2 < 0$, then there exists $N \in \mathbb{N}$ such that

$$D_n^2 - B^2 \geq 0 \text{ for } n \geq N, \text{ and } D_n^2 - B^2 < 0 \text{ for } 0 \leq n < N. \tag{18}$$

If the condition $(\mathcal{H})$ holds, then

$$D_0 > 0, \ (a + u^*)^2 - v^* > 0, \text{ and } d^2 - v^{*2} \leq 0.$$

Therefore

$$D_0^2 - B^2 < 0 \Leftrightarrow D_0 < B \Leftrightarrow f < \frac{ab(d^2 + v^{*2})^2}{(a + u^*)[(a + u^*)^2 - v^*](d^2 - v^{*2})}.$$

Notice (13), if we define a value f^* as follows, we will be able to study the impact of predation of fish on the dynamics of the system. So, we define

$$f^* = \frac{ab(d^2 + v^{*2})^2}{(a + u^*)[(a + u^*)^2 - v^*](d^2 - v^{*2})}. \tag{19}$$

Since f is a nonnegative parameter, it is easy to see that, if $f < f^*$, then $D_0^2 - B^2 < 0$; if $f \geq f^*$, then $D_0^2 - B^2 \geq 0$.

Let $\omega_n = \sqrt{Z_n}$ and

$$\tau_n^j = \frac{1}{\omega_n}\left(\arccos\frac{\omega_n^2 - D_n}{B} + 2j\pi\right), \quad j \in \mathbb{N}_0, \ 0 \leq n < N. \tag{20}$$

Then Eq. (15) has a pair of purely imaginary roots $\pm i\omega_n$ provided that $f < f^*$ and $\tau = \tau_n^j$. Now, we are ready to define the critical value of the delay parameter in the following,

$$\tau^* = \tau_{k_0}^0 = \min\{\tau_n^0 : 0 \leq n < N\}, \quad \omega^* = \omega_{k_0}. \tag{21}$$

It is easy to see that τ^* can be viewed as a function of f since τ_n^j is a function of f from the equation (11). We consider the eigenvalue λ as a function of τ. Then, we have the following statement about the sign of the derivative of $\lambda(\tau)$ at τ_n^j, and then the sign of the derivative $\lambda(\tau)$ at τ^*.

Theorem 3.1 *Suppose that the condition $(\mathcal{H})$ is satisfied. If $0 < f < f^*$, then*

$$Re\lambda'(\tau_n^j) > 0, \ for \ j \in \mathbb{N}_0, \ 0 \leq n < N,$$

where N is defined by (18).

Proof Differentiating the two sides of (11) with respect to τ, it follows that

$$(2\lambda + T_n - B\tau e^{-\lambda\tau})\frac{d\lambda}{d\tau} - B\lambda e^{-\lambda\tau} = 0.$$

Thus

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\lambda + T_n - B\tau e^{-\lambda\tau}}{B\lambda e^{-\lambda\tau}}.$$

From (15)-(17), we have

$$Re\left(\frac{d\lambda}{d\tau}\right)^{-1}\Bigg|_{\tau=\tau_n^j} = Re\left(\frac{(i\omega_n + T_n)(\cos\omega_n\tau_n^j + i\sin\omega_n\tau_n^j) - B\tau_n^j}{Bi\omega_n}\right)$$

$$
= \frac{2\omega_n \cos \omega_n \tau_n^j + T_n \sin \omega_n \tau_n^j}{B\omega_n}
$$

$$
= \frac{2\omega_n(\omega_n^2 - D_n) + T_n^2 \omega_n}{B^2 \omega_n}
$$

$$
= \frac{\sqrt{T_n^4 - 4T_n^2 D_n + 4B^2}}{B^2} > 0.
$$

The proof is completed. $\qquad\square$

According to the discussion above and Corollary 2.4 in Ruan and Wei (2003), we know that the roots of (11) have negative real parts when $0 \leq \tau < \tau^*$, and the $(n+1)$th equation of (11) has a pair of simple purely imaginary roots when $\tau = \tau_n^j$. We can also get that (11) has at least one pair of conjugate complex roots with positive real parts when $\tau > \tau^*$. Combining the property (14) and Equation (19), we write the results above as the following theorem.

Theorem 3.2 *Suppose the condition* ($\mathcal{H}$) *is satisfied.*

(1) If $f^* \leq f < \infty$, then the equilibrium state $E^*(u^*, v^*)$ of the system (2) is locally asymptotically stable for $\tau \geq 0$.
(2) If $0 < f < f^*$, then
  (a) the equilibrium state $E^*(u^*, v^*)$ of the system (2) is locally asymptotically stable for $0 \leq \tau < \tau^*$, the equilibrium state $E^*(u^*, v^*)$ is unstable for $\tau > \tau^*$, where τ^* is a function of f.
  (b) the system (2) undergoes Hopf bifurcations at the equilibrium point $E^*(u^*, v^*)$ when $\tau = \tau_n^j$ for $j \in \mathbb{N}_0$, $0 \leq n < N$ with N satisfying (18).

3.2 Stability and Direction of the Hopf Bifurcations

Theorem 3.2 says that a family of spatially homogeneous or inhomogeneous periodic solutions may bifurcate from the positive homogeneous equilibrium state E^* of the system (2) when τ crosses through the critical value τ^*. In this subsection, we investigate the stability and direction of Hopf bifurcations by using the center manifold theorem and the normal formal theory of partial functional differential equation (Faria 2000; Wu 1996). Basically, the system (2) firstly is represented as an abstract ODE system. Secondly, at the center manifold of the ODE system corresponding to E^*, the normal form or Taylor expansion of the ODE system is computed. Then, the coefficients of the first 4 terms of the normal form will reveal all the properties of the periodical solutions (Hassard et al. 1981).

