

# Dynamical analysis of toxin producing Phytoplankton–Zooplankton interactions

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## Abstract

In the present paper we consider a toxin producing phytoplankton–zooplankton model in which the toxin liberation by phytoplankton species follows a discrete time variation. Firstly we consider the elementary dynamical properties of the toxic-phytoplankton–zooplankton interacting model system in absence of time delay. Then we establish the existence of local Hopf-bifurcation as the time delay crosses a threshold value and also prove the existence of stability switching phenomena. Explicit results are derived for stability and direction of the bifurcating periodic orbit by using normal form theory and center manifold arguments. Global existence of periodic orbits is also established by using a global Hopf-bifurcation theorem. Finally, the basic outcomes are mentioned along with numerical results to provide some support to the analytical findings.

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## 1. Introduction

Almost all aquatic life is based upon plankton, which are the most abundant form of life floating freely near the surfaces of all aquatic environments, namely, lakes, rivers, estuaries and oceans [1,2]. The plant forms of plankton community are known as phytoplankton, they are capable of photo-synthesis in presence of sunlight and serve as the basic food source and occupy the first trophic level for all aquatic food chains. The animals in the plankton community are known as zooplankton. Phytoplankton are consumed by zooplankton which are a most favourable food source for fish and other aquatic animals. Phytoplankton are not only the basis for all aquatic food chains, they render very useful service by producing a huge amount of oxygen for human and other living animals after absorbing carbon-dioxide from surrounding environments [3]. The most common features of the phytoplankton population is rapid increase of biomass due to rapid cell proliferation and almost equally rapid decrease in population, separated by some fixed time period. This type of rapid change in phytoplankton population density is known as ‘*bloom*’. The excitable nature of blooms is the main characteristics in the plankton ecosystem. Due to the accumulation of high biomass or to the presence of toxicity, some of these blooms, more adequately called “harmful algal blooms” (HABs, [4]), are noxious to marine ecosystems or to human health and can produce great socioeconomic damage. Reduction of

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grazing pressure of zooplankton due to release of toxic substances by phytoplankton is one of the most interesting topics of research in the last few decades [1,5–10]. Chattopadhyay et al. [8] proposed a mathematical model for toxic phytoplankton (*Noctiluca Scintillans* belonging to the group Dinoflagellates of the division Dinophyta) and zooplankton (*Paracalanus* belonging to the group Copepoda) interaction and explores the role of toxin producing phytoplankton (TPP) behind harmful algal blooms. The general form of mathematical model they have considered is the following two nonlinear coupled ordinary differential equations

$$\frac{dP}{dt} = rP \left( 1 - \frac{P}{k} \right) - \beta f(P)Z \tag{1a}$$

$$\frac{dZ}{dt} = \beta_1 f(P)Z - \delta Z - \rho g(P)Z \tag{1b}$$

where  $P \equiv P(t)$  is the density of toxin producing phytoplankton (TPP) population and  $Z \equiv Z(t)$  is the density of zooplankton population at any instant of time ‘ $t$ ’ subject to the non-negative initial condition  $P(0) = P_0 \geq 0$  and  $Z(0) = Z_0 \geq 0$ . In above model system ‘ $r$ ’ is the intrinsic growth rate and ‘ $k$ ’ is the environmental carrying capacity of TPP population. ‘ $f(P)$ ’ represents the functional response for the grazing of phytoplankton by zooplankton and ‘ $g(P)$ ’ describes the distribution of toxic substance which ultimately contributes to the death of zooplankton populations.  $\beta(>0)$  is the maximum uptake rate for zooplankton species,  $\beta_1(>0)$  denotes the ratio of biomass conversion (satisfying the obvious restriction  $0 < \beta_1 < \beta$ ) and  $\delta(>0)$  is the natural death rate of zooplankton. Finally  $\rho(>0)$  denotes the rate of toxic substances produced by per unit biomass of phytoplankton. They have analyzed the above model system by taking various combinations of functional response terms. In [10], the authors have analyzed the following type of model system

$$\frac{dP}{dt} = rP \left( 1 - \frac{P}{k} \right) - \beta f(P)Z \tag{2a}$$

$$\frac{dZ}{dt} = \beta_1 f(P)Z - \delta Z - \rho g(P(t - \tau))Z \tag{2b}$$

with  $f(P) = P$  and  $g(P) = P/(\gamma + P)$  based upon the assumption that the process of toxin liberation follows a discrete variation and ‘ $\tau$ ’ is the discrete time period required for the maturation of phytoplankton cells to liberate toxic substances. Based upon the model system (2), the authors studied the oscillation of phytoplankton and zooplankton populations along with the stability condition for oscillatory behaviour.

Based upon their ideas, we intend to study a model system similar to (2) with the assumption that  $f(P)$  and  $g(P)$  are described by same type of function, namely, Holling type-II functions. With this assumption the model system (2) takes a new form as follows

$$\frac{dP}{dt} = rP \left( 1 - \frac{P}{k} \right) - \beta f(P)Z \tag{3a}$$

$$\frac{dZ}{dt} = \beta_1 f(P)Z - \delta Z - \rho f(P(t - \tau))Z \tag{3b}$$

subject to the initial condition  $P(\theta) \geq 0, Z(0) = Z_0 \geq 0$  where  $P(\theta)$  is a continuous function in  $-\tau \leq \theta \leq 0$ . As phytoplankton is the most favourable food source for zooplankton within aquatic environments and the Holling type-II functional form is a reasonable assumption to describe the law of predation we will assume Holling type-II functional form for ‘ $f(P)$ ’ [10,11]. It is quite reasonable to assume that the law of grazing must be same whether it contributes toward the growth of zooplankton species or it suppresses the rate of grazing due to presence of toxic substances. In this paper we are mainly interested in the dynamics of the toxic-phytoplankton–zooplankton model system with the same functional form for  $f(P)$  and  $g(P)$  in presence of time delay. So far as our knowledge goes, in most of the works authors have assumed  $f(P)$  and  $g(P)$  are of different type. Based upon the above model system we intend to study the periodic oscillatory nature of phytoplankton and zooplankton populations by considering a discrete time delay as bifurcation parameter. After finding the conditions for stable periodic oscillation we also study the global existence of periodic solutions for the model system (3).

The paper is organized as follows. In the next section we briefly mention the basic local dynamical behaviour of the model system near steady states, where we make the assumption that the process of toxin liberation follows no time

lag, that is its effect is instantaneous to the grazers. In Section 3 we consider the delayed phytoplankton–zooplankton model whose construction is based upon the assumption that process of toxin liberation follows a discrete time variation, then we deduce the condition for exchange of stability behaviour around the coexisting equilibrium point through a Hopf-bifurcation by considering the discrete time delay as bifurcation parameter. Section 4 consists of a purely algebraic technique based on normal form theory and center manifold arguments for retarded functional differential equations [12] to investigate the stability of small amplitude periodic solutions arising from Hopf-bifurcation. Using the technique for global Hopf-bifurcation results due to Wu [13], we prove the global existence of periodic solutions in Section 5. In Section 6, we give some numerical simulation results in support of the analytical findings. Finally, we mention basic outcomes of our mathematical findings and their ecological significance in the concluding section.

## 2. Basic mathematical model: Stability analysis

The interaction of toxic-phytoplankton–zooplankton systems and their dynamical behaviour will be considered in this paper based upon the following nonlinear ordinary differential equation model system (with  $\tau = 0$ )

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{k}\right) - \frac{\beta PZ}{\gamma + P} \quad (4a)$$

$$\frac{dZ}{dt} = \frac{\beta_1 PZ}{\gamma + P} - \delta Z - \frac{\rho PZ}{\gamma + P} \quad (4b)$$

subject to the initial condition  $P(0) = P_0 \geq 0$ ,  $Z(0) = Z_0 \geq 0$ . Here ‘ $r$ ’ is the intrinsic growth rate of phytoplankton species in absence of zooplankton and ‘ $\gamma$ ’ is the half saturation constant for a Holling type II functional response. The biological significance of all other parameters have already been mentioned in the introduction. Now we make a basic assumption that  $\beta_1 > \rho$ , that is, the ratio of biomass consumed by zooplankton is greater than the rate of toxic substance liberation by phytoplankton species. The vector fields associated with the model system (4) are smooth within  $R_+^2$  and thus the existence and uniqueness criteria hold good and it is easy to verify that  $P(t), Z(t) > 0$  whenever  $P(0), Z(0) > 0$  [14]. Regarding the boundedness of the solution for the model system (4) we state the following lemma:

**Lemma 1.** *All the solutions of the model system (4) with the positive initial conditions  $P_0, Z_0$  are uniformly bounded within a region  $B \subseteq R_+^2$  where  $B = \{(P, Z) \in R_+^2 : \beta_1 P + \beta Z = \frac{L}{\delta} + \epsilon; L = \frac{(r+\delta)\beta_1 k}{2}\}$ .*

This lemma is obvious and we omit its proof (interested readers may consult the work [15]).

The equilibrium states for the model system (4) are given by  $E_0(0, 0)$  (trivial equilibrium),  $E_1(k, 0)$  (axial equilibrium) and  $E_*(P^*, Z^*)$  (positive interior equilibrium), where  $P^* = \frac{\delta\gamma}{\beta_1 - \rho - \delta}$  and  $Z^* = \frac{r}{\beta} \left(1 - \frac{P^*}{k}\right) (\gamma + P^*)$ . Thus for existence of  $E_*$  we must have  $\beta_1 > \rho + \delta$  and  $P^* < k$ . For local stability of these equilibrium states we have to find the Jacobian matrix at these equilibrium states corresponding to the model system (4). We then have to calculate eigenvalues of the corresponding Jacobian matrices to characterize the local stability of these equilibrium states. The Jacobian matrix for the model system (4) at any point  $(P, Z)$  within positive quadrant is given by

$$J(P, Z) = \begin{pmatrix} r - \frac{2rP}{k} - \frac{\beta\gamma Z}{(\gamma + P)^2} & -\frac{\beta P}{\gamma + P} \\ \frac{(\beta_1 - \rho)\gamma Z}{(\gamma + P)^2} & \frac{(\beta_1 - \rho)P}{\gamma + P} - \delta \end{pmatrix}. \quad (5)$$

It is easy to check that  $E_0$  is always a saddle point,  $E_1$  is locally asymptotically stable whenever  $E_*$  does not exist and a saddle point whenever  $E_*$  exists. At  $E_*$  the Jacobian matrix takes the form

$$J_* = \begin{pmatrix} r - \frac{2rP^*}{k} - \frac{\beta\gamma Z^*}{(\gamma + P^*)^2} & -\frac{\beta P^*}{\gamma + P^*} \\ \frac{(\beta_1 - \rho)\gamma Z^*}{(\gamma + P^*)^2} & 0 \end{pmatrix}.$$

Thus by Routh–Hurwitz criteria  $E_*$  is locally asymptotically stable whenever  $k < 2P^* + \gamma$ . In this case  $E_*$  is a global attractor also. The stability behaviour changes as  $k$  passes through the critical value  $k = k^* = 2P^* + \gamma$  and the system exhibits Hopf-bifurcation. Thus the existence criteria for Hopf-bifurcation can be stated as follows:

**Lemma 2.** *If  $k = k^* = 2P^* + \gamma$  with  $\beta_1 > \rho + \delta$ , then the model system (4) exhibits a Hopf-bifurcation around  $E_*$ . This implies that a small amplitude periodic orbit bifurcates near  $E_*$  whenever  $k$  passes through its critical value  $k^*$ .*

A detailed analysis in this direction can be found in [8].

