

# A space-time state-space model of phytoplankton allelopathy

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## Abstract

An integro-differential equation system with nonlocal effects of interspecific allelopathic interaction has been studied to investigate the formation of spatio-temporal structures in toxin producing phytoplankton population. The model is inherently more realistic than the usual kind of reaction-diffusion model. Bifurcation from uniform steady-state solution has been examined. Evolution of steady-state spatially periodic structure and periodic standing waves have been studied. The model helps to investigate the blooms, pulses and succession in different patches of phytoplankton population. Numerical simulations for a hypothetical set of parameter values and experimental observations have been presented to substantiate the analytical findings.

*Keywords:* Phytoplankton; Allelopathy; Nonlocal effects; Time delay; Spatial structures

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## 1. Introduction

Plankton is the basis of all aquatic food chain. Phytoplankton in particular occupies the first trophic level in the food chain. Plankton does huge service for the earth: food for marine life, oxygen for human life and it also absorb carbon-di-oxide from the earth atmosphere. Harmful effects and allelochemical effect of planktonic algal are the recent topics in aquatic research. Bloom forming phytoplankton are directly harmful to the other planktonic biota including human beings. Patchiness in phytoplankton population is a commonly observed phenomenon. Several workers have noted that the increased population of one species of phytoplankton might affect the growth of one or several other species by the production of allelopathic toxins or stimulators, influencing the

formation of patches, each patch having the properties of exhibiting blooms, pulses and succession. It is now well established that quite a good number of phytoplankton species produce toxin (see the elegant review of Hellebust [5] and the book by Rice [13]) and a lot of theoretical works have been done on plankton patchiness with the help of reaction-diffusion mechanisms (see [11], [4]). When a bloom of a particular harmful phytoplankton occurs, the cumulative effect of the entire toxin released may effect the other organism, causing mass mortality. Such extreme concentrations or blooms are responsible for the massive localized mortality observed in fish and invertebrates in various places [13].

Maynard Smith [7] incorporated the effect of toxic substances in a two species Lotka–Volterra competitive system by assuming that each species produces a substance toxic to the other, but only when the other is present. Mukhopadhyay et al. [8] suggested that a species needs some time to mature before producing a substance which is toxic (or stimulatory) to the other, i.e., the production of an allelopathic substance by the competing species is not instantaneous, but occur after some discrete time lag required for maturity of the species. In a competing system, the allelopathic effect on that system needs its past history. So, instead of discrete time delay, continuous delay is more appropriate.

Britton [1] introduced the concept of double convolution in population models as time convolution is necessarily effective to rise to a convolution in space. It is evident that the nonlocal spatial effect occurs not only due to diffusion but also due to allelopathic interaction between the species. So, it also seems reasonable to assume that the production of toxic substance by one of the competing species allelopathic to the other and will be effective within a certain range of area, beyond which there will be no effect. Presence of nonlocal term brings about a variety of solution behavior which is not possible to obtain from a scalar local reaction diffusion equation [3]. So, considering all above, we modify our model [8] in general.

In this paper, we have considered a computational method for determining regions in parameter space corresponding to linear stability or instability of a uniform steady-state solution of the considered system in plankton allelopathy. Investigation on nonlocal allelopathic effect as well as effect of distributed time delay on planktonic world is our main objective of study.

In an earlier work [8], we observed that the two species competitive and allelopathic system as proposed by a delay differential equations model where spatial variation was absent showed that the time delay could drive the competitive system to sustained oscillations only when the allelopathy is of stimulatory nature but no such phenomenon had been observed when the allelopathy was of inhibitory type. In the latter case it was also observed that at the steady-state one species has always a lower value than the other. Hence, although the delay effect produced by delayed allelochemical production can regulate the densities of the different competing species in the aquatic ecosystem by influencing seasonal succession, blooms or pulses when the allelochemical is stimulatory, no such effect of regulation could be noted if the allelochemical was inhibitory. But as in the planktonic world, most of the allelochemical interactions are of inhibitory type, one should conceptualize a well-posed model that can explain the important attributes of planktonic growth such as blooms, pulses and succession when

the interacting species produce toxic allelochemicals. The present work is an attempt towards developing such a model. The integro-differential reaction-diffusion model of phytoplankton population involving competition and allelopathic interaction proposed by us in this paper is thus a modification and improvement of the delay-differential equations model as proposed in our earlier work.

## 2. The mathematical model

Generally two types of blooms, “spring” bloom and “red tides” occur in aquatic system. Spring blooms and red tides may be explained by sustained oscillation and multistability, respectively. Several researchers tried to explain the nature of planktonic blooms by different approaches: for example, nutrient upwelling by Edwards and Brindley [2], spatial patchiness by Matthews and Brindley [6], species diversity by Pitchford and Brindley [12], etc. But the nature of planktonic blooms through nonlocal delay differential model is still unknown. In this paper a Lotka–Volterra competitive model will be modified and analyzed to explain the nature of planktonic blooms. Lotka–Volterra competitive model is well studied [9] and the results obtained from this dynamics may be tested in real life situation. In the formulation of the model we consider two toxin producing competitive plankton species, namely, *Nitzschia* sp. and *Chaetoceros* spp. and the growth of the species follows the law of logistic growth [10]. We assume that each species produces toxin only in the presence of other and require some time for maturity of the species to produce toxin. The effect of toxin substance on each species is not depend only on the population density at one point in space, but depends on the weighted average involving values at all points in space as the species moving (by diffusion) and hence nonlocality arises in the system.

Considering the above assumptions and facts, the following two species competition model with nonlocal effect may be formulated by means of partial differential equations.

The modified two species competition model [8] in general, can be written as

$$\begin{aligned} \frac{\partial N_1}{\partial T} &= N_1 \left[ K_1 - \alpha_1 N_1 - \beta_{12} N_2 - \gamma_1 N_2 \int_{-R_1}^{R_1} \int_{-\infty}^t F_{12}(\mathbf{r}_1, \tau_1) \right. \\ &\quad \left. \times N_1(\mathbf{r} - \mathbf{r}_1, t - \tau_1) d\tau_1 d\mathbf{r}_1 \right], \\ \frac{\partial N_2}{\partial T} &= N_2 \left[ K_2 - \alpha_2 N_2 - \beta_{21} N_1 - \gamma_2 N_1 \int_{-R_2}^{R_2} \int_{-\infty}^t F_{21}(\mathbf{r}_2, \tau_2) \right. \\ &\quad \left. \times N_2(\mathbf{r} - \mathbf{r}_2, t - \tau_2) d\tau_2 d\mathbf{r}_2 \right], \end{aligned} \quad (2.1)$$

where  $N_j \equiv N_j(\mathbf{r}, t)$ 's ( $j = 1, 2$ ) are the population densities (number of cells per litre) of two competing species at a certain position  $\mathbf{r}$  with respect to certain frame of references at time  $t$ ;  $K_1, K_2$  are the rates of cell proliferation per hour;  $\alpha_1, \alpha_2$  are the rates of intraspecific competition of the first and second species, respectively;  $\beta_{12}, \beta_{21}$  are the rates of inter-specific competition of the first and second species, respectively

and  $K_j/\alpha_j$  ( $j = 1, 2$ ) are environmental carrying capacities (representing the number of cells per liter). The units of  $\alpha_1, \alpha_2, \beta_{12}$  and  $\beta_{21}$  are per hour per cell, and the unit of time is in hours.  $\gamma_1, \gamma_2$  are the rates of toxic inhibition of the first species by the second and vice versa.  $\tau_1, \tau_2 > 0$  are the times (in hours) required to produce the “allelochemical” of the first and second species, respectively [8].  $\mathbf{r}_j \in [0, R_j]$  ( $j = 1, 2$ ) are the range upto which the allelopathic effects are effective. We make the following assumption on  $F_{pq}(\mathbf{r}, t)$  ( $p \neq q; p, q = 1, 2$ ) [1]:

H1.  $F \equiv F_{pq}(\mathbf{r}, t) \geq 0$  (as a weighting function);  $F \in L^1(\mathbb{R}^n \times (0, \infty))$  indicates that the convolution is spatio-temporal and  $tF \in L^1(\mathbb{R}^n \times (0, \infty))$ .

