

## Pattern Formation and Synchronism in an Allelopathic Plankton Model with Delay in a Network\*

Canrong Tian<sup>†</sup> and Shigui Ruan<sup>‡</sup>

**Abstract.** A network is introduced to describe the spatiotemporal dynamics of two-species competitive and allelopathic plankton models, where the network structure represents the movement directions between every two patches. Time delay is also incorporated to describe the time required to produce stimulatory effect of one species on the growth of the other species. The model is described by a system of discrete-space and continuous-time equations with time delay in a network. Using the time delay as a bifurcation parameter, it is shown that a Hopf bifurcation occurs in the system. The stability of the Hopf bifurcation is also considered by applying the center manifold theory. Numerical simulations reveal that the stability of Hopf bifurcation leads to the emergence of planktonic blooms. Moreover, it is found that the network structure can switch the types of spatiotemporal patterns, a new feature observed only in delay differential equations with network structure.

**Key words.** pattern formation, Hopf bifurcation, network

**AMS subject classifications.** 34C23, 35B36, 92C15

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**1. Introduction.** Plankton refer to floating organisms of different sorts of phyla living in pelagic sea, freshwater lakes, or large rivers (Sommer [39], Baretta-Bekker, Duursma, and Kuipers [4], Fasham [11]). Plankton is one of the most important components of marine ecosystems. They not only compose the basis of all aquatic food chains but also carry out very useful services by providing oxygen and absorbing carbohydrates to human life (Duinker and Wefer [9]). Seasonal succession phenomenon is widely observed because the increased population of one species might affect the population growth of another species by producing allelopathic toxin stimulators (Rice [30]). There have been many examples for two plankton species competing over resources and stimulating each other's growth at the same time. For instance, Berglund [5] noted that the green alga, *Enteromorpha linza*, produces substances stimulatory to the growth of *Enteromorpha* species; Monahan and Trainor [25] also found that the green alga *Hormotila blemista* stimulated its own growth and also stimulated one strain of *Scenedesmus*. Folt and Goldman [12] reported that the filtering rate of the copepod *Diaptomus tyrrelli* is reduced in the presence of its potential competitor, *Epischura nevadensis*, by as much as 60% caused by a chemical released into the water by *Epischura*.

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<sup>†</sup>Department of Basic Sciences, Yancheng Institute of Technology, Yancheng, Jiangsu 224002 ([tiancanrong@163.com](mailto:tiancanrong@163.com)).

<sup>‡</sup>Department of Mathematics, University of Miami, Coral Gables, FL 33146 ([ruan@math.miami.edu](mailto:ruan@math.miami.edu)).

Since the production of allelopathic substance is not instantaneous but mediated by some time lag required for maturity, it is reasonable to take account of the effect of time delay when the interplay between the two allelopathic substances is investigated. By incorporating the allelopathic interaction into the classical Lotka–Volterra competition model, Mukhopadhyay, Chattopadhyay, and Tapaswi [26] proposed the following delay differential equations (DDEs),

$$(1.1) \quad \begin{aligned} \frac{du}{dt} &= u(t)(a_1 - b_{11}u(t) - b_{12}v(t) + e_1u(t)v(t)), \\ \frac{dv}{dt} &= v(t)(a_2 - b_{21}u(t) - b_{22}v(t) + e_2u(t - \tau)v(t)), \end{aligned}$$

where  $u(t)$  and  $v(t)$  are the densities of the two competitive and allelopathic plankton populations at time  $t$ ;  $a_1$  and  $a_2$  are the proliferation rates,  $b_{11}$  and  $b_{22}$  are the intraspecific competition rates,  $b_{12}$  and  $b_{21}$  are the interspecific competition rates of these two species, respectively;  $e_i$  ( $i = 1, 2$ ) is the stimulatory rate of species  $i$  by the other species;  $\tau$  is the time required to produce stimulatory effect of the first species on the growth of the second species. It was shown in [26] that system (1.1) has a stable limit cycle when the time delay takes some critical value. The periodicity of limit cycles gives rise to an regular pattern, which can interpret the scenario of seasonal succession in nature.

In addition to inducing seasonal successions, the allelopathic interaction can also cause planktonic blooms (Smetacek [37]). Planktonic blooms are the occurrence of a rapid increase or accumulation in the population, which cause the large amounts of carbon in the oceans. In view of the field observations in Abbott [1] and Fasham [11], the bloom phenomenon can be seen as a spatially heterogeneous solution where the population evolve with space and time. Spatial heterogeneity of plankton densities is called “patchiness” (for a review, see Malchow et al. [22], Medvinsky et al. [23], and Okubo and Levin [27]). In the marine environment, owing to strong water current, plankton populations move both horizontally and vertically. Therefore, diffusion plays an important role in the modeling of aquatic ecosystems. Steele [41] and Sjoberge [36] studied the effects of diffusion on plankton dynamics. Taking the diffusion of the plankton populations into consideration, Tian [43] generalized (1.1) to the following reaction-diffusion equations with delay:

$$(1.2) \quad \begin{aligned} \frac{\partial u}{\partial t} - D_u \Delta u &= u(t, x)(a_1 - b_{11}u(t, x) - b_{12}v(t, x) + e_1u(t, x)v(t, x)), \\ \frac{\partial v}{\partial t} - D_v \Delta v &= v(t, x)(a_2 - b_{21}u(t, x) - b_{22}v(t, x) + e_2u(t - \tau, x)v(t, x)), \end{aligned}$$

where  $u(t, x)$  and  $v(t, x)$  are the densities of the two competitive and allelopathic plankton populations at time  $t$  and location  $x \in \Omega$ ,  $\Delta$  denotes the Laplacian operator, which describes the diffusion of the plankton population under the assumption that individuals of the plankton population are performing a Brownian random walk. It is easy to see that the population flux is proportional to the gradient concentration.  $D_u$  and  $D_v$  are the diffusive coefficients of the two plankton species, respectively. System (1.2) has been shown to have a Hopf bifurcation when the time delay is chosen as a bifurcation parameter. Owing to the onset of Hopf bifurcation, if the initial data is an inhomogeneous perturbation, system (1.2) admits a spatially inhomogeneous and temporally quasiperiodic solution. This solution has been shown (Tian and Zhang [44]) to induce regular spiral waves.

The diffusion in system (1.2) is a depiction of the standard Brownian motion; i.e., nearest jumps for individuals of the plankton population are characterized by the fact that both waiting time distribution and jump size distribution must have finite moments. However, the individuals of the plankton population do not necessarily always execute the nearest jumps, but instead they can wait between successive jumps and perform long jumps (Viswanathan et al. [46]). When the conditions of finite moments in the distributions of waiting time and jump size are not met, plankton undergoes anomalous diffusion. In order to take account of the anomalous diffusion of plankton, we propose a network structured type of plankton movement to study an analogous system in discrete space and continuous time, where each node of network owns the homogeneous densities of a small plankton community. The motion between different nodes depends upon the topological network structure, because instead of moving to the nearby regions some marine organisms may move directly to faraway regions owing to the affection of ocean currents (Schmitt and Seuront [33], Toner, Tu, and Ramaswamy [45], Viswanathan et al. [46]).

For a classical Lotka–Volterra competition model, Liao and Lou [21] investigated the long time behavior of the solutions for two different connected habitats. In a similar way for a mosquito population model, Gourley and Ruan [14] divided the whole mosquito community into several patches where in each patch the mosquitoes form a small community, and each small community has completely different competitive interactions. Inspired by these approaches, we introduce a network into the plankton population dynamics, where each node of the network owns the homogeneous densities of a small plankton community. Thus, we propose the following two-species competitive and allelopathic plankton model with time delay in a network:

$$\begin{aligned} \dot{u}_i(t) &= u_i(t)(a_1 - b_{11}u_i(t) - b_{12}v_i(t) + e_1u_i(t)v_i(t - \tau)) + D_u \sum_{j=1}^n L_{ij}u_j(t), \\ (1.3) \quad \dot{v}_i(t) &= v_i(t)(a_2 - b_{21}u_i(t) - b_{22}v_i(t) + e_2u_i(t)v_i(t)) + D_v \sum_{j=1}^n L_{ij}v_j(t), \quad \forall i = 1, 2, \dots, n. \end{aligned}$$

In system (1.3), we assume that the allelopathic interplay follows two principles. First the toxin stimulator of one species is dependent on the density of the other species so that the allelopathic effect is zero when either species is absent. Hence, we describe it by the term  $e_1u_i(t)v_i(t)$ . Second the production of the toxin stimulator is not instantaneous but mediated by some time lag required for maturity. Hence, the term is described by  $e_2u_i(t - \tau)v_i(t)$ . Here the time-dependent densities of the two competitive species locating in node  $i$  are denoted by  $u_i(t)$  and  $v_i(t)$ , respectively.  $a_1$  and  $a_2$  are the rates of cell proliferation per unit time of the first and the second species, respectively, while  $b_{11}$  and  $b_{22}$  are the rates of intraspecific competition among the first and the second species, respectively;  $b_{12}$  and  $b_{21}$  are the rates of interspecific competition of the first and the second species, respectively;  $\frac{a_i}{b_{ii}}$  ( $i = 1, 2$ ) are environmental carrying capacities (representing the number of cells per liter);  $e_1$  and  $e_2$  are the rates of allelopathic stimulation of the first species by the second and vice versa;  $\tau$  is a positive constant representing that the production of allelopathic substance by the competitive species will not be instantaneous but mediated by some time lag required for maturity of the species.

In order to ensure the ecological meaning, we consider system (1.3) under the following initial conditions:

$$(1.4) \quad \begin{aligned} &0 \leq v_i(\zeta) \leq \frac{b_{11}}{e_1} \text{ is continuous on } -\tau \leq \zeta \leq 0, \text{ and } v_i(0) > 0, \\ &0 < u_i(0) \leq \frac{b_{22}}{e_2}. \end{aligned}$$

By using the existence theorem (Theorem 3.1 of [38]) of DDEs, we know that system (1.3) has a global solution except for the blow-up case. By using the Method of Steps (section 3.1 of [38]), the initial condition (1.4) ensures that the solution of system (1.3) has a uniform upper bound. Thus no blow-up occurs.

This plankton model is defined on an undirected network with  $n$  nodes and no self-loops. The direction motion of every patch is described by the adjacent matrix of the network,  $G$ , and  $k_i = \sum_{j=1}^n G_{ij}$  denotes the degree of the  $i$ th node. The Laplacian matrix  $L$  of the network is defined by  $L_{ij} = G_{ij} - k_i \delta_{ij}$ , where  $\delta_{ij}$  is a Dirac delta function. Hence,  $L_{ij}$  ( $i \neq j$ ) means the interspecific dispersal direction: when  $L_{ij} = 1$ , it means that there exists a routine such that species moves from patch  $i$  to patch  $j$ , where the disperse speeds of the two species are positive constants  $D_u$  and  $D_v$ , respectively; when  $L_{ij} = 0$ , it means that there exists no such routine from patch  $i$  to patch  $j$ .

We would like to mention that patch or lattice structure has been used to model competition for resource, including the effect of allelopathy. For example, Atkinson and Shorrocks [3] and Ives and May [19] studied models for two species competing for use of a patchy and ephemeral resource and found that an inferior competitor may persist if the superior competitor clumps or aggregates. Durrett and Levin [10] showed that in a spatially structured population of *Escherichia coli*, both colicin-producing and colicin-sensitive strains can coexist and the competition outcome is determined by the effectiveness of allelopathy. Iwasa, Nakamaru, and Levin [20] analyzed a lattice version of the Durrett–Levin model based on pair approximation (forming a system of ODEs of global and local densities) and found that there is a relatively narrow parameter region of bistability which disappears when the model is considered on a lattice of infinitely large size. Our network population dynamical model can be regarded as a generalization of the patch structure models, but there are some differences. Most analytic studies on patch structure models focus on only two patches (see for example Liao and Lou [21]), while in our network structure model (1.3) there are more than two habitats described by the nodes of the species. Most patch structure models deal with neighborhood patches (see for example Durrett and Levin [10]), while in our network structure model (1.3) each two nodes do not necessarily have the edges of direct connection where the mechanism of connection is dependent on the probability. Hence the network structure belongs to the complex network, just as the examples of numerical simulations on the small-world network and free-scale network in section 4 show. Moreover, the network structure plays an important role in the pattern formation of spatial-temporal solutions. Our examples in section 4 illustrate that when the average degree is small (i.e., the number of edges is small) the steady state solution is spatially inhomogeneous; when the average degree is large (i.e., the number of edges is large) the steady state solution is spatially homogeneous, which is similar to the behavior of ODEs. Finally, in a finite patch model the long distance movement is less

important, in particular if the primary goal is to understand the long term effects of local dispersal and patch geometry on population dynamics, while the network model (1.3) involves both long and local dispersals. Furthermore, patch models treat local population dynamics implicitly in terms of presence or absence of populations, while we will study the nonlinear dynamics of the network model (1.3).