### 3. Mathematical model with delay: Local stability analysis

The delayed model system is developed based upon the fact that the liberation of toxic substances by phytoplankton species is not an instantaneous phenomena rather it must be mediated by some time lag which is required for the maturity of toxic-phytoplankton. If we assume ‘ $\tau$ ’ is the discrete time period required for the maturity of toxic-phytoplankton then model system (4) can be extended as a delay differential equation model system as follows

$$\frac{dP}{dt} = rP \left( 1 - \frac{P}{k} \right) - \frac{\beta P Z}{\gamma + P} \tag{6a}$$

$$\frac{dZ}{dt} = \frac{\beta_1 P Z}{\gamma + P} - \delta Z - \frac{\rho P(t - \tau) Z}{\gamma + P(t - \tau)} \tag{6b}$$

subject to the initial condition  $P(\theta) \geq 0, Z(0) = Z_0 \geq 0$  where  $P(\theta)$  for  $-\tau \leq \theta \leq 0$ . Under these assumptions the model system (6) must possess a unique solution [16,17]. We will consider here the time delay as a control parameter starting with the assumption that  $E_*$  is locally asymptotically stable whenever  $\tau = 0$ . For local asymptotic stability analysis of  $E_*(P^*, Z^*)$  for the model system (6), we linearize the model system (6) with help of the transformations  $P(t) = P^* + x_1(t), Z(t) = Z^* + x_2(t)$  ( $x_1$  and  $x_2$  are small perturbation terms whose second and higher order terms can be neglected) and which results in the following system of linear delay differential equations :

$$\frac{dx_1}{dt} = ax_1 + bx_2 \tag{7a}$$

$$\frac{dx_2}{dt} = cx_1 + dx_1(t - \tau) \tag{7b}$$

where the coefficients are given by

$$a = \frac{rP^*}{\gamma + P^*} \left( 1 - \frac{2P^*}{k} - \frac{\gamma}{k} \right), \quad b = -\frac{\beta P^*}{\gamma + P^*}, \quad c = \frac{\beta_1 \gamma Z^*}{(\gamma + P^*)^2}, \quad d = -\frac{\rho \gamma Z^*}{(\gamma + P^*)^2}.$$

The characteristic equation corresponding to the linearized system (7) is given by

$$G(\lambda, \tau) \equiv \lambda^2 - a\lambda - b(c + de^{-\lambda\tau}) = 0. \tag{8}$$

At  $\tau = 0, E_*$  is locally asymptotically stable whenever  $k < 2P^* + \gamma$ . Now  $E_*$  will be locally asymptotically stable for  $\tau \geq 0$  if the real part of  $G(\lambda, 0)$  is negative and  $G(i\omega, \tau) \neq 0$  for every real  $\omega$  and  $\tau \geq 0$ . We assume that for some values of  $\tau (\neq 0)$ , there exists a real number  $\omega > 0$  such that  $\lambda = i\omega$  is a root of the characteristic Eq. (8). Then separating real and imaginary parts of  $G(i\omega, \tau) = 0$  we get

$$\omega^2 + bc + bd \cos \omega\tau = 0 \tag{9}$$

$$bd \sin \omega\tau - a\omega = 0. \tag{10}$$

The above two equations can be combined as

$$\omega^4 + \omega^2(a^2 + 2bc) + b^2(c^2 - d^2) = 0. \tag{11}$$

Let us denote

$$\Delta = (a^2 + 2bc)^2 - 4b^2(c^2 - d^2)$$

Then the roots of biquadratic equation (11) are given by

$$\omega_{\pm}^2 = \frac{1}{2} \left[ -(a^2 + 2bc) \pm \sqrt{\Delta} \right].$$

Now as we need  $\omega(>0)$  as a real quantity, we have to consider the following cases

- (i)  $\Delta < 0$  imply no purely imaginary roots of the form  $i\omega$ ,
- (ii)  $\Delta > 0, c^2 > d^2, a^2 + 2bc > 0$  imply no purely imaginary roots of the form  $i\omega$ ,
- (iii)  $\Delta > 0, c^2 < d^2, a^2 + 2bc > 0$  imply one purely imaginary root  $i\omega_+$ ,
- (iv)  $\Delta > 0, c^2 < d^2, a^2 + 2bc < 0$  implies one purely imaginary root  $i\omega_+$ ,
- (v)  $\Delta > 0, c^2 > d^2, a^2 + 2bc < 0$  imply two purely imaginary roots  $i\omega_{\pm}$ .

Since the existence of the positive interior equilibrium  $E_*$  demands  $c^2 > d^2$ , the cases (iii) and (iv) can be excluded. For the cases (i) and (ii) we don't have any purely imaginary roots of the characteristic Eq. (8). This shows that the positive interior equilibrium point  $E_*$  is absolutely stable (locally asymptotically stable for all  $\tau \geq 0$ ) under the parametric restrictions  $P^* < k < 2P^* + \gamma, \beta_1 > \rho + \delta$  with the conditions (i) and (ii).

We now consider the case (v), which implies  $c^2 > d^2, a^2 + 2bc < 0$ ; in this case there are two purely imaginary roots given by  $\omega_{\pm} = \sqrt{\frac{1}{2}[-(a^2 + 2bc) \pm \sqrt{\Delta}]}$  where  $0 < \omega_- < \omega_+$ . From the Eqs. (9) and (10) we have

$$\sin(\omega_{\pm}\tau) = \frac{a\omega_{\pm}}{bd} < 0 \tag{12}$$

$$\cos(\omega_{\pm}\tau) = \frac{(-a^2 \pm \sqrt{\Delta})}{2bd}. \tag{13}$$

Since in this case  $(-a^2 \pm \sqrt{\Delta}) < 0, \cos(\omega_{\pm}\tau) < 0$ . Thus  $\tau_k^{\pm} = \frac{1}{\omega_{\pm}}[\arcsin(\frac{a\omega_{\pm}}{bd}) + 2k\pi], k = 0, 1, 2, \dots$  Let us define  $\theta_{\pm} = \arcsin(\frac{a\omega_{\pm}}{bd})$ . Then  $\pi < \theta_- < \theta_+ < 3\frac{\pi}{2}, 0 < \omega_- < \omega_+$  and arcsin is decreasing. We have thus two sequences of delays  $\tau_k^+ = \frac{\theta_+ + 2k\pi}{\omega_+}$  and  $\tau_k^- = \frac{\theta_- + 2k\pi}{\omega_-}$  for which there are two purely imaginary roots of the Eq. (8).

We will now study how the real parts of the roots of (8) vary as  $\tau$  varies in a small neighborhood of  $\tau_k^+$  as well as  $\tau_k^-$ . Let  $\lambda = u + i\omega$  be a root of (8), then substituting  $\lambda = u + i\omega$  in the characteristic equation and separating real and imaginary parts we have

$$H_1(u, \omega, \tau) \equiv u^2 - au - bc - \omega^2 - bde^{-u\tau} \cos \omega\tau = 0$$

$$H_2(u, \omega, \tau) \equiv 2u\omega - a\omega + bde^{-u\tau} \sin \omega\tau = 0.$$

Now we have  $H_1(0, \omega_{\pm}, \tau_k^{\pm}) = H_2(0, \omega_{\pm}, \tau_k^{\pm}) = 0$ . Also we have  $|J|_{(0, \omega_{\pm}, \tau_k^{\pm})} > 0$  where

$$J = \begin{pmatrix} \frac{\partial H_1}{\partial u} & \frac{\partial H_1}{\partial \omega} \\ \frac{\partial H_2}{\partial u} & \frac{\partial H_2}{\partial \omega} \end{pmatrix}.$$

Hence by the implicit function theorem  $H_1(u, \omega, \tau) = 0 = H_2(u, \omega, \tau)$  defines  $u, \omega$  as a function of  $\tau$  in a neighborhood of  $(0, \omega_{\pm}, \tau_k^{\pm})$  such that  $u_+(\tau_k^+) = 0, \omega_+(\tau_k^+) = \omega_+, \frac{du_+}{d\tau}(\tau_k^+) > 0$  and  $u_-(\tau_k^-) = 0, \omega_-(\tau_k^-) = \omega_-, \frac{du_-}{d\tau}(\tau_k^-) < 0$ . Now we are in a position to state the following theorem regarding the Hopf-bifurcation:

**Theorem 1.** For the delayed model system (6),

- (i) if  $P^* < k < 2P^* + \delta$  with  $\beta_1 > \rho + \delta$ , either  $(a^2 + 2bc)^2 < 4b^2(c^2 - d^2)$  or  $a^2 + 2bc > 0$ , and  $(a^2 + 2bc)^2 - 4b^2(c^2 - d^2) > 0$  then  $E_*$  is locally asymptotically stable for all  $\tau \geq 0$
- (ii) if  $P^* < k < 2P^* + \gamma$  with  $\beta_1 > \rho + \delta$ , and  $a^2 + 2bc < 0, (a^2 + 2bc)^2 - 4b^2(c^2 - d^2) > 0$  then there exists a positive integer  $n$ , such that the equilibrium  $E_*$  switches  $n$  times from stability to instability to stability and so on such that  $E_*$  is locally asymptotically stable whenever  $\tau \in [0, \tau_0^+) \cup (\tau_0^-, \tau_1^+) \cup \dots \cup (\tau_{n-1}^-, \tau_n^+)$  and is unstable whenever  $\tau \in (\tau_0^+, \tau_0^-) \cup (\tau_1^+, \tau_1^-) \cup \dots \cup (\tau_{n-1}^+, \tau_{n-1}^-)$  and  $\tau > \tau_n^+$ . The model system (6) undergoes a Hopf-bifurcation around  $E_*$  for every  $\tau = \tau_k^{\pm}$ .