H2.  $F$  satisfies the normalization condition, i.e.,

$$\int_{-\infty}^{\infty} \int_0^{\infty} F_{pq}(\mathbf{r}, t) dt d\mathbf{r} = 1.$$

H3.  $F = F(r, t)$ . The Kernel  $F$  assumes that the nonlocal effect depends only on the distance, and not on the direction.

Besides the above-mentioned assumptions (H1–H3) the following assumption on  $F_{pq}(\mathbf{r}, t)$  is made as there will be no allelopathic effect when  $|\mathbf{r}| > R_p (> 0)$   $p = 1, 2$ , i.e.,

H4.  $F_{pq}(\mathbf{r}, t)$  is an even function of  $\mathbf{r}$  vanishing outside an interval  $[0, R_p]$ . So,  $F_{pq}(\mathbf{r}, t)$  is defined as  $F_{pq}(\mathbf{r}, t) = 0$ , when  $\mathbf{r} \ni [0, R_p]$   $p = 1, 2$ .

We consider such Kernel functions satisfying all the above assumptions on them. Therefore,

$$\begin{aligned} & \int_{-R_p}^{R_p} \int_{-\infty}^t F_{pq}(\mathbf{r}_p, \tau_p) N_p(\mathbf{r} - \mathbf{r}_p, t - \tau_p) d\tau_p d\mathbf{r}_p \\ & \equiv \int_{-\infty}^{\infty} \int_{-\infty}^t F_{pq}(\mathbf{r} - \mathbf{r}_p, t - \tau_p) N_p(\mathbf{r}_p, \tau_p) d\tau_p d\mathbf{r}_p = F_{pq} * N_p. \end{aligned} \quad (2.2)$$

Alternatively, the model system is considered as follows

$$\begin{aligned} \frac{\partial N_1}{\partial T} &= N_1 [K_1 - \alpha_1 N_1 - \beta_{12} N_2 - \gamma_1 N_2 F_{12} * N_1], \\ \frac{\partial N_2}{\partial T} &= N_2 [K_2 - \alpha_2 N_2 - \beta_{21} N_1 - \gamma_2 N_1 F_{21} * N_2]. \end{aligned} \quad (2.3)$$

The double convolution  $F_{pq} * N_p$  will be reduced to be purely temporal or purely spatial form by taking the Kemels in the form  $F_{pq}(\mathbf{r} - \mathbf{r}_p, t - \tau_p) = \delta(\mathbf{r}) F_{pq}(t - \tau_p)$  and  $F_{pq}(\mathbf{r} - \mathbf{r}_p, t - \tau_p) = \delta(t) F_{pq}(\mathbf{r} - \mathbf{r}_p)$ , respectively, where  $\delta$  represents the Dirac delta function. The suffixes  $t$  and  $s$  denote temporal and the spatial cases, respectively.

Note that  $F_{pq}(\mathbf{r} - \mathbf{r}_p, t - \tau_p)$  ( $p, q = 1, 2; p \neq q$ ) represent Kernel functions quantifying the effect of  $N_p(r_p, \tau_p)$  on  $N_q(r, t)$ .

### 3. Equilibria

The uniform steady states of allelopathic Inhibitory system are as follows:

$$\begin{aligned} E_0 &= (0, 0), \\ E_1 &= \left( \frac{\alpha_1}{K_1}, 0 \right), \\ E_2 &= \left( 0, \frac{\alpha_2}{K_2} \right), \\ E^* &= (N_1^*, N_2^*). \end{aligned} \quad (3.1)$$

It was observed [8] that both the species will persist when  $K_p/K_q < \alpha_p\beta_{qp}$  ( $p, q = 1, 2; p \neq q$ ). The system has unique positive interior equilibrium if  $\alpha_p/\beta_{qp} > \gamma_p/\gamma_q$ ,  $\gamma_p > 0$  ( $p, q = 1, 2; p \neq q$ ). So the required condition for the existence of unique positive equilibrium as well as for the persistence of the system is

$$\frac{\alpha_p}{\beta_{qp}} > \max \left( \frac{\gamma_p}{\gamma_q}, \frac{K_p}{K_q} \right) \quad \text{when } \gamma_p, \gamma_q > 0 \quad (p, q = 1, 2; p \neq q). \quad (3.2)$$

### 4. Local stability of interior equilibrium

Before dealing local stability properties of the system, we first rescale the system by changing the variables as follows:

$$\begin{aligned} u &= \frac{N_1}{K_1/\alpha_1}, \quad v = \frac{N_2}{K_2/\alpha_2}, \quad \text{and} \quad t = K_1 T, \\ \alpha_{12} &= \frac{\beta_{12}}{\alpha_2} \frac{K_2}{K_1}, \quad \alpha_{21} = \frac{\beta_{21}}{\alpha_1} \frac{K_1}{K_2}, \\ b_1 &= \frac{\gamma_1}{\alpha_1} \frac{K_2}{\alpha_2}, \quad b_2 = \frac{\gamma_2}{\alpha_2} \frac{K_1}{\alpha_1}, \\ K &= \frac{K_2}{K_1}. \end{aligned} \quad (4.1)$$

To avoid complexity, we here consider only the nonlocal as well as time delay effect of  $u$  on  $v$  by considering  $F_{12}(\mathbf{r} - \mathbf{r}_1, t - \tau_1) = \delta(\mathbf{r})\delta(t)$  i.e., the reduced dimensionless system of equations reduces to

$$\begin{aligned} \frac{\partial u}{\partial t} &= u[1 - u - \alpha_{12}v - b_1uv], \\ \frac{\partial v}{\partial t} &= Kv[1 - v - \alpha_{21}u - b_2uF_{21} * v]. \end{aligned} \quad (4.2)$$

The corresponding equilibria would be expressed accordingly. Here we are dealing with the stability problem of interior equilibrium  $E^* = (u^*, v^*)$  corresponding to the original equilibrium of the system (2.3).

To investigate the linear stability of the nonzero equilibrium ( $E^* = (u^*, v^*)$ ) substitute  $u = n_1 + u^*$  and  $v = n_2 + v^*$  and the corresponding initial conditions are  $u \equiv u^*$ , and  $v \equiv v^*$  for  $t < 0$  (so that  $n_j \equiv 0$  for  $t \leq 0$ ) and  $u(\mathbf{x}, 0) = u_0(\mathbf{x})$ ;  $v(\mathbf{x}, 0) = v_0(\mathbf{x})$ ; ( $j = 1, 2$ ).

Consider the linearized system in the following forms for the system (4.2),

$$\begin{aligned}\frac{\partial n_1}{\partial t} &= An_1 + Bn_2, \\ \frac{\partial n_2}{\partial t} &= Cn_1 + Dn_2 + EF_{21} * n_2,\end{aligned}\quad (4.3)$$

where  $A$ ,  $B$ ,  $C$ ,  $D$  and  $E$  are defined as

$$\begin{aligned}A &= -(1 + b_1 v^*) u^*, \\ B &= -(a_{12} + b_1 u^*) u^*, \\ C &= -K(a_{21} + b_2 v^*) v^*, \\ D &= -K v^*, \\ E &= -K b_2 u^* v^*.\end{aligned}\quad (4.4)$$

Note that all the constant parameters in the linearized system are negative.

As we are interested for the spatially structured solution, we consider the solution in the form

$$\begin{pmatrix} n_1(\mathbf{r}, t) \\ n_2(\mathbf{r}, t) \end{pmatrix} = \begin{pmatrix} P(t) \\ Q(t) \end{pmatrix} e^{i\mathbf{m}\mathbf{r}}.$$

The characteristic equation of the linearized system takes the form as

$$\Phi(\lambda, m^2) \equiv \lambda^2 - (A + D + E\bar{F}_{21}(\lambda, m^2))\lambda + AD - BC + AE\bar{F}_{21}(\lambda, m^2) = 0, \quad (4.5)$$

where  $\mathbf{m}$  is the wave vector in one-dimensional coordinate system;  $\lambda$  is the growth factor and  $\bar{F}_{21}(\lambda, m^2) = \int_{-\infty}^{\infty} \int_0^{\infty} F_{21}(\mathbf{r}_2, \tau_2) e^{-\lambda t} e^{-i\mathbf{m}\mathbf{r}_2} d\mathbf{r}_2 d\tau_2$ .  $A$ ,  $B$ ,  $C$ ,  $D$  and  $E$  are defined in (4.4).