To write the system (2) as an ODE system, we need to define some function spaces. Let's define a function space

$$
X = \left\{ (u_1, u_2) \in W^{2,2}(0, \pi) : \frac{\partial u_1}{\partial x} = \frac{\partial u_2}{\partial x} = 0, \text{ at } x = 0, \pi \right\},
$$

where $u_1(\cdot, t) = u(\cdot, \tau t) - u^*$, $u_2(\cdot, t) = v(\cdot, \tau t) - v^*$, $U(t) = (u_1(\cdot, t), u_2(\cdot, t))^{\mathrm{T}}$. Then the system (2) can be written as an equation in the function space $\mathscr{C} = C([-1, 0], X)$:

$$\frac{\mathrm{d}U(t)}{\mathrm{d}t} = \tau \tilde{D} \Delta U(t) + L(\tau)(U_t) + f(U_t, \tau), \tag{22}$$

where $\tilde{D} = \mathrm{diag}(1, D)$, $L(\tau)(\cdot) : \mathscr{C} \to X$ and $f : \mathscr{C} \times \mathbb{R} \to X$ are given, respectively, by

$$L(\tau)(\varphi) = \tau L_1 \varphi(0) + \tau L_2 \varphi(-1),$$
$$f(\varphi, \tau) = \tau (f_1(\varphi, \tau), \ f_2(\varphi, \tau))^{\mathrm{T}},$$

with

$$f_1(\varphi, \tau) = a_1 \varphi_1^2(0) + a_2 \varphi_1(0)\varphi_2(0) + a_3 \varphi_1^3(0) + a_4 \varphi_1^2(0)\varphi_2(0) + \mathcal{O}(4),$$
$$f_2(\varphi, \tau) = a_5 \varphi_1^2(-1) + a_6 \varphi_1(-1)\varphi_2(0) + a_7 \varphi_2^2(0) + a_8 \varphi_1^3(-1)$$
$$+ a_9 \varphi_1^2(-1)\varphi_2(0) + a_{10}\varphi_2^3(0) + \mathcal{O}(4),$$

$$a_1 = \frac{av^*}{(a+u^*)^3} - 1, \ a_2 = \frac{-a}{(a+u^*)^2}, \ a_3 = \frac{-av^*}{(a+u^*)^4}, \ a_4 = \frac{a}{(a+u^*)^3},$$
$$a_5 = \frac{-abv^*}{(a+u^*)^3}, \ a_6 = \frac{ab}{(a+u^*)^2}, \ a_7 = \frac{fd^2(3v^{*2} - d^2)}{(d^2 + v^{*2})^3},$$
$$a_8 = \frac{abv^*}{(a+u^*)^4}, \ a_9 = \frac{-ab}{(a+u^*)^3}, \ a_{10} = \frac{4fd^2v(d^2 - v^{*2})}{(d^2 + v^{*2})^4},$$

for $\varphi = (\varphi_1, \varphi_2)^{\mathrm{T}} \in \mathscr{C}$.

Let $\tau = \tau^* + \mu$. Then (22) can be rewritten as

$$\frac{\mathrm{d}U(t)}{\mathrm{d}t} = \tau^* \tilde{D} \Delta U(t) + L(\tau^*)(U_t) + F(U_t, \mu), \tag{23}$$

where

$$F(\varphi, \mu) = \mu \tilde{D} \Delta \varphi(0) + L(\mu)(\varphi) + f(\varphi, \tau^* + \mu),$$

for $\varphi \in \mathscr{C}$.

From the previous subsection, when $\mu = 0$ (i.e. $\tau = \tau^*$), the system (23) undergoes Hopf bifurcation at the equilibrium $(0, 0)$. It is also clear that $\pm i\omega^*\tau^*$ are simply purely imaginary eigenvalues of the linearized system of (23) at the origin

$$\frac{\mathrm{d}U(t)}{\mathrm{d}t} = (\tau^* + \mu)\tilde{D} \Delta U(t) + L(\tau^* + \mu)(U_t), \tag{24}$$

with $\mu = 0$ and all other eigenvalues of (24) at $\mu = 0$ have negative real parts.

The eigenvalues of $\tau \tilde{D} \Delta$ on X are $-\tau k^2$ and $-\tau D k^2$, $k \in \mathbb{N}_0$, with corresponding eigenfunctions $\beta_k^1(x) = (\gamma_k(x), 0)^{\mathrm{T}}$ and $\beta_k^2(x) = (0, \gamma_k(x))^{\mathrm{T}}$, where $\gamma_k = \frac{\cos kx}{\|\cos kx\|_{2,2}}$.

We define a space as $M_k = \text{span}\{\langle\varphi, \beta_k^i\rangle\beta_k^i : \varphi \in \mathscr{C}, i = 1, 2\}$, $k \in \mathbb{N}_0$, and the inner product $\langle\cdot, \cdot\rangle$ is defined by

$$\langle u, v\rangle = \int_0^\pi u^\mathrm{T} v dx, \text{ for } u, v \in X.$$

Then, on M_k, the Eq. (24) is equivalent to the ODE on $\mathbb{R}^2$:

$$\frac{dU(t)}{dt} = -(\tau^* + \mu)k^2\tilde{D}U(t) + L(\tau^* + \mu)(U_t). \tag{25}$$

Now, we compute the normal form in the center manifold. There are several steps. We first compute eigenvectors of the infinitesimal generator of the semigroup defined by linearized system at $\tau = \tau^*$. From the Riesz representation theorem, there exists a bounded variation function $\eta_k(\mu, \theta)$ for $\theta \in [-1, 0]$, such that

$$-(\tau^* + \mu)k^2\tilde{D}\varphi(0) + L(\tau^* + \mu)(\varphi) = \int_{-1}^0 d\eta_k(\mu, \theta)\varphi(\theta) \tag{26}$$

for $\varphi \in C([-1, 0], \mathbb{R}^2)$. In fact, we can choose

$$\eta_k(\mu, \theta) = \begin{cases} (\tau^* + \mu)(L_1 - k^2\tilde{D}), & \theta = 0, \\ 0, & \theta \in (-1, 0), \\ -(\tau^* + \mu)L_2, & \theta = -1. \end{cases}$$