**4. Stability of periodic solutions**

In the previous section we have obtained the conditions for which the model system (6) undergoes a Hopf bifurcation by considering ‘ $\tau$ ’ as bifurcation parameter. In this section we determine the stability of periodic solutions

bifurcating from  $E_*$  at  $\tau = \tau_k^\pm$ . For this purpose we deduce the normal form of the model system (6) by following the way as introduced by Faria and Magalhaes [12], choosing ‘ $\tau$ ’ as bifurcation parameter in a small neighborhood of  $\tau = \tau_k^\pm$ . Introducing the time scaling  $t \rightarrow \frac{t}{\tau}$  in Eq. (6) we get the following transformed system of equations

$$\frac{dP}{dt} = \tau \left[ rP \left( 1 - \frac{P}{k} \right) - \frac{\beta PZ}{\gamma + P} \right] \tag{14a}$$

$$\frac{dZ}{dt} = \tau \left[ \frac{\beta_1 PZ}{\gamma + P} - \delta Z - \frac{\rho P(t-1)Z(t)}{\gamma + P(t-1)} \right]. \tag{14b}$$

We now apply the transformation  $x_1(t) = P(t) - P^*$ ,  $x_2(t) = Z(t) - Z^*$ , thus (14) reduces to

$$\frac{dx_1(t)}{dt} = \tau \left[ ax_1(t) + bx_2(t) + \sum_{m \geq 2} \frac{1}{m!} h_m^{(11)} x_1^m(t) + \sum_{i+j \geq 2} \frac{1}{i!j!} h_{ij}^{(11)} x_1^i(t) x_2^j(t) \right] \tag{15a}$$

$$\begin{aligned} \frac{dx_2(t)}{dt} = \tau \left[ cx_1(t) + dx_2(t-1) + \sum_{m \geq 2} \frac{1}{m!} h_m^{(2)} x_1^m(t) + \sum_{i+j \geq 2} \frac{1}{i!j!} h_{ij}^{(21)} x_1^i(t) x_2^j(t) \right. \\ \left. + \sum_{i+j \geq 2} h_{ij}^{(22)} x_1^i(t-1) x_2^j(t) \right] \end{aligned} \tag{15b}$$

where  $a, b, c, d$  have the same expression as given in Section 3 and the  $h$ ’s are given as follows

$$\begin{aligned} h^{(11)} &= rP \left( 1 - \frac{P}{k} \right), & h^{(2)} &= \frac{\beta_1 PZ}{\gamma + P}, & h^{(21)} &= Z \left( \frac{\beta_1 P}{\gamma + P} - \delta \right), & h^{(22)} &= -Z \left( \delta + \frac{\rho P}{\gamma + P} \right) \\ h_m^{(11)} &= \left( \frac{\partial^m h^{(11)}}{\partial P^m} \right)_{(P^*, Z^*)}, & h_{ij}^{(11)} &= \left( \frac{\partial^{i+j} h^{(11)}}{\partial P^i \partial Z^j} \right)_{(P^*, Z^*)}, & h_m^{(2)} &= \left( \frac{\partial^m h^{(2)}}{\partial P^m} \right)_{(P^*, Z^*)} \\ h_{ij}^{(21)} &= \left( \frac{\partial^{i+j} h^{(21)}}{\partial P^i \partial Z^j} \right)_{(P^*, Z^*)}, & h_{ij}^{(22)} &= \left( \frac{\partial^{i+j} h^{(22)}}{\partial P^i \partial Z^j} \right)_{(P^*, Z^*)}. \end{aligned}$$

The system of Eq. (15) in a phase space  $C := C([-1, 0], R_+^2)$  can be written in matrix form as follows

$$\frac{dX}{dt} = \tau L(X_t) + \tau F(X_t) \tag{16}$$

where  $X \equiv X(t)$  is a column vector  $(x_1(t), x_2(t))^T$ ,  $X_t \in C$  satisfying the condition  $X_t(\theta) = X(t + \theta)$ ,  $-1 \leq \theta \leq 0$ .  $L$  is a continuous linear function, mapping  $C$  into  $R_+^2$  and is defined by

$$L(\phi) = \begin{pmatrix} a\phi_1(0) + b\phi_2(0) \\ c\phi_1(0) + d\phi_1(-1) \end{pmatrix}, \quad \phi \in C.$$

This hypothesis implies that there exist an  $2 \times 2$  matrix  $\eta(\theta)$  for  $-1 \leq \theta \leq 0$  whose elements are of bounded variation such that

$$L(\phi) = \int_{-1}^0 [d\eta(\theta)]\phi(\theta) \tag{17}$$

and

$$d\eta(\theta) = \left[ \begin{pmatrix} a & b \\ c & 0 \end{pmatrix} \delta(\theta) + \begin{pmatrix} 0 & 0 \\ 0 & d \end{pmatrix} \delta(\theta + 1) \right] d\theta \tag{18}$$

where  $\delta$  denotes the Dirac-delta function. Also  $F : C \rightarrow R_+^2$  is given by

$$F(\phi) = \left( \begin{array}{c} \sum_{m \geq 2} \frac{1}{m!} h_m^{(11)} \phi_1^m(0) + \sum_{i+j \geq 2} \frac{1}{i!j!} h_{ij}^{(11)} \phi_1^i(0) \phi_2^j(0) \\ \sum_{m \geq 2} \frac{1}{m!} h_m^{(2)} \phi_1^m(0) + \sum_{i+j \geq 2} \frac{1}{i!j!} h_{ij}^{(21)} \phi_1^i(0) \phi_2^j(0) + \sum_{i+j \geq 2} h_{ij}^{(22)} \phi_1^i(-1) \phi_2^j(0) \end{array} \right).$$

We now expand  $F(\phi)$  in a Taylor series about  $\phi$

$$F(\phi) = F_0(\phi) + F_1(\phi) + \frac{1}{2!} F_2(\phi) + \dots$$

Comparing we get  $F_0(\phi) = F_1(\phi) = (0, 0)^T$  and

$$\frac{1}{n!} F_n(\phi) = \left( \begin{array}{c} \frac{1}{n!} h_n^{(11)} \phi_1^n(0) + \sum_{i+j=n} \frac{1}{i!j!} h_{ij}^{(11)} \phi_1^i(0) \phi_2^j(0) \\ \frac{1}{n!} h_n^{(2)} \phi_1^n(0) + \sum_{i+j=n} \frac{1}{i!j!} h_{ij}^{(21)} \phi_1^i(0) \phi_2^j(0) + \sum_{i+j=n} h_{ij}^{(22)} \phi_1^i(-1) \phi_2^j(0) \end{array} \right). \tag{19}$$

Introducing a new parameter  $\kappa = \tau - \tau_k$  we rewrite (16) as

$$\frac{dX}{dt} = \tau_k L(X_t) + \tilde{F}(X_t, \kappa) \tag{20}$$

where  $\tilde{F}(X_t, \kappa) = \kappa L(X_t) + (\kappa + \tau_k) F(X_t)$  and  $\tau_k$  denotes any one of the critical values  $\tau_k^\pm$  ( $k = 0, 1, 2, \dots$ ) at which Eq. (8) has a pair of purely imaginary roots  $\pm i\omega$ . The linear operator defined by (17) generates a strong continuous semigroup of bounded linear operators with the infinitesimal generator

$$A\phi = \begin{cases} \frac{d\phi}{d\theta}, & -1 \leq \theta < 0 \\ \int_{-1}^0 [d\eta(\theta)]\phi(\theta), & \theta = 0. \end{cases} \tag{21}$$

At  $\tau = \tau_k$ , the infinitesimal generator  $A$  has a pair of imaginary eigenvalues  $\pm i\sigma_k$  where  $\sigma_k = \omega\tau_k$ . Let us consider  $\wedge = \{-i\sigma_k, i\sigma_k\}$ . Let  $P$  be the eigen-space associated with  $\wedge$  and we decompose  $C$  by  $\wedge$  as  $C = P \oplus Q$  where  $Q$  is the complementary space of  $P$  in  $C$  and  $\dim P = 2$ . Let us define  $C^* = C([0, 1], R_+^{2*})$ , where  $R_+^{2*}$  is the two dimensional vector space of row vectors and for any  $\psi$  in  $C^*$  consider the adjoint bilinear form  $(\cdot, \cdot)$  on  $C^* \times C$  associated with the linear equation

$$(\psi, \phi) = \psi(0)\phi(0) - \int_{-1}^0 \int_0^\theta \psi(\xi - \theta) d\eta(\theta) \phi(\xi) d\xi \tag{22}$$

and the adjoint operator  $A^*$  of  $A$  is defined as

$$A^*\psi(s) = \begin{cases} -\frac{d\psi(s)}{ds} & 0 \leq s \leq 1 \\ \int_{-1}^0 d\eta(s)\psi(-s) & s = 0. \end{cases} \tag{23}$$

Let  $\Phi = (\Phi_1, \Phi_2)$  be a basis for  $P$  and  $\Psi = \begin{pmatrix} \Psi_1 \\ \Psi_2 \end{pmatrix}$  be a basis for the dual space  $P^*$  in  $C^*$  associated with the eigenvalues  $\pm i\sigma_k$  of the adjoint equations. Then it can be normalized so that  $(\Psi, \Phi) = I$  where  $I$  is a  $2 \times 2$  identity matrix. We consider (20) in  $C([-1, 0] : C)$  and still denote it by  $C$ . Thus we write the  $2 \times 2$  matrices  $\Phi$  and  $\Psi$  of the form  $\Phi(\theta) = (\Phi_1(\theta) \quad \Phi_2(\theta))$ ,  $\Phi_1(\theta) = e^{i\sigma_k\theta} v$ ,  $\Phi_2(\theta) = \overline{\Phi_1(\theta)}$ ,  $-1 \leq \theta \leq 0$  and  $\Psi(s) = \begin{pmatrix} \Psi_1(s) \\ \Psi_2(s) \end{pmatrix}$ ,  $\Psi_1(s) = e^{-i\sigma_k s} u^T$ ,  $\Psi_2(s) = \overline{\Psi_1(s)}$ ,  $0 \leq s \leq 1$  where  $v = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$  and  $u = \begin{pmatrix} u_1 \\ u_2 \end{pmatrix}$  are vectors in  $C^2$  and also  $\dot{\Phi} = \Phi B$ ,

where  $B$  is a  $2 \times 2$  diagonal matrix  $B = \begin{pmatrix} i\sigma_k & 0 \\ 0 & -i\sigma_k \end{pmatrix}$ . With the help of (22) after some computation, we have

$$v = \begin{pmatrix} 1 \\ \frac{i\sigma_k - a\tau_k}{b\tau_k} \end{pmatrix}, \quad u = \begin{pmatrix} u_1 \\ \frac{b\tau_k u_1}{i\sigma_k} \end{pmatrix} \tag{24a}$$

where

$$u_1 = \frac{i\sigma_k}{(2 + d\tau_k e^{-i\sigma_k})i\sigma_k - a\tau_k(1 + d\tau_k e^{-i\sigma_k})}. \tag{24b}$$