Let us now state the properties of  $\bar{F}_{pq}(\lambda, m^2)$  due to Britton [1].

- P1. When  $\lambda$  is real,  $\bar{F}_{pq}(\lambda, m^2)$  is a real valued function of  $\lambda$  and  $m^2$ .
- P2.  $\bar{F}_{pq}(0, 0) = 1$ ,  $\bar{F}_{pq}(\mathbf{0}) = 1$  and  $\bar{F}_{pq}(0) = 1$ .
- P3. If  $\text{Re } \lambda \geq 0$  then  $\bar{F}_{pq}(\lambda, m^2) \leq 1$  and  $|\bar{F}_{pq}(\lambda, m^2)| \leq 1$ .
- P4. If  $\lambda$  is real and nonnegative and  $(\lambda, m^2) \neq (0, 0)$  then  $\bar{F}_{pq}(\lambda, m^2) < 1$ .
- P5. If  $(\omega, m^2) \neq (0, 0)$  then  $\bar{F}_{pq}(i\omega, m^2) \neq 1$ .

The proofs of the above properties may be found in detail in Britton [1] and Gourley and Britton [3]. We also state the following

$$\bar{F}_{pq}(i\omega, m^2) = C_{pq}(\omega) - iS_{pq}(\omega), \quad (4.6a)$$

where

$$\begin{aligned}
 C_{pq}(\omega) &= \int_{-\infty}^{\infty} \int_0^{\infty} F_{pq}(\mathbf{x}, t) \cos \omega t \cos \mathbf{m} \cdot \mathbf{x} \, dt \, d\mathbf{x}, \\
 S_{pq}(\omega) &= \int_{-\infty}^{\infty} \int_0^{\infty} F_{pq}(\mathbf{x}, t) \sin \omega t \cos \mathbf{m} \cdot \mathbf{x} \, dt \, d\mathbf{x}.
 \end{aligned}
 \tag{4.6b}$$

Note that  $|C_{pq}(\omega)| \leq 1$ ,  $|S_{pq}(\omega)| \leq 1$ , for all  $\omega \geq 0$ ;  $p, q = 1, 2$ ,  $p \neq q$ .

It is found that the particular time delay and wave number  $\mathbf{m}$  of the perturbation and the uniform state will make the system unstable if  $\Phi(\lambda, m^2) = 0$  has roots in the right half complex plane. The number of roots can be obtained by the formula  $n(\infty) = \lim_{\omega \rightarrow \infty} (1 - 1/\pi \arg \Phi(i\omega, m^2))$ . Therefore stability depends upon the geometric properties of curve traced out (in the complex plane) by  $\Phi(i\omega, m^2)$  as  $\omega$  runs from 0 to  $\infty$ . From the properties of  $\bar{F}_{pq}(\lambda, m^2)$ , in general, it is found that  $\bar{F}_{pq}(\lambda, m^2) \leq 1$ .

Since  $A + D + E\bar{F}_{21}(\lambda, m^2) < 0$ , the steady-state will be linearly unstable at  $AD - BC + AE\bar{F}_{21}(\lambda, m^2) \leq 0$  along with  $BC > AD$ , i.e.,  $\bar{F}_{21}(\lambda, m^2) \leq (BC - AD)/AE$  and stable at  $\bar{F}_{21}(\lambda, m^2) > (BC - AD)/AE$ . So, the system will pass from stability to instability at the bifurcation point  $\gamma(m^2, b_1, b_2)$  where

$$\begin{aligned}
 \gamma(m^2, b_1, b_2) &= \frac{BC - AD}{AE} = \bar{F}_{21}(\lambda, m^2). \\
 (\alpha_{pq}, p \neq q, p, q = 1, 2, \text{ and } b_1 \text{ fixed}).
 \end{aligned}
 \tag{4.7}$$

Note that  $\gamma$  is not only a function of  $m^2$  but also depends on the bifurcating parameter  $b_2$ . At the critical wave number  $m = m_c$  equated from (4.7) the system will spontaneously emerge into a steady spatially periodic solution (population patches) according to Turing sense.

### 5. Bifurcation

In this section, we deal with the problem of bifurcation of the solution from the coexisting steady-state  $(u^*, v^*)$  of the system (4.3). Here we adopt the method of perturbation. We consider two of the bifurcations, namely bifurcation to steady spatially periodic solutions and Hopf bifurcation to periodic standing waves. We are not considering the Hopf bifurcation to periodic traveling wave solutions as the concerned dynamics of plankton allelopathy are in aquatic system. Following Britton [1], we have that as  $m^2 \rightarrow \infty$ , in  $n$  dimensions,

$$\bar{F}_{21}(\lambda, m^2) \sim -\frac{2\pi^{n/2}}{\Gamma(n/2)m^2} F_{21(n)}(\lambda) + o\left(\frac{1}{m^2}\right),
 \tag{5.1}$$

where

$$F_{21(n)}(\lambda) = \lim_{r \rightarrow 0^+} \mathcal{L}(F_{21(r)}(r, \lambda)r^{n-1})
 \tag{5.2}$$

and  $\mathcal{L}$  denotes Laplace transform. It is to be noted that  $F_{21(n)}(0) < 0$  and  $F'_{21(n)}(0) > 0$ . The Pade' approximation of  $F_{21(n)}(\lambda)$  in the simplest form is

$$F_{21(n)}(\lambda) \approx \frac{F_{21(n)}(0)}{1 - (F'_{21(n)}(0)/F_{21(n)}(0))\lambda}. \quad (5.3)$$

We then approximate the characteristic equation (4.5) of polynomial type as

$$\Phi(\lambda, m^2) \approx \tilde{\Phi}(\lambda, m^2) = 0. \quad (5.4)$$

Equivalently, the above equation can be written in the form as

$$\frac{1}{AE} \lambda^3 - \frac{1}{AE} \left\{ \frac{F_{21(n)}(0)}{F'_{21(n)}(0)} + (A + D) \right\} \lambda^2 + \left\{ \frac{1}{AE} \left( \frac{F_{21(n)}(0)}{F'_{21(n)}(0)} \right) (A + D - E \frac{2\pi^{n/2} F_{21(n)}(0)}{\Gamma(n/2)m^2}) \right\} \lambda - \left\{ \gamma - \frac{2\pi^{n/2} F_{21(n)}(0)}{\Gamma(n/2)m^2} \right\} \frac{F_{21(n)}(0)}{F'_{21(n)}(0)} = 0. \quad (5.5)$$

We shall analyze  $\tilde{\Phi}(\lambda, m^2) = 0$  instead of  $\Phi(\lambda, m^2) = 0$  and assume that the dominant roots of  $\Phi(\lambda, m^2) = 0$  are close to those of  $\tilde{\Phi}(\lambda, m^2) = 0$ .

Firstly, we consider the root  $\lambda = 0$ . Then

$$\gamma = \frac{2\pi^{n/2}}{\Gamma(n/2)m^2} F_{21(n)}(0). \quad (5.6)$$

Next to observe the change of  $\lambda$ . For this we differentiate partially  $\tilde{\Phi}(\lambda, m^2) = 0$  with respect to  $\gamma$ , keeping  $m$  fixed and obtain that

$$\frac{\partial \lambda}{\partial \gamma} = \left\{ \gamma + \frac{1}{AE} \frac{F_{21(n)}(0)}{F'_{21(n)}(0)} \left\{ (A + D) + E \frac{2\pi^{n/2}}{\Gamma(n/2)m^2} \right\} \right\}^{-1}.$$

If the case when  $\frac{\partial \lambda}{\partial \gamma} < 0$  then the relevant root of  $\tilde{\Phi}(\lambda, m^2) = 0$  crosses from the right half plane as  $\gamma$  increases, so that the corresponding mode loses linear stability, but on the other hand when  $\partial \lambda / \partial \gamma > 0$  it moves from right to left, implying a gain of linear stability. In either case, transversality condition holds, and this is the situation in which bifurcation at a simple eigenvalue occurs in a system of differential equations.

