Toxic phytoplankton-induced spatiotemporal patterns

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Abstract Here we consider a reaction diffusion system of three plankton populations, a zooplankton feeding on two phytoplankton populations, in two different settings. Firstly, the two phytoplanktons are both non-toxic and both enhance the growth of the grazing zooplankton. Secondly, we assume that one of the phytoplankton releases toxin and thereby inhibits the growth of the zooplankton. Our analytic and numerical study shows that the spatiotemporal distribution of the plankton species is uniform when both phytoplankton populations are non-toxic. However, in the presence of toxin-producing phytoplankton, the biomass distribution of all the plankton populations becomes inhomogeneous.

Keywords Plankton dynamics · Toxin-producing phytoplankton · Toxin inhibition · Diffusion · Paradox of plankton · Diffusive instability

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1 Introduction

Marine plankton dynamics has become an important contemporary research area due to the fact that plankton is at the bottom of the oceanic food web. Field studies have assessed its physical and biological properties. From these, several models have been proposed for the investigation of plankton dynamics. They lead to the insurgence of pattern structures. For a review of some of them, the reader should consult Part III and for stochastic effects Part IV of [1].

One line of investigation is particularly concerned with the negative impact of eutrophication. This is the consequence of the so-called red, or sometimes brown, tides [2–4], which have been found to recur ever more often in recent times. 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 reaching, 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) [5–8].

Several various possible mechanisms that aim to understand how the diversity of plankton communities is maintained have been proposed and analyzed in the literature [9–12]. 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 [13].

Of particular interest here is a model recently proposed [14] consisting of a system of two phytoplankton and one zooplankton populations. It will be considered under two different scenarios. Firstly, the two phytoplankton populations enhance the growth of the zooplankton grazing on them. Secondly, one of the phytoplankton is assumed instead to be toxic to the grazer zooplankton, thereby inhibiting its growth via a nonlinear response.

This paper is then mainly focused on the consideration of how diffusive plankton movement influences the evolution of the models presented in [14]. An important finding of our investigation is that the action of the toxin-producing phytoplankton is not only harmful to the grazing zooplankton but can also act as a triggering mechanism to generate spatial inhomogeneities.

The organization of the paper is as follows. In Section 2 we extend to space the two phytoplankton-zooplankton models already considered in the literature [14], by adding diffusion. Next the non-toxic releasing model is analyzed in Section 3, while Section 4 considers the system in the presence of toxic phytoplankton. In Section 5 we then study the same problems in a two-dimensional context. Finally, in Section 6, a brief discussion concludes the paper.

2 The models

In this research we want to investigate the spatial behavior of two plankton models earlier presented in the literature as purely time-dependent population models.

The main purpose of [14] was to study the effects of toxic phytoplankton on zooplankton. In that paper, the study of equilibria was performed, and bifurcation diagrams were reported. No chaotic behavior was discovered. To investigate the spatial behavior for this model, it is

necessary to set up two systems in a symmetrical fashion. In fact, since the action of toxic phytoplankton needs to be examined when non-toxic phytoplankton are also present, for comparison purposes, we also consider a second model in which two different non-toxic phytoplankton populations are present. In this way, the systems are well balanced for the required comparison.

Let Z denote the zooplankton population, N_1 and N_2 be the two phytoplankton populations. The former will always be non-toxic, while the latter will be non-toxic in the first model and toxin-releasing in the second.

The spatial extension of the model presented in [14] is obtained as follows. We assume that both the non-toxic (NTP) and toxic phytoplankton grow logistically in the absence of the other, and, while when both are present, they compete for resources. An interspecific competition term then comes into play. The zooplankton predation on both kinds of phytoplankton is described by simple mass action terms. Under these assumptions, the spatial reaction-diffusion model for NTP can be written as

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= N_1 \left\{ r_1 \left(1 - \frac{N_1 + \psi_1 N_2}{K} \right) - \alpha_1 Z \right\} + D_1 \frac{\partial^2 N_1}{\partial x^2}, \\ \frac{\partial N_2}{\partial t} &= N_2 \left\{ r_2 \left(1 - \frac{N_2 + \psi_2 N_1}{K} \right) - \alpha_2 Z \right\} + D_2 \frac{\partial^2 N_2}{\partial x^2}, \\ \frac{\partial Z}{\partial t} &= Z \{ \beta_1 N_1 + \delta N_2 - c \} + D_3 \frac{\partial^2 Z}{\partial x^2}.\end{aligned}\quad (1)$$

The parameters r_1 and r_2 are the intrinsic growth rates of the phytoplankton populations. K is the carrying capacity for phytoplankton, common therefore to both N_1 and N_2 ; ψ_1 and ψ_2 represent the interspecific competition coefficients of N_1 on N_2 and N_2 on N_1 , respectively; α_1 and α_2 are the specific predation rates of