Our main goal is to study Hopf bifurcation of the model caused by the instability of the positive equilibrium, which consequently induces self-organized spatiotemporal patterns. The effects of time delay were first considered in predator-prey systems by Volterra [47] who showed that under certain conditions the spatial distributions possess a certain oscillatory behavior. Recently there are some investigations about the delay-driven spatial patterns in various systems (Bertram and Mikhailov [6], Beta et al. [7], Boccaletti et al. [8], Mikhailov and Showalter [24], Sen et al. [34], Yan and Li [50], Shi, Shi, and Song [35], Song et al. [40]). Moreover, experimentally delayed feedback has been introduced in Grill, Zykov, and Müller [15] to induce spiral waves. In this paper, a profound distinction from the above studies lies in that our system evolves on a discrete domain, i.e., a network. That is, all the interactions between the plankton take place in every discrete node with all the nodes linked up with no self-loops and directions. Delayed network has been recently investigated by Petit et al. [29] who studied a delayed reaction-diffusion equation on a complex network and showed that, even with one single species, Turing-like traveling waves can emerge but never stationary patterns. This result improves the classical ones by Turing mechanism where at least two species are necessary to generate Turing patterns. Petit et al. [28] further showed that the complex network composed with a two-component delayed reaction-diffusion system can also generate Turing patterns due to the interaction between the time delay and the diffusion. The joint effects of diffusion and time delay on the nonlinear dynamics of reaction-diffusion equations with delay were studied in Haderl and Ruan [17]. For the fundamental, stability, and bifurcation theories of partial differential equations with delay, we refer to the monograph of Wu [49].

We will study how many types of regular spatiotemporal patterns there are when system (1.3) generates self-organization patterns, and which factors can shift the pattern transition between different patterns. Note that the DDE model (1.1) possesses periodic solutions, which means that it has synchronism, and the PDE model (1.2) possesses spatially inhomogeneous and temporally quasiperiodic solutions, which means that it loses synchronism when the diffusion is included. Thus, we also aim to study whether the network system has synchronism; namely, temporally periodic solutions. Hopf bifurcation analysis is an effective approach to achieve this goal. But quasiperiodic solutions driven by the loss of stability for periodic solutions usually occur in codimension-two Hopf bifurcations. We think that the network structure may induce quasiperiodic solutions corresponding to the loss of synchronism and apply the method of numerical computation to study the effect of network structure on synchronism. The Hopf bifurcation analysis in such a discrete-space and continuous-time model with time delay is new, and the temporally oscillatory modes in the competitive plankton species can be used to explain the plankton bloom phenomenon. We also find that system (1.3) has both temporally homogeneous periodic solutions and spatially inhomogeneous and temporally quasiperiodic solutions, a new feature that the DDE model (1.1) and the delay reaction-diffusion equation model (1.2) do not have.

The paper is structured as follows. In section 2 we first carry out the linear analysis for the two-component discrete-space and continuous-time system with time delay in a network, then study local stability of the coexistent equilibrium and the existence of Hopf bifurcation. In section 3, the center manifold theory is applied to study the stability and direction of the Hopf bifurcation. In section 4 we perform some numerical simulations to illustrate that the effect of network structure can switch the pattern transition and synchronism. The paper ends with some ecological explanations of our analytical findings and numerical simulations.

**2. Spatiotemporal pattern induced by Hopf bifurcation.** In this section we show that system (1.3) without time delay does not generate any spatial pattern but can create spatial patterns when time delay is present.

The problem (1.3) has four homogeneous equilibria: three boundary equilibria  $(0, 0)$ ,  $(\frac{a_1}{b_{11}}, 0)$ ,  $(0, \frac{a_2}{b_{22}})$  and an interior equilibrium  $(\hat{u}, \hat{v})$  (coexistent equilibrium), where

$$\hat{u} = \left( -q_{12} - \sqrt{q_{12}^2 - 4p_{12}r_{12}/2p_{12}} \right), \quad \hat{v} = \left( -q_{21} - \sqrt{q_{21}^2 - 4p_{21}r_{21}/2p_{21}} \right),$$

$$p_{ij} = -b_{ij}e_i + b_{ii}e_j, \quad q_{ij} = -a_ie_j + a_j e_i - b_{ii}b_{jj} + b_{ij}b_{ji}, \quad r_{ij} = a_ib_{jj} - a_j b_{ij}.$$

The interior equilibrium  $(\hat{u}, \hat{v})$  exists if and only if

$$(2.1) \quad \frac{e_1}{e_2} < \frac{b_{12}}{b_{22}} < \frac{a_1}{a_2} < \frac{b_{11}}{b_{21}} \quad \text{and} \quad a_2 e_1 + b_{12} b_{21} < a_1 e_2 + b_{11} b_{22},$$

or

$$(2.2) \quad \frac{b_{12}}{b_{22}} < \frac{a_1}{a_2} < \frac{b_{11}}{b_{21}} < \frac{e_1}{e_2} \quad \text{and} \quad a_1 e_2 + b_{12} b_{21} < a_2 e_1 + b_{11} b_{22}.$$

The above conditions ensure that  $(\hat{u}, \hat{v})$  is in the biologically meaningful region  $u_i > 0, v_i > 0$ .

It is easy to see that the equilibrium of total extinction  $(0, 0)$  is a saddle point. The boundary equilibrium  $(\frac{a_1}{b_{11}}, 0)$  is a saddle point if  $\frac{a_1}{a_2} \geq \frac{b_{11}}{b_{21}}$  and a stable node otherwise. The other boundary equilibrium  $(0, \frac{a_2}{b_{22}})$  is a saddle point if  $\frac{a_2}{a_1} \geq \frac{b_{22}}{b_{12}}$  and a stable node otherwise. The interior equilibrium  $(\hat{u}, \hat{v})$  exists if and only if (2.1) or (2.2) holds. From the biological perspective, we are interested in studying the stability behavior of the coexistent equilibrium, i.e., the interior equilibrium  $(\hat{u}, \hat{v})$ .

Now, we conduct the linear stability analysis of (1.3) with respect to the homogeneous equilibrium. Let us denote by  $(u_i, v_i)_{1 \leq i \leq n} = (\hat{u}, \hat{v})$  the homogeneous equilibrium. In order to determine its stability we translate the equilibrium  $(\hat{u}, \hat{v})$  to the origin via defining the small perturbations  $\delta u_i = u_i - \hat{u}$ ,  $\delta v_i = v_i - \hat{v}$ . The linearized system of (1.3) around the equilibrium can be therefore expressed by

$$(2.3) \quad \begin{pmatrix} \delta \dot{u}_i \\ \delta \dot{v}_i \end{pmatrix} = \mathbf{J}_1 \begin{pmatrix} \delta u_i \\ \delta v_i \end{pmatrix} + \mathbf{J}_2 \begin{pmatrix} \delta u_{i,\tau} \\ \delta v_i \end{pmatrix} + \mathbf{D} \begin{pmatrix} \sum_{j=1}^n L_{ij} \delta u_j \\ \sum_{j=1}^n L_{ij} \delta v_j \end{pmatrix},$$

where  $\delta u_{i,\tau} = \delta u_i(t - \tau)$ , and

$$(2.4) \quad \mathbf{J}_1 = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \quad \mathbf{J}_2 = \begin{pmatrix} 0 & a_{13} \\ 0 & 0 \end{pmatrix}, \quad \mathbf{D} = \begin{pmatrix} D_u & 0 \\ 0 & D_v \end{pmatrix}.$$

Here  $a_{11} = -\hat{u}(b_{11} - e_1 \hat{v})$ ,  $a_{12} = -b_{12} \hat{u}$ ,  $a_{21} = \hat{v}(-b_{21} + e_2 \hat{v})$ ,  $a_{22} = -\hat{v}(b_{22} - e_2 \hat{u})$ ,  $a_{13} = \hat{u}^2 e_1$ .

For the diffusional network system (2.3), we use the same notation as that in Petit et al. [28] to deal with the Laplacian matrix. Let  $0 = \Lambda^1 > \Lambda^2 > \dots > \Lambda^n$  be the eigenvalues of the Laplacian matrix  $L$ , and the eigenbasis  $\{\Phi^\alpha : \alpha = 1, 2, \dots, n\}$  being each eigenvector associated to a topological eigenvalue  $\Lambda^\alpha$ . For any small perturbation  $(\delta u_i(t), \delta v_i(t))^T$  ( $T$  denotes the transpose) from the equilibrium, we have the following basis decomposition:

$$(2.5) \quad \begin{pmatrix} \delta u_i(t) \\ \delta v_i(t) \end{pmatrix} = \sum_{\alpha=1}^n \begin{pmatrix} c_1^\alpha \\ c_2^\alpha \end{pmatrix} e^{\lambda_\alpha t} \Phi_i^\alpha, \quad (i = 1, 2, \dots, n).$$

Inserting (2.5) into (2.3), noticing that  $\sum_{j=1}^n L_{ij} \Phi_j^\alpha = \Lambda^\alpha \Phi_i^\alpha$ , and using the orthogonality of the eigenvectors, we get for each mode  $\alpha$  ( $\alpha = 1, \dots, n$ ) that

$$\lambda_\alpha \begin{pmatrix} c_1^\alpha \\ c_2^\alpha \end{pmatrix} e^{\lambda_\alpha t} = \mathbf{J}_1 \begin{pmatrix} c_1^\alpha \\ c_2^\alpha \end{pmatrix} e^{\lambda_\alpha t} + \mathbf{J}_2 \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} e^{\lambda_\alpha(t-\tau)} + \Lambda^\alpha \mathbf{D} \begin{pmatrix} c_1^\alpha \\ c_2^\alpha \end{pmatrix} e^{\lambda_\alpha t}.$$

Hence we obtain the characteristic equation:

$$(2.6) \quad \Delta(\lambda_\alpha, \tau) = 0, \quad \text{where } \Delta(\lambda_\alpha, \tau) = \det \left( \lambda_\alpha \mathbf{I} - (\mathbf{J}_1 + e^{-\lambda_\alpha \tau} \mathbf{J}_2 + \Lambda^\alpha \mathbf{D}) \right).$$

Substituting (2.4) into (2.6), the characteristic equation of (1.3) becomes

$$(2.7) \quad \lambda_\alpha^2 + (-a_{11} - a_{22} - D_u \Lambda^\alpha - D_v \Lambda^\alpha) \lambda_\alpha + (a_{11} + D_u \Lambda^\alpha)(a_{22} + D_v \Lambda^\alpha) - a_{21}(a_{12} + a_{13} e^{-\lambda_\alpha \tau}) = 0.$$

After some direct computation, the characteristic equation of (1.3) is reduced to

$$(2.8) \quad \lambda_\alpha^2 + A_1 \lambda_\alpha + A_2 + A_3 e^{-\lambda_\alpha \tau} = 0,$$

where  $A_1 = -a_{11} - a_{22} - D_u \Lambda^\alpha - D_v \Lambda^\alpha$ ,  $A_2 = a_{11} a_{22} - a_{12} a_{21} + D_u D_v \Lambda^{2\alpha} + (a_{11} D_v + a_{22} D_u) \Lambda^\alpha$ ,  $A_3 = -a_{21} a_{13}$ .

By analyzing the characteristic equation (2.6) (Ruan [31]), we have the following results on the stability of the homogeneous steady state of system (1.3).