The other way of change in stability can occur is by two complex conjugate eigenvalues crossing the imaginary axis. We therefore look for the locus in the  $(\gamma, m^2)$  plane where  $\tilde{\Phi}(\lambda, m^2) = 0$  has purely imaginary roots.

So our analysis suggests that if we focus attention on a certain particular wave number  $m$  (i.e., if we fix a wave vector  $\mathbf{m}$  and only consider stability to perturbations of that particular wave vector), then regarding  $b_2$  as bifurcation parameter, we should get a bifurcation at simple eigenvalue to the steady spatially periodic solutions, and a hopf bifurcation to solutions which are spatially and temporally periodic. We confirm those bifurcations in the following section by constructing the bifurcating solutions using perturbation methods and with numerical results.



### 5.1. Bifurcation to steady spatially periodic solutions

We consider the bifurcation that occur in (4.2) in the light of Gourley and Britton [3]. When  $\gamma$  is increased, a root of the eigenvalue equation (4.5) crosses the imaginary axis through the origin. Such a crossing always occurs if  $m^2 \neq 0$ . When  $\lambda=0$  is a root, the linearized equations have solutions proportional to  $e^{i\mathbf{m}\cdot\mathbf{x}}$ , so this suggests that we should consider the possibility of a bifurcation of steady spatially periodic plane wave solutions from the steady-state solution  $(u^*, v^*)$ . Let  $\mathbf{m}$  be any nonzero vector; define  $\xi = \mathbf{m}\cdot\mathbf{x}$  and look for a solution which is  $2\pi$ -periodic of the form  $u(\mathbf{x}, t) = u(\mathbf{m}\cdot\mathbf{x}) = u(\xi)$ ,  $v(\mathbf{x}, t) = v(\mathbf{m}\cdot\mathbf{x}) = v(\xi)$ . The system (4.2) in the system becomes

$$\begin{aligned} 0 &= u[1 - u - \alpha_{12}v - b_1uv], \\ 0 &= Kv[1 - v - \alpha_{21}u - b_2uF_{21} * *v] \end{aligned} \tag{5.7}$$

with the periodic boundary conditions at  $\xi=0$  and  $\xi=2\pi$ . Again the system is invariant under the transformation  $\xi \rightarrow -\xi$  but we may ensure that the eigenvalue of the linearized system is simple if we look for the solutions symmetric in  $\xi$ . Thus we look for the solutions on  $(0, \pi)$  which satisfy the conditions

$$u'(0) = u'(\pi) = v'(0) = v'(\pi) = 0. \tag{5.8}$$

For general kernels, the term  $F_{21} * *v$  requires  $v$  to be defined on the whole real line; a solution on  $(0, \pi)$  satisfying (5.8) is therefore understood to be extended to an even function on  $(\pi, -\pi)$  and then periodically over all  $\mathbb{R}$ .

We can check that an appropriate transversality condition holds as  $\lambda$  passes through 0. Differentiating (5.4) with respect to  $b_2$  and setting  $\lambda = 0$  yields

$$\left. \frac{\partial \lambda}{\partial b_2} \right|_{\lambda=0} = \frac{-Kv^2B + Ku^*v^*\bar{F}_{21,\lambda}(0, m^2) + Ku^*v^*A\hat{E}\bar{F}_{21,\lambda}(0, m^2)}{A + D + E\hat{E}\bar{F}_{21,\lambda}(0, m^2) - AE\hat{E}\bar{F}_{21,\lambda}(0, m^2)}. \tag{5.9}$$

Since  $m^2 \neq 0$ , properties of  $\bar{F}_{21}$  under parametric conditions imply that the above quantity is nonzero and therefore that the transversality condition does indeed hold. We now construct the first few terms in the bifurcating solution using standard perturbation procedure, regarding  $m^2$  as fixed and working on suitable space of functions satisfying (5.8) with the inner product

$$[(u_1, u_2), (v_1, v_2)] = \int_0^\pi (u_1(\xi)\bar{v}_1(\xi) + u_2(\xi)\bar{v}_2(\xi)) d\xi.$$

We seek a solution of (5.7) with (5.8) of the form

$$\begin{aligned} \begin{pmatrix} u \\ v \end{pmatrix} &= \begin{pmatrix} u^* \\ v^* \end{pmatrix} + \varepsilon \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} + \varepsilon^2 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} + \dots, \\ b_2 &= b_{20} + \varepsilon b_{21} + \varepsilon^2 b_{22} + \dots, \end{aligned} \tag{5.10}$$

where

$$u'_n(0) = u'_n(\pi) = v'_n(0) = v'_n(\pi) = 0, \quad n = 1, 2, \dots \tag{5.11}$$

We substitute (5.9) into (5.7) and equate powers of  $\varepsilon$  upto the third order. If we define the linear operator  $L_1$  by

$$L_1 = \begin{pmatrix} (1 + b_1 v^*)u^* & (\alpha_{12} + b_1 u^*)u^* \\ K v^*(\alpha_{21} + b_{20} v^*) & K v^*(1 + b_{20} u^* F_{21}^{**}) \end{pmatrix}, \quad (5.12)$$

where the operator  $F_{21}^{**}$  is defined in (2.2), then the first three perturbation equations are

$$L_1 \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \mathbf{0}, \quad (5.13)$$

$$L_1 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \begin{pmatrix} \{u_1\{(1 + b_1 v^*)u_1 + (\alpha_{12} + 2b_1 u^*)v_1\}\} \\ \{K v_1\{(\alpha_{21} u_1 + v^* b_{20} u_1) + (v_1 + b_{20} u^* F_{21}^{**} v_1)\}\} \\ + K v^*(b_{20} u_1 F_{21}^{**} v_1 + b_{21} v^* u_1 + b_{21} u^* F_{21}^{**} v_1)\} \end{pmatrix}, \quad (5.14)$$

$$L_1 \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} \{u^*(b_1 u_1 v_2 + b_1 u_2 v_1) + u_1((1 + b_1 v^*)u_2 + (\alpha_{12} + b_1 u^*)v_2) \\ + u_2((1 + b_1 v^*)u_1 + (\alpha_{12} + b_1 u^*)v_1)\} \\ \{b_{20}(u_1 F_{21}^{**} v_2 + u_2 F_{21}^{**} v_1) + b_{21}(v^* F_{21}^{**} v_2 + u_1 F_{21}^{**} v_1 \\ + u_2 v^*) + b_{22}(v^* u_1 + u^* F_{21}^{**} v_1) + v_1((\alpha_{21} u_2 \\ + v^* b_{20} u_2) + (v_2 + b_{20} F^{**} v_2) + b_{20} u_1 F_{21}^{**} v_1 + b_{21} u^* F^{**} v_1 \\ + b_{21} v^* u_1) + v_2((\alpha_{21} u_1 + v^* b_{20} u_1) \\ + (v_1 + b_{20} u^* F^{**} v_1))\} \end{pmatrix}. \quad (5.15)$$

Next we have the simple result as

$$F_{21}^{**} \cos n\xi = \bar{F}_{21}(0, n^2 m^2) \cos n\xi, \quad n = 0, 1, 2, \dots$$

