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Spatiotemporal Dynamic of Toxin Producing Phytoplankton (TPP)-Zooplankton Interaction

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Abstract. The present paper deals with a toxin producing phytoplankton (TPP)-zooplankton interaction in spatial environment in the context of phytoplankton bloom. In the absence of diffusion the stability of the given system in terms of co-existence and hopf bifurcation has been discussed. After that TPP-zooplankton interaction is considered in spatiotemporal domain by assuming self diffusion in both population. It has been obtained that in the presence of diffusion given system becomes unstable (Turing instability) under certain conditions. Moreover, by applying the normal form theory and the center manifold reduction for partial differential equations (PDEs), the explicit algorithm determining the direction of Hopf bifurcations and the stability of bifurcating periodic solutions is derived. Finally, numerical simulations supporting the theoretical analysis are also included.

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1. Introduction

A remarkable feature associated with many phytoplankton population is the occurrence of rapid and massive bloom formation. Such events are characterized by

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a dramatic sharp rise in algae population numbers of up to several orders of magnitude [1] followed by a sudden collapse whereby the phytoplankton population returns to its original low level as if nothing had ever occurred.

These harmful algal blooms are due to increased production of poisoning chemicals by some phytoplankton species. In the last decades of the past century, a global increase of toxin-producing phytoplankton (TPP) has been observed. Red tides have a negative impact on the zooplankton and then on the species feeding on it, affecting the large fish in the ocean and ultimately affecting, the human food chain. Mathematical models for the understanding of the occurrence of red tides have been proposed, based on the idea that they are caused by toxin-producing phytoplankton (TPP) [2–5]

Observational evidence for the patchiness of phytoplankton is abundant and is relatively easy to obtain [6]. Information on zooplankton distribution, vital for theoretical modeling of the dynamics, is however scarcer and difficult to obtain. Many authors have included the spatial variation of phytoplankton population in bloom models [7, 8].

Recently, spatial movements of planktonic systems in the presence of toxin-producing phytoplankton have been found to generate and maintain inhomogeneous biomass distribution of competing phytoplankton as well as grazer zooplankton [9].

To explain the periodicity of bloom, Mukopadhyay and Bhattacharyya [10] have considered a plankton interaction model which exploits spatial variation of plankton with self and cross diffusion induced by toxin producing phytoplankton population. Tian et. al. [11] have also shown in their study that cross diffusion of plankton populations lead to the formation of spatial patterns and hence induces diffusive instability. Recently interaction of toxin producing phytoplankton-zooplankton have been studied with and without delay for obtaining possible mechanism of controlling bloom of plankton. Instabilities and patterns in zooplankton-phytoplankton with self diffusion has been discussed in Upadhyay et. al. [20]. In the present paper we have considered the interaction of toxin producing phytoplankton(TPP)-zooplankton with spatial heterogeneity and self diffusion and the main aim is to obtain the effect of spatial heterogeneity on the stability of TPP and zooplankton. The organisation of this paper is as follows: In the next section we develop mathematical model followed by its stability analysis in section 3. The bifurcation analysis of the given model system with and without diffusion stating its dynamic flow is given in section 4 and 5. The stability and bifurcation properties are provided in section 6. The justification of our analytical findings are provided numerically followed by conclusion in final sections.

2. The Mathematical Model

The mathematical model representing the TPP-zooplankton interaction is governed by the system of ordinary differential equation,

$$\begin{cases} \frac{dp}{dt} = rp(1-p/k) - c\frac{p}{a+p}z + d_1\nabla^2 p & t>0, x\in\Omega \\ \frac{dz}{dt} = c_1\frac{p}{a+p}z - \delta_2 z - \eta\frac{p}{a+p}z + d_2\nabla^2 z & t>0, x\in\Omega \\ \partial_n p = \partial_n z = 0 & t>0, x\in\partial\Omega \\ p(0,x) = p_0 \geqslant 0, z(0,x) = z_0 \geqslant 0 & x\in\Omega \end{cases} \tag{1}$$

where p(t,x) and z(t,x) denote the population densities of prey(toxin producing phytoplankton) and predator(zooplankton) species at time t and space x, respectively; the positive constants d_1 and d_2 represent the diffusion rates of prey and predator species, respectively; $r > 0$ denotes the intrinsic growth rate of prey species, $k > 0$ denotes the carrying capacity of prey species, $c > 0$, $c_1 > 0$ be the capturing rate and conversion rate of the predator population; $\delta > 0$ denotes the death rate of predator species, $a > 0$ is the half saturation constant and $\eta > 0$ be the rate of toxication by the TPP population, ∇^2 denotes the Laplacian operator