Enlarge the phase space  $C$  to the space  $BC$  of the functions from  $[-1, 0]$  to  $R_+^2$  uniformly continuous on  $[-1, 0)$  and with a jump discontinuity at 0. The elements of  $BC$  are of the form  $\phi + X_0\alpha$  where  $\phi \in C, \alpha \in R_+^2$  that is we can identify  $BC$  with  $C \times R_+^2$ . The projection of  $C$  upon  $P, \phi \rightarrow \Phi(\Psi, \phi)$  associated with decomposition  $C = P \oplus Q$  is now replaced by  $\pi : BC \rightarrow P$  such that  $\pi(\phi + X_0\alpha) = \Phi[(\Psi, \phi) + \Psi(0)\alpha]$  leading to the decomposition  $BC = P \oplus \ker \pi$  with the property  $Q \subset \ker \pi$ . We decompose  $X_t = \Phi n(t) + s_t, n(t) \in C^2, s_t \in Q' = \ker \pi \cap C^1$  and Eq. (20) is equivalent to

$$\dot{n} = Bn(t) + \psi(0)\tilde{F}(\Phi n + s, \kappa) \tag{25a}$$

$$\frac{ds}{dt} = A_{Q'}s + (I - \pi)X_0\tilde{F}(\Phi n + s, \kappa) \tag{25b}$$

where  $X_0 = X_0(\theta)$  is given by

$$X_0(\theta) = \begin{cases} I & \theta = 0 \\ 0 & -1 \leq \theta < 0 \end{cases} \tag{26}$$

and  $A_{Q'} : Q' \rightarrow \ker \pi$ . We refer to [12] for detailed explanation of the notations described above. We consider the Taylor expansion of the second terms of the right hand sides of Eq. (14)

$$\psi(0)\tilde{F}(\Phi n + s, \kappa) = \frac{1}{2!}f_2^1(n, s, \kappa) + \frac{1}{3!}f_3^1(n, s, \kappa) + h.o.t \tag{27a}$$

$$(I - \pi)X_0\tilde{F}(\Phi n + s, \kappa) = \frac{1}{2!}f_2^2(n, s, \kappa) + \frac{1}{3!}f_3^2(n, s, \kappa) + h.o.t \tag{27b}$$

where  $f_j^1(n, s, \kappa)$  and  $f_j^2(n, s, \kappa)$  are homogeneous polynomials in  $(n, s, \kappa)$  of degree  $j, j = 2, 3$  with coefficients in  $C^2$  and  $\ker \pi$ , h.o.t. stands for higher order terms. The flow of (25) on the center manifold tangent to the invariant subspace  $P$  at  $n = 0, \kappa = 0$  is given by

$$\dot{n} = Bn + \frac{1}{2}h_2^1(n, 0, \kappa) + \frac{1}{3!}h_3^1(n, 0, \kappa) + h.o.t. \tag{28}$$

where  $h_j^1, j = 2, 3$  are homogeneous polynomials of degree  $j$  in  $(n, \kappa)$ , which is in normal form. We consider  $V_j^{(m+p)}(X)$  as the linear space of homogeneous polynomials of degree  $j$  in  $m + p$  variables,  $n = (n_1, n_2, \dots, n_m), \kappa = (\kappa_1, \kappa_2, \dots, \kappa_p)$  with coefficients in  $X$ . For  $j \geq 2$ , let  $M_j$  denote operator defined in  $V_j^{m+p}(R^m \times \ker \pi)$  with values in the same space by

$$\begin{aligned} M_j(p, h) &= (M_j^1 p, M_j^2 h) \\ (M_j^1 p)(n, \kappa) &= [B, p(\cdot, \kappa)](n) \\ (M_j^2 h)(n, \kappa) &= D_x h(n, \kappa) Bn - A_{Q'}(h(n, \kappa)) \end{aligned}$$

where  $[B, p(\cdot, \kappa)]$  denotes the Lie bracket defined by

$$[B, p(\cdot, \kappa)](n) = D_n p(n, \kappa) Bn - Bp(n, \kappa)$$



Here the operator  $M_j^1$  acts on  $V_j^3(\mathcal{C}^2)$  and we consider the decomposition  $V_j^3(\mathcal{C}^2) = (\text{Im } M_j^1) \oplus (\text{ker } M_j^1)$ . We have  $\text{ker}(M_j^1) = \text{span}\{n^q \kappa^l e_k : (q, \bar{\lambda}) = \lambda_k, k = 1, 2, q \in N, l \in N, |(q, l)| = j\}$  where  $\{e_1, e_2\}$  is the canonical basis for  $\mathcal{C}^2$ . We have now

$$(M_j p)(n, \kappa) = i\sigma_k \begin{pmatrix} n_1 \frac{\partial p_1}{\partial n_1} - n_2 \frac{\partial p_1}{\partial n_2} - p_1 \\ n_1 \frac{\partial p_2}{\partial n_1} - n_2 \frac{\partial p_2}{\partial n_2} + p_2 \end{pmatrix}.$$

Thus

$$\text{ker}(M_2^1) = \text{span} \left\{ \begin{pmatrix} n_1 \kappa \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ n_2 \kappa \end{pmatrix} \right\}$$

and

$$\text{ker}(M_3^1) = \text{span} \left\{ \begin{pmatrix} n_1^2 n_2 \\ 0 \end{pmatrix}, \begin{pmatrix} n_1 \kappa^2 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ n_1 n_2^2 \end{pmatrix}, \begin{pmatrix} 0 \\ n_2 \kappa^2 \end{pmatrix} \right\}.$$

From (27a)

$$f_2^1(n, s, \kappa) = \psi(0)[2L(\kappa)(\Phi n + s) + F_2(\Phi n + s, \tau_k)].$$

We have now

$$\Phi n = \begin{pmatrix} e^{i\sigma_k \theta} v_1 n_1 + e^{-i\sigma_k \theta} \bar{v}_1 n_2 \\ e^{i\sigma_k \theta} v_2 n_1 + e^{-i\sigma_k \theta} \bar{v}_2 n_2 \end{pmatrix}$$

with the help of (19) we get

$$f_2^{(1)}(n, 0, \kappa) = \begin{pmatrix} 2A_1 n_1 \kappa + 2A_2 n_2 \kappa + a_{20} n_1^2 + 2a_{11} n_1 n_2 + a_{02} n_2^2 \\ 2\bar{A}_1 n_2 \kappa + 2\bar{A}_2 n_1 \kappa + \bar{a}_{02} n_1^2 + 2\bar{a}_{11} n_1 n_2 + \bar{a}_{20} n_2^2 \end{pmatrix}$$

where  $A_1 = \frac{i\sigma_k}{\tau_k} u^T v$ ,  $A_2 = -\frac{i\sigma_k}{\tau_k} u^T \bar{v}$  and bar denotes the complex conjugate.

$$\begin{aligned} a_{20} &= \tau_k \begin{pmatrix} u_1 h_2^{(11)} v_1^2 + 2u_1 h_{11}^{(11)} v_1 v_2 + u_2 h_2^{(2)} v_1^2 + 2u_2 h_{11}^{(21)} v_1 v_2 \\ + 2u_2 h_{11}^{(22)} e^{-i\sigma_k} v_1 v_2 + u_2 h_{20}^{(22)} e^{-2i\sigma_k} v_1^2 \end{pmatrix} \\ a_{11} &= \tau_k \begin{pmatrix} u_1 h_2^{(11)} v_1 \bar{v}_1 + u_1 h_{11}^{(11)} (v_1 \bar{v}_2 + v_2 \bar{v}_1) + u_2 h_2^{(2)} v_1 \bar{v}_1 + u_2 h_{11}^{(21)} (v_1 \bar{v}_2 + v_2 \bar{v}_1) \\ + u_2 h_{11}^{(22)} (e^{-i\sigma_k} v_1 \bar{v}_2 + e^{i\sigma_k} v_2 \bar{v}_1) + u_2 h_{20}^{(22)} v_1 \bar{v}_1 \end{pmatrix} \\ a_{02} &= \tau_k \begin{pmatrix} u_1 h_2^{(11)} \bar{v}_1^2 + 2u_1 h_{11}^{(11)} \bar{v}_1 v_2 + u_2 h_2^{(2)} \bar{v}_1^2 + 2u_2 h_{11}^{(21)} \bar{v}_1 v_2 \\ + 2u_2 h_{11}^{(22)} e^{i\sigma_k} \bar{v}_1 v_2 + u_2 h_{20}^{(22)} e^{2i\sigma_k} \bar{v}_1^2 \end{pmatrix}. \end{aligned}$$

Following [12], the second order terms in  $(n, \kappa)$  of the normal form on the center manifold are given by

$$h_2^1(n, 0, \kappa) = \text{Proj}_{\text{ker}(M_2^1)} f_2^1(n, 0, \kappa).$$

Thus we get

$$h_2^1(n, 0, \kappa) = \begin{pmatrix} 2A_1 n_1 \kappa \\ 2\bar{A}_1 n_2 \kappa \end{pmatrix}.$$

For the cubic terms in the normal form, we have

$$h_3^1(n, 0, \kappa) \in \text{ker}(M_3^1).$$

In order to study the local stability of the periodic orbit arising from Hopf-bifurcation the terms  $o(|n|\kappa^2)$  are irrelevant. Hence we only need to compute the coefficients of  $\begin{pmatrix} n_1^2 n_2 \\ 0 \end{pmatrix}$  and  $\begin{pmatrix} 0 \\ n_1 n_2^2 \end{pmatrix}$ . The canonical basis for  $V_2^3(\mathcal{C}^2)$  consists of

following twelve elements

$$\begin{pmatrix} n_1^2 \\ 0 \end{pmatrix}, \begin{pmatrix} n_1 n_2 \\ 0 \end{pmatrix}, \begin{pmatrix} n_1 \kappa \\ 0 \end{pmatrix}, \begin{pmatrix} n_2^2 \\ 0 \end{pmatrix}, \begin{pmatrix} n_2 \kappa \\ 0 \end{pmatrix}, \begin{pmatrix} \kappa^2 \\ 0 \end{pmatrix}$$

$$\begin{pmatrix} 0 \\ n_1^2 \end{pmatrix}, \begin{pmatrix} 0 \\ n_1 n_2 \end{pmatrix}, \begin{pmatrix} 0 \\ n_1 \kappa \end{pmatrix}, \begin{pmatrix} 0 \\ n_2^2 \end{pmatrix}, \begin{pmatrix} 0 \\ n_2 \kappa \end{pmatrix}, \begin{pmatrix} 0 \\ \kappa^2 \end{pmatrix}.$$