Let A denote the infinitesimal generator of the semigroup defined by (25) with $\mu = 0$, $k = k_0$ and A^* denote the formal adjoint of A under the bilinear form

$$(\psi_k, \phi_k)_k = \psi_k(0)\phi_k(0) - \int_{-1}^0\int_0^\theta \psi_k(\xi - \theta)d\eta_k(\mu, \theta)\phi_k(\xi)d\xi \tag{27}$$

for $\phi_k \in C([-1, 0], \mathbb{R}^2)$ and $\psi_k \in C([0, 1], \mathbb{R}^{2^\mathrm{T}})$. Then, we know that $\pm i\omega^*\tau^*$ are simple purely imaginary eigenvalues of A, and they are also eigenvalues of A^*. By direct computations, we get $q(\theta) = q(0)e^{i\omega^*\tau^*\theta} = (1, C_1)^\mathrm{T}e^{i\omega^*\tau^*\theta}$ is eigenvector of A corresponding to $i\omega^*\tau^*$, where

$$C_1 = -\frac{a + u^*}{u^*}\left[i\omega^* + k_0^2 + u^* - \frac{u^*v^*}{(a + u^*)^2}\right].$$

Similarly, we get $q^*(s) = e^{-i\omega^*\tau^*s}(C_2, 1)$ is eigenvector of A^* corresponding to $i\omega^*\tau^*$, where

$$C_2 = -\frac{a + u^*}{u^*}\left[i\omega^* + Dk_0^2 - \frac{fv^*(v^{*2} - d^2)}{(d^2 + v^{*2})^2}\right].$$

Let $\Phi = (\Phi_1, \Phi_2) = (\text{Re}q, \text{Im}q)$ and $\Psi^* = (\Psi_1^*, \Psi_2^*)^{\text{T}} = (\text{Re}q^*, \text{Im}q^*)^{\text{T}}$. After some straightforward calculations using (27), we obtain

$$(\Psi^*, \Phi)_{k_0} = \begin{pmatrix} (\Psi_1^*, \Phi_1)_{k_0} & (\Psi_1^*, \Phi_2)_{k_0} \\ (\Psi_2^*, \Phi_1)_{k_0} & (\Psi_2^*, \Phi_2)_{k_0} \end{pmatrix}$$

with

$$(\Psi_1^*, \Phi_1)_{k_0} = \text{Re}(C_1 + C_2) + M\left(\cos\omega^*\tau^* + \frac{\sin\omega^*\tau^*}{\omega^*\tau^*}\right),$$

$$(\Psi_1^*, \Phi_2)_{k_0} = \text{Im}C_1 - M\sin\omega^*\tau^*,$$

$$(\Psi_2^*, \Phi_1)_{k_0} = \text{Im}C_2 + M\sin\omega^*\tau^*,$$

$$(\Psi_2^*, \Phi_2)_{k_0} = M\left(\cos\omega^*\tau^* - \frac{\sin\omega^*\tau^*}{\omega^*\tau^*}\right),$$

where $M = \frac{abv^*\tau^*}{2(a+u^*)^2}$. Let $\Psi = (\Psi_1, \Psi_2)^{\text{T}} = (\Psi^*, \Phi)_{k_0}^{-1}\Psi^*$, $(\Psi, \Phi)_{k_0} = I_2$, and I_2 is a 2×2 identity matrix.

We now write the reduced equation on the center manifold. The center subspace of linear equation (24) with $\mu = 0$ is given by $P_{\text{CN}}\mathscr{C}$, where

$$P_{\text{CN}}\varphi = \varphi(\Psi, \langle\varphi, \beta_{k_0}\rangle)_{k_0} \cdot \beta_{k_0}, \ \varphi \in \mathscr{C},$$

with $\beta_{k_0} = (\beta_{k_0}^1, \beta_{k_0}^2)$ and $c \cdot \beta_{k_0} = c_1\beta_{k_0}^1 + c_2\beta_{k_0}^2$ for $c = (c_1, c_2)^{\text{T}} \in \mathscr{C}$. Let $P_S\mathscr{C}$ denote the stable subspace of linear equation (24) with $\mu = 0$, then $\mathscr{C} = P_{\text{CN}}\mathscr{C} \bigoplus P_S\mathscr{C}$.

Using the decomposition $\mathscr{C} = P_{\text{CN}}\mathscr{C} \bigoplus P_S\mathscr{C}$ and following Wu (1996), Zuo and Wei (2011), the flow of (23) with $\mu = 0$ in the center manifold is given by the following formulae:

$$(x_1(t), x_2(t))^{\text{T}} = (\Psi, \langle U_t, \beta_{k_0}\rangle)_{k_0},$$
$$U_t = \Phi(x_1(t), x_2(t))^{\text{T}} \cdot \beta_{k_0} + h(x_1, x_2, 0), \tag{28}$$
$$\begin{pmatrix} \dot{x}_1(t) \\ \dot{x}_2(t) \end{pmatrix} = \begin{pmatrix} 0 & \omega^*\tau^* \\ -\omega^*\tau^* & 0 \end{pmatrix}\begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} + \Psi(0)\langle F(U_t, 0), \beta_{k_0}\rangle, \tag{29}$$

with $h(0, 0, 0) = 0$ and $Dh(0, 0, 0) = 0$.

Let us write the reduced equation in complex form. Set $z = x_1 - ix_2$ and $\Psi(0) = (\Psi_1(0), \Psi_2(0))^{\text{T}}$, then $q = \Phi_1 + i\Phi_2$ and $\Phi(x_1(t), x_2(t))^{\text{T}} \cdot \beta_{k_0} = (qz + \overline{qz}) \cdot \beta_{k_0}/2$. Thus, (28) can be written as

$$U_t = \frac{1}{2}(qz + \overline{qz}) \cdot \beta_{k_0} + w(z, \overline{z}), \tag{30}$$

where

$$w(z, \overline{z}) = h \left(\frac{z + \overline{z}}{2}, \frac{i(z - \overline{z})}{2}, 0 \right).$$

From (29) and (30), we obtain that z satisfies

$$\dot{z} = i\omega^* \tau^* z + g(z, \overline{z}), \tag{31}$$

where

$$g(z, \overline{z}) = (\Psi_1(0) - i\Psi_2(0))\langle F(U_t, 0), \beta_{k_0} \rangle = (\Psi_1(0) - i\Psi_2(0))\langle f(U_t, \tau^*), \beta_{k_0} \rangle.$$

Now, let's compute $g(z, \overline{z})$. Set

$$g(z, \overline{z}) = g_{20}\frac{z^2}{2} + g_{11}z\overline{z} + g_{02}\frac{\overline{z}^2}{2} + g_{21}\frac{z^2\overline{z}}{2} + \cdots,$$

$$w(z, \overline{z}) = w_{20}\frac{z^2}{2} + w_{11}z\overline{z} + w_{02}\frac{\overline{z}^2}{2} + \cdots. \tag{32}$$