The nontrivial solution of (5.13) with (5.11) is of the form

$$\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} \cos \xi \quad (5.16)$$

as long as

$$\begin{aligned} \phi(0; b_{20}, m^2) &= AD|_{b_2=b_{20}} - BC|_{b_2=b_{20}} + AE|_{b_2=b_{20}} \bar{F}_{21}(0, m^2) \\ &= K u^* v^* \{(1 + b_1 v^*) - (\alpha_{12} + b_1 u^*)(\alpha_{21} + b_{20} v^*) \\ &\quad + u^* b_{20} (1 + b_1 v^*) \bar{F}_{21}(0, m^2)\} = 0 \end{aligned} \quad (5.17)$$

and in this case either component of (5.13) gives the ratio of  $a_1$  to  $a_2$ ;

$$\frac{a_1}{a_2} = -\frac{\alpha_{12} + b_1 u^*}{1 + b_1 v^*}.$$

This the only solution of (5.13) provided that

$$\phi(0; b_{20}, n^2 m^2) \neq 0 \quad \text{for all integers } n \geq 2$$

which we assume to be the case. Then (5.17) defines  $b_{20}$  as a function of  $m^2$ ,

$$b_{20} = b_{20}(m^2) = \frac{\alpha_{21}(\alpha_{12} + b_1 u^*) - (1 + b_1 v^*)}{(1 + b_1 v^*)u^* \bar{F}_{21}(0, m^2) - (\alpha_{12} + b_1 u^*)v^*}. \tag{5.18}$$

We define the adjoint  $L_1^*$  of the linear operator  $L_1$  is given by

$$L_1^* = \begin{pmatrix} (1 + b_1 v^*)u^* & K v^*(\alpha_{21} + b_{20} v^*) \\ (\alpha_{12} + b_1 u^*)u^* & K v^*(1 + b_{20} u^* F_{21} ** ) \end{pmatrix}, \tag{5.19}$$

$L_1^*$  satisfies the properties  $[L_1 \mathbf{u}, \mathbf{v}] = [\mathbf{u}, L_1^* \mathbf{v}]$  showing that

$$\int_0^\pi v F_{21} ** u d\xi = \int_0^\pi u F_{21} ** v d\xi$$

for all functions  $u, v$  such that  $u'(0) = u'(\pi) = v'(0) = v'(\pi) = 0$ . It can be easily verified by expanding  $u, v$  in their Fourier cosine series and evaluating each integrand and using the orthogonality properties of the function  $\cos n\xi$  over the interval  $(0, \pi)$ . We have the Fredholm Alternative to obtain the solution  $(u_1^*, v_1^*)^T$  of the adjoint equation:

$$L_1^* \begin{pmatrix} u_1^* \\ v_1^* \end{pmatrix} = \mathbf{0}. \tag{5.20}$$

Consider the solution is  $(u_1^*, v_1^*)^T = (d_1, d_2)^T \cos \xi$  where

$$\frac{d_1}{d_2} = -\frac{K(\alpha_{21} + b_{20} v^*)v^*}{(1 + b_1 v^*)u^*} \tag{5.21}$$

and this solution is unique upto normalization. With  $u_1 = a_1 \cos \xi$  and  $v_1 = a_2 \cos \xi$ , it follows from Fredholm Alternative that (5.14) has a solution if and only if the inner product of its right-hand side with  $(u_1^*, v_1^*)^T$  is zero. Since the quadratic terms  $u_1^2, u_1 v_1$  and  $u_1 F_{21} ** u_1$  do not involve first harmonics we are left with

$$\int_0^\pi v^* b_{21}(v^* + u^* \bar{F}_{21}(0, m^2)) a_1 d_1 \cos^2 \xi d\xi = 0 \tag{5.22}$$

or  $b_{21}(v^* + u^* \bar{F}_{21}(0, m^2)) a_1 d_1 = 0$  implying that  $b_{21} = 0$  (as  $a_1, d_1$  cannot be zero). Changing Eq. (5.14) by using the above results and applying Fredholm Alternative

theorem we have

$$\begin{aligned}
 & b_{22} \left( v^* + \frac{a_2}{a_1} u^* \bar{F}_{21}(0, m^2) \right) \\
 &= \frac{d_1}{d_2} \left\{ (\alpha_{12} + 3b_1 u^*) \left\{ \left( A_2 + \frac{a_2}{a_1} A_1 \right) + \frac{1}{2} \left( B_2 + \frac{a_2}{a_1} B_1 \right) \right. \right. \\
 &\quad \left. \left. + 2(1 + b_1 v^*) \left( A_1 + \frac{1}{2} B_1 \right) + \frac{3}{4} b_1 a_1 a_2 \right\} - \left\{ b_{20} \left\{ A_2 + \frac{a_2}{a_1} A_1 \bar{F}_{21}(0, m^2) \right. \right. \right. \\
 &\quad \left. \left. + \frac{1}{2} (B_2 \bar{F}_{21}(0, 4m^2) + \frac{a_2}{a_1} B_1 \bar{F}_{21}(0, m^2)) \right\} \right. \\
 &\quad \left. + \frac{a_2}{a_1} \left\{ (\alpha_{21} + v^* b_{20}) \left( A_1 + \frac{1}{2} B_1 \right) \right. \right. \\
 &\quad \left. \left. + (1 + u^* b_{20}) A_2 + \frac{1}{2} (1 + u^* b_{20} \bar{F}_{21}(0, 4m^2)) B_2 \right\} + \frac{1}{4} b_{20} \frac{a_2}{a_1} a_2 \bar{F}_{21}(0, m^2) \right. \\
 &\quad \left. + \left( A_2 + \frac{1}{2} B_2 \right) \left\{ (\alpha_{21} + v^* b_{20}) + \frac{a_2}{a_1} (1 + b_{20} u^* \bar{F}_{21}(0, m^2)) \right\} \right\}, \quad (5.23)
 \end{aligned}$$

where

$$\begin{aligned}
 A_1 &= \frac{1}{\Phi(0, b_{20}, 0)} \left\{ (1 + b_{20} u^*) \left( \frac{1}{2u^*} ((1 + b_1 v^*) a_1^2 + (\alpha_{12} + 2b_1 u^*) a_1 a_2) \right) \right. \\
 &\quad \left. - \frac{1}{2Kv^*} (2(1 + b_1 v^*) (1 + 2b_{20} u^*) a_1 a_2 + (\alpha_{12} + b_1 u^*) (1 + b_{20} u^*) a_2^2) \right\}, \\
 A_2 &= \frac{1}{\alpha_{12} + b_1 u^*} \left\{ \frac{1}{2u^*} ((\alpha_{12} + 2b_1 u^*) a_1 a_2 + (1 + b_1 u^*) a_1^2) - (1 + b_1 v^*) A_1 \right\}, \\
 B_1 &= \frac{\Phi(0, b_{20}, 0)}{\Phi(0, b_{20}, 4m^2)} A_1, \\
 B_2 &= \frac{1}{\alpha_{12} + b_1 u^*} \left\{ \frac{1}{2u^*} ((\alpha_{12} + 2b_1 u^*) a_1 a_2 + (1 + b_1 v^*) a_1^2) \right. \\
 &\quad \left. - (1 + b_1 v^*) B_1 \right\}. \quad (5.24)
 \end{aligned}$$

Hence the sign of  $b_{22}$  indicates whether the bifurcation is sub or super critical. We assume the following numerical values of the constants [8]:  $K_1 = 2$ ,  $K_2 = 1$ ,  $\alpha_1 = 0.07$ ,  $\alpha_2 = 0.08$ ,  $\beta_{12} = 0.05$ ,  $\beta_{21} = 0.015$ ,  $\gamma_1 = 0.009$ ,  $\gamma_2 = 0.008$ . Then after some algebraic computations we can find have,  $b_{22} > 0$  for all  $m \geq 2$ . Hence the bifurcation is super-critical in this parametric space.