**Lemma 2.1.** *Suppose that (2.1) or (2.2) holds, and*

$$(2.9) \quad a_{11} + a_{22} < 0, \quad a_{21} a_{13} < a_{11} a_{22} - a_{12} a_{21} < -a_{21} a_{13},$$

where  $a_{11} = -\hat{u}(b_{11} - e_1 \hat{v})$ ,  $a_{12} = -\hat{u}(b_{12} - e_1 \hat{u})$ ,  $a_{21} = -\hat{v} b_{21}$ ,  $a_{22} = -\hat{v}(b_{22} - e_2 \hat{u})$ ,  $a_{13} = \hat{u}^2 e_1$ . Then

- (i) if the delay is absent, that is,  $\tau = 0$ , then all characteristic roots of (2.8) have negative real parts;
- (ii) if the delay is present, that is,  $\tau > 0$ , then the characteristic equation (2.8) has a pair of purely imaginary roots  $\pm i\omega^*$  at  $\tau = \tau_j$ , where

$$(2.10) \quad \omega^{*2} = \frac{1}{2} \left( 2A_2 - A_1^2 + \sqrt{A_1^4 - 4A_1^2 A_2 + 4A_3^2} \right)$$

and

$$(2.11) \quad \tau_j = \frac{1}{\omega^*} \left( 2j\pi + \arccos \left( \frac{\omega^{*2} - A_2}{A_3} \right) \right), \quad j = 0, 1, 2, \dots$$

Here  $A_1 = -a_{11} - a_{22} - D_u \Lambda^\alpha - D_v \Lambda^\alpha$ ,  $A_2 = a_{11}a_{22} - a_{12}a_{21} + D_u D_v \Lambda^{2\alpha} + (a_{11}D_v + a_{22}D_u)\Lambda^\alpha$ ,  $A_3 = -a_{21}a_{13}$ .

*Proof.* (i) We first consider the case  $\tau = 0$ . The characteristic equation (2.8) is reduced to

$$\lambda_\alpha^2 + (-a_{11} - a_{22} - D_u \Lambda^\alpha - D_v \Lambda^\alpha)\lambda_\alpha + A_2 + A_3 = 0.$$

In view of (2.9), we deduce that  $-a_{11} - a_{22} - D_u \Lambda^\alpha - D_v \Lambda^\alpha > 0$  and  $A_2 + A_3 > 0$ . Hence, the roots of characteristic equation (2.6) have negative real parts.

(ii) We let  $\pm i\omega$  be a pair of pure imaginary roots. Substituting  $\pm i\omega$  into characteristic equation (2.8) and separating real and imaginary parts, we have

$$(2.12) \quad \begin{aligned} -\omega^2 + A_2 + A_3 \cos \omega\tau &= 0, \\ A_1\omega - A_3 \sin \omega\tau &= 0, \end{aligned}$$

which lead to

$$\omega^4 + (A_1^2 - 2A_2)\omega^2 + A_2^2 - A_3^2 = 0.$$

The above equation has a unique positive real root  $\omega^{*2}$  if and only if  $A_2 < A_3$ , which is guaranteed by condition (2.9). Moreover, by solving the above equation, the expression of  $\omega^*$  is written in the form of (2.10). Hence, the corresponding  $\tau_j$  in (2.11) can be obtained by substituting (2.10) into (2.12). ■

**Theorem 2.2.** *Suppose that (2.1) or (2.2) is satisfied. If (2.9) holds, then system (1.3) is locally stable at equilibrium  $(\hat{u}, \hat{v})$  for  $\tau \in [0, \tau_0)$  and unstable for  $\tau \in [\tau_0, \infty)$ ; here  $\tau_0$  is given in (2.11). Moreover, system (1.3) undergoes a Hopf bifurcation at  $\tau = \tau_0$ . There exist a constant  $\sigma > 0$  and a smooth curve  $\lambda(\tau) : (\tau_0 - \sigma, \tau_0 + \sigma) \rightarrow \mathbb{C}$  such that  $\lambda(\tau_0) = i\omega^*$  and  $\Delta(i\omega^*, \tau_0) = 0$  for all  $\tau \in (\tau_0 - \sigma, \tau_0 + \sigma)$ .*

*Proof.* We use the similar argument as Theorem 3.6 in Ruan [31]. Since  $\tau_0$  is the smallest value such that characteristic equation (2.8) has a root with zero real part, we apply G.J. Butler's Lemma (see Appendix 2 in Freedman and Rao [13]) to obtain that the real parts of the characteristic roots are all negative for  $t \in [0, \tau_0)$ . Hence  $(\hat{u}, \hat{v})$  is locally stable for  $\tau \in [0, \tau_0)$ . We need to show the following transversality condition

$$(2.13) \quad \frac{d}{d\tau} \operatorname{Re} \lambda(\tau) |_{\tau=\tau_0} > 0.$$

Substituting a complex eigenvalue  $\lambda_\alpha = \mu + i\omega$  into (2.8) and separating real and imaginary parts, we have

$$(2.14) \quad \begin{aligned} \mu^2 - \omega^2 + A_1\mu + A_2 + A_3 e^{-\mu\tau} \cos \omega\tau &= 0, \\ 2\mu\omega + A_1\omega - A_3 e^{-\mu\tau} \sin \omega\tau &= 0. \end{aligned}$$



Differentiating (2.14) with respect  $\tau$ , we get

$$(2\mu + A_1 - A_3\tau e^{-\mu\tau} \cos \omega\tau) \frac{d\mu}{d\tau} - (2\omega + A_3\tau e^{-\mu\tau} \sin \omega\tau) \frac{d\omega}{d\tau} = A_3 e^{-\mu\tau} (\mu \cos \omega\tau + \omega \sin \omega\tau),$$

$$(2\omega + A_3\tau e^{-\mu\tau} \sin \omega\tau) \frac{d\mu}{d\tau} + (2\mu + A_1 - A_3\tau e^{-\mu\tau} \cos \omega\tau) \frac{d\omega}{d\tau} = A_3 e^{-\mu\tau} (\mu \sin \omega\tau + \omega \cos \omega\tau).$$

Eliminating terms involving  $\frac{d\omega}{d\tau}$  from the above equations, we have

$$\begin{aligned} & [(2\mu + A_1 - A_3\tau e^{-\mu\tau} \cos \omega\tau)^2 + (2\omega + A_3\tau e^{-\mu\tau} \sin \omega\tau)^2] \frac{d\mu}{d\tau} \\ &= A_3 e^{-\mu\tau} [(\mu \cos \omega\tau + \omega \sin \omega\tau)(2\mu + A_1 - A_3\tau e^{-\mu\tau} \cos \omega\tau) \\ &+ (\mu \sin \omega\tau + \omega \cos \omega\tau)(2\omega + A_3\tau e^{-\mu\tau} \sin \omega\tau)]. \end{aligned}$$

(2.15)

In view of some positive terms of (2.15), to show  $\frac{d\mu}{d\tau} > 0$ , it is sufficient to verify that

$$\begin{aligned} & (\mu \cos \omega\tau + \omega \sin \omega\tau)(2\mu + A_1 - A_3\tau e^{-\mu\tau} \cos \omega\tau) \\ &+ (\mu \sin \omega\tau + \omega \cos \omega\tau)(2\omega + A_3\tau e^{-\mu\tau} \sin \omega\tau) > 0. \end{aligned}$$

(2.16)

Now at  $\tau = \tau_0$ ,  $\mu = 0$ ,  $\omega = \omega^*$ , (2.14) becomes

$$\begin{aligned} & -\omega^{*2} + A_2 + A_3 \cos \omega^* \tau_0 = 0, \\ & A_1 \omega^* - A_3 \sin \omega^* \tau_0 = 0, \\ & \omega^{*4} + (A_1^2 - 2A_2)\omega^{*2} + A_2^2 - A_3^2 = 0, \end{aligned}$$

(2.17)

and (2.16) becomes

$$\omega^* \sin \omega^* \tau_0 (A_1 - A_3 \tau_0 \cos \omega^* \tau_0) + \omega^* \cos \omega^* \tau_0 (2\omega^* + A_3 \tau_0 \sin \omega^* \tau_0) > 0.$$

Simplifying the above inequality, we have to check

$$A_1 \omega^* \sin \omega^* \tau_0 + 2\omega^{*2} \cos \omega^* \tau_0 > 0.$$

(2.18)

Substituting the first and second equations of (2.17) into (2.18) yields

$$\frac{1}{A_3} A_1^2 \omega^{*2} - \frac{1}{A_3} [2\omega^{*2} (A_2 - 2\omega^{*2})] > 0.$$

(2.19)

Since  $A_3 > 0$ , we need only to verify that

$$2\omega^{*4} + (A_1^2 - 2A_2)\omega^{*2} > 0.$$

(2.20)

Substituting the third equation of (2.17) into (3.3), we only need to verify that

$$\omega^{*4} - A_2^2 + A_3^2 > 0.$$

(2.21)

The above inequality holds because  $0 < A_2 < A_3$ , which can be immediately deduced by (2.9). The conditions for Hopf bifurcation are then satisfied.

Moreover, by applying the implicit function theorem to  $\Delta(\lambda, \tau)$ , there exist a constant  $\sigma > 0$  and a smooth curve  $\lambda(\tau) : (\tau_0 - \sigma, \tau_0 + \sigma) \rightarrow \mathbb{C}$  such that  $\lambda(\tau_0) = i\omega^*$  and  $\Delta(i\omega^*, \tau_0) = 0$ .

Now by using Proposition 6.5 in [38], we obtain that  $(\hat{u}, \hat{v})$  is locally unstable for  $\tau \in [\tau_0, \infty)$ . ■

*Remark 2.3.* Planktonic blooms are the phenomena of the instability of the planktonic population. From Theorem 2.2, we can see that system (1.3) will undergo a Hopf bifurcation for  $\tau > \tau_0$  when the parameter restrictions of (2.1), (2.2), and (2.9) are satisfied. Hence our system (1.3) is able to exhibit the periodic nature of blooms. Hence, an increase of delay may destabilize a planktonic allelopathic ecosystem which ultimately gives rise to the bloom phenomenon.

**3. The stability of the Hopf bifurcation.** In Theorem 2.2, we obtained conditions under which a family of periodic solutions bifurcated from the interior equilibrium  $(\hat{u}, \hat{v})$  at critical values  $\tau_0$ . As pointed out in Hassard, Kazarinoff, and Wan [16], it is interesting and important to determine the direction, stability, and period of these periodic solutions. The method of Hassard, Kazarinoff, and Wan [16] has been applied to study delayed population dynamics (Ruan and Wolkowicz [32]), neural network dynamics (Wei and Ruan [48]), and has been developed to partial functional differential equations (Wu [49]) with applications to delayed reaction-diffusion population models (Su, Wei, and Shi [42], Yan and Li [50]). We will derive explicit formulas determining these factors at the critical value  $\tau_0$  using the center manifold theory and the normal form theory in Hassard, Kazarinoff, and Wan [16]. In this section, we always assume that (2.9) hold and  $\pm i\omega$  are the only purely imaginary roots, where  $\omega = \omega^*$ .