Let $(\psi_1, \psi_2) = \Psi_1(0) - i\Psi_2(0)$. From (28), (30) and (31), we can get the following quantities:

$$g_{20} = \frac{\tau^*}{2} \int_0^\pi \gamma_{k_0}^3 \mathrm{d}x \left[(a_1 + a_2 C_1)\psi_1 + \left(a_5 \mathrm{e}^{-2i\omega^*\tau^*} + a_6 C_1 \mathrm{e}^{-i\omega^*\tau^*} + a_7 C_1^2 \right) \psi_2 \right],$$

$$g_{11} = \frac{\tau^*}{4} \int_0^\pi \gamma_{k_0}^3 \mathrm{d}x \left\{ [2a_1 + a_2(C_1 + \overline{C}_1)]\psi_1 \right.$$
$$\left. + \left[2a_5 + a_6 \left(C_1 \mathrm{e}^{i\omega^*\tau^*} + \overline{C}_1 \mathrm{e}^{-i\omega^*\tau^*} \right) + 2a_7 C_1 \overline{C}_1 \right] \psi_2 \right\},$$

$$g_{02} = \frac{\tau^*}{2} \int_0^\pi \gamma_{k_0}^3 \mathrm{d}x \left[(a_1 + a_2\overline{C}_1)\psi_1 + \left(a_5 \mathrm{e}^{2i\omega^*\tau^*} + a_6 \overline{C}_1 \mathrm{e}^{i\omega^*\tau^*} + a_7 \overline{C}_1^2 \right) \psi_2 \right],$$

and

$$g_{21} = \frac{\tau^*}{4} \int_0^\pi \gamma_{k_0}^4 \mathrm{d}x [3a_3 + a_4(2C_1 + \overline{C}_1)]\psi_1$$
$$+ \frac{\tau^*}{4} \int_0^\pi \gamma_{k_0}^4 \mathrm{d}x \left[3a_8 \mathrm{e}^{-i\omega^*\tau^*} + a_9 \left(2C_1 + \overline{C}_1 \mathrm{e}^{-2i\omega^*\tau^*} \right) + 3a_{10}C_1^2\overline{C}_1 \right] \psi_2$$
$$+ \frac{\tau^*}{2} \left\langle \left[a_1 \left(4w_{11}^{(1)}(0) + 2w_{20}^{(1)}(0) \right) \right.\right.$$
$$\left.\left. + a_2 \left(2w_{11}^{(2)}(0) + w_{20}^{(2)}(0) + 2C_1 w_{11}^{(1)}(0) + \overline{C}_1 w_{20}^{(1)}(0) \right) \right] \gamma_{k_0}, \gamma_{k_0} \right\rangle \psi_1$$
$$+ \frac{\tau^*}{2} \left\langle \left[a_5 \left(4w_{11}^{(1)}(-1)\mathrm{e}^{-i\omega^*\tau^*} + 2w_{20}^{(1)}(-1)\mathrm{e}^{i\omega^*\tau^*} \right) \right.\right.$$

$$+a_6 \left(2w_{11}^{(2)}(0)e^{-i\omega^*\tau^*} + w_{20}^{(2)}(0)e^{i\omega^*\tau^*} + 2C_1 w_{11}^{(1)}(-1) + \overline{C}_1 w_{20}^{(1)}(-1) \right)$$

$$+a_7(4C_1 w_{11}^{(2)}(0) + 2\overline{C}_1 w_{20}^{(2)}(0)) \bigg] \gamma_{k_0}, \gamma_{k_0} \bigg\rangle \psi_2.$$

Here w_{11} and w_{20} are need to be computed. The calculation of w_{11} and w_{20} is somewhat tedious. Let A_U denote the generator of the semigroup generated by the linear system (24) with $\mu = 0$. From (30) and (31), we have

$$\dot{w} = \dot{U}_t - \frac{1}{2}(q\dot{z} + \overline{q}\dot{\overline{z}}) \cdot \beta_{k_0}$$

$$= \begin{cases} A_U w - \frac{1}{2}(qg + \overline{q}\overline{g}) \cdot \beta_{k_0}, & \theta \in [-1, 0], \\ A_U w - \frac{1}{2}(qg + \overline{q}\overline{g}) \cdot \beta_{k_0} + f\left(\frac{1}{2}(q\dot{z} + \overline{q}\dot{\overline{z}}) \cdot \beta_{k_0} + w, \tau^* \right), & \theta = 0, \end{cases}$$

$$= A_U w + H(z, \overline{z}, \theta),$$ (33)

where

$$H(z, \overline{z}, \theta) = H_{20}(\theta) \frac{z^2}{2} + H_{11}(\theta) z\overline{z} + H_{02}(\theta) \frac{\overline{z}^2}{2} + \cdots.$$

Let

$$f\left(\frac{1}{2}(q\dot{z} + \overline{q}z) \cdot \beta_{k_0} + w, \tau^* \right) = f_{z^2} \frac{z^2}{2} + f_{z\overline{z}} z\overline{z} + f_{\overline{z}^2} \frac{\overline{z}^2}{2} + \cdots.$$

Furthermore, by comparing the coefficients, we obtain that

$$H_{20}(\theta) = \begin{cases} -\frac{1}{2}(q(\theta)g_{20} + \overline{q}(\theta)\overline{g}_{02}) \cdot \beta_{k_0}, & \theta \in [-1, 0), \\ -\frac{1}{2}(q(\theta)g_{20} + \overline{q}(\theta)\overline{g}_{02}) \cdot \beta_{k_0} + f_{z^2}, & \theta = 0, \end{cases}$$

$$H_{11}(\theta) = \begin{cases} -\frac{1}{2}(q(\theta)g_{11} + \overline{q}(\theta)\overline{g}_{11}) \cdot \beta_{k_0}, & \theta \in [-1, 0), \\ -\frac{1}{2}(q(\theta)g_{11} + \overline{q}(\theta)\overline{g}_{11}) \cdot \beta_{k_0} + f_{z\overline{z}}, & \theta = 0. \end{cases}$$ (34)