3. Stability Properties of Equilibria

All solutions of (1) are nonnegative and bounded for all $t > 0$ [20] when $d_1 = 0$, $d_2 = 0$. If $r > \delta_1$ and $c_1 - \eta > \delta_2$ system (1) has a unique interior equilibrium $E^*(p, z)$, where $p = \frac{\gamma\delta_2}{c_1-\eta-\delta_2}$ and $z = \frac{r(1-\frac{p}{K})(\gamma+p)}{c}$. In fact, under the Neumann boundary conditions, we know that E^* is still the steady-state solutions of system (1). From the point of view of ecology, the properties of positive constant steady-state solution are important and interesting. Therefore, in the following, we shall focus on the stability of $E^*(p, z)$ and the existence of Hopf bifurcation. Using transformation $u = p - p^*$ and $v = z - z^*$, system (1) can be rewritten as,

$$\begin{cases} \frac{du}{dt} = a_{10}u + a_{01}v + d_1\frac{\partial^2 u}{\partial x^2} + f(u, v, d_1) \\ \frac{dv}{dt} = b_{10}u + b_{01}v + d_2\frac{\partial^2 v}{\partial x^2} + g(u, v, d_2) \end{cases} \tag{2}$$

Where

$$f(u, v, d_1) = a_{20}u^2 + a_{11}uv + a_{02}v^2 + a_{30}u^3 + a_{21}u^2v + ...$$
$$g(u, v, d_2) = b_{20}u^2 + a_{11}uv + +b_{30}u^3 + a_{21}u^2v + ...h.o.d. \tag{3}$$

$a_{10} = r - \frac{2rp^*}{K} - \frac{c\gamma z^2}{(\gamma+p^*)^2}$,
$a_{01} = -\frac{cp^*}{\gamma+p^*}$,$a_{20} = -\frac{2r}{K} - \frac{2c\gamma z^*}{(\gamma+p^*)^3}$,$a_{11} = -\frac{c\gamma}{(\gamma+p^*)^2}$,
$a_{02} = 0$,$a_{30} = -\frac{6c\gamma z^*}{(\gamma+p^*)^4}$,$a_{21} = \frac{2c\gamma}{(\gamma+p)^3}$,$a_{03} = 0$,$b_{10} = \frac{(c_1-\eta)\gamma z^*}{(\gamma+p^*)^2}$,$b_{01} = \frac{(c_1-\eta)p^*}{\gamma+p^*} - \delta_2$,$b_{20} = -\frac{2(c_1-\eta)\gamma z^*}{(\gamma+p)^3}$,
$b_{11} = \frac{(c_1-\eta)\gamma}{(\gamma+p^*)^2}$,$b_{30} = \frac{6(c_1-\eta)\gamma z^*}{(\gamma+p^*)^4}$,$b_{21} = -\frac{2(c_1-\eta)}{(\gamma+p^*)^3}$,$b_{03} = 0$

4. Stability Without Diffusion

Theorem. In the absence of diffusion (k=0), choosing η the rate of toxin liberation as the bifurcation parameter;
(i)System remained asymptotically stable if $T_0 < 0$ and $D_0 > 0$ which is equivalent to $\eta > \eta_0$, $r > Max(\frac{\delta_2}{2}, 1)$ and where $\eta_* = c_1 - \frac{\delta_2(1-r)+\frac{2r(\delta_2+\gamma)}{K}}{2r-\delta_2}$.
(ii) A hopf-bifurcation occurs as η passes through a critical value η_0.
Proof The Jacobian matrix of the system (2) at (u^*, v^*) is
$J = \begin{pmatrix} a_{10} & a_{01} \\ b_{10} & b_{01} \end{pmatrix}$
The characteristic equation is given by,

$$\lambda^2 - T\lambda + D = 0 \tag{4}$$

where $T = a_{10} + b_{01}$, $D = a_{10}b_{01} - a_{01}b_{10}$
It is well known that the stability of trivial solution of (2) depends on the locations