For the sake of convenience, let  $\tau = \tau_0 + \nu$ . Then  $\nu = 0$  is the Hopf bifurcation value for system (1.3). In order to simplify the Hopf bifurcation for  $(\hat{u}, \hat{v})$ , we can translate this equilibrium at the origin by performing a coordinate shift. We perform the change of variables  $u_i - \hat{u} = \bar{u}_i$ ,  $v_i - \hat{v} = \bar{v}_i$ . For ease of notation, we omit the bars of  $\bar{u}_i$  and  $\bar{v}_i$ . Thus we rewrite system (1.3) around the interior equilibrium in the form

$$\begin{aligned}\dot{u}_i(t) &= D_u \sum_{j=1}^n L_{ij} u_j(t) + a_{11} u_i(t) + a_{12} v_i(t) + a_{13} v_i(t - \tau) + (-b_{11} - e_1 \hat{v}) u_i^2(t) \\ &\quad + (-b_{12}) u_i(t) v_i(t) + (-2e_1 \hat{u}) u_i(t) v_i(t - \tau) + (-e_1) u_i^2(t) v_i(t - \tau), \\ \dot{v}_i(t) &= D_v \sum_{j=1}^n L_{ij} v_j(t) + a_{21} u_i(t) + a_{22} v_i(t) + (-b_{21} - 2e_2 \hat{v}) u_i(t) v_i(t) \\ &\quad + (-b_{22} - e_2 \hat{u}) v_i^2(t) + (-e_2) u_i(t) v_i^2(t).\end{aligned}$$

Since  $\pm i\omega^*$  are the only purely imaginary roots of the above linear operator, by using the orthogonality of the eigenvectors of  $L_{ij}$ , the above equations can be rewritten as

$$\begin{aligned}(3.1) \quad \dot{u}_i(t) &= D_u \Lambda^\alpha u_i(t) + a_{11} u_i(t) + a_{12} v_i(t) + a_{13} v_i(t - \tau) + (-b_{11} - e_1 \hat{v}) u_i^2(t) \\ &\quad + (-b_{12}) u_i(t) v_i(t) + (-2e_1 \hat{u}) u_i(t) v_i(t - \tau) + (-e_1) u_i^2(t) v_i(t - \tau), \\ \dot{v}_i(t) &= D_v \Lambda^\alpha v_i(t) + a_{21} u_i(t) + a_{22} v_i(t) + (-b_{21} - 2e_2 \hat{v}) u_i(t) v_i(t) \\ &\quad + (-b_{22} - e_2 \hat{u}) v_i^2(t) + (-e_2) u_i(t) v_i^2(t) \quad \forall i = 1, 2, \dots, n.\end{aligned}$$

We denote the solution of (3.1) as  $\mathbb{X}(t) = (u_i(t), v_i(t))^T$  and set  $\mathbb{X}_t(\theta) = \mathbb{X}(t + \theta)$ ,  $\theta \in [-\tau, 0]$ , where  $T$  denotes the transpose,  $\mathbb{X}_t \in C([-\tau, 0], \mathbb{R}^2) \triangleq \mathcal{C}$ . It can be verified that system (3.1) undergoes a Hopf bifurcation at the critical value  $\tau = 0$  in which the corresponding eigenvalues are  $\pm i\omega^*$ . We rewrite (3.1) as the following functional differential equation,

$$(3.2) \quad \dot{\mathbb{X}}_t = L_\nu(\mathbb{X}_t) + R_\nu(\mathbb{X}_t),$$

where  $L_\nu : \mathcal{C} \rightarrow \mathbb{R}^2$ ,  $R_\nu : \mathcal{C} \rightarrow \mathbb{R}^2$  are given by

$$L_\nu(\phi) = M_0 \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} + M_1 \begin{pmatrix} \phi_1(-\tau) \\ \phi_2(-\tau) \end{pmatrix},$$

$$M_0 = \begin{pmatrix} a_{11} + D_u \Lambda^\alpha & a_{12} \\ a_{21} & a_{22} + D_v \Lambda^\alpha \end{pmatrix}, \quad M_1 = \begin{pmatrix} 0 & a_{13} \\ 0 & 0 \end{pmatrix},$$

$$R_\nu(\phi) = \begin{pmatrix} (-b_{11} - e_1 \hat{v})\phi_1^2(0) + (-b_{12})\phi_1(0)\phi_2(0) + (-2e_1 \hat{u})\phi_1(0)\phi_2(-\tau) + (-e_1)\phi_1^2(0)\phi_2(-\tau) \\ (-b_{21} - 2e_2 \hat{v})\phi_1(0)\phi_2(0) + (-b_{22} - e_2 \hat{u})\phi_2^2(0) + (-e_2)\phi_1(0)\phi_2^2(0) \end{pmatrix}.$$

We can choose

$$(3.3) \quad \eta(\theta, \nu) = M_0 \delta(\theta) + M_1 \delta(\theta + \tau),$$

where  $\delta(\cdot)$  is the Dirac function. By using Riesz representation theorem, we have

$$(3.4) \quad L_\nu(\phi) = \int_{-\tau}^0 \phi(\theta) d\eta(\theta, \nu) \quad \text{for } \phi \in \mathcal{C},$$

where

$$d\eta(\theta, \nu) = M_0 \delta(\theta) d\theta + M_1 \delta(\theta + \tau) d\theta.$$

Next, we define two operators  $A_\nu$  and  $F_\nu$  on  $C^1([-\tau, 0], \mathbb{R}^2) \triangleq \mathcal{C}^1$  by

$$(3.5) \quad (A_\nu \phi)(\theta) = \begin{cases} \frac{d\phi}{d\theta}, & \theta \in [-\tau, 0), \\ \int_{-\tau}^0 \phi(\xi) d\eta(\xi, \nu), & \theta = 0; \end{cases}$$

$$(3.6) \quad (F_\nu \phi)(\theta) = \begin{cases} 0, & \theta \in [-\tau, 0), \\ R_\nu(\phi), & \theta = 0. \end{cases}$$

Then (3.2) is transformed into

$$(3.7) \quad \dot{\mathbb{X}}_t = A_\nu(\mathbb{X}_t) + F_\nu(\mathbb{X}_t).$$

Note that the adjoint operator  $A_\nu^*$  of  $A_\nu$  is defined as

$$(3.8) \quad (A_\nu^* \psi)(\theta^*) = \begin{cases} -\frac{d\psi}{d\theta^*}, & \theta^* \in (0, \tau], \\ \int_{-\tau}^0 \psi(-\xi) d\eta^T(\xi, \nu), & \theta^* = 0, \end{cases}$$

where  $\psi \in C^1([0, \tau], \mathbb{R}^2)$ . We choose the solution space of (3.7) as the complex space  $\mathbb{C}^2$  instead of merely  $\mathbb{R}^2$ . Define the following bilinear form

$$(3.9) \quad \langle \psi(\theta^*), \phi(\theta) \rangle = \bar{\psi}^T(0)\phi(0) - \int_{\theta=-\tau}^0 \int_{\xi=0}^\theta \bar{\psi}^T(\xi - \theta) d\eta(\theta)\phi(\xi) d\xi$$

for  $\phi \in C([-\tau, 0], \mathbb{C}^2)$ ,  $\psi \in C^1([0, \tau], \mathbb{C}^2)$ , where  $\eta(\theta) = \eta(\theta, 0)$ , to determine the coordinates of the center manifold near the origin of (3.2). Note that the overline stands for the complex conjugate.

By the analysis in Lemma 2.1, we know that  $\pm i\omega^*$  are eigenvalues of (2.8). Accordingly,  $\pm i\omega^*$  are eigenvalues of  $A_0$  and  $A_0^*$ , respectively. We first need to compute the eigenvectors  $q(\theta)$  and  $q^*(\theta^*)$  of  $A_0$  and  $A_0^*$  corresponding to  $i\omega^*$  and  $-i\omega^*$ , respectively; namely,

$$(3.10) \quad A_0 q(\theta) = i\omega^* q(\theta) \text{ and } A_0^* q^*(\theta^*) = -i\omega^* q^*(\theta^*),$$

which satisfy the normalized conditions  $\langle q^*, q \rangle = 1$  and  $\langle q^*, \bar{q} \rangle = 0$ . Thus, we set

$$(3.11) \quad q(\theta) = q(0)e^{i\omega^*\theta} = \begin{pmatrix} q_1 \\ q_2 \end{pmatrix} e^{i\omega^*\theta} \text{ and } q^*(\theta^*) = q^*(0)e^{i\omega^*\theta^*} = \begin{pmatrix} q_1^* \\ q_2^* \end{pmatrix} e^{i\omega^*\theta^*}$$

for  $\theta \in [-\tau, 0)$ ,  $\theta^* \in (0, \tau]$ .

Noting that  $q(0)$  can also be solved by the characteristic equation (2.8), we have

$$q(\theta) = \begin{pmatrix} 1 \\ \frac{-a_{22} + i\omega^*}{a_{21}} \end{pmatrix} e^{i\omega^*\theta}.$$

Similarly substituting (3.11) into (3.10), we have

$$q^*(\theta^*) = \rho \begin{pmatrix} \frac{-a_{11} - i\omega^*}{a_{21}} \\ 1 \end{pmatrix} e^{i\omega^*\theta^*}.$$

In order to ensure  $\langle q^*, q \rangle = 1$ , we need to determine the value of  $\rho$ . From (3.9), we have

$$\begin{aligned} \langle q^*(s), q(\theta) \rangle &= \bar{q}^*(0)q(0) - \int_{-\tau}^0 \int_0^\theta \bar{q}^*(\xi - \theta) d\eta(\theta) q(\xi) d\xi \\ &= \bar{\rho}(\bar{q}_1^*, \bar{q}_2^*)(q_1, q_2)^T - \int_{-\tau}^0 \int_0^\theta \bar{\rho}(\bar{q}_1^*, \bar{q}_2^*) e^{-i\omega^*(\xi - \theta)} d\eta(\theta) (q_1, q_2)^T e^{i\omega^*\xi} d\xi \\ &= \bar{\rho}(\bar{q}_1^* q_1 + \bar{q}_2^* q_2 + \tau_0 e^{-i\omega^*\tau_0} a_{13} q_2) \\ &= \bar{\rho}(\bar{q}_1^* + q_2 + \tau_0 e^{-i\omega^*\tau_0} a_{13} q_2). \end{aligned}$$

Thus we can choose  $\rho$  as

$$\bar{\rho} = 1/(\bar{q}_1^* + q_2 + \tau_0 e^{-i\omega^*\tau_0} a_{13} q_2).$$

Next, by using  $q$  and  $q^*$ , we can construct a coordinate for the center manifold  $C_0$  at  $\nu = 0$  with the method of Hassard, Kazarinoff, and Wan [16]. Denote  $x_t = x_t(\theta)$  as a solution of (3.7) when  $\nu = 0$ , and define

$$(3.12) \quad z(t) \triangleq \langle q^*, x_t \rangle,$$

$$(3.13) \quad W(t, \theta) \triangleq x_t(\theta) - 2\text{Re}\{z(t)q(\theta)\}.$$

In term of the center manifold reduction, we have  $W(t, \theta) = W(z(t), \bar{z}(t), \theta)$  on  $C_0$ . According to the center eigenspace at the equilibrium, we further have

$$(3.14) \quad W(t, \theta) = W(z(t), \bar{z}(t), \theta) \triangleq W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + W_{30}(\theta) \frac{z^3}{6} + \dots,$$

where  $z$  and  $\bar{z}$  are the local coordinates of the center manifold  $C_0$  in directions  $q$  and  $q^*$ , respectively.

Note that  $W$  is real if  $\mathbb{X}(t)$  is real. We are only concerned with real solutions. For a solution  $\mathbb{X}(t) \in C_0$  of (3.7) with  $\nu = 0$ , (3.13) implies that

$$(3.15) \quad \begin{aligned} \dot{z}(t) &= \langle q^*, \dot{x}_t \rangle \\ &= i\omega^* z + \bar{q}^*(0) F_0(W(z, \bar{z}, \theta) + 2\text{Re}\{z(t)q(\theta)\}) \\ &\triangleq i\omega^* z + \bar{q}^*(0) F_0(z, \bar{z}). \end{aligned}$$

We rewrite the above equation as

$$(3.16) \quad \dot{z}(t) = i\omega^* z + g(z, \bar{z}),$$

where

$$(3.17) \quad \begin{aligned} g(z, \bar{z}) &= \bar{q}^*(0) F_0(z, \bar{z}) \\ &\triangleq \frac{g_{20}}{2} z^2 + g_{11} z\bar{z} + \frac{g_{02}}{2} \bar{z}^2 + \frac{g_{30}}{6} z^3 + \frac{g_{21}}{2} z^2 \bar{z} + \frac{g_{12}}{2} z \bar{z}^2 + \frac{g_{03}}{6} \bar{z}^3 + \dots \end{aligned}$$

Regarding (3.16), we need to give the explicit expressions of  $g_{ij}$ . We highlight this in the following lemma.

**Lemma 3.1.** *If we set*

$$(3.18) \quad \begin{aligned} k_1 &= -b_{11} - e_1 \hat{v}, & k_2 &= -b_{12}, & k_3 &= -2e_1 \hat{u}, & k_4 &= -e_1, \\ k_5 &= -b_{21} - 2e_2 \hat{v}, & k_6 &= -b_{22} - e_2 \hat{u}, & k_7 &= -e_2, \end{aligned}$$

then  $g_{ij}$  can be explicitly expressed by (3.21).