By using the chain rule

$$\dot{w} = \frac{\partial w(z, \overline{z})}{\partial z} \dot{z} + \frac{\partial w(z, \overline{z})}{\partial \overline{z}} \dot{\overline{z}},$$

we obtain, from (32) and (33), that

$$\begin{cases} H_{20} = (2i\omega^*\tau^* - A_U)w_{20}, \\ H_{11} = -A_U w_{11}. \end{cases}$$ (35)

As $2i\omega^*\tau^*$ and 0 are not characteristic values of (24), (35) has unique solutions w_{20} and w_{11} in $P_S\mathscr{C}$, given by

$$
\begin{cases}
w_{20} = (2i\omega^*\tau^* - A_U)^{-1} H_{20}, \\
w_{11} = -A_U^{-1} H_{11}.
\end{cases}
\tag{36}
$$

Using the definition of A_U, we get, from the first equation (34) and (35), that for $\theta \in [-1, 0]$,

$$
\dot{w}_{20} = 2i\omega^*\tau^* w_{20}(\theta) + \frac{1}{2}(q(\theta)g_{20} + \overline{q}(\theta)\overline{g}_{02}) \cdot \beta_{k_0}.
$$

Therefore

$$
w_{20}(\theta) = \frac{1}{2}\left[\frac{ig_{20}}{\omega^*\tau^*}q(\theta) + \frac{i\overline{g}_{02}}{3\omega^*\tau^*}\overline{q}(\theta) \right] \cdot \beta_{k_0} + E e^{2i\omega^*\tau^*\theta},
$$

where E is a 2-dimensional vectors in X. Notice that

$$
\tau^*\tilde{D}\Delta q(0) \cdot \beta_{k_0} + L(\tau^*)(q(\theta) \cdot \beta_{k_0}) = i\omega^* q(0) \cdot \beta_{k_0},
$$
$$
\tau^*\tilde{D}\Delta \overline{q}(0) \cdot \beta_{k_0} + L(\tau^*)(\overline{q}(\theta) \cdot \beta_{k_0}) = -i\omega^* \overline{q}(0) \cdot \beta_{k_0},
$$

From (35), we get that

$$
2i\omega^*\tau^* E - \tau^*\tilde{D}\Delta E - L(\tau^*)(E e^{2i\omega^*\tau^*\theta}) = f_{z^2}.
\tag{37}
$$

Representing E and f_{z^2} by series: $E = \sum_{k=0}^{\infty} E_k \cdot \beta_k = \sum_{k=0}^{\infty} E_k \gamma_k$ ($E_k \in \mathbb{R}^2$), and $f_{z^2} = \sum_{k=0}^{\infty}\langle f_{z^2}, \beta_k \rangle \cdot \beta_k = \sum_{k=0}^{\infty}\langle f_{z^2}, \beta_k \rangle \gamma_k$, we get from (37) that

$$
2i\omega^*\tau^* E_k + \tau^*\tilde{D}k^2 E_k - L(\tau^*)(E_k e^{2i\omega^*\tau^*}) = \langle f_{z^2}, \beta_k \rangle, \ k \in \mathbb{N}_0.
$$

So, E_k could be calculated by

$$
E_k = \tilde{E}_k^{-1}\langle f_{z^2}, \beta_k \rangle,
$$

where

$$
\tilde{E}_k = \tau^* \begin{pmatrix} 2i\omega^* + k^2 + u^* - \dfrac{u^*v^*}{(a+u^*)^2} & \dfrac{u^*}{a+u^*} \\ \dfrac{abv^*}{(a+u^*)^2}e^{-2i\omega^*\tau^*} & 2i\omega^* + Dk^2 - \dfrac{fv^*(v^{*2}-d^2)}{(d^2+v^{*2})^2} \end{pmatrix},
$$

$$
\langle f_{z^2}, \beta_k \rangle = \begin{cases} \frac{1}{\sqrt{\pi}}\tilde{f}_{z^2}, & k_0 \neq 0, \ k = 0, \\ \frac{1}{\sqrt{2\pi}}\tilde{f}_{z^2}, & k_0 \neq 0, \ k = 2k_0, \\ \frac{1}{\sqrt{\pi}}\tilde{f}_{z^2}, & k_0 = 0, \ k = 0, \\ 0, & \text{other,} \end{cases}
$$

with

$$\tilde{f}_{z^2} = \frac{\tau^*}{2} \left(\begin{array}{c} a_1 + a_2 C_1 \\ a_5 e^{-2i\omega^*\tau^*} + a_6 C_1 e^{-i\omega^*\tau^*} + a_7 C_1^2 \end{array} \right).$$

Similarly, we get

$$w_{11}(\theta) = \frac{1}{2} \left[\frac{-ig_{11}}{\omega^*\tau^*} q(\theta) + \frac{i\overline{g}_{11}}{\omega^*\tau^*} \overline{q}(\theta) \right] \cdot \beta_{k_0} + F,$$

$$F = \sum_{k=0}^{\infty} F_k \gamma_k \ (F_k \in \mathbb{R}^2), \quad F_k = \tilde{F}_k^{-1} < f_{z\bar{z}}, \beta_k >,$$

where

$$\tilde{F}_k = \tau^* \left(\begin{array}{cc} k^2 + u^* - \dfrac{u^* v^*}{(a+u^*)^2} & \dfrac{u^*}{a+u^*} \\ \dfrac{abv^*}{(a+u^*)^2} & Dk^2 - \dfrac{f v^*(v^{*2} - d^2)}{(d^2 + v^{*2})^2} \end{array} \right),$$

$$\langle f_{z\bar{z}}, \beta_k \rangle = \begin{cases} \frac{1}{\sqrt{\pi}} \tilde{f}_{z\bar{z}}, & k_0 \neq 0, \ k = 0, \\ \frac{1}{\sqrt{2\pi}} \tilde{f}_{z\bar{z}}, & k_0 \neq 0, \ k = 2k_0, \\ \frac{1}{\sqrt{\pi}} \tilde{f}_{z\bar{z}}, & k_0 = 0, \ k = 0, \\ 0, & \text{other,} \end{cases}$$

with

$$\tilde{f}_{z\bar{z}} = \frac{\tau^*}{4} \left(\begin{array}{c} 2a_1 + a_2(C_1 + \overline{C}_1) \\ 2a_5 + a_6(C_1 e^{i\omega^*\tau^*} + \overline{C}_1 e^{-i\omega^*\tau^*}) + 2a_7 C_1 \overline{C}_1 \end{array} \right).$$

So, the coefficient g_{21} is completely determined.