The image of each one of the elements of this basis under  $M_2^1/i\sigma_k$  are respectively

$$\begin{pmatrix} n_1^2 \\ 0 \end{pmatrix}, -\begin{pmatrix} n_1 n_2 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 0 \end{pmatrix}, -3\begin{pmatrix} n_2^2 \\ 0 \end{pmatrix}, -2\begin{pmatrix} n_2 \kappa \\ 0 \end{pmatrix}, -\begin{pmatrix} \kappa^2 \\ 0 \end{pmatrix}$$

$$3\begin{pmatrix} 0 \\ n_1^2 \end{pmatrix}, \begin{pmatrix} 0 \\ n_1 n_2 \end{pmatrix}, 2\begin{pmatrix} 0 \\ n_1 \kappa \end{pmatrix}, -\begin{pmatrix} 0 \\ n_2^2 \end{pmatrix}, \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \kappa^2 \end{pmatrix}.$$

We have

$$\begin{aligned} \frac{1}{3!}h_3^1(n, 0, \kappa) &= \frac{1}{3!}\text{Proj}_{\ker(M_3^1)}\overline{f_3^1}(n, 0, \kappa) \\ &= \frac{1}{3!}\text{Proj}_{\ker'(M_3^1)}\overline{f_3^1}(n, 0, 0) + o(|n| \kappa^2) \end{aligned}$$

where  $\ker'(M_3^1) = \text{span} \left\{ \begin{pmatrix} n_1^2 n_2 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ n_1 n_2^2 \end{pmatrix} \right\}$  and  $\overline{f_3^1}(n, 0, 0)$  is the third order terms of the equation after computing the normal form of the equation up to second order. Following the computation scheme given in [12] we have

$$\overline{f_3^1}(n, 0, 0) = f_3^1(n, 0, 0) + \frac{3}{2} \left[ (D_n f_2^1)U_2 - (D_n U_2)h_2^1 \right]_{(n,0,0)} + \frac{3}{2} \left[ (D_s f_2^1)g \right]_{(n,0,0)}$$

We now compute  $\frac{1}{3!}h_3^1(n, 0, \kappa)$  step by step

Step 1: Computation for  $\text{Proj}_{\ker'(M_3^1)} \left[ (D_n f_2^1)U_2 \right]_{(n,0,0)}$

Following the procedure in [12] we get

$$U_2(n, 0, 0) = (M_2^1)^{-1} P_{1,2}^1 f_2^1(n, 0, 0)$$

where  $(M_2^1)^{-1}$  is the right inverse of  $(M_2^1)$  and  $P_{1,2}^1 f_2^1(n, 0, 0)$  is the projection of  $f_2^1(n, 0, 0)$  on the image space of  $(M_2^1)$ . Now

$$f_2^1(n, 0, 0) = \begin{pmatrix} a_{20}n_1^2 + 2a_{11}n_1n_2 + a_{02}n_2^2 \\ \overline{a}_{02}n_1^2 + 2\overline{a}_{11}n_1n_2 + \overline{a}_{20}n_2^2 \end{pmatrix}.$$

Hence

$$U_2(n, 0, 0) = \begin{pmatrix} \frac{1}{i\sigma_k} (a_{20}n_1^2 - 2a_{11}n_1n_2 - \frac{1}{3}a_{02}n_2^2) \\ \frac{1}{i\sigma_k} \left( \frac{1}{3}\overline{a}_{02}n_1^2 + 2\overline{a}_{11}n_1n_2 - \overline{a}_{20}n_2^2 \right) \end{pmatrix}.$$

Again

$$D_n f_2^1 = \begin{pmatrix} 2a_{20}n_1 + 2a_{11}n_2 & 2a_{11}n_1 + 2a_{02}n_2 \\ 2\overline{a}_{02}n_1 + 2\overline{a}_{11}n_2 & 2\overline{a}_{11}n_1 + 2\overline{a}_{20}n_2 \end{pmatrix}$$

and after some algebraic calculations we get

$$\text{Proj}_{\ker'(M_3^1)} \left[ (D_n f_2^1)U_2 \right]_{(n,0,0)} = \begin{pmatrix} \frac{2i}{\sigma_k} (a_{20}a_{11} - 2|a_{11}|^2 - \frac{1}{3}|a_{02}|^2)n_1^2 n_2 \\ -\frac{2i}{\sigma_k} (\overline{a}_{20}a_{11} - 2|a_{11}|^2 - \frac{1}{3}|a_{02}|^2)n_1 n_2^2 \end{pmatrix}.$$

Step 2: Computation for  $\text{Proj}_{\ker'(M_3^1)} [(D_n U_2)h_2^1]_{(n,0,0)}$

We have  $h_2^1(n, 0, 0) = 0$  and so

$$\text{Proj}_{\ker'(M_3^1)} [(D_n U_2)h_2^1]_{(n,0,0)} = 0.$$

Step 3: Computation for  $\text{Proj}_{\ker'(M_3^1)} f_3^1(n, 0, 0)$

We have  $f_3^1(n, 0, 0) = \Psi(0)F_3(\Phi n, \tau_k)$  and from (19)

$$\frac{1}{3!} F_3(\Phi n, \tau_k) = \tau_k \left( \begin{array}{c} \frac{1}{3!} h_3^{(11)} \phi_1^3(0) + \frac{1}{2!} h_{21}^{(11)} \phi_1^2(0) \phi_2(0) \\ \frac{1}{3!} h_3^{(2)} \phi_1^3(0) + \frac{1}{2!} h_{21}^{(21)} \phi_1^2(0) \phi_2(0) + \frac{1}{2!} h_{21}^{(22)} \phi_1^2(-1) \phi_2(0) + \frac{1}{3!} h_{30}^{(22)} \phi_1^3(-1) \end{array} \right).$$

After computing we have

$$\text{Proj}_{\ker'(M_3^1)} f_3^1(n, 0, 0) = \begin{pmatrix} 3a_{21}n_1^2n_2 \\ 3\bar{a}_{21}n_1n_2^2 \end{pmatrix}$$

where

$$a_{21} = \tau_k \begin{pmatrix} u_1 h_3^{(11)} v_1^2 \bar{v}_1 + u_1 h_{21}^{(11)} (v_1^2 \bar{v}_2 + 2v_1 \bar{v}_1 v_2) + u_2 h_3^{(2)} v_1^2 \bar{v}_1 \\ + u_2 h_{21}^{(21)} (v_1^2 \bar{v}_2 + 2v_1 \bar{v}_1 v_2) + u_2 h_{21}^{(22)} (e^{-2i\sigma_k} v_1^2 \bar{v}_2 + 2v_1 \bar{v}_1 v_2) \\ + u_2 h_{30}^{(22)} e^{-2i\sigma_k} v_1^2 \bar{v}_1 \end{pmatrix}.$$

Step 4: Computation for  $\text{Proj}_{\ker'(M_3^1)} [(D_s f_2^1)g]_{(n,0,0)}$

Here  $g$  is a second order homogeneous polynomial in  $(n_1, n_2, \kappa)$  with coefficients in  $Q'$ . Let

$$g(n_1, n_2, \kappa) = g_{110}n_1n_2 + g_{101}n_1\kappa + g_{011}n_2\kappa + g_{200}n_1^2 + g_{020}n_2^2 + g_{002}\kappa^2$$

where  $g = \begin{pmatrix} g_1 \\ g_2 \end{pmatrix}$  is the unique solution of

$$(M_2^2 g)(n, \kappa) = (I - \pi) [2L(\kappa)(\Phi n) + F_2(\Phi n, \tau_k)]$$

which acts in  $V_2^3(Q')$ . Following [12] we have

$$\begin{aligned} (M_2^2 g)(n, \kappa) &= D_n g(n, \kappa) Bn - A_{Q'}(g(n, \kappa)) \\ &= D_n g(n, \kappa) Bn - \dot{g}(n, \kappa) - X_0 [L(\tau_k)(g(n, \kappa)) - \dot{g}(n, \kappa)(0)] \\ &= (I - \pi) X_0 [2l(\kappa)(\Phi n) + F_2(\Phi n, \tau_k)]. \end{aligned}$$

Thus from the above it follows that  $h = h(n, 0)(\theta)$  can be evaluated by the system

$$\dot{g}(n) - D_n g(n) Bn = \Phi \Psi(0) [2L(0)(\Phi n) + F_2(\Phi n, \tau_k)] \tag{29}$$

$$\dot{g}(n)(0) - L(\tau_k)(g(n)) = 2L(0)(\Phi n) + F_2(\Phi n, \tau_k) \tag{30}$$

where we have used  $\pi(\phi + X_0\kappa) = \Phi[(\Psi, \phi) + \Psi(0)\kappa]$  and  $\dot{g}$  denotes the derivative of  $g(n)(\theta)$  with respect to  $\theta$ . We have now

$$\begin{aligned} f_2^1(n, s, 0) &= \Psi(0) [2L(0)(\Phi n + s) + F_2(\Phi n + s, \tau_k)] \\ &= \tau_k \begin{pmatrix} u_1 & u_2 \\ \bar{u}_1 & \bar{u}_2 \end{pmatrix} \begin{pmatrix} h_2^{(11)} c_1^2 + 2h_{11}^{(11)} c_1 d_1 \\ h_2^{(2)} c_1^2 + 2h_{11}^{(21)} c_1 d_1 + 2h_{11}^{(22)} c_2 d_1 + h_{20}^{(22)} c_2^2 \end{pmatrix} \end{aligned}$$

where

$$\begin{aligned} c_1 &= v_1 n_1 + \bar{v}_1 n_2 + s_1(0) \\ c_2 &= e^{-i\sigma_k} v_1 n_1 + e^{i\sigma_k} \bar{v}_1 n_2 + s_1(-1) \\ d_1 &= v_2 n_1 + \bar{v}_2 n_2 + s_2(0). \end{aligned}$$

After some computation, we have the second order column matrix

$$\left[ (D_s f_2^1) g \right]_{(n,0,0)} = 2\tau_k \begin{pmatrix} u_1 & u_2 \\ \bar{u}_1 & \bar{u}_2 \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix}$$

where

$$\begin{aligned} w_1 &= \left[ b_0(h_2^{(11)} g^1(0) + h_{11}^{(11)} g^2(0) + h_2^{(2)} g^1(0) + h_{11}^{(11)} g^2(0)) + c_0(h_{11}^{(22)} g^2(0) + h_{20}^{(22)} g^1(-1)) \right. \\ &\quad \left. + d_0(h_{11}^{(21)} g^1(0) + h_{11}^{(11)} g^1(0) + h_{11}^{(22)} g^1(-1)) \right] \\ w_2 &= [b_0(h_2^{(11)} g^1(0) + h_{11}^{(11)} g^2(0) + h_2^{(2)} g^1(0) + h_{11}^{(11)} g^2(0)) + c_0(h_{11}^{(22)} g^2(0) + h_{20}^{(22)} g^1(-1)) \\ &\quad + d_0(h_{11}^{(21)} g^1(0) + h_{11}^{(22)} g^1(-1) + h_{11}^{(11)} g^1(0))] \end{aligned}$$

and

$$b_0 = v_1 n_1 + \bar{v}_1 n_2, \quad c_0 = e^{-i\sigma_k} v_1 n_1 + e^{i\sigma_k} \bar{v}_1 n_2, \quad d_0 = v_2 n_1 + \bar{v}_2 n_2$$

with

$$g^1(0) = g^1 \frac{\partial s_1(0)}{\partial s_1}, \quad g^2(0) = g^2 \frac{\partial s_2(0)}{\partial s_2}, \quad g^1(-1) = g^1 \frac{\partial s_1(-1)}{\partial s_1}.$$