*Proof.* From (3.13) and (3.14), we obtain that

$$(3.19) \quad \begin{aligned} x_t(\theta) &= W(t, \theta) + 2\text{Re}\{z(t)q(\theta)\} \\ &= W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + zq + \bar{z}\bar{q} + \dots \\ &= W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + (1, q_2)^T e^{i\omega^* \theta} z + (1, \bar{q}_2)^T e^{-i\omega^* \theta} \bar{z} + \dots \end{aligned}$$

In view of (3.18), substituting (3.19) into (3.17) yields

$$(3.20) \quad \begin{aligned} g(z, \bar{z}) &= \bar{q}^*(0) F_0(z, \bar{z}) = \bar{q}^*(0) F_0(x_t(\theta)) \\ &= \bar{\rho}(\bar{q}_1^*, 1) \begin{pmatrix} k_1 \phi_1^2(0) + k_2 \phi_1(0) \phi_2(0) + k_3 \phi_1(0) \phi_2(-\tau) + k_4 \phi_1^2(0) \phi_2(-\tau) \\ k_5 \phi_1(0) \phi_2(0) + k_6 \phi_2^2(0) + k_7 \phi_1(0) \phi_2^2(0) \end{pmatrix} \\ &\triangleq \frac{g_{20}}{2} z^2 + g_{11} z\bar{z} + \frac{g_{02}}{2} \bar{z}^2 + \frac{g_{30}}{6} z^3 + \frac{g_{21}}{2} z^2 \bar{z} + \frac{g_{12}}{2} z \bar{z}^2 + \frac{g_{03}}{6} \bar{z}^3 + h.o.t., \end{aligned}$$

where h.o.t. stands for higher order terms, and

$$\begin{aligned}
g_{20} &= 2\bar{\rho}(\bar{q}_1^* k_1 + \bar{q}_1^* q_2 k_2 + \bar{q}_1^* q_2 k_3 e^{-i\omega^* \tau_0} + q_2 k_5 + q_2^2 k_6), \\
g_{11} &= 2\bar{\rho}(\bar{q}_1^* k_1 + \bar{q}_1^* \operatorname{Re}(q_2) k_2 + \bar{q}_1^* \operatorname{Re}(q_2 e^{-i\omega^* \tau_0}) k_3 + \operatorname{Re}(q_2) k_5 + |q_2|^2 k_6), \\
g_{02} &= 2\bar{\rho}(\bar{q}_1^* k_1 + \bar{q}_1^* \bar{q}_2 k_2 + \bar{q}_1^* \bar{q}_2 k_3 e^{i\omega^* \tau_0} + \bar{q}_2 k_5 + \bar{q}_2^2 k_6), \\
g_{30} &= 6\bar{\rho} \left[ \bar{q}_1^* k_1 W_{20}^{(1)}(0) + \bar{q}_1^* k_2 \left( \frac{W_{20}^{(1)}(0) q_2}{2} + \frac{W_{20}^{(2)}(0)}{2} \right) + \bar{q}_1^* k_3 \left( \frac{W_{20}^{(1)}(0) q_2}{2} + \frac{W_{20}^{(2)}(-\tau)}{2} \right) \right. \\
&\quad \left. + \bar{q}_1^* k_4 q_2 e^{-i\omega^* \tau_0} + k_5 \left( \frac{W_{20}^{(1)}(0) q_2}{2} + \frac{W_{20}^{(2)}(0)}{2} \right) + q_2 k_6 W_{20}^{(2)}(0) + k_7 q_2^2 \right], \\
g_{21} &= 2\bar{\rho} \left[ \bar{q}_1^* k_1 \left( W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0) \right) + \bar{q}_1^* k_2 \left( \frac{W_{20}^{(1)}(0) q_2}{2} + \frac{W_{20}^{(2)}(0)}{2} + q_2 W_{11}^{(1)}(0) + W_{11}^{(2)}(0) \right) \right. \\
&\quad \left. + \bar{q}_1^* k_3 \left( \frac{W_{20}^{(1)}(0) \bar{q}_2 e^{i\omega^* \tau_0}}{2} + \frac{W_{20}^{(2)}(-\tau) \bar{q}_2}{2} + W_{11}^{(1)}(0) q_2 e^{-i\omega^* \tau_0} + W_{11}^{(2)}(-\tau) \right) \right. \\
&\quad \left. + \bar{q}_1^* k_4 \left( \bar{q}_2 e^{i\omega^* \tau_0} + 2q_2 e^{-i\omega^* \tau_0} \right) + k_5 \left( \frac{W_{20}^{(1)}(0) \bar{q}_2}{2} + \frac{W_{20}^{(2)}(0)}{2} + q_2 W_{11}^{(1)}(0) + W_{11}^{(2)}(0) \right) \right. \\
(3.21) \quad &\quad \left. + k_6 \left( \bar{q}_2 W_{20}^{(2)}(0) + 2q_2 W_{11}^{(2)}(0) \right) + k_7 \left( \bar{q}_2^2 + 2|q_2|^2 \right) \right], \\
g_{12} &= 2\bar{\rho} \left[ \bar{q}_1^* k_1 \left( W_{02}^{(1)}(0) + 2W_{11}^{(1)}(0) \right) + \bar{q}_1^* k_2 \left( q_2 \frac{W_{02}^{(1)}(0)}{2} + \frac{W_{02}^{(2)}(0) q_2}{2} + \bar{q}_2 W_{11}^{(1)}(0) + W_{11}^{(2)}(0) \right) \right. \\
&\quad \left. + \bar{q}_1^* k_3 \left( \frac{W_{02}^{(1)}(0) q_2}{2} + \frac{W_{02}^{(2)}(-\tau)}{2} + W_{11}^{(1)}(0) \bar{q}_2 e^{i\omega^* \tau_0} + W_{11}^{(2)}(-\tau) \right) \right. \\
&\quad \left. + \bar{q}_1^* k_4 \left( q_2 e^{-i\omega^* \tau_0} + 2\bar{q}_2 e^{i\omega^* \tau_0} \right) + k_5 \left( \frac{W_{02}^{(1)}(0) q_2}{2} + \frac{W_{02}^{(2)}(0)}{2} + \bar{q}_2 W_{11}^{(1)}(0) + W_{11}^{(2)}(0) \right) \right. \\
&\quad \left. + k_6 \left( q_2 W_{02}^{(2)}(0) + 2\bar{q}_2 W_{11}^{(2)}(0) \right) + k_7 \left( \bar{q}_2^2 + 2|q_2|^2 \right) \right], \\
g_{03} &= 6\bar{\rho} \left[ \bar{q}_1^* k_1 W_{02}^{(1)}(0) + \bar{q}_1^* k_2 \left( \frac{W_{02}^{(1)}(0) \bar{q}_2}{2} + \frac{W_{02}^{(2)}(0)}{2} \right) + \bar{q}_1^* k_3 \left( \frac{W_{02}^{(1)}(0) \bar{q}_2 e^{i\omega^* \tau_0}}{2} + \frac{W_{02}^{(2)}(-\tau)}{2} \right) \right. \\
&\quad \left. + \bar{q}_1^* k_4 \bar{q}_2 e^{i\omega^* \tau_0} + k_5 \left( \frac{W_{02}^{(1)}(0) \bar{q}_2}{2} + \frac{W_{02}^{(2)}(0)}{2} \right) + \bar{q}_2 k_6 W_{02}^{(2)}(0) + k_7 \bar{q}_2^2 \right],
\end{aligned}$$

where  $W_{20}^{(k)}$ ,  $W_{11}^{(k)}$ , and  $W_{02}^{(k)}$  are the  $k$ th components of  $W_{20}$ ,  $W_{11}$ , and  $W_{02}$ , respectively, for  $-\tau \leq \theta \leq 0$ .

Since  $g_{21}$  depends on  $W_{20}(\theta)$  and  $W_{11}(\theta)$ , we need to find the values of  $W_{20}(\theta)$  and  $W_{11}(\theta)$ . From (3.7) and (3.13), we have

$$\begin{aligned}
 \dot{W} &= \dot{x}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\
 (3.22) \quad &= \begin{cases} A_0W - 2\text{Re}\{\bar{q}^*(0)F_0q(\theta)\}, & -\tau \leq \theta < 0, \\ A_0W - 2\text{Re}\{\bar{q}^*(0)F_0q(\theta)\} + F_0, & \theta = 0 \end{cases} \\
 &\triangleq A_0W + H(z, \bar{z}, \theta),
 \end{aligned}$$

where

$$(3.23) \quad H(z, \bar{z}, \theta) = H_{20} \frac{z^2}{2} + H_{11}z\bar{z} + H_{02} \frac{\bar{z}^2}{2} + \dots$$

From (3.14), we have

$$\begin{aligned}
 \dot{W} &= \dot{W}_z \dot{z}(t) + \dot{W}_{\bar{z}} \dot{\bar{z}}(t) \\
 (3.24) \quad &= (W_{20}(\theta)z + W_{11}(\theta)\bar{z} + \dots)(i\omega^*z(t) + g(z, \bar{z})) \\
 &\quad + (W_{11}(\theta)z + W_{02}(\theta)\bar{z} + \dots)(-i\omega^*\bar{z}(t) + \bar{g}(z, \bar{z})).
 \end{aligned}$$

Substituting (3.14) to (3.22) yields that

$$\begin{aligned}
 \dot{W} &= A_0(W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + \dots) + H_{20}(\theta) \frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta) \frac{\bar{z}^2}{2} + \dots \\
 (3.25) \quad &= (A_0W_{20}(\theta) + H_{20}(\theta)) \frac{z^2}{2} + (A_0W_{11}(\theta) + H_{11}(\theta))z\bar{z} + (A_0W_{02}(\theta) + H_{02}(\theta)) \frac{\bar{z}^2}{2} + \dots
 \end{aligned}$$

Comparing the coefficients of  $z^2$  and  $z\bar{z}$  from (3.24) and (3.25), we get

$$\begin{aligned}
 (3.26) \quad &(A_0 - 2i\omega^*I)W_{20}(\theta) = -H_{20}(\theta), \\
 &A_0W_{11}(\theta) = -H_{11}(\theta).
 \end{aligned}$$

For  $\theta \in [0, \tau]$ , it follows from (3.13), (3.14), (3.23), and (3.24) that

$$\begin{aligned}
 H(z, \bar{z}, \theta) &= -2\text{Re}\{\bar{q}^*(0)F_0q(\theta)\} \\
 &= -\bar{q}^*(0)F_0q(\theta) - q^*(0)\bar{F}_0\bar{q}(\theta) \\
 (3.27) \quad &= -g(z, \bar{z})q(\theta) - \bar{g}(z, \bar{z})\bar{q}(\theta) \\
 &= -\left(g_{20} \frac{z^2}{2} + g_{11}z\bar{z} + g_{02} \frac{\bar{z}^2}{2} + \dots\right)q(\theta) - \left(\bar{g}_{20} \frac{\bar{z}^2}{2} + \bar{g}_{11}z\bar{z} + \bar{g}_{02} \frac{z^2}{2} + \dots\right)\bar{q}(\theta).
 \end{aligned}$$

Comparing the coefficients of  $z^2$  and  $z\bar{z}$  between (3.23) and (3.27), we get

$$\begin{aligned}
 (3.28) \quad &H_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{20}\bar{q}(\theta), \\
 &H_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta).
 \end{aligned}$$

From the definition of  $A_\nu(\theta)$  and (3.26) and (3.28), we have

$$(3.29) \quad \dot{W}_{20}(\theta) = 2i\omega^*W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta).$$