Let $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ denote the eigenvalues of (24). Thus we can compute the following quantities:

$$\begin{aligned} c_1(0) &= \frac{i}{2\omega^*\tau^*} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2 \right) + \frac{1}{2}g_{21}, \\ \mu_2 &= -\frac{\text{Re}(c_1(0))}{\alpha'(\tau^*)}, \\ \beta_2 &= 2\text{Re}(c_1(0)), \\ T_2 &= -\frac{1}{\omega^*\tau^*} (\text{Im}(c_1(0)) + \mu_2\omega'(\tau^*)). \end{aligned} \quad (38)$$

According to the Hopf bifurcation theory (see Hassard et al. 1981), we know that μ_2 determines the direction of the Hopf bifurcation (forward if $\mu_2 > 0$, backward if $\mu_2 < 0$); β_2 determines the stability of the bifurcating periodic solutions (stable if

$\beta_2 < 0$, unstable if $\beta_2 > 0$); and T_2 determines the period of the bifurcating periodic solutions (the period increases if $T_2 > 0$, decreases if $T_2 < 0$).

Since $\mathrm{Re}(\lambda'(\tau^*)) > 0$, from Theorem 3.1, we obtain the following conclusions: If $\mathrm{Re}(c_1(0)) < 0(> 0)$, then $\mu_2 > 0(< 0)$, $\beta_2 < 0(> 0)$, the bifurcating periodic solutions exists for $\tau > \tau^*(< \tau^*)$ and are orbitally stable(unstable).

The symbolic formula of $c_1(0)$ is difficult to obtain for our problem. However, we will demonstrate some cases of numerical computation in the next Sect. 3.3. Particularly, we will be interested in how the sign of $c_1(0)$ is related to the predation rate f of fish on herbivorous zooplankton.

3.3 Biological Implications of Oscillations Induced by Delay

It is well known that the delay may drive a stable positive equilibrium state to an unstable one and may cause oscillations in the system. This mechanism of destabilising is different from Turing instability. For the plankton ecosystem we studied, the maturation period of herbivorous zooplankton is built into the model as a delay parameter τ. The plankton ecosystem has nutrient supplied and also has predator population of fish. The nutrient levels and predation of fish both have impacts on the dynamics of the system. When the nutrient level is fixed, the per capita growth rate and carrying capacity of phytoplankton are constants in our model. We look at how the predation rate of the present fish on herbivorous zooplankton, $F = f\frac{wr^2}{\gamma}$, influences the system. We already know from the Sect. 2.3, under eutrophic condition ($\mathcal{H}$), F has no upper bounds. Now, under the same biologically reasonable condition ($\mathcal{H}$), we found that, there is a critical value for the predation rate of fish on herbivorous zooplankton, F^*, the equilibrium state E^* is locally asymptotically stable when $F \geq F^*$ no matter what the maturation period of herbivorous zooplankton τ is, while the equilibrium E^* will be unstable or the system will oscillate when $0 < F < F^*$ and $\tau > \tau^*$. Ecologically, the predation of fish on zooplankton must be great enough to keep the plankton ecosystem stable at the equilibrium without influence of life cycle of herbivorous zooplankton. This seems to counter intuitive, since the predation of fish on zooplankton will reduce the density of herbivorous zooplankton and the equilibrium density of herbivorous zooplankton is decreasing as the predation rate of fish increases (see Sect. 2.3), and so it may increase a collapsibility of herbivorous zooplankton population. However, under the eutrophic condition ($\mathcal{H}$), the plankton ecosystem is still able to maintain its equilibrium state. The ecological implication is that, under the eutrophic condition and the fish predation rate is below the critical value, increasing the fish predation delays occurrence of oscillations. However, the system will be in the coexistent equilibrium when the fish predation rate is above the critical value. This means that the fish predation damps oscillations. This conclusion is consistent with that planktivorous fish tends to damp zooplankton-phytoplankton oscillation in the early study (Scheffer 1991).

When the predation rate of fish on herbivorous zooplankton is satisfied $0 < F < F^*$, the maturation period of herbivorous zooplankton comes to effect on the dynamics of the plankton ecosystem. We found that there is a critical length for the maturation period of herbivorous zooplankton, τ^* for each F. When the maturation period τ is
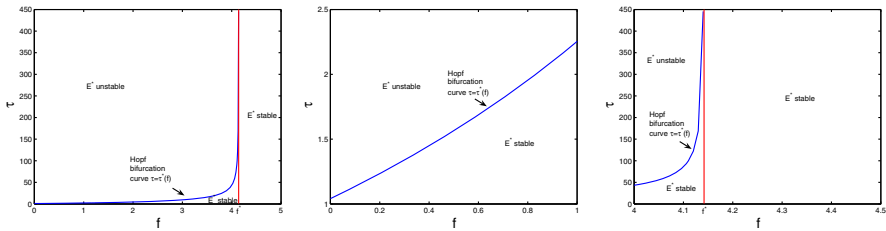
Fig. 2 Bifurcation diagram in the space of parameters: scaled fish predation rate f on zooplankton and the critical length τ^* of the maturation period of herbivorous zooplankton. The second and third plot are a part of the first one zoomed in. The parameter values are taken as $a = 0.5, b = 2, c = 1, d = 2.5, D = 2$ and $f^* = 4.1418$

smaller than τ^*, the equilibrium state E^* is still locally asymptotical stable; when the maturation period τ is greater than τ^*, the equilibrium state E^* is unstable. Around the equilibrium point E^*, the system undergoes a Hopf bifurcation. That is, the model system oscillates, and it has periodical solutions. The plankton ecosystem has been studied experimentally and theoretically for a long period of time. It has been established that the predator–prey mechanism is a major cause of plankton oscillation (Mccauley and Murdoch 1987; Scheffer 1991). However, the predator–prey mechanism is largely caused by life cycles of plankton (phytoplankton and zooplankton), while life cycles of plankton go with or are controlled by the annual seasonality. The seasonal growth of phytoplankton causes growth of herbivorous zooplankton; the growth of herbivorous zooplankton influence back on phytoplankton while predation of fish on zooplankton also impacts the plankton system. It is biologically obvious that, if the growth period of herbivorous zooplankton is too long, say exceeding one year, there would be no oscillation at all; if the growth period of herbivorous zooplankton is too short comparing with the growth period of phytoplankton (which is not included in this study), it is also difficult to expect population oscillations. From the literatures, we know that some zooplankton have a life cycle of 200 days while some phytoplankton has a life cycle of 6 days (Larsson 1978; Allan 1976; Dasson and Montresor 2011; Meadows and Campbell 1988). The annual seasonality is reflected in the life cycle of zooplankton. So, we may conclude that the maturation period of herbivorous zooplankton plays a major role in the oscillation of the plankton ecosystem.