**5.2. Hopf bifurcation to periodic standing waves**

Following Gourley and Britton [3] next we consider the bifurcation that occurs in (4.2) when as  $\gamma$  is increased, two roots of the eigenvalue equation (4.5) cross the imaginary axis as a pair of complex conjugates. Here the linear equations have the solutions of the form  $Ae^{i\mathbf{m}\cdot\mathbf{x}}e^{i\omega t}$  and this suggests that we are to consider the possibility that from the uniform steady-state solution  $(u^*, v^*)$ , a family of plane wave solutions which is periodic in both space and time bifurcates. Let us look for a solution of (4.2) of the form  $u(\mathbf{x}, t) = u(\xi, \tau)$ ,  $v(\mathbf{x}, t) = v(\xi, \tau)$  where  $\xi = \mathbf{m}\cdot\mathbf{x}$  and  $\tau = \omega t$  ( $\mathbf{m}$  being any fixed nonzero vector) such that  $u, v$  are  $2\pi$ –periodic in both arguments. We have

$$\begin{aligned} \omega u_\tau &= u[1 - u - \alpha_{12}v - b_1uv], \\ \omega v_\tau &= Kv[1 - v - \alpha_{21}u - b_2u \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} F_{21}(\mathbf{r} - \mathbf{r}_2, t - \tau_2)v(\mathbf{r}_2, \tau_2) d\tau_2 d\mathbf{r}_2] \end{aligned} \tag{5.25}$$

for  $(\xi, \tau) \in (0, 2\pi) \times (0, 2\pi)$  with the periodic boundary conditions. Again the solutions are symmetric in  $\xi$ . Thus we look for the solutions which satisfy the conditions

$$u_\xi(0, \tau) = u_\xi(\pi, \tau) = v_\xi(0, \tau) = v_\xi(\pi, \tau) = 0 \tag{5.26}$$

and the conditions

$$\begin{aligned} u(\xi, 0) &= u(\xi, 2\pi), & u_\tau(\xi, 0) &= u_\tau(\xi, 2\pi), \\ v(\xi, 0) &= v(\xi, 2\pi), & v_\tau(\xi, 0) &= v_\tau(\xi, 2\pi). \end{aligned} \tag{5.27}$$

We look for a solution of (5.25) with (5.27) in the form

$$\begin{aligned} \begin{pmatrix} u \\ v \end{pmatrix} &= \begin{pmatrix} u^* \\ v^* \end{pmatrix} + \varepsilon \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} + \varepsilon^2 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} + \dots, \\ b_2 &= b_{20} + \varepsilon b_{21} + \varepsilon^2 b_{22} + \dots, \\ \omega &= \omega_0 + \varepsilon \omega_1 + \varepsilon^2 \omega_2 + \dots \end{aligned} \tag{5.28}$$

Substitute (5.28) into (5.25) and equate powers of  $\varepsilon$  upto the third power. We have

$$F_{21} * * u_n = (F_{21} * * u_n)^0 + \varepsilon (F_{21} * * u_n)_\varepsilon^0 + \frac{1}{2} \varepsilon^2 (F_{21} * * u_n)_{\varepsilon\varepsilon}^0 + \dots, \tag{5.29}$$

where the superscript zero denotes evaluation at  $\varepsilon = 0$ . Let us define the linear operator  $L_2$  by

$$L_2 = \omega_0 \frac{\partial}{\partial \tau} - \begin{pmatrix} (1 + b_1 v^*)u^* & (\alpha_{12} + b_1 u^*)u^* \\ Kv^*(\alpha_{21} + b_{20} v^*) & Kv^*(1 + b_{20} u^*(F_{21} * *)^0) \end{pmatrix}, \tag{5.30}$$

where the operator  $F_{21} **$  is defined in (2.2). The first three perturbation equations are then obtained as

$$L_2 \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \mathbf{0}, \tag{5.31}$$

$$L_2 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \begin{pmatrix} \{-\omega_1 u_{1\tau} + u_1 \{(1 + b_1 v^*) u_1 + (\alpha_{12} + 2b_1 u^*) v_1\} \\ \{-\omega_1 v_{1\tau} - K \{v_1 \{(\alpha_{21} + b_{20} v^*) u_1 + v_1 + u^* b_{20} (F_{21} ** v_1)^0\} \\ + v^* \{(\alpha_{21} + b_{20}) u_2 + v_2 + b_{21} (v^* u_1 + u^* (F_{21} ** v_1)^0) \\ + b_{20} \{u_1 (F_{21} ** v_1)^0 + u^* (F_{21} ** v_1)_\varepsilon^0 + (F_{21} ** u_2)^0\}\}\} \} \end{pmatrix}, \quad (5.32)$$

$$L_2 \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} \{-\omega_2 u_{1\tau} - \omega_1 u_{2\tau} + 2(1 + b_1 v^*) u_1 u_2 \\ + (\alpha_{12} + 2b_1 u^*) u_1 v_2 + b_1 u_1^2 v_1 + (\alpha_{12} + 2b_1 u^*) u_2 v_1\} \\ \{-\omega_2 v_{1\tau} - \omega_1 v_{2\tau} - K \{v_2 \{(\alpha_{21} + v^* b_{20}) u_1 \\ + (v_1 + b_{20} u^* (F_{21} ** v_1)^0) + v_1 \{(\alpha_{21} + b_{20} v^*) u_2 + v_2 \\ + b_{22} u^* v^* + b_{21} v^* u_1 + b_{21} u^* (F_{21} ** v_1)^0 + b_{20} u_1 (F_{21} ** v_1)^0 \\ + b_{20} u^* ((F_{21} ** v_1)_\varepsilon^0 + (F_{21} ** v_2)^0)\} + v^* \{b_{22} (u^* (F_{21} ** v_1)^0 \\ + u_1 F_{21} ** v^*\} + b_{21} (v^* u_2 + u_1 (F_{21} ** v_1)^0 \\ + u^* ((F_{21} ** v_1)_\varepsilon^0 + (F_{21} ** v_2)^0)) \\ + b_{20} (u_2 (F_{21} ** v_1)^0 + u_1 ((F_{21} ** v_1)_\varepsilon^0 + (F_{21} ** v_2)^0) \\ + u^* (\frac{1}{2} (F_{21} ** v_1)_{\varepsilon\varepsilon}^0 + (F_{21} ** v_2)_\varepsilon^0 + (F_{21} ** v_3)^0)\}\} \} \end{pmatrix}, \quad (5.33)$$

for  $(\zeta, \tau) \in (0, \pi) \times (0, 2\pi)$  with the conditions of the form (5.26) and (5.27) for each  $(u_n, v_n)$ . Gourley and Britton [3] gives the value of  $F_{21} ** e^{i p \tau} \cos n \zeta$  as

$$F_{21} ** e^{i p \tau} \cos n \zeta = \bar{F}_{21}(p i \omega, n^2 m^2) e^{i p \tau} \cos n \zeta, \quad p, n = 0, 1, 2, \dots \quad (5.34)$$

For function  $u$  of the form  $v_{p,n}(\zeta, \tau) = e^{i p \tau} \cos n \zeta$  we have, from (5.34),  $(F_{21} ** v_{p,n})^0 = \bar{F}_{21}(p i \omega_0, n^2 m^2) v_{p,n}$ . For other functions  $v(F_{21} ** v)^0$  would be calculated by first writing  $v$  as Fourier series in terms of the function  $v_{p,n}$ . The nontrivial solution of (5.31) is of the form

$$\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \begin{pmatrix} a_1 \\ 1 \end{pmatrix} e^{i \tau} \cos \zeta + \text{c.c.} \quad (5.35)$$

which satisfies (5.31) as long as

$$\begin{aligned} \phi(i\omega_0; b_{20}, m^2) &= -\omega_0^2 - i(A + D + E\bar{F}_{21}(i\omega_0, m^2))\omega_0 + (AD - BC) \\ &+ AE\bar{F}_{21}(i\omega_0, m^2) = 0 \end{aligned} \quad (5.36)$$

and in this case either component of (5.31) implies that

$$a_1 = -\frac{(\alpha_{12} + b_1 u^*)u^*}{i\omega_0 - (1 + b_1 v^*)u^*}. \tag{5.37}$$

This is the only solution (upto scalar multiples) of (5.31) if we assume

$$\phi(pi\omega_0; b_{20}, n^2 m^2) \neq 0 \quad \text{for any pair of nonnegative integers } (p, n) \neq (1, 1). \tag{5.38}$$

The real and imaginary parts of (5.36) give  $b_{20}$  and  $\omega_0$  implicitly in terms of  $m^2$ ,  $b_{20} = b_{20}(m^2)$ ,  $\omega_0 = \omega_0(m^2)$ .

It is evident that the adjoint  $L_2^*$  of the linear operator  $L_2$  is given by

$$L_2^* = -\omega_0 \frac{\partial}{\partial \tau} - \begin{pmatrix} (1 + b_1 v^*)u^* & K v^*(\alpha_{21} + b_{20} v^*) \\ (\alpha_{12} + b_1 u^*)u^* & K u^* v^* \end{pmatrix} - K b_{20} u^* v^* L_2^{*'}, \tag{5.39}$$

where the linear operator  $L_2^{*'}$  acts on the Fourier components as follows:

$$L_2^{*'} \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} e^{pi\tau} \cos n\zeta = \begin{pmatrix} 0 \\ \bar{F}_{21}(pi\omega_0, n^2 m^2) e^{pi\tau} \cos n\zeta \end{pmatrix} \tag{5.40}$$

and on any other functions satisfying (5.26), (5.27) by expressing it as a Fourier series and using linearity. The term  $L_2^{*'}$  is in fact the contribution to the adjoint from the nonlocal term in the operator  $L_2$ .

The solution  $(u_1^*, v_1^*)^T$  of the adjoint equation

$$L_2^* \begin{pmatrix} u_1^* \\ v_1^* \end{pmatrix} = 0$$

is of the form

$$\begin{pmatrix} u_1^* \\ v_1^* \end{pmatrix} = \begin{pmatrix} d_1 \\ 1 \end{pmatrix} e^{i\tau} \cos \zeta + \text{c.c.} \tag{5.41}$$

with

$$d_1 = -\frac{K(\alpha_{21} + b_{20} v^*)v^*}{i\omega_0 - (1 + b_1 v^*)u^*}. \tag{5.42}$$

For values of  $b_2$  near  $b_{20}$ , let  $\lambda(b_2)$  be the root of the eigenvalue equation (4.5) such that  $\lambda(b_{20}) = i\omega_0$ . Then

$$\begin{aligned} & -\lambda^2(b_{20}) - i(A + D + E)|_{b_2=b_{20}} \bar{F}_{21}(\lambda(b_{20}), m^2) \lambda(b_{20}) \\ & + (AD - BC) + AE|_{b_2=b_{20}} \bar{F}_{21}(\lambda(b_{20}), m^2) = 0. \end{aligned} \tag{5.43}$$

Differentiating the above equation with respect to  $b_2$  and evaluating at  $b_2 = b_{20}$  we have

$$\begin{aligned} & \lambda'(b_{20}) \left\{ \left( -B \frac{a_1}{|a_1|^2} (2 - E \bar{F}_{21, \lambda}(i\omega_0, m^2)) + (A - D) + E \bar{F}_{21}(i\omega_0, m^2) \right) \right\} \\ & = K v^* \left\{ u^* \frac{a_1}{|a_1|^2} \bar{F}_{21}(i\omega_0, m^2) u^* A - B v^* \right\}. \end{aligned} \tag{5.44}$$

Using the values of  $a_1$  from (5.37),  $d_1$  from (5.42) and from the Pade' approximation of

$$F_{21(n)}(\lambda) \approx \frac{F_{21(n)}(0)}{1 - (F'_{21(n)}(0)/F_{21(n)}(0))\lambda},$$

we find the approximate value of  $\lambda'(b_{20})$  and  $\omega_0 = \omega_0^*$  at  $b_2 = b_{20}$  for large  $m^2$ . From (5.43), separating real and imaginary parts and using the approximate value of the Kernel function, we get approximate values of  $\lambda(b_{20})$  and  $\omega_0 = \omega_0^*$ , where  $\omega_0^*$  can be evaluated from the following:

$$\omega_0^* = \sqrt{\frac{AD - BC + AE\left(\frac{2\pi n^2}{\Gamma(\frac{n}{2})m^2}\right)}{1 + (A + D + E\left(\frac{2\pi n^2}{\Gamma(\frac{n}{2})m^2}\right))\frac{F'_{21(n)}(0)}{F_{21(n)}(0)}}}. \quad (5.45)$$

Here we derive certain condition which will be needed to demonstrate the transversality condition required for this bifurcation. Assume that  $\text{Re } \mu'(b_{20}) \neq 0$ . It is obvious that  $(F_{21} * v_1)_\xi^0 = i\omega_1 \bar{F}_{21(s)}(i\omega_0, m^2) e^{i\xi} \cos \xi + \text{complex conjugate (c.c.)}$ . By taking the inner product of the right-hand side of (5.32) with  $(u_1^*, v_1^*)^T$  we have after some algebraic calculation and applying solvability condition of (5.32)  $b_{21} = 0$  and  $\omega_1 = 0$  and consequently we also have  $(F_{21} * v_1)_\xi^0 = 0$ . Let

$$\begin{aligned} \delta_1 = \xi_1 &= (1 + b_1 v^*) a_1^2 + (\alpha_{12} + 2b_1 u^*) a_1, \\ \delta_2 = \xi_2 &= -K \{ (\alpha_{21} + b_{20} v^*) a_1 + (1 + 2b_{20} u^* \bar{F}_{21}(0, m^2)) \} \end{aligned} \quad (5.46)$$

and let

$$\begin{aligned} A_1 &= \frac{1}{2\phi(2i\omega_0, b_{20}, 0)} \{ 2i\omega_0 \delta_1 - \delta_1 K v^* (1 + b_{20} u^*) + \delta_2 (\alpha_{12} + b_1 u^*) u^* \}, \\ A_2 &= \frac{1}{2\phi(2i\omega_0, b_{20}, 0)} \{ 2i\omega_0 \delta_2 - \delta_2 u^* (1 + b_1 v^*) + \delta_1 K (\alpha_{21} + b_{20} v^*) v^* \}, \\ B_1 &= \frac{1}{2\phi(2i\omega_0, b_{20}, 4m^2)} \{ 2i\omega_0 \delta_1 - \delta_1 K v^* (1 + b_{20} u^* \bar{F}_{21}(2i\omega_0, 4m^2)) \\ &\quad + \delta_2 (\alpha_{12} + b_1 u^*) u^* \}, \\ B_2 &= \frac{1}{2\phi(2i\omega_0, b_{20}, 4m^2)} \{ 2i\omega_0 \delta_2 - \delta_2 u^* (1 + b_1 v^*) + \delta_1 K (\alpha_{21} + b_{20} v^*) v^* \}, \\ C_1 = D_1 &= \frac{1}{2\phi(0, b_{20}, 0)} \{ -\xi_1 K v^* (1 + b_{20} u^*) - \xi_2 (\alpha_{12} + b_1 u^*) u^* \}, \\ C_2 = D_2 &= \frac{1}{2\phi(0, b_{20}, 0)} \{ -\xi_2 u^* (1 + b_1 v^*) - \xi_1 K v^* (\alpha_{21} + b_{20} v^*) \}. \end{aligned} \quad (5.47)$$



Now with  $b_{21} = \omega_1 = 0$  we have  $(F_{21} * v_2)_z^0 = 0$  and  $(F_{21} * v_2)_{zz}^0 = 2i\omega_2 \bar{F}_{21(s)}(i\omega_0, m^2) e^{iz} \cos \xi + \text{c.c.}$  After some algebra using the solvability conditions, we have

$$b_{22} = -\frac{1}{\text{Re}\{Kv^*(u^*(1 + \bar{F}_{21}(i\omega_0, m^2)) + v^*a_1)\}} \text{Re}(\bar{d}_1 \tilde{\rho}_{11} + \tilde{\rho}_{12}),$$

where

$$\begin{aligned} \rho_{11} = & -i\omega_2 a_1 + 2(1 + b_1 v^*)(\bar{a}_1 + \frac{1}{2} \bar{a}_1 B_1 + a_1(2 \text{Re } C_1 + \text{Re } D_1)) \\ & + (\alpha_{12} + 2b_1 u^*)(A_1 + \frac{1}{2} B_1 + 2 \text{Re } C_1 + \text{Re } D_1) \\ & + (\alpha_{12} + 2b_1 u^*)(\bar{a}_1 A_2 + \frac{1}{2} \bar{a}_1 B_2 + a_1(2 \text{Re } C_2 + \text{Re } D_2)) \\ & + b_1(\frac{1}{4} a_1^2 + \frac{3}{4} |a_1|^2) \end{aligned}$$

$$\begin{aligned} \rho_{12} = & -i\omega_2(1 + Kb_{20}u^* \bar{F}_{21,\lambda}(i\omega_0, m^2)) \\ & + Kb_{22}v^*(u^*(1 + \bar{F}_{21}(i\omega_0, m^2)) + v^*a_1) \\ & - K\{(\alpha_{21} + v^*b_{20} + b_{20}\bar{F}_{21}(i\omega_0, 4m^2))(\bar{a}_1 A_2 + \frac{1}{2} \bar{a}_1 B_2 \\ & + a_1(2 \text{Re } C_2 + \text{Re } D_2)) + (\alpha_{21} + b_{20}v^* \\ & + b_{20}\bar{F}_{21}(i\omega_0, m^2))(A_1 + \frac{1}{2} B_1 + 2 \text{Re } C_1 + \text{Re } D_1) \\ & + (2 + u^*b_{20}\bar{F}_{21}(i\omega_0, m^2) + v^*\bar{F}_{21}(i\omega_0, 4m^2))(A_2 + \frac{1}{2} B_2 \\ & + (2 \text{Re } C_2 + \text{Re } D_2)) + b_{20}\bar{F}_{21}(i\omega_0, m^2)a_1 \end{aligned}$$

and

$$\begin{aligned} \rho_{11} = & -i\omega_2 a_1 + \tilde{\rho}_{11}, \\ \rho_{12} = & -i\omega_2(1 + Kb_{20}u^* \bar{F}_{21,\lambda}(i\omega_0, m^2)) \\ & + Kb_{22}v^*(u^*(1 + \bar{F}_{21}(i\omega_0, m^2)) + v^*a_1) + \tilde{\rho}_{12}. \end{aligned} \tag{5.48}$$

The above quantity determines whether the bifurcation is super-critical or subcritical. Applying Pade approximation on  $\bar{F}_{21}(i\omega_0, m^2)$  and using the same parametric values as in section (5.1), we work out  $\omega_0^* = 0.21$ ,  $b_{22} = 72.53 > 0$ . Hence the Hopf bifurcation is super-critical implying that the system (4.2) has stable limit cycle spatially periodic solutions.

## 6. Discussion

An integro-differential equation model of toxin producing phytoplankton dynamics involving distributed time delay in the production of allelochemicals and nonlocal

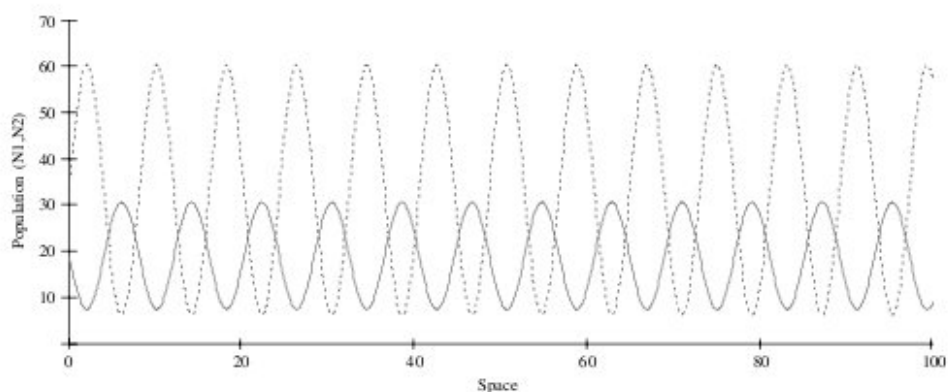


Fig. 1.

allelopathic effect has been considered. The important findings can be summarized as the following:

- (1) The nonlocal effect drives the system into a steady-state spatially periodic and symmetric solution by bifurcation at some higher values of the wave numbers explaining the formation of phytoplanktonic patches (stationary dissipative structure).
- (2) The time delay factor drives the spatial system into a limit cycle by Hopf bifurcation at some value of  $\tau > 0$  (periodic standing wave) describing phytoplanktonic blooms, pulses and succession through out the year.

To observe the spatial pattern, plankton samples were collected from Talsari (Orissa, India) to Digha Mohana (West Bengal, India) during the period 1999–2001. Frequency of sampling was once in every fortnight except the months of September and October. During this time due to roughness of sea sampling programme had to be suspended. The study area is situated between  $21^{\circ}37'$  Northern latitude and  $87^{\circ}25'$  Eastern Longitude to  $21^{\circ}42'$  Northern latitude and  $87^{\circ}31'$  Eastern Longitude. There were altogether 30 sampling dates (in Fig. 2, the collection dates are mentioned as 1, 2, ..., 30) and the collection region is divided into seven stations, the distance between two subsequent stations is 2 km. Six species of the diatoms, viz., *Chaetoceros* spp., *Skeletonema costatum*, *Cerratatulina* spp., *Leptocylindricus* spp., *Nitzschia* spp. and *Phaeocystis* spp. are toxin producing plankton (TPP). Soumia [15] also mentioned that these species are TPP species. *Dinophysics acuta*, *Noctiluca scintillans* and *Prorocentrum* sp. of Dinoflagellate group are also TPP. Richardson [14] mentioned that these species are TPP.

Our analytical results show that the proposed model may generate spatial pattern. To substantiate our analytical findings numerical simulation is presented for a hypothetical set of parameter values (see Section 5.1 for the parameter values and Fig. 1.) The qualitative behavior of the spatial pattern generated by *Nitzschia* sp. and *Chaetoceros*

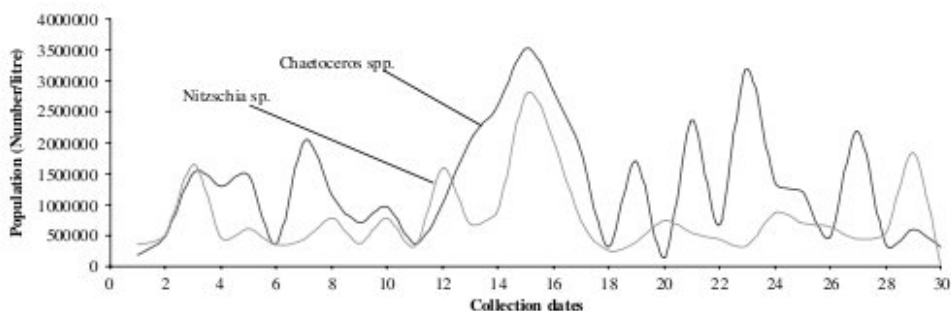


Fig. 2.

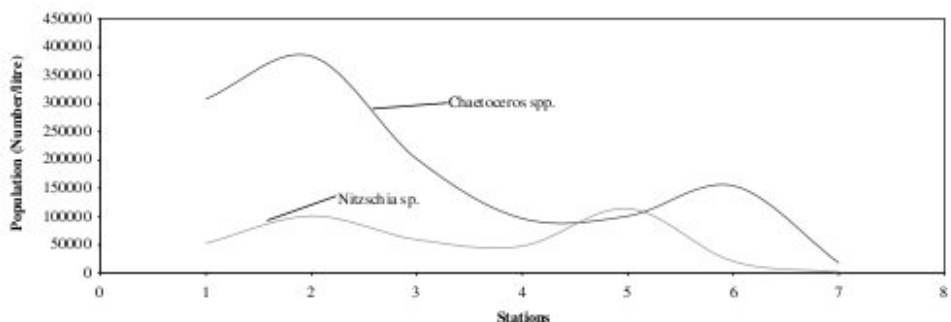


Fig. 3.

spp. is similar to the pattern observed by numerical solution of the proposed model (see Figs. 2 and 3).

Thus the model proposed here can adequately describe the dynamics of planktonic communities involving toxic allelopathic interaction, in aquatic still water ecosystem.

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