Since  $q(\theta) = (q_1, q_2)^T e^{i\omega^*\theta}$ , we obtain

$$(3.30) \quad W_{20}(\theta) = \frac{ig_{20}}{\omega^*} q(0) e^{i\omega^*\theta} + \frac{i\bar{g}_{02}}{3\omega^*} \bar{q}(0) e^{-i\omega^*\theta} + G_1 e^{2i\omega^*\theta},$$

where  $G_1 = (G_1^{(1)}, G_1^{(2)})^T$  is a constant vector. Similarly, we have

$$(3.31) \quad W_{11}(\theta) = \frac{-ig_{11}}{\omega^*} q(0) e^{i\omega^*\theta} + \frac{i\bar{g}_{11}}{\omega^*} \bar{q}(0) e^{-i\omega^*\theta} + G_2,$$

where  $G_2 = (G_2^{(1)}, G_2^{(2)})^T$  is a constant vector. Now, we shall find the values of  $G_1$  and  $G_2$ . From the definition of  $A_0$  and (3.26), we have

$$(3.32) \quad \int_{-\tau}^0 d\eta(\theta) W_{20}(\theta) = 2i\omega^* W_{20}(0) - H_{20}(0)$$

and

$$(3.33) \quad \int_{-\tau}^0 d\eta(\theta) W_{11}(\theta) = -H_{11}(0),$$

where  $\eta(\theta) = \eta(\theta, 0)$ . In view of (3.22), we deduce that when  $\theta = 0$ ,

$$(3.34) \quad H(z, \bar{z}, 0) - 2\text{Re}\{\bar{q}^*(0)F_0q(0)\} + F_0 = -g(z, \bar{z})q(0) - \bar{g}(z, \bar{z})\bar{q}(0) + F_0.$$

Then we have

$$(3.35) \quad \begin{aligned} H_{20} \frac{z^2}{2} + H_{11} z\bar{z} + H_{02} \frac{\bar{z}^2}{2} + \cdots &= - \left( g_{20} \frac{z^2}{2} + g_{11} z\bar{z} + g_{02} \frac{\bar{z}^2}{2} + \cdots \right) q(0) \\ &\quad - \left( \bar{g}_{20} \frac{\bar{z}^2}{2} + \bar{g}_{11} z\bar{z} + \bar{g}_{02} \frac{z^2}{2} + \cdots \right) \bar{q}(0) + F_0. \end{aligned}$$

Comparing both sides of (3.35), we obtain

$$(3.36) \quad H_{20} = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + 2 \begin{pmatrix} k_1 + k_2q_2 + k_3q_2e^{-i\omega^*\tau} \\ k_5q_2 + k_6q_2^2 \end{pmatrix}$$

and

$$(3.37) \quad H_{11} = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + \begin{pmatrix} 2k_1 + 2k_2\text{Re}(q_2) + 2k_3\text{Re}(q_2e^{-i\omega^*\tau}) \\ 2k_5\text{Re}(q_2) + 2k_6|q_2|^2 \end{pmatrix}.$$

Since  $i\omega^*$  is the eigenvalue of  $A_0$  and  $q(0)$  is the corresponding eigenvector, we get

$$(3.38) \quad \left( i\omega^* I - \int_{-\tau}^0 e^{i\omega^*\theta} d\eta(\theta) \right) q(0) = 0$$



and

$$(3.39) \quad \left( -i\omega^* I - \int_{-\tau}^0 e^{-i\omega^*\theta} d\eta(\theta) \right) \bar{q}(0) = 0.$$

Therefore, substituting (3.30) and (3.32) into (3.36), we have

$$(3.40) \quad \left( 2i\omega^* I - \int_{-\tau}^0 e^{2i\omega^*\theta} d\eta(\theta) \right) G_1 = 2 \begin{pmatrix} k_1 + k_2q_2 + k_3q_2e^{-i\omega^*\tau} \\ k_5q_2 + k_6q_2^2 \end{pmatrix},$$

that is,

$$(3.41) \quad H^*G_1 = 2 \begin{pmatrix} k_1 + k_2q_2 + k_3q_2e^{-i\omega^*\tau} \\ k_5q_2 + k_6q_2^2 \end{pmatrix},$$

where

$$(3.42) \quad H^* = \begin{pmatrix} 2i\omega^* - a_{11} - D_u\Lambda^\alpha & -a_{12} - a_{13}e^{-2i\omega^*\tau} \\ -a_{21} & 2i\omega^* - a_{22} - D_v\Lambda^\alpha \end{pmatrix}.$$

Thus,

$$(3.43) \quad G_1^{(1)} = \frac{\text{Det} \begin{pmatrix} 2(k_1 + k_2q_2 + k_3q_2e^{-i\omega^*\tau}) & -a_{12} - a_{13}e^{-2i\omega^*\tau} \\ 2(k_5q_2 + k_6q_2^2) & 2i\omega^* - a_{22} - D_v\Lambda^\alpha \end{pmatrix}}{\text{Det}(H^*)},$$

$$G_1^{(2)} = \frac{\text{Det} \begin{pmatrix} 2i\omega^* - a_{11} - D_u\Lambda^\alpha & 2(k_1 + k_2q_2 + k_3q_2e^{-i\omega^*\tau}) \\ -a_{21} & 2(k_5q_2 + k_6q_2^2) \end{pmatrix}}{\text{Det}(H^*)}.$$

In a similar way, substituting (3.31) and (3.33) into (3.37), we have

$$(3.44) \quad P^*G_2 = \begin{pmatrix} 2k_1 + 2k_2\text{Re}(q_2) + 2k_3\text{Re}(q_2e^{-i\omega^*\tau}) \\ 2k_5\text{Re}(q_2) + 2k_6|q_2|^2 \end{pmatrix},$$

where

$$(3.45) \quad P^* = \begin{pmatrix} -a_{11} - D_u\Lambda^\alpha & -a_{12} - a_{13} \\ -a_{12} & -a_{22} - D_v\Lambda^\alpha \end{pmatrix}.$$

Thus,

$$(3.46) \quad G_2^{(1)} = \frac{\text{Det} \begin{pmatrix} 2k_1 + 2k_2\text{Re}(q_2) + 2k_3\text{Re}(q_2e^{-i\omega^*\tau}) & -a_{12} - a_{13} \\ 2k_5\text{Re}(q_2) + 2k_6|q_2|^2 & -a_{22} - D_v\Lambda^\alpha \end{pmatrix}}{\text{Det}(P^*)},$$

$$G_2^{(2)} = \frac{\text{Det} \begin{pmatrix} -a_{11} - D_u\Lambda^\alpha & 2k_1 + 2k_2\text{Re}(q_2) + 2k_3\text{Re}(q_2e^{-i\omega^*\tau}) \\ -a_{12} & 2k_5\text{Re}(q_2) + 2k_6|q_2|^2 \end{pmatrix}}{\text{Det}(P^*)}.$$

Therefore, we can determine  $W_{20}(\theta)$  and  $W_{11}(\theta)$  from (3.30) and (3.31). ■

**Theorem 3.2.** *Suppose that  $\operatorname{Re}\{\lambda'(0)\}$  and  $\operatorname{Im}\{\lambda'(0)\}$  are solutions of (3.49). If  $\operatorname{Re}\{C_1(0)\} \neq 0$ , then system (1.3) has a branch of Hopf bifurcating solutions for  $\tau = \tau_0 + \nu$  with  $\nu$  satisfying  $\nu \operatorname{Re}\{\lambda'(0)\} B(\tau_0, \nu) < 0$ , where  $C_1(0)$  and  $B(\tau_0, \nu)$  will be defined in (3.48) and (3.52). Also the bifurcating periodic solutions have the following properties:*

- (i)  $\operatorname{Re}\{C_1(0)\}$  determines the stability of the bifurcating periodic solutions: the bifurcating periodic solutions are orbitally stable (resp., unstable) if  $\operatorname{Re}\{C_1(0)\} < 0$  (resp.,  $\operatorname{Re}\{C_1(0)\} > 0$ );
- (ii)  $-\frac{\operatorname{Re}\{C_1(0)\}}{\operatorname{Re}\{\lambda'(0)\}}$  determines the direction of the Hopf bifurcation: if  $-\frac{\operatorname{Re}\{C_1(0)\}}{\operatorname{Re}\{\lambda'(0)\}} > 0$  (resp.,  $-\frac{\operatorname{Re}\{C_1(0)\}}{\operatorname{Re}\{\lambda'(0)\}} < 0$ ), the bifurcating periodic solutions exist for  $\nu > 0$  (resp.,  $\nu < 0$ ), which is also called a supercritical (resp., subcritical) Hopf bifurcation;
- (iii) the period of the bifurcating periodic solution is  $\frac{2\pi}{\omega^* \tau_0}$  as  $\nu = 0$ , the period  $T(\tau_0, \nu)$  is increasing in parameter  $\nu$  (resp., decreasing) if  $N(\tau_0) > 0$  (resp.,  $N(\tau_0) < 0$ ). Here  $T(\tau_0, \nu)$  and  $N(\tau_0)$  are defined in (3.55).

*Proof.* By a standard normal form method, we can perform nonlinear (complex) coordinate transform to (3.16) such as all quadratic terms and fourth order terms are eliminated, namely, (3.16) becomes

$$(3.47) \quad z'(t) = \lambda(\nu)z + \frac{1}{2}C_1(\nu)z^2\bar{z} + (o|z|^3),$$

where  $\lambda(\nu) = i\omega^*\tau_0 + \nu\lambda'(0) + (o|\nu|^3)$  with  $\lambda(\nu)$  being a smooth function defined by Theorem 2.2 and

$$(3.48) \quad C_1(0) = \frac{i}{2\omega^*}(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2) + \frac{1}{2}g_{21}.$$

In view of (2.15), we have

$$(3.49) \quad \begin{aligned} (A_1 - A_3\tau_0 \cos \omega^*\tau_0)\operatorname{Re}\lambda'(0) - (2\omega + A_3\tau_0 \sin \omega^*\tau_0)\operatorname{Im}\lambda'(0) &= A_3\omega^* \sin \omega^*\tau_0, \\ (2\omega^* + A_3\tau_0 \sin \omega^*\tau_0)\operatorname{Re}\lambda'(0) + (A_1 - A_3\tau_0 \cos \omega^*\tau_0)\operatorname{Im}\lambda'(0) &= A_3\omega^* \cos \omega^*\tau_0. \end{aligned}$$

Letting  $z = re^{i\theta}$ , then (3.47) can be written as

$$(3.50) \quad \begin{aligned} \frac{dr}{dt} &= \nu r \operatorname{Re}\lambda'(0) + \frac{1}{2}r^3 \operatorname{Re}\{C_1(0)\} + h.o.t., \\ \frac{d\theta}{dt} &= \omega^*\tau_0 + \nu \operatorname{Im}\lambda'(0) + \frac{1}{2}r^2 \operatorname{Im}\{C_1(0)\} + h.o.t. \end{aligned}$$

Hence

$$(3.51) \quad \begin{aligned} \frac{dr}{d\theta} &= \frac{\nu r \operatorname{Re}\{\lambda'(0)\} + \frac{1}{2}r^3 \operatorname{Re}\{C_1(0)\} + h.o.t.}{\omega^*\tau_0 + \nu \operatorname{Im}\{\lambda'(0)\} + \frac{1}{2}r^2 \operatorname{Im}\{C_1(0)\} + h.o.t.} \\ &= \frac{1}{A(\tau_0, \nu)} (\nu \operatorname{Re}\{\lambda'(0)\}r + B(\tau_0, \nu)r^3) + h.o.t., \end{aligned}$$

where

$$(3.52) \quad \begin{aligned} A(\tau_0, \nu) &= \omega^*\tau_0 + \nu \operatorname{Im}\{\lambda'(0)\}, \\ B(\tau_0, \nu) &= \frac{1}{2} \operatorname{Re}\{C_1(0)\} - \frac{\operatorname{Im}\{C_1(0)\} \operatorname{Re}\{\lambda'(0)\} \nu}{2A(\tau_0, \nu)}. \end{aligned}$$

Let

$$r(\theta, r_0) = r_1(\theta)r_0 + r_2(\theta)r_0^2 + r_3(\theta)r_0^3 + O(r_0^4)$$

be a solution of (3.51) satisfying  $r(0, r_0) = r_0$ . Then  $r_1(0) = 1$ ,  $r_i(0) = 0$  for  $i \geq 2$ . Inserting the above into (3.51), we have

$$r_1'(\theta)r_0 + r_2'(\theta)r_0^2 + r_3'(\theta)r_0^3 + O(r_0^4) = \frac{1}{A(\tau_0, \nu)} (\nu \operatorname{Re}\{\lambda'(0)\}r + B(\tau_0, \nu)r^3) + h.o.t.$$