We are also curious about how the predation rate of fish on zooplankton is related to the critical length of the maturation period of herbivorous zooplankton τ^*, although we know there is an abstract functional relation. However, an analytical relation between these two parameters is difficult to obtain. To demonstrate, we produce some numerical plots as the bifurcation curve in the parameter space as shown in Fig. 2.

From the plots in Fig. 2, we get some qualitative view that, the critical length τ^* of the maturation period of herbivorous zooplankton is increasing as f increases. We also obtain that there is a critical value f^* of f, which corresponds to F^*, that τ^* will increase indefinitely when f approaches f^*. When f is greater than f^*, E^* is stable. So, the influence of the fish predation upon zooplankton on the plankton ecosystem is complex. We may say that within certain range the fish predation would delay the occurrence of oscillations.
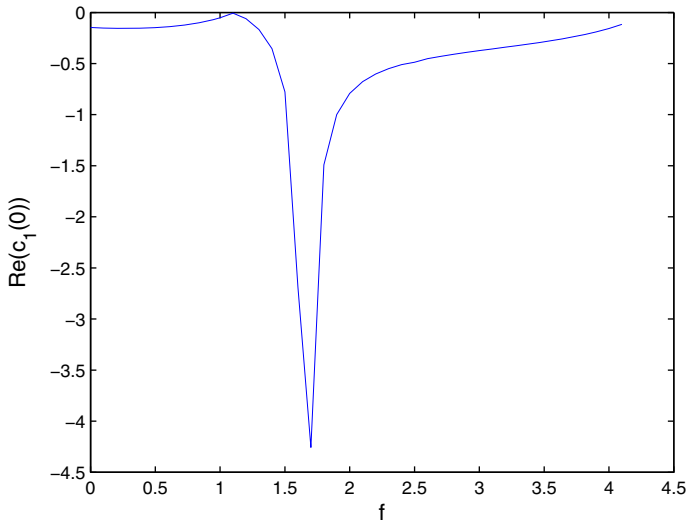
Fig. 3 The relation between the predation rate f of fish on herbivorous zooplankton and the real part of $c_1(0)$, where $a = 0.5, b = 2, c = 1, d = 2.5, D = 2$

It is interesting to know how the predation of fish on herbivorous zooplankton affects the stability of oscillation in the plankton system (1). In the previous subsection, we did the calculation about the properties of the Hopf bifurcations. But, the analytical formulas are difficult to reach. We conduct some numerical computation as shown in Fig. 3. From Fig. 3, we see that $\text{Re}(c_1(0)) < 0$ with the choices of the parameter values. That means that the Hopf bifurcation occurs just after the critical value τ^* (supercritical), and the oscillations as periodic solutions are orbitally stable. The predation of fish on herbivorous zooplankton does not influence the stability of the oscillations, and also does not change the direction of the Hopf bifurcations.
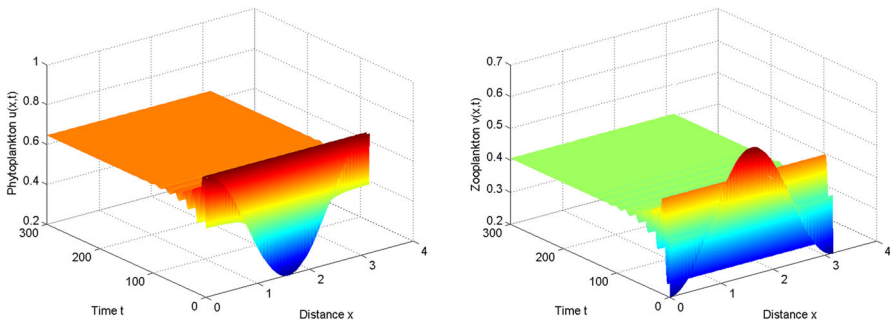
4 Numerical Simulations

To demonstrate our analytical results, we conduct some numerical simulations in this section.

Example 1 Taking $a = 2, b = 2, f = 8, c = 0.8, d = 2.5, D = 2, \tau = 1$ such that $h = -0.1333 < 0$. For this set of parameter values we observe that $h < 0$ and the boundary equilibrium $E_1(1, 0)$ of (2) is globally asymptotically stable(see Fig. 4). In the numerical simulations for Fig. 4, the initial conditions are $u(x, t) = 1 - 0.2 \cos 2x, v(x, t) = 0.01 + 0.01 \cos x, (x, t) \in [0, \pi] \times [-\tau, 0]$.