Also we may write

$$\begin{aligned} g^1(0) &= g_{110}^1(0) n_1 n_2 + g_{200}^1(0) + g_{020}^1(0) n_2^2 \\ g^1(-1) &= g_{110}^1(-1) n_1 n_2 + g_{200}^1(-1) + g_{020}^1(-1) n_2^2 \\ g^2(0) &= g_{110}^2(0) n_1 n_2 + g_{200}^2(0) + g_{020}^2(0) n_2^2. \end{aligned}$$

Thus

$$\text{Proj}_{\ker(M_3^1)} \left[ (D_s f_2^1) g \right]_{(n,0,0)} = \begin{pmatrix} 2c_3 n_1^2 n_2 \\ 2\bar{c}_3 n_1 n_2^2 \end{pmatrix}$$

where  $c_3$  is given by

$$c_3 = u^T \tau_k \begin{pmatrix} [h_2^{(11)} g_{110}^1(0) v_1 + h_2^{(11)} g_{200}^1(0) \bar{v}_1 + h_{11}^{(11)} g_{110}^1(0) v_2 + h_{11}^{(11)} g_{200}^1(0) \bar{v}_2 + h_{11}^{(11)} g_{110}^2(0) v_1] \\ [h_{11}^{(11)} g_{200}^2(0) \bar{v}_1 + h_2^{(2)} g_{110}^1(0) v_1 + h_2^{(2)} g_{200}^1(0) \bar{v}_1 + h_{11}^{(21)} g_{110}^1(0) v_2 + h_{11}^{(21)} g_{200}^1(0) \bar{v}_2 \\ + h_{11}^{(11)} g_{110}^2(0) v_1 + h_{11}^{(11)} g_{200}^2(0) \bar{v}_1 + h_{11}^{(22)} g_{110}^1(-1) v_2 + h_{11}^{(22)} g_{200}^1(-1) \bar{v}_2 \\ + h_{11}^{(22)} e^{-i\sigma_k} g_{110}^2(0) v_1 + h_{11}^{(22)} e^{i\sigma_k} g_{200}^2(0) \bar{v}_1 + h_{20}^{(22)} e^{-i\sigma_k} g_{110}^1(-1) v_1 + h_{20}^{(22)} e^{i\sigma_k} g_{200}^1(-1) \bar{v}_1] \end{pmatrix}.$$

Again from (29) and (30) we obtain the differential equation for  $g_{110}(\theta)$  and  $g_{200}(\theta)$  as

$$\dot{g}_{110}(\theta) = (\phi_1 \quad \phi_2) \begin{pmatrix} 2a_{11} \\ 2\bar{a}_{11} \end{pmatrix} \tag{31}$$

$$\dot{g}_{200}(\theta) - 2i\sigma_k g_{200}(\theta) = (\phi_1 \quad \phi_2) \begin{pmatrix} a_{20} \\ \bar{a}_{02} \end{pmatrix} \tag{32}$$

with the conditions

$$\dot{g}_{110}(0) - L(\tau_k)(g_{110}) = \tau_k \begin{pmatrix} a_1 \\ b_1 \end{pmatrix} \tag{33}$$

$$\dot{g}_{200}(0) - L(\tau_k)(g_{200}) = \tau_k \begin{pmatrix} a_2 \\ b_2 \end{pmatrix} \tag{34}$$

where

$$g_{110}(\theta) = \begin{pmatrix} g_{110}^1(\theta) \\ g_{110}^2(\theta) \end{pmatrix}, \quad g_{200}(\theta) = \begin{pmatrix} g_{200}^1(\theta) \\ g_{200}^2(\theta) \end{pmatrix}$$

and

$$\begin{aligned}
 a_1 &= 2h_2^{(11)}v_1\bar{v}_1 + 2h_{11}^{(1)}(v_1\bar{v}_2 + v_2\bar{v}_1) \\
 b_1 &= 2h_2^{(2)}v_1\bar{v}_1 + 2h_{11}^{(21)}(v_1\bar{v}_2 + v_2\bar{v}_1) + 2h_{11}^{(22)}(e^{-i\sigma_k}v_1\bar{v}_2 + e^{i\sigma_k}\bar{v}_1v_2) + 2h_{20}^{(22)}v_1\bar{v}_1 \\
 a_2 &= h_2^{(11)}v_1^2 + 2h_{11}^{(1)}v_1v_2 \\
 b_2 &= h_2^{(2)}v_1^2 + 2h_{11}^{(21)}v_1v_2 + 2h_{11}^{(22)}e^{-i\sigma_k}v_1v_2 + h_{20}^{(22)}e^{-2i\sigma_k}v_1^2.
 \end{aligned}$$

Solving (31) and (32) subject to the conditions (33) and (34) we get

$$g_{110}(\theta) = \frac{2}{i\sigma_k} \left( a_{11}e^{i\sigma_k\theta}v - \bar{a}_{11}e^{-i\sigma_k\theta}\bar{v} \right) + C_1 \tag{35}$$

$$g_{200}(\theta) = -\frac{1}{i\sigma_k} \left( a_{20}e^{i\sigma_k\theta}v + \frac{1}{3}\bar{a}_{02}e^{-i\sigma_k\theta}\bar{v} \right) + C_2e^{2i\sigma_k\theta} \tag{36}$$

where  $C_1 = \begin{pmatrix} c_1^{(1)} & c_1^{(2)} \end{pmatrix}$  and  $C_2 = \begin{pmatrix} c_2^{(1)} & c_2^{(2)} \end{pmatrix}$  are as follows

$$\begin{aligned}
 c_1^{(1)} &= -\frac{b_1}{c+d} \\
 c_1^{(2)} &= \frac{1}{b} \left( \frac{ab_1}{c+d} - a_1 \right) \\
 c_2^{(1)} &= \frac{bb_2\tau_k^2 + 2i\sigma_k a_2\tau_k}{2i\sigma_k(2i\sigma_k - a\tau_k) + b\tau_k^2(c + de^{-2i\sigma_k})} \\
 c_2^{(2)} &= \frac{a_2\tau_k^2(c + de^{-2i\sigma_k}) + b_2\tau_k(2i\sigma_k - a\tau_k)}{2i\sigma_k(2i\sigma_k - a\tau_k) + b\tau_k^2(c + de^{-2i\sigma_k})}.
 \end{aligned}$$

Thus the above four steps together give the result

$$\frac{1}{3!}h_3^1(n, 0, \kappa) = \begin{pmatrix} A_3n_1^2n_2 \\ \bar{A}_3n_1n_2^2 \end{pmatrix}$$

where  $A_3 = \frac{i}{2\sigma_k}(a_{20}a_{11} - 2|a_{11}|^2 - \frac{1}{3}|a_{02}|^2) + \frac{1}{2}(a_{21} + c_3)$ . Hence the normal form (28) becomes

$$\dot{n} = Bn + \begin{pmatrix} A_1n_1\kappa \\ \bar{A}_1n_2\kappa \end{pmatrix} + \begin{pmatrix} A_3n_1^2n_2 \\ \bar{A}_3n_1n_2^2 \end{pmatrix} + o(|n|\kappa^2 + |n|^4). \tag{37}$$

This normal form relative to P can be written in terms of the co-ordinates  $(x, y)$  by using the change of variables  $n_1 = x - iy, n_2 = x + iy$ , where  $i = \sqrt{-1}$ . Finally using the polar co-ordinates  $x = r \cos \theta, y = r \sin \theta$ , the normal form (37) becomes

$$\dot{r} = k_1r\kappa + k_2r^3 + o(\kappa^2\rho + |(r, \kappa)|^4) \tag{38a}$$

$$\dot{\theta} = -\sigma_k + o(|(r, \kappa)|) \tag{38b}$$

where  $k_1 = \text{Re}(A_1), k_2 = \text{Re}(A_3)$ . Summarizing the results obtained above leads us to the following theorem,

**Theorem 2.** *The flow of the Eq. (20) on the center manifold of the origin at  $\kappa = 0$  is given by (38). Moreover if  $k_2 \neq 0$  (generic Hopf bifurcation) the periodic orbits of Eq. (38) bifurcating from the origin  $r = 0, \kappa = 0$  are given by*

$$\begin{aligned}
 r(t, \kappa) &= \left[ -\frac{k_1\kappa}{k_2} \right]^{\frac{1}{2}} + o(\kappa) \\
 \theta(t, \kappa) &= -\sigma_k + o\left(|\kappa|^{\frac{1}{2}}\right)
 \end{aligned}$$

and the stability of periodic orbits depends upon the following conditions

- (i) if  $k_1 k_2 < 0$  (respectively  $k_1 k_2 > 0$ ) there exists a unique non trivial periodic orbit in the neighborhood of  $(r, \kappa) = (0, 0)$  for  $\kappa > 0$  (respectively  $\kappa < 0$ ) and no periodic orbit for  $\kappa < 0$  (respectively  $\kappa > 0$ ),
- (ii) the non trivial periodic orbit is stable if  $k_2 < 0$  and unstable if  $k_2 > 0$ .

**5. Global existence of periodic solutions**

In the earlier sections we have established that the model system (6) undergoes a Hopf bifurcation at  $E_*$  for  $\tau = \tau_k^\pm$  and also investigated the stability of bifurcating periodic solutions. In this section by using a global Hopf bifurcation theorem due to Wu [13] we study the global continuation of periodic solutions bifurcating from the point  $(E_*, \tau_k^+)$ ,  $k = 0, 1, 2, \dots$  for the model system (6). For convenience we write the model system (6) as

$$\dot{I} = F(I_t, \tau, T) \tag{39}$$

where  $I_t(\theta) = I(t + \theta) \in C([-\tau, 0], R_+^2)$  and  $I_t = (P_t, Z_t)$ . We use the following notations

$$\begin{aligned} \ell &= C([-\tau, 0], R_+^2) \\ \Sigma &= cl\{(I, \tau, T) \in \ell \times R_+ \times R_+ : I \text{ is a } T\text{-periodic solution of (39)}\} \\ N &= \{(\bar{I}, \bar{\tau}, \bar{T}) : F(\bar{I}, \bar{\tau}, \bar{T}) = 0\}. \end{aligned}$$

Let  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  denote the connected component of  $(E_*, \tau_k^+, \frac{2\pi}{\omega_+})$  in  $\Sigma$  where the expression for  $\tau_k^+$  and  $\omega_+$  are given in Section 3.

**Lemma 3.** *Whenever  $E_*$  exists, all the nontrivial periodic solution of (39) are uniformly bounded within  $R_+^2$ .*

**Proof.** Let  $\xi_1, \xi_2, \eta_1$  and  $\eta_2$  be the real quantities defined by

$$\begin{aligned} P(\xi_1) &= \min\{P(t)\} & P(\eta_1) &= \max\{P(t)\} \\ Z(\xi_2) &= \min\{Z(t)\} & Z(\eta_2) &= \max\{Z(t)\} \end{aligned}$$

where  $P(t)$  and  $Z(t)$  are nonconstant periodic solutions to (39). As our state space is  $R_+^2$ , we will look only for positive periodic solutions. From (6a) we get

$$0 = r - \frac{r}{k} P(\eta_1) - \frac{\beta Z(\eta_1)}{\gamma + P(\eta_1)} < r \left(1 - \frac{P(\eta_1)}{k}\right).$$

This implies

$$P(\eta_1) < k.$$

From (6b)

$$0 = \frac{\beta_1 P(\eta_2)}{\gamma + P(\eta_2)} - \delta - \frac{\rho P(\eta_2 - \tau)}{\gamma + P(\eta_2 - \tau)} < \frac{\beta_1 P(\eta_2)}{\gamma + P(\eta_2)} - \delta.$$

This shows

$$P(\eta_2) > \frac{\delta \gamma}{\beta_1 - \delta}.$$

Hence

$$\frac{\delta \gamma}{\beta_1 - \delta} < P(\eta_2) < P(\eta_1) < k. \tag{40}$$

Again from (6a)

$$0 = r \left(1 - \frac{P(\eta_2)}{k}\right) - \frac{\beta Z(\eta_2)}{\gamma + P(\eta_2)} < r - \frac{\beta Z(\eta_2)}{\gamma + P(\eta_2)}.$$

This implies

$$\beta Z(\eta_2) < r(\gamma + P(\eta_2)) < r(\gamma + k).$$

That is

$$Z(\eta_2) < \frac{r(\gamma + k)}{\beta}. \tag{41}$$

Hence by the relation (40) and (41) the lemma is confirmed.  $\square$

**Lemma 4.** Suppose  $E_*$  exists and  $k < 2P^* + \gamma$ . Then there is no any nontrivial  $\tau$ -periodic solution for the system (6).

**Proof.** Let us assume that the model system (6) has a nontrivial  $\tau$ -periodic solution. Then the model system (3) has also a periodic solution. For the model system (3) we note that the  $P$ -axis and  $Z$ -axis are invariant and the orbits of the model system (3) do not intersect each other. There is no solution which will cross the co-ordinate axes. If there be any periodic solution within the first quadrant, then there must be equilibrium in its interior and obviously  $E_*$  is there. Now if  $k < 2P^* + \gamma$  holds with the existence of  $E_*$  then  $E_*$  is globally asymptotically stable. Hence by the Benedixon-Dulac criterion the system (3) does not have any periodic orbit under the restriction mentioned in the lemma and the lemma is confirmed.  $\square$

**Theorem 3.** Suppose that  $E_*$  exists with  $k < 2P^* + \gamma$  and  $a^2 + 2bc < 0$ . Then for each  $\tau > \tau_k^+$  ( $k = 0, 1, \dots$ ), system (6) has at least  $k + 1$  periodic solutions.

**Proof.** The characteristic matrix of Eq. (6) at an equilibrium  $\bar{T} = (\bar{P}, \bar{Z})$  is given by

$$\nabla(\bar{T}, \tau, T)(\lambda) = \begin{pmatrix} \lambda - \bar{a} & -\bar{b} \\ -\bar{c} - \bar{d}e^{-\lambda\tau} & \lambda - \bar{e} \end{pmatrix} \tag{42}$$

where

$$\begin{aligned} \bar{a} &= r \left( 1 - \frac{2\bar{P}}{k} \right) - \frac{\beta\gamma\bar{Z}}{(\gamma + \bar{P})^2}, & \bar{b} &= -\frac{\beta\bar{P}}{\gamma + \bar{P}}, & \bar{c} &= \frac{\beta_1\gamma\bar{Z}}{(\gamma + \bar{P})^2}, \\ \bar{d} &= -\frac{\rho\gamma\bar{Z}}{(\gamma + \bar{P})^2} & \text{and} & & \bar{e} &= \frac{(\beta_1 - \rho)\bar{P}}{\gamma + \bar{P}} - \delta \end{aligned}$$

$(\bar{T}, \bar{\tau}, \bar{T})$  is called a center if  $F(\bar{T}, \bar{\tau}, \bar{T}) = 0$  and  $\det(\nabla(\bar{T}, \bar{\tau}, \bar{T})(\frac{2\pi}{T}i)) = 0$ . A center is said to be isolated if it is the only center in some neighbourhood of  $(\bar{T}, \bar{\tau}, \bar{T})$ . The model system (6) has three equilibria  $E_0(0, 0)$ ,  $E_1(k, 0)$  and  $E_*(P^*, Z^*)$ . It is clear from Section 2 that the equilibria  $E_0(0, 0)$  and  $E_1(k, 0)$  are not centers. From the discussion about the local Hopf-bifurcation theorem in Section 3, it follows that  $(E_*, \tau_k^+, \frac{2\pi}{\omega_+})$  is an isolated center and there exist  $\epsilon > 0$ ,  $\delta > 0$  and a smooth curve  $\lambda : (\tau_k^+ - \delta, \tau_k^+ + \delta) \rightarrow C$  such that  $\det(\nabla(\lambda(\tau))) = 0$ ,  $|\lambda(\tau) - i\omega_+| < \epsilon$  for all  $\tau \in [\tau_k^+ - \delta, \tau_k^+ + \delta]$  and

$$\lambda(\tau_k^+) = i\omega_+, \quad \left. \frac{d\text{Re}\lambda(\tau)}{d\tau} \right|_{\tau=\tau_k^+} > 0.$$

Let

$$\Omega_{\epsilon, \frac{2\pi}{\omega_+}} = \left\{ (u, T) : 0 < u < \epsilon, \left| T - \frac{2\pi}{\omega_+} \right| < \epsilon \right\}.$$

Now if  $|\tau - \tau_k^+| \leq \delta$  and  $(u, T) \in \partial\Omega_{\epsilon, \frac{2\pi}{\omega_+}}$ , then  $\det(\nabla(E_*, \tau, T)(u + \frac{2\pi}{T}i)) = 0$  iff  $u = 0$ ,  $\tau = \tau_k^+$  and  $T = \frac{2\pi}{\omega_+}$ .

Hence all the assumptions  $(A_1) \sim (A_4)$  of Theorem 8 in [13] are satisfied for  $m = 1$ . Moreover if we define  $H^\pm(E_*, \tau_k^+, \frac{2\pi}{\omega_+})(u, T) = \det(\nabla(E_*, \tau_k^+ \pm \delta, T)(u + \frac{2\pi}{T}i))$  then we have the crossing number of isolated centers  $(E_*, \tau_k^+, \frac{2\pi}{\omega_+})$  as follows

$$\begin{aligned} \gamma_1 \left( E_*, \tau_k^+, \frac{2\pi}{\omega_+} \right) &= \text{deg}_B \left( H^-(E_*, \tau_k^+, \frac{2\pi}{\omega_+}), \Omega_{\epsilon, \frac{2\pi}{\omega_+}} \right) - \text{deg}_B \left( H^+ \left( E_*, \tau_k^+, \frac{2\pi}{\omega_+} \right), \Omega_{\epsilon, \frac{2\pi}{\omega_+}} \right) \\ &= -1 \neq 0. \end{aligned}$$

Thus by Theorem 8 of [13], we conclude that the connected component  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  through  $(E_*, \tau_k^+, \frac{2\pi}{\omega_+})$  in  $\Sigma$  is unbounded. We will now show that the projection of  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  onto  $\tau$ -space is  $[\tau_k^+, \infty]$ . With the help of Lemma 4 the projection of  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  onto  $\tau$ -space is away from zero. Let us suppose that the projection of  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  onto  $\tau$ -space is bounded. This implies that the projection of  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  onto  $\tau$  space must include an interval of the form  $(0, \hat{\tau})$ . With the help of Lemma 4 this shows that the projection of  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  onto  $T$ -space is bounded. Hence by Lemma 3 the connected component  $\mu_{(E_*, \tau_k^+, \frac{2\pi}{\omega_+})}$  is bounded and we have a contradiction and consequently the theorem is confirmed.  $\square$

### 6. Numerical results

In this section, we present some numerical results for some particular values of the parameters associated with the model system (6). For ecological justification behind the choice of numerical values and related information, interested readers may consult the literature by Chattopadhyay et al. [8]. We consider the following model system

$$\frac{dP}{dt} = 2P \left( 1 - \frac{P}{108} \right) - \frac{0.7PZ}{5 + P} \tag{43a}$$

$$\frac{dZ}{dt} = \frac{0.6PZ}{5 + P} - .3654Z - \frac{0.2P(t - \tau)Z}{5 + P(t - \tau)} \tag{43b}$$

which has an interior equilibrium point  $E_*(52.80346820809254, 84.40611033414001)$  and this set of parameter values satisfies the local asymptotic stability conditions of  $E_*$  in absence of time delay. Substituting  $P(t) = 52.80346820809254 + x_1(t)$  and  $Z(t) = 84.40611033414001 + x_2(t)$  in (43) and then linearizing we get

$$\begin{aligned} \frac{dx_1}{dt} &= -0.0441006743738x_1 - 0.63945x_2, \\ \frac{dx_2}{dt} &= 0.07578571428571x_1 - 0.0252619047619x_1(t - \tau). \end{aligned} \tag{44}$$

As the conditions  $\Delta > 0$ ,  $c^2 > d^2$  and  $a^2 + 2bc < 0$  are satisfied, we find two purely imaginary roots  $i\omega_{\pm}$  with  $\omega_+ = 0.24583783672861$ ,  $\omega_- = 0.18585273350794$

After some usual algebraic calculations one can find the minimum value of the delay parameter ‘ $\tau$ ’ for the model system (43) for which the stability behaviour changes and the first critical values are given by

$$\tau_0^+ = 15.77200313837373, \quad \text{and} \quad \tau_0^- = 19.7669696683186$$

such that,  $E_*$  is locally stable for  $\tau \in [0, 15.77200313837373)$  and is unstable for  $\tau \in (15.77200313837373, 19.7669696683186)$ . The eigenvectors as defined in (24) are given by

$$\begin{aligned} u &= \begin{pmatrix} 0.42399156898581 + 0.09428853634629i \\ -0.2452543732444 + 1.1028465446809i \end{pmatrix} \\ v &= \begin{pmatrix} 1 \\ -0.06896657185675 - 0.38445200833312i \end{pmatrix}. \end{aligned}$$

Now one can calculate the relevant quantities to obtain the normal form by using any mathematical software (e.g. MATLAB, MAPLE), which results in the desired normal form (see Eq. (38)) as follows

$$\dot{r} = -0.02766106548628r\kappa - 0.00483827117482r^3 + o(\kappa^2\rho + |(r, \kappa)|^4) \tag{45a}$$

$$\dot{\theta} = -3.87735513241468 + o(|(r, \kappa)|). \tag{45b}$$

Finally the stability determining quantities for Hopf-bifurcating periodic solutions are given by

$$k_1 = -0.02766106548628,$$

$$k_2 = \text{Re}(-0.00483827117482 - 0.00917806049283i) = -0.00483827117482.$$



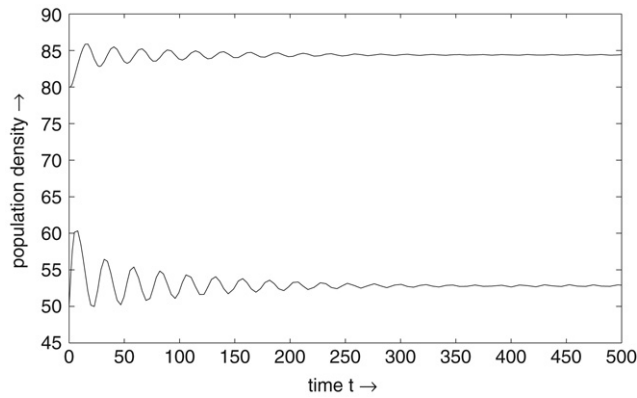


Fig. 1. Solution of (43) for  $\tau = 14.5 < \tau_0^+$  showing  $E_* = (52.80, 84.41)$  is stable.

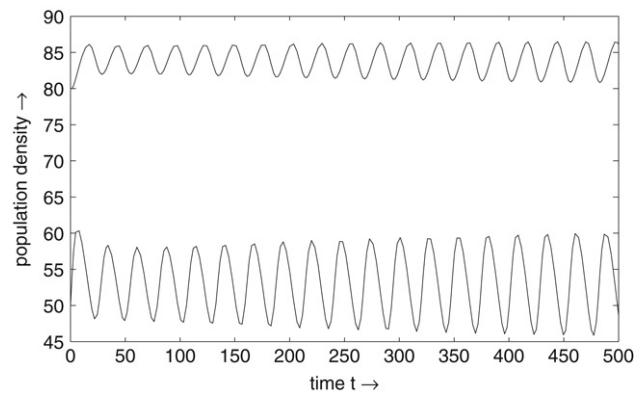


Fig. 2. Hopf bifurcating periodic solution of (43) for  $\tau = 16.2 > \tau_0^+$ .

As  $k_2 < 0$ , the periodic solution is stable. Interested readers may verify the results with other sets of parametric values or with some realistic field data.

From our analytical findings we have seen that  $E_*$  is locally asymptotically stable for  $\tau < \tau_0^+$ , Fig. 1 shows the simulation result for the model system (43) with  $\tau = 15.4 < \tau_0^+$ . Interior equilibrium point loses its stability as  $\tau$  passes through its critical value  $\tau = \tau_0^+$  and a Hopf bifurcation occurs, a stable Hopf-bifurcating periodic solution is depicted in Fig. 2.  $E_*$  remains unstable whenever  $\tau_0^+ < \tau < \tau_0^-$  and regains its stability for  $\tau > \tau_0^-$ . The equilibrium point  $E_*$  remains locally asymptotically stable whenever the delay parameter lies in the range  $\tau_0^- < \tau < \tau_1^+$  (see Fig. 3).  $E_*$  again switches from stability to instability as  $\tau$  passes through  $\tau = \tau_1^+$  and an unstable solution for the model system (43) is shown in Fig. 4. The numerical simulations we have done here illustrate the stable periodic solution arising from Hopf bifurcation at  $\tau = \tau_0^+$  and the switching of stability that occurs as the magnitude of the delay parameter increases gradually.

## 7. Discussion

Aquatic environments are not only a common habitat for phytoplankton as well as zooplankton but they constitute the aquatic ecosystem as it is. Global increase of harmful phytoplankton blooms in the last two decades have received a great deal of attention from several researchers, but the pattern and mechanism behind the planktonic blooms as well as its possible control have not yet taken a proper shape and hence it emerges as an interesting subject area for theoretical ecologists and their co-researchers. It is established by many of the present day researchers that one of the key factors behind phytoplankton bloom and succession is the toxic substance released by some phytoplankton species. The main objective of the present paper is to study the qualitative behaviour of an interacting phytoplankton–zooplankton system in presence of toxic substances with the help of a delay differential equation model system with same type

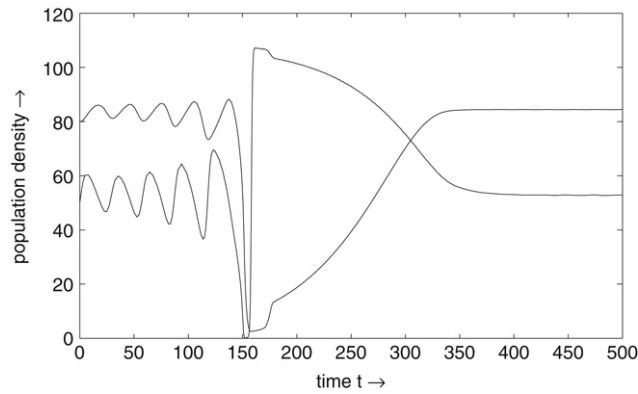


Fig. 3.  $E_*$  regains its stability for  $\tau_0^- < \tau = 20.5$ .

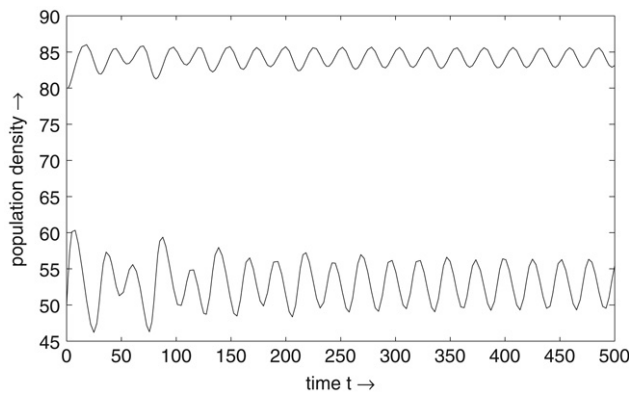


Fig. 4.  $E_*$  switches from stability to instability at  $\tau = 42.5 > \tau_1^+$ .

of functional response associated with the growth of zooplankton due to grazing of phytoplankton and the term which has a negative effect on the zooplankton growth due to presence of toxic substances. Analysis of the delayed model system is based upon the assumption that the toxin liberation by the phytoplankton species follows a discrete time variation and we have established that when the time delay ‘ $\tau$ ’ crosses a threshold value ‘ $\tau_k^\pm$ ’, the delayed toxic-phytoplankton–zooplankton model system enters into a Hopf bifurcation and we have a periodic orbit around a coexisting equilibrium point  $E_*$  for  $k = 0, 1, 2, \dots$ . We have shown that there are two possible cases for local asymptotic stability of  $E_*$  for the delayed model system, in the first possible case the positive interior equilibrium  $E_*$  is absolutely stable under certain parametric restrictions mentioned in the theorem of Section 3, (in this situation bloom phenomena never arise for the model system under consideration) and the second possible case includes a sequence of two time delays  $\tau_k^+(k = 0, 1, 2, \dots)$  and  $\tau_k^-(k = 0, 1, 2, \dots)$  under certain parametric restrictions for which the interior equilibrium point  $E_*$  is stable whenever  $\tau \in [0, \tau_0^+) \cup (\tau_0^-, \tau_1^+) \cup \dots$  and unstable for  $\tau \in (\tau_0^+, \tau_0^-) \cup (\tau_1^+, \tau_1^-) \cup \dots$ . This phenomenon is known as switching of stability which arises for our model system. The most interesting as well as mathematically important results we have presented in this paper is the stability criteria for the Hopf-bifurcating periodic solution by considering the discrete time lag ‘ $\tau$ ’ as bifurcation parameter. In order to understand the importance of the delay differential model system in studying the toxic-phytoplankton–zooplankton interaction compared to the non-delayed version and the effect of discrete time delays on dynamical behaviour of the model system we have considered ‘ $\tau$ ’ as bifurcation parameter. The local stability analysis of bifurcating periodic solutions is based on normal form theory and we have obtained the criterion for stable and unstable periodic solutions. According to the analytical results obtained in Section 4 our numerical example shows that the model system does not have any periodic orbit whenever  $0 \leq \tau < 15.77200313837373$  and all trajectories eventually approach the coexisting equilibrium point  $E_*$  starting from any point within the positive quadrant of state space. A unique periodic orbit emerges in the vicinity of  $E_*$  when ‘ $\tau$ ’ crosses the critical value  $\tau = 15.7720$  and for  $\tau < 19.7669696683186$

the periodic orbit is stable (see numerical results). This result indicates that there is a threshold limit of toxin liberation by the phytoplankton species below which the system does not have any excitable nature and above which the system shows excitability. These results are consistent with the dynamical behaviour of the toxic-phytoplankton–zooplankton interaction model with discrete time lag ‘ $\tau$ ’, and agree well with some earlier works. We have established the global existence of the bifurcating periodic solutions indicating the global oscillatory nature for the solution of the delayed model system when it exhibits oscillatory behaviour. Numerical simulations which we have performed show the switching of stability behaviour for the coexisting equilibrium point as the time delay crosses its different threshold values; interested readers may check the stability of oscillatory solutions obtained for  $\tau > \tau_1^+$ .

There is still a tremendous amount of work to do with the phytoplankton–zooplankton model, especially in presence of toxic substances. It would be interesting to study the emerging dynamical behaviour with various types of functional response terms to describe the grazing of phytoplankton by zooplankton and the effect of toxic substances liberated by the phytoplankton on their grazers in presence of discrete and continuous time delay in various terms associated with the model system. On the other hand, the study of dynamical behaviour of planktonic interaction models with varying magnitude of different parameters involved with the model system keeping the discrete time delay as a constant and verification of these results with some practical data set may suggest some control mechanism for harmful phytoplankton blooms. We hope, these issues will be well addressed in the near future and we leave them for the subject matter of our future research. Finally we would like to remark that the subject area, namely, ‘harmful phytoplankton blooms’ demands more in-depth and consistent research to understand the underlying mechanism behind recurrent bloom formations of different phytoplankton species along with possible control mechanisms.

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