Thus,

$$r_1'(\theta) = \frac{\nu \operatorname{Re}\{\lambda'(0)\}}{A(\tau_0, \nu)}, \quad r_2'(\theta) = 0, \quad r_3'(\theta) = \frac{B(\tau_0, \nu)}{A(\tau_0, \nu)}.$$

Hence,

$$r_1(\theta) = \frac{\nu \operatorname{Re}\{\lambda'(0)\}}{A(\tau_0, \nu)}\theta + 1, \quad r_2(\theta) = 0, \quad r_3(\theta) = \frac{B(\tau_0, \nu)}{A(\tau_0, \nu)}\theta.$$

Then the Poincaré map  $P(r_0) = r(2\pi, r_0)$  has the form

$$(3.53) \quad P(r_0) = \left( \frac{2\nu \operatorname{Re}\{\lambda'(0)\}\pi}{A(\tau_0, \nu)} + 1 \right) r_0 + \frac{2\pi B(\tau_0, \nu)}{A(\tau_0, \nu)} r_0^3 + O(r_0^5).$$

Near  $r_0 = 0$ , the map has a unique fixed point

$$(3.54) \quad r_0^* = \sqrt{\frac{-\nu \operatorname{Re}\{\lambda'(0)\}}{B(\tau_0, \nu)}} (1 + O(|\nu|)).$$

We can compute the period of the bifurcated periodic solution as follows:

$$(3.55) \quad \begin{aligned} T(\tau_0, \nu) &= \int_0^{2\pi} \frac{d\theta}{A(\tau_0, \nu) + \frac{1}{2}\operatorname{Im}\{C_1(0)\}r^2 + h.o.t.} \\ &= \frac{1}{A(\tau_0, \nu)} \int_0^{2\pi} \left( 1 + \frac{\operatorname{Im}\{C_1(0)\}\operatorname{Re}\{\lambda'(0)\}\nu}{2A(\tau_0, \nu)B(\tau_0, \nu)} \right) d\theta + o(|\nu|) \\ &= \frac{2\pi}{\omega^*\tau_0} (1 + N(\tau_0)\nu + o(|\nu|)), \end{aligned}$$

where

$$N(\tau_0) = \frac{\operatorname{Im}\{C_1(0)\}\operatorname{Re}\{\lambda'(0)\} - \operatorname{Re}\{C_1(0)\}\operatorname{Im}\{\lambda'(0)\}}{\omega^*\tau_0 \operatorname{Re}\{C_1(0)\}}.$$

By applying the method of Hassard, Kazarinoff, and Wan [16], we obtain all the conclusions. ■

**4. Numerical simulations.** In this section, we carry out numerical simulations to confirm our analytical findings. By choosing the type of the adjacent matrix  $D$ , we obtain different types of networks, such as Watts–Strogatz network and Barabási–Albert network. In term of  $D$ , we thus have the Laplacian matrix  $L$ . By putting  $L$  into system (1.3), we perform the numerical simulations via the DDEs. We consider the following set of parameters:

$$(4.1) \quad \begin{aligned} a_1 = 1, a_2 = 2, \quad b_{11} = 0.08, \quad b_{12} = 0.015, \quad b_{21} = 0.05, \quad b_{22} = 0.07, \\ e_1 = 0.003, \quad e_2 = 0.0008, \quad \tau = 0.3, \quad D_u = 0.05, \quad D_v = 0.05. \end{aligned}$$

For this particular choice, the positive uniform equilibrium is  $(\hat{u}, \hat{v}) = (23.6972, 15.9699)$ . In Theorem 3.2 we showed that the network can generate spatial patterns if the delay is beyond a threshold. For the given parameters in (4.1), condition (2.11) yields the threshold  $\tau_0 = 2.45$ . Here, taking the delay  $\tau = 3$  such that spatial patterns appear, we notice that these parameters (the original data were given in Mukhopadhyay, Chattopadhyay, and Tapaswi [26] and Tian and Zhang [43]) are not the actual values from experimental observations. However, they make biological senses:  $a_1 = 1$  and  $a_2 = 2$  mean that the two species reproduce 1 and 2 cell divisions per hour, respectively. The carrying capacities  $\frac{a_1}{b_{11}} = 12.5$  and  $\frac{a_2}{b_{22}} = 28.5714$  are reasonable because the theoretical maximum densities of the two species are approximately 6,000 and 14,000 units per liter, respectively. Other parameters such as the intraspecies competition coefficients  $b_{ii}$ , interspecies competition coefficients  $b_{ij}$ , and allelopathic coefficients  $e_i$  are also appropriate to the plankton allelopathy model.

Firstly, we assume that the network is a Watts–Strogatz one made by 100 nodes, with an average degree of 4 and the probability to rewire a link of 0.15. From a mathematical point of view, a Watts–Strogatz network is an undirected graph, and some of the connections between the nodes are determined, and some of them are random. It possesses the homogeneous degree distribution. If the average degree is 4, each node is connected with 2 nodes adjacent to each other on the left and right. If the probability to rewire a link is 0.15, the probability that each node is connected to any node in the graph is 0.15. The role of the rewired edge is to introduce some stochastic routine between two patches in model (1.3), because the individual population movement is usually subject to the random walk. On the left-top panel in Figure 4.1, we illustrate the initial density of the first species in the network, which is taken as a uniformly distributed random perturbation around the equilibrium and in fact does not affect on the regular spatiotemporal structure of pattern formation mechanism. Using a Runge–Kutta scheme for the time integration, we can depict the spatial densities of the first plankton population on the network for times  $t = 400, 800, 1200$  in the second, third, and fourth panels of Figure 4.1. This figure shows that the network exhibits a spatially inhomogeneous behavior for different times. But we cannot see the asymptotic behavior of the plankton population in each node. In order to do it, we depict the temporal solution of (1.3), where we did not consider the network structure and just arranged the nodes in a vertical column. From the right panel of Figure 4.2, we see that the solution for each node exhibits temporally periodic oscillatory behavior. On the other hand, if the delay is absent, the solution is asymptotically stable in the left panel of Figure 4.2. Hence, we found that system (1.3) evolves a regular spatiotemporal pattern because the delay induces Hopf bifurcation.

Although our analytical result in Theorem 3.2 predicts temporally periodic oscillatory solutions, it has not considered the structure of the network. Next, we perform numerical simulations to see when we increase the average degree in the Watts–Strogatz network, whether the spatiotemporal patterns of system (1.3) will change. We can see three types of spatiotemporal patterns in the left column panels of Figure 4.3. The left-top panel presents sloping stripes when the system evolves in the terminal state, in the left-bottom panel the terminal state is in vertical stripes, and in the left-middle panel, however, the transient state

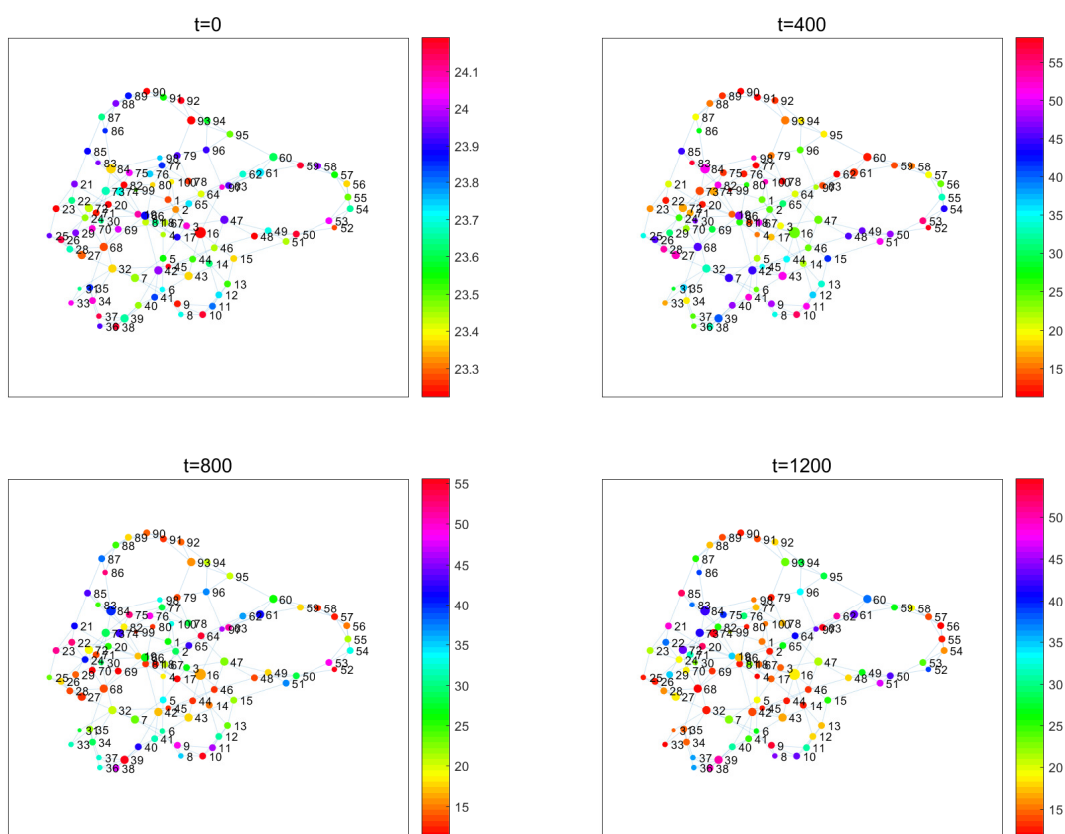


Figure 4.1. Solutions of  $u$  at time instants  $t = 0, 400, 800, 1200$  in the Watts–Strogatz network. The node size corresponds to node degree. Here  $\tau = 0.3$ . Other parameters are given in (4.1).