Example 2 If we choose $a = 0.5, b = 2, f = 2, c = 1, d = 2.5, D = 2$ such that the condition $(\mathcal{H})$ holds. Then we get that system (2) exits a unique positive equilibrium $E^*(0.6451, 0.4064)$ and E^* is asymptotically stable for $\tau = 0$. From calculation, we find $f^* = 4.1418$ and only for $n = 0$ equation (17) has positive roots, and
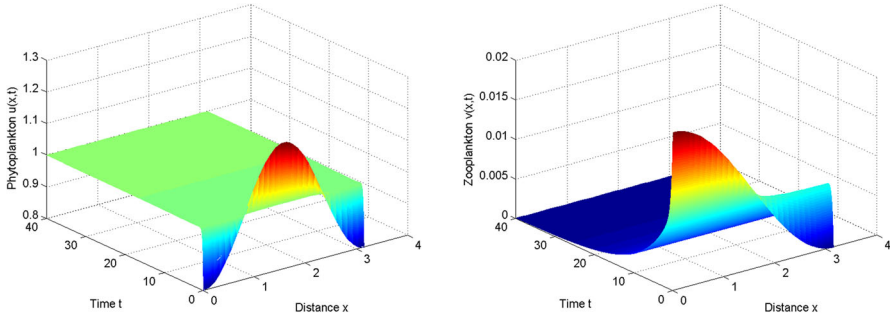
Fig. 4 Numerical simulations of the system (2) for $a = 2, b = 2, f = 8, c = 0.8, d = 2.5, D = 2, \tau = 1$. The boundary equilibrium $E_1(1, 0)$ of (2) is asymptotically stable
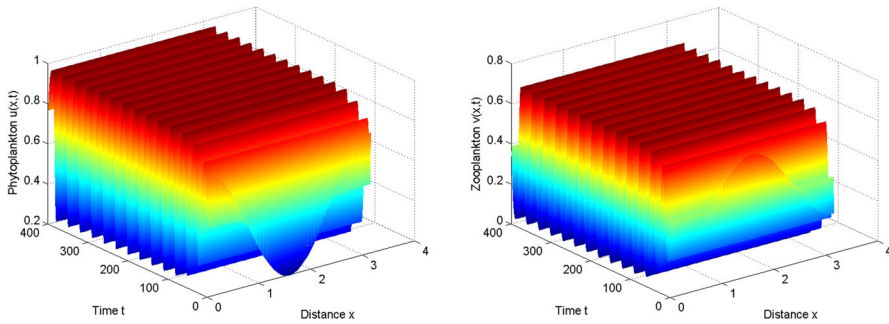

Fig. 5 Numerical simulations of system (2) for $a = 0.5, b = 2, f = 2, c = 1, d = 2.5, D = 2$ and $\tau = 3 < \tau^*$. The positive equilibrium $E^*(0.6451, 0.4064)$ of (2) is asymptotically stable

$$\tau_0^j \approx 4.4896 + 20.8288 j, \text{ for } j \in \mathbb{N}_0.$$

So, $\tau^* = \tau_0^0 \approx 4.4896$. From Theorem 3.2, we know that the equilibrium point E^* of system (2) is locally asymptotically stable for $0 \leq \tau < \tau^*$ (see Fig. 5), the equilibrium point $E^*(u^*, v^*)$ is unstable for $\tau > \tau^*$, and system (2) undergoes Hopf bifurcation at the equilibrium E^* when $\tau = \tau_0^j$ for $j \in \mathbb{N}_0$. By the formulas derived in previous section, we get $c_1(0) \approx -0.7918 + 0.0810i$. Because $\text{Re}(c_1(0)) \approx -0.7918 < 0$, so we know that when $\tau > \tau^*$, there exits orbitally stable periodic solutions (see Fig. 6). In the numerical simulations for Figs. 5 and 6, the initial conditions are $u(x, t) = 0.5 + 0.3 \cos 2x, \ v(x, t) = 0.4 - 0.2 \cos 2x, (x, t) \in [0, \pi] \times [-\tau, 0]$.

5 Conclusions and Discussion

We revisited the minimal model proposed by Scheffer (1991) with extensions – spatial diffusion of both phytoplankton and herbivorous zooplankton and the delay of zooplankton maturation period. Since our focus is effects of zooplankton maturation period on the dynamics of plankton systems, we only study the case of spatial dimension 1 for spatial diffusion. However, the results about delay effects should be valid

Fig. 6 Numerical simulations of system (2) for $a = 0.5, b = 2, f = 2, c = 1, d = 2.5, D = 2$ and $\tau = 6 > \tau^*$. The positive equilibrium $E^*(0.6451, 0.4064)$ of (2) is unstable and there exist stable spatially homogeneous periodic solutions

for spatial dimension 2 or higher. The dynamics picture of the plankton system we obtained is as follows. When the nutrient level is sufficient low such that the maximal per capita growth rate $e\gamma \frac{w}{H_p + w}$ of herbivorous zooplankton is less than its death rate δ, that is, the parameter h, a scaled maximal net growth rate of herbivorous zooplankton, is negative, herbivorous zooplankton will collapse and then phytoplankton population will grow into its carrying capacity. Mathematically, the boundary equilibrium is globally stable. When the nutrient level increases so that $h > 0$, and other two conditions that nutrients is not too high and the half-saturation rate is not too fast, forming an eutrophic condition $(\mathcal{H})$, are satisfied, the system has a unique coexistent homogeneous equilibrium E^*. The equilibrium density of phytoplankton increases, while the equilibrium density of herbivorous zooplankton decreases as the fish predation rate is increasing. However, the system will never collapses under the eutrophic condition unless the fish predation rate approaches infinite. This is one of new phenomena we derived. For the fish predation rate, we find a critical value F^*, the coexistent equilibrium is locally asymptotical stable when the fish predation rate is above F^*. When the fish predation rate is below this critical value, the coexistent equilibrium may stable or unstable or the system oscillates, which depends on the delay parameter τ. It means that fish predation damps oscillations. This functional relation of two biological significant parameters is also a new phenomenon we obtained.

Comparing with the study in Scheffer (1991), we not only largely enhance its conclusions in more mathematical ways under a broader setting where spatial diffusion and maturation delays are counted, but also obtain new dynamical patterns. We see that under eutrophic conditions (or the condition $(\mathcal{H})$), the gradual change of fish density (represented by the predation rate of fish on zooplankton F) leads the system to switch its dynamical behaviors. We concluded that planktivorous fish is one of major players who change the dynamical patterns of plankton systems. In addition, phytoplankton–zooplankton oscillations are largely attributed to the predator–prey mechanism. However, we argue that the phytoplankton–zooplankton oscillations originate from the annually seasonal changes which is represented as the maturation period of herbivorous zooplankton (see Sect. 3.3). We may conclude that oscillations are mainly caused by maturation periods of zooplankton in plankton ecosystems.

A review of field or experimental data would be important for the mathematical analysis to be verified, although our focus in this study is to explore the new dynamical patterns induced by the delay of the maturation period of zooplankton in the extended minimal model. We will leave the data review and verification and the following possible improvements as our future studies. We know that phytoplankton also need time to be mature and their maturation period have different lengthes. We will consider to include two delay parameters for both phytoplankton and zooplankton in the minimal model for further study. It is known that there are many fish that feed on both phytoplankton and zooplankton. We will also consider to build this fact into the minimal model in the future.

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