of roots of (4), when all roots of (4) have negative real parts, the trivial solution of (2) is stable; otherwise, it is unstable.
Thus if $T < 0$ and $D > 0$, then E^* is locally asymptotically stable.
Next we analyze the Hopf bifurcation occurring at E^* by choosing η as the bifurcation parameter.
For the occurrence of hopf bifurcation at $\eta = \eta_0$, Jacobian J has a pair of imaginary eigenvalues, say $\lambda = \pm\iota\sqrt{D}$ and let $\lambda(\eta) = \sigma(\eta) + \iota\omega(\eta)$ be the root of (4), then $\sigma(\eta) = \frac{T}{2}$, $\omega(\eta) = \frac{\sqrt{4D-T}}{2}$
and, $|\frac{\partial\sigma(\eta)}{\partial\eta}|_{\eta=\eta_0} = \frac{-2r\delta_2\gamma}{K(c_1-\eta-\delta_2)^2} + \frac{\delta_2(1-\frac{r\gamma^2}{K})}{(c_1-\eta)^2} \neq 0$
By the Hopf Bifurcation Theorem , we know that system (1) undergoes a Hopf bifurcation at E^* when $\eta = \eta_0$.

5. Diffusion-Driven Instability of the Equilibrium Solution

In this part, we will derive conditions for the diffusion-driven instability with respect to the equilibrium solution E^*, the spatially homogenous solution of the (1).
It is well known that the operator $-\Delta\phi = \lambda\phi$, $x \in \Omega$, with the above no-flux boundary condition has eigenvalues and eigenfunctions as follows:

$$\mu_0 = 0,\ \phi_0(x) = \sqrt{\tfrac{1}{\pi}},\ \mu_k = k^2,\ \phi_k(x) = \sqrt{\tfrac{2}{\pi}}\cos(kx),\ \text{k=1,2,3,....}$$

From the standard linear operator theory, it is known that if all the eigenvalues of the operator L have negative real parts, then $E^* = (u_1, u_2)$ is asymptotically stable, and if some eigenvalues have positive real parts, the $E^* = (u_1, u_2)$ is unstable.

We consider the following characteristic equation of the operator L:

$$L\begin{pmatrix}\phi\\ \psi\end{pmatrix} = \mu\begin{pmatrix}\phi\\ \psi\end{pmatrix}$$

Let $(\phi(x), \psi(x))^T$ be the eigenfunction of L corresponding to eigenvalue μ and let

$$\begin{pmatrix}\phi\\ \psi\end{pmatrix} = \Sigma_{k=0}^{\infty}\begin{pmatrix}a_k\\ b_k\end{pmatrix}\cos(kx)$$

where a_k and b_k are coefficients, we obtain that

$$-k^2D\Sigma_{k=0}^{\infty}\begin{pmatrix}a_k\\ b_k\end{pmatrix}\cos(kx) + J\Sigma_{k=0}^{\infty}\begin{pmatrix}a_k\\ b_k\end{pmatrix}\cos(kx) = \mu\Sigma_{k=0}^{\infty}\begin{pmatrix}a_k\\ b_k\end{pmatrix}\cos(kx)$$

$$(J - k^2D)\Sigma_{k=0}^{\infty}\begin{pmatrix}a_k\\ b_k\end{pmatrix} = \mu\Sigma_{k=0}^{\infty}\begin{pmatrix}a_k\\ b_k\end{pmatrix} \qquad (k = 0.1.2., ...,)$$

Denote

$$J_k = J - k^2D = \left[\begin{pmatrix}a_{10} & a_{01}\\ b_{10} & b_{01}\end{pmatrix} - \begin{pmatrix}d_1\mu_k & 0\\ 0 & d_2\mu_k\end{pmatrix}\right] = 0$$

It follows from this, that the eigenvalues of L are given by the eigenvalues of J_k for k=0,1,2,.. The characteristic equation of J_k is

$$\mu^2 - \mu T_k + D_k = 0, \qquad k = 0, 1, 2, ... \tag{5}$$

where
$T_k = (d_1 + d_2)k^2 - (a_{10} + b_{01})$
$D_k = d_1d_2k^4 - (d_1b_{01} + d_2a_{10})k^2 + (a_{10}b_{01} - a_{01}b_{10})$

Theorem. (i)The positive equilibrium E^* is locally asymptotically stable in the presence of diffusion if and only if $T_k < 0$ and $D_k > 0$ i.e. (5) do not possess a positive root for any $k \geqslant 0$
(ii) Diffusion instability (Turing instability) occurs if the following inequality holds, $4d_1d_2(a_{10}b_{01} - a_{01}b_{10}) < (d_1b_{01} + d_2a_{10})^2$.
Proof. From the definition of $T_k(T_0 < 0)$ we have $T_k < 0$ for all $k > 0$ satisfying $k < \frac{a_{10}+b_{01}}{d_1+d_2}$ where $\eta > \eta_*$.
Thus the diffusion driven instability only occurs if $D_k(k^2) = d_1d_2k^4 - (d_1b_{01} + d_2a_{10})k^2 + (a_{10}b_{01} - a_{01}b_{10}) < 0$ i.e. (5) has at least one positive root. Since D_k is quadratic in k^2 and the graph of $D_k = 0$ is a parabola. The minimum of $D_k(k^2)$ is occur at $k^2 = k^2_{min}$, where

$$k^2_{min} = \frac{d_1b_{01}+d_2a_{10}}{2d_1d_2} > 0$$

Consequently, the condition for diffusive instability is $D_k(k^2) < 0$,
i.e. $4d_1d_2(a_{10}b_{01} - a_{01}b_{10}) < (d_1b_{01} + d_2a_{10})^2$.

6. Properties of Bifurcating Solutions

The PDE (2.1) possesses any periodic solution of corresponding ODE as a spatially homogeneous periodic solution, including the ones from Hopf bifurcation. We can also perform a Hopf bifurcation analysis of PDE 2.1 at the same bifurcation point of ODE and bifurcating spatially homogeneous periodic solutions exist near $\eta = \eta_0$. So we shall applying the normal form theory and center manifold theorem introduced by Hassard et al [12]. to study the direction of Hopf bifurcations. To determine the stability of bifurcated periodic solutions, we need to know the restriction of the system to its center manifold at $\mu = \mu_0$. Denote by L the operator

$$\begin{pmatrix} u \\ v \end{pmatrix} = L \begin{pmatrix} u \\ v \end{pmatrix}$$

with domain

$$\{(u, v) \in H^2(\Omega) \times H^2(\Omega) | \partial u_w, \partial v_w = 0, x \in \Omega\}$$

, where the $H^2(\Omega)$ is the standard Sobolev space and

$$L^* = \begin{pmatrix} a_{10} + d_1\Delta & b_{10} \\ a_{01} & b_{01} + d_2\Delta \end{pmatrix}.$$

In fact, we can choose

$$q = \begin{pmatrix} 1 \\ \frac{(\iota\omega_0 - a_{10})}{a_{01}} \end{pmatrix} = \begin{pmatrix} a_0 \\ b_0 \end{pmatrix}, \qquad q^* = D^* \begin{pmatrix} \frac{(-\omega_0 - \iota a_{10})}{a_{01}} \\ \iota \end{pmatrix} = \begin{pmatrix} a_* \\ b_* \end{pmatrix}, \quad D^* = \frac{a_{01}}{2\pi\omega_0}$$

For all $\alpha \in D_{L^*}$, $\beta \in D_L$, it is not difficult to verify that
$< L^*\alpha, \beta >=< \alpha, L\beta >$, $Lq = \iota\omega_0 q$
$L^*q^* = -\iota\omega_0 q^*$, $< q^*, q >= 1$, $< q^*, \bar{q} >= 0$.
where $< \alpha, \beta >= \int_\Omega \alpha^T \beta dx$ denotes the inner product in $L^2(\Omega) \times L^2(\Omega)$.
Noticing that
$(u, v) = zq + \bar{z}\bar{q} + W, \qquad z =< q^*, (u_1, u_2)^T >$
Then

$$\begin{cases} u = z + \bar{z} + W_1 \\ v = z(\frac{(\iota\omega_0 - a_{10})}{a_{01}}) + \bar{z}(\frac{(-\iota\omega_0 - a_{10})}{a_{01}}) + W_2 \end{cases} \tag{6}$$

System in (z, W) coordinates becomes ,

$$\begin{cases} \frac{dz}{dz} = \iota\omega_0 z + < q^*, \tilde{f} > \\ \frac{dW}{dt} = LW + [\tilde{f} - < q^*, \tilde{f} > q - < \bar{q^*}, \tilde{f} > \bar{q}] \end{cases} \tag{7}$$

where $\tilde{f} = (f, g)$ defined in (3).
Then, straightforward but tedious calculations show that

$< q^*, \tilde{f} >= \frac{a_{01}}{2\omega_0}[(\frac{(\omega_0 - \iota a_{10})}{a_{01}})f + \iota g]$

$< \bar{q^*}, \tilde{f} >= \frac{a_{01}}{2\omega_0}[(\frac{(\omega_0 + \iota a_{10})}{a_{01}})f - \iota g]$

$< q^*, \tilde{f} > q = \frac{a_{01}}{2\omega_0}[(\frac{(\omega_0 - \iota a_{10})}{a_{01}})f + \iota g, \frac{(\iota\omega_0 - a_{10})}{a_{01}}((\frac{(\omega_0 - \iota a_{10})}{a_{01}})f + \iota g)]$

$< \bar{q^*}, \tilde{f} > \bar{q} = \frac{a_{01}}{2\omega_0}[\frac{((\omega_0 + \iota a_{10})}{a_{01}})f - \iota g), ((\frac{(\omega_0 + \iota a_{10})}{a_{01}})f - \iota g)\frac{(-\iota\omega_0 - a_{10})}{a_{01}}]$
Noticing that

$$H = \frac{H_{20}}{2}z^2 + H_{11}z\bar{z} + \frac{H_{02}}{2}\bar{z}^2 + ... \tag{8}$$

$$W = \frac{W_{20}}{2}z^2 + W_{11}z\bar{z} + \frac{W_{02}}{2}\bar{z}^2 + ... \tag{9}$$

On the center manifold, we have

$\begin{cases} (2\iota\omega - L)W_{20} = H_{20} \\ (-L)W_{11} = H_{11} \\ W_{02} = \bar{W_{20}} \end{cases}$ and
$< q^*, \tilde{f} > q + < \bar{q^*}, \tilde{f} > \bar{q} = (f, g)$

$H(z, \bar{z}, W) =< q^*, \tilde{f} > q + < \bar{q^*}, \tilde{f} > \bar{q} - (f, g) = 0$

This implies that

W_{20}=W_{02}=W_{11}=0
Therefore

$$\frac{dz}{dt} = \iota\omega z + \frac{g_{20}}{2}z^2 + g_{11}z\bar{z} + \frac{g_{02}}{2}\bar{z}^2 + \frac{g_{21}}{2}z^2\bar{z} + O(|z|^4) \tag{10}$$

where

$$\begin{aligned} g_{20} &= 2D^*[\bar{a_0^*}(a_{20} + b_0 a_{11} + b_0^2 a_{02}) + \bar{b_0^*}(b_{20} + b_0 b_{11})], \\ g_{11} &= D^*[\bar{a_0^*}(2a_{20} + 2Re(b_0)a_{11} + 2a_{02}b_0\bar{b_0}) + \bar{b_0^*}(2b_{20} + 2Re(b_0)b_{11})], \\ g_{02} &= 2D^*[\bar{a_0^*}(a_{20} + a_{11}\bar{b_0} + a_{02}\bar{b_0^2} + 2a_{21}\bar{b_0}) + \bar{b_0^*}(b_{20} + \bar{b_0}b_{11} + 2\bar{b_0}b_{21})], \\ g_{21} &= 2D^*[\bar{a_0^*}(3a_{30} + a_{21}\bar{b_0} + 2a_{21}b_0) + \bar{b_0^*}(3b_{30} + 2(2b_0 + \bar{b_0})b_{21})] \end{aligned}$$

According to [12], we can obtain

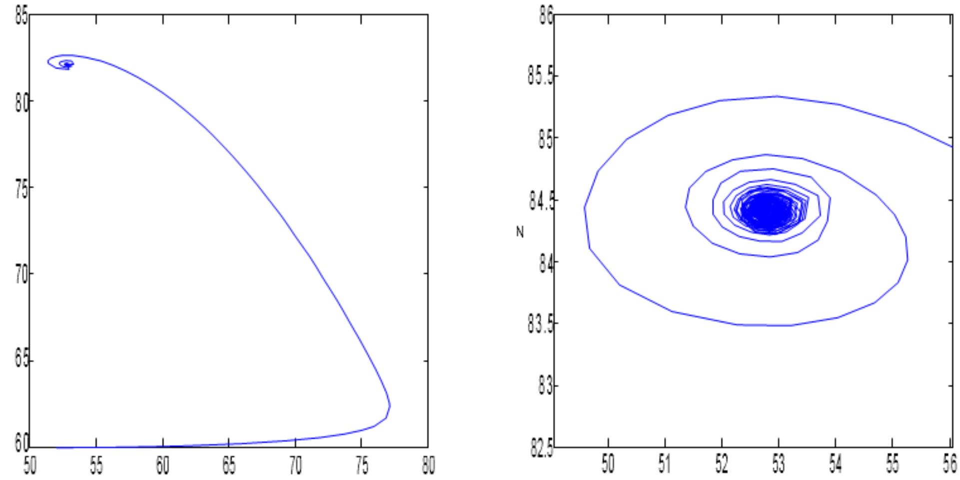

Figure 1. Left: the positive equilibrium is asymptotically stable and right: positive equilibrium is unstable, and there exists a stable limit cycle

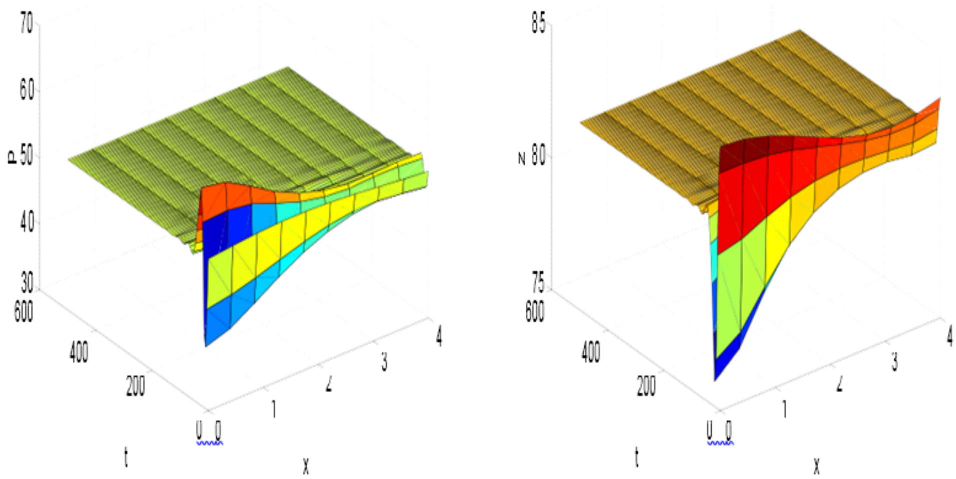

Figure 2. Numerical simulations of the stable equilibrium solution of system (2.1). The solution appears to converge to a homogeneous steady state.

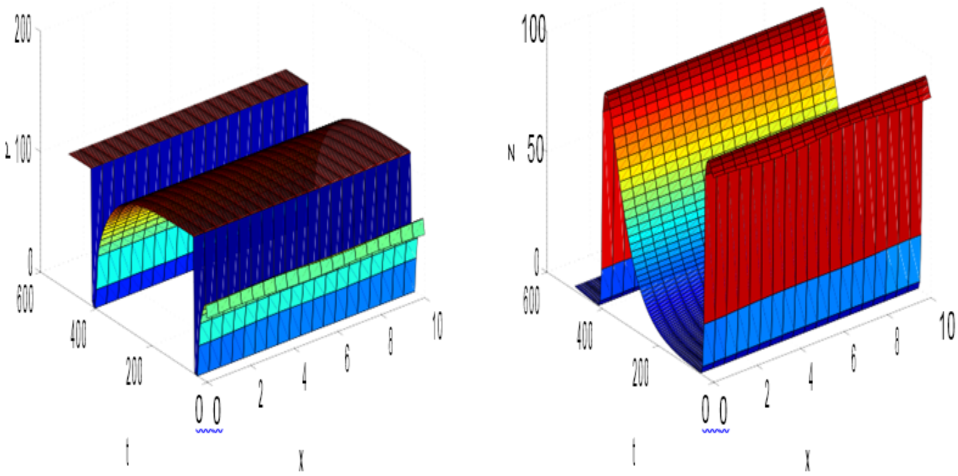

Figure 3. Numerical simulations of an unstable homogeneous equilibrium solution driven by diffusion. Left: component p(unstable); right: component z (unstable).

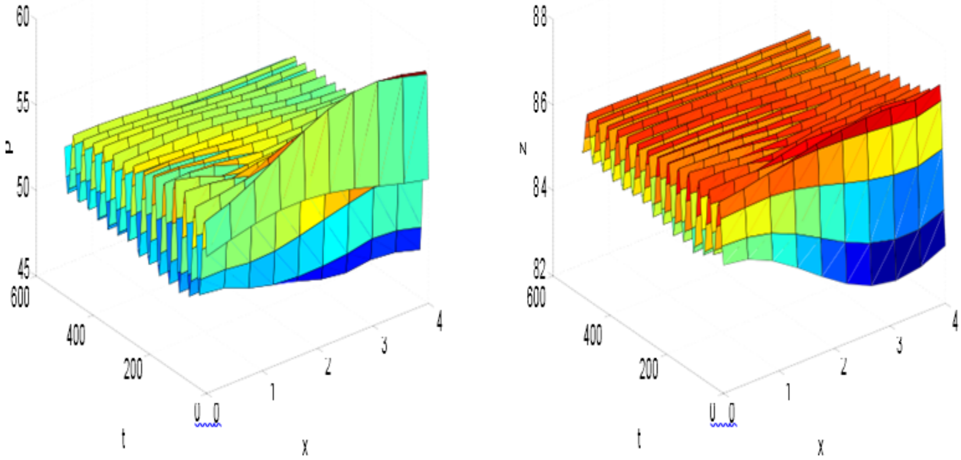

Figure 4. Numerical simulations of inhomogeneous stable periodic solution of given system with diffusion. Left: orbitally stable periodic solution (component p); right: orbitally stable periodic solution (component z).

$$c_1(0) = \frac{\iota\{g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\}}{2\omega_0} + \frac{g_{21}}{2}$$

$$\mu_2 = -\frac{Re\{c_1(0)\}}{Re\{\lambda'(\eta)\}},$$

$$\beta_2 = 2Re\{c_1(0)\},$$

7. Numerical Simulation

In this section, we gives the numerical validation of results derived analytically in above sections to observe the effects of diffusion on the given plankton system. We considered the following model system,

$$\begin{cases} \frac{dp}{dt} = 3p(1 - p/105) - 0.7\frac{p}{5+p}z + d_1\Delta^2 p \\ \frac{dz}{dt} = 0.6\frac{p}{5+p}z - 0.364z - 0.2\frac{p}{5+p}z + d_2\Delta^2 z \end{cases} \tag{11}$$

which has an interior equilibrium point $E^*(52.80, 84.40)$ in the absence of diffusion. From the sign of T(trace)=-0.0976 and D(det)=0.0314, it is clear that (4) has eigen values with negative real parts which ensure the local asymptotic stability of E^* when $\eta > \eta_0 = 0.1871$. When $\eta = \eta_0 = 0.1871$ and K=108, it can be calculated that the jacobian has pair of imaginary eigen values and system enters into hopf bifurcation with the existence of limit cycles (see fig1). For PDE, taking $d_1 = 1 \times 10^{-3}$, $d_2 = 1 \times 10^{-3}$, K=105, $\eta = 0.2071$, it is found that the homogenous equilibrium solution which are also spatially homogeneous are stable, which is shown numerically in fig 2.

Again taking $d_1 = 1 \times 10^{0}$, $d_2 = 1 \times 10^{0}$, K=113, $\eta = 0.2071 > \eta_0$, it is found that the homogenous equilibrium solution which are the spatially homogeneous become unstable which is shown numerically in fig 3.

Choosing another set of parameters $d_1 = 1 \times 10^{-3}$, $d_2 = 1 \times 10^{-5}$, K=108, $\eta = 0.1871$, it is obtained that Hopf bifurcation occurs at$\eta = \eta_0$, the direction of the bifurcation is supercritical, and the bifurcating periodic solutions are locally asymptotically stable. This is shown in fig 4., where the initial condition is taken at $(52 + \sin x, 84 + \cos x)$.

8. Discussion and Conclusion

In this paper the TPP-zooplankton interaction in spatiotemporal domain were studied where both populations are subject to self diffusion. We have first analysed the given system by taking diffusion coefficients $d_1 = 0$, $d_2 = 0$. It is observed that under certain conditions the positive equilibrium E^* remained asymptotically stable and a hopf bifurcation occurs when η, the rate of toxication passes through its critical value $\eta = \eta_0$. In the presence of diffusion, it is found that the spatially homogeneous solution remained stable under certain conditions and Turing instability arises when some of these conditions are violated. Further using normal form the direction of spatially homogeneous periodic solution are derived and their stability is discussed.

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