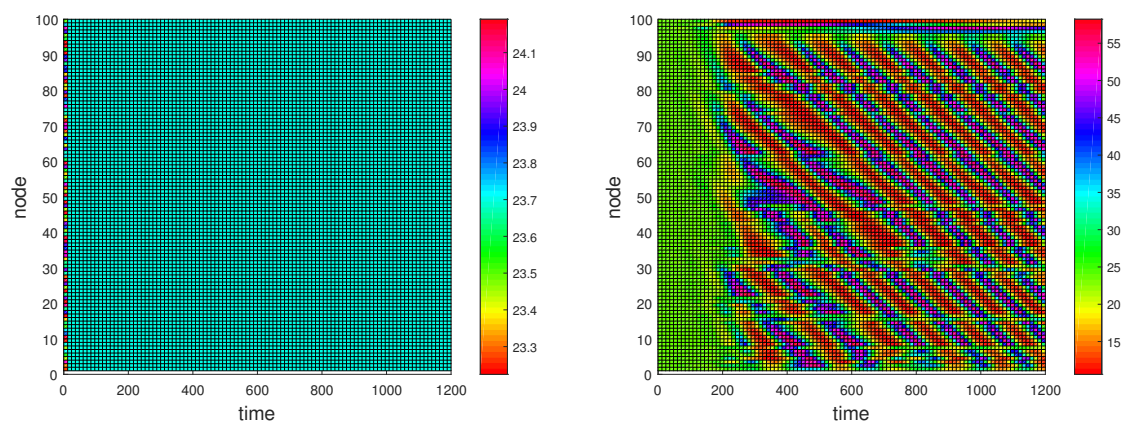
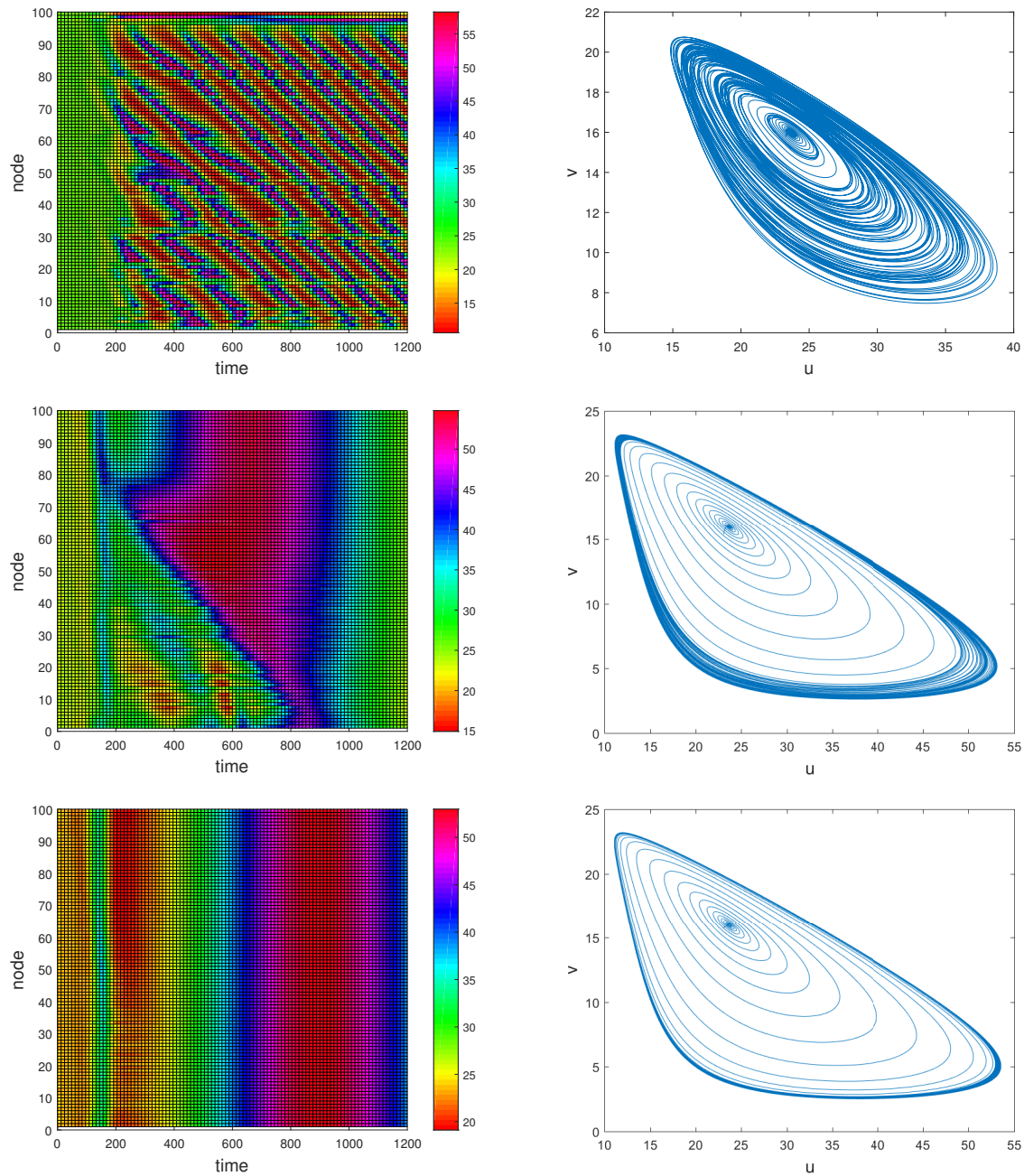


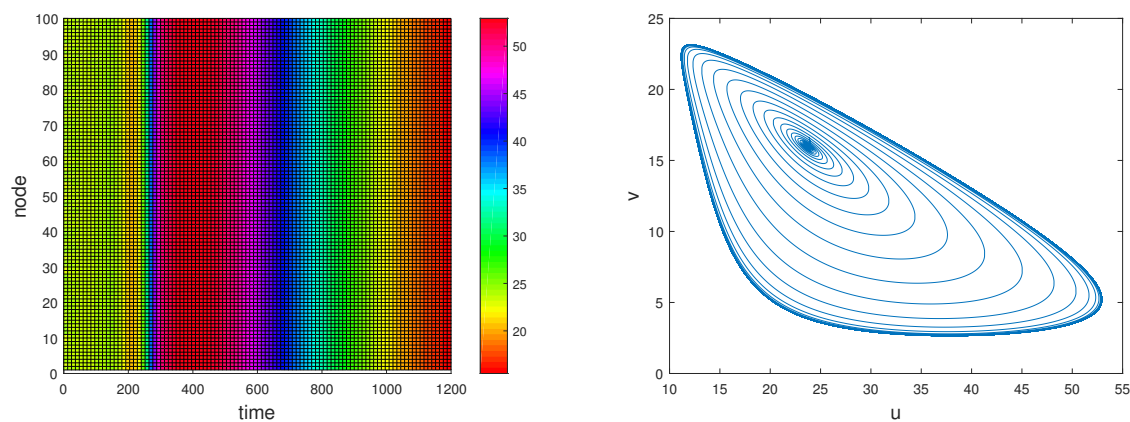
Figure 4.2. Spatiotemporal patterns of  $u$  in the Watts–Strogatz network for different delay. Here every grid of the vertical coordinate represents a node. Left panel ( $\tau = 0$ ): In the absence of delay it is the asymptotically stable solution. Right panel ( $\tau = 0.3$ ): In the presence of delay it is the temporally periodic oscillatory solution.



**Figure 4.3.** A comparison of spatiotemporal patterns of  $u$  between different average degrees: 4 (top panels), 6 (middle panels), and 8 (bottom panels). The right panels are the corresponding phase portraits of the left patterns.

is in sloping stripes ( $t < 1000$ ) while the terminal state is in vertical stripes ( $t > 1000$ ). Hence, the left-middle panel shows a mixed spatiotemporal pattern with sloping stripes and vertical stripes. From the diffusion point of view, when the average degree is small, the effect of the single node cannot diffuse to the whole network, the sloping stripes are spatially inhomogeneous but temporally oscillatory. When the average degree is large, the effect of the single node can diffuse to the whole network, the vertical stripes are spatially homogeneous and temporally oscillatory. When the average degree is moderate, the effect of the single node cannot diffuse to the whole network in the transient state, but it can diffuse to the whole network in the terminal state. The right panels show the phase trajectories at fixed nodes. The right-bottom phase portrait is a limit cycle, where the terminal trajectory is periodic. In the right-top phase portrait the whole domain inside the limit cycle is densely packed, where the terminal trajectory is quasiperiodic.

Finally, we choose our network as a Barabási–Albert free scale network, which consists of 100 nodes, with 3 initial nodes. Similar to the Watts–Strogatz network, Barabási–Albert free scale network is an undirected graph possessing both determined paths and random paths. Different from the Watts–Strogatz network, Barabási–Albert network possesses a scale-free degree distribution. In the left panel of Figure 4.4 the terminal state is the regular vertical striped spatiotemporal pattern, while the right phase portrait is the corresponding limit cycle. By comparing the spatiotemporal patterns between Watts–Strogatz network and Barabási–Albert free scale network, we find that the latter is more likely to generate vertical stripes instead of sloping stripes. Hence it has a faster diffusion speed to spread over the whole network.



**Figure 4.4.** Spatiotemporal pattern of  $u$  in the Barabási–Albert free scale network. The left panel is the vertical striped pattern. The right panel is the corresponding phase portrait.

In ecological meaning, the temporal periodic solutions describe the bloom phenomenon. From Figure 4.2, we can see that when delay  $\tau > \tau_0$ , system (1.3) exhibits a bloom phenomenon. Even if the same delay drives the bloom phenomenon, the structure of the network plays an important role on the spatial heterogeneity of system (1.3). In Figure 4.3, we see three different spatial distributions of bloom phenomena. In the left-top panel of Figure 4.3,

the spatial distribution is heterogeneous, which is also called “patchiness.” In the left-middle panel of Figure 4.3, the spatial distribution is heterogeneous in short-time but homogeneous in long-time. In the left-bottom panel of Figure 4.3, the spatial distribution is homogeneous. Figure 4.4 indicates that Barabási–Albert free scale network induces the spatially homogeneous bloom.

**5. Discussions.** Planktonic blooms have important implications for marine ecosystems (Abbott [1], Fasham [11], Smetacek [37]). Though the process by which the bloom phenomenon forms is not well understood, researchers have been trying to explain it by different population dynamical models (Malchow et al. [22], Medvinsky et al. [23], Mukhopadhyay, Chattopadhyay, and Tapaswi [26]) in which the causes of the bloom phenomenon are the interplay of planktonic competition and allelopathic toxins. Many experimental findings have provided evidence to indicate that allelopathic stimulatory interaction maintains a balanced phytoplankton ecology (Berglund [5], Hellebust [18], Monahan and Trainor [25], Rice [30]). Allelopathy has been described as one of the factors that control blooms, pulses, and successions in the abundance of phytoplankton species in all kinds of bodies of water. In this paper we have aimed to study allelopathic stimulatory plankton communities by using a Lotka–Volterra type competition model with anomalous diffusion. Allelopathic stimulatory effect in the model has been incorporated by introducing the production of an allelopathic substance by each of the species. The newly born plankton takes some time to mature before it can produce effective allelochemicals, which induces a delay effect in the model. The interplay of multipatch inhabit has been investigated by introducing a network to describe the dispersal directions of plankton species in different inhabitants. Plankton species in each node share no relationship with the geometrical distance among nodes but are dependent on the topological structure of the network instead. To our knowledge, there is no population dynamical model taking into account the network structure to describe the bloom phenomenon in the literature.

It is shown that the time delay destabilizes the system and leads to a limit cycle through Hopf bifurcation. Applying a linear stability analysis and a center manifold theory, we investigated stability of the Hopf bifurcation. It is worth mentioning that owing to the introduction of a network, our numerical simulations have brought out some dynamical features that the analytical theorems cannot attain. For the Watts–Strogatz network containing 100 nodes, we have obtained three dynamical pattern features:

- (i) When the average degree is 4, the system possesses temporally quasiperiodic solutions. The population distribution is the spatially heterogeneous regular pattern.
- (ii) When the average degree is 8, the system possesses temporally periodic solutions. The population distribution is the spatially homogeneous regular pattern.
- (iii) When the average degree is 6, the system possesses temporally periodic solutions with a quasiperiodic transient solution. The population distribution is a mixed pattern which is both spatially heterogeneous and spatially homogeneous.

Moreover, we have observed that the network with Barabási–Albert free scale type admits temporally periodic solutions. The population distribution is the spatially homogeneous regular pattern. Hence, our model has temporally periodic solutions, which is in good agreement with the periodic nature of blooms (Abbott [1], Abraham [2], Rice [30]).



In model (1.3), it was assumed that only species  $u_i$  has a time delay for maturity. If we assume that the species  $v_i$  also has a time delay, then the model takes the following form ( $i = 1, 2, \dots, n$ ):

$$(5.1) \quad \begin{aligned} \dot{u}_i(t) &= u_i(t)(a_1 - b_{11}u_i(t) - b_{12}v_i(t) + e_1u_i(t)v_i(t - \tau_1)) + D_u \sum_{j=1}^n L_{ij}u_j(t), \\ \dot{v}_i(t) &= v_i(t)(a_2 - b_{21}u_i(t) - b_{22}v_i(t) + e_2u_i(t - \tau_2)v_i(t)) + D_v \sum_{j=1}^n L_{ij}v_j(t). \end{aligned}$$

Then the technique of Wei and Ruan [48] can be applied to discuss the stability and bifurcation of the two-delay model (5.1). Following the procedure in section 2, we can find a critical value  $\tau_{1,0}$  of the first delay such that the steady state of system (1.3) (with  $\tau_1$  only) is asymptotically stable when  $\tau_1 < \tau_{1,0}$  and unstable when  $\tau_1 > \tau_{1,0}$ . Now consider the two-delay model (5.1) and let  $\tau_1 \in (0, \tau_{1,0})$  be fixed. Using a similar argument we can find a critical value  $\tau_{2,0}(\tau_1)$  of the second delay such that the steady state of system (5.1) (with both  $\tau_1$  and  $\tau_2$ ) is asymptotically stable when  $\tau_2 < \tau_{2,0}(\tau_1)$ . Thus, when  $(\tau_1, \tau_2) \in [0, \tau_{1,0}) \times [0, \tau_{2,0}(\tau_1))$ , the steady state of the two-delay model (5.1) is asymptotically stable. (Note that the actual stability region could be larger than  $[0, \tau_{1,0}) \times [0, \tau_{2,0}(\tau_1))$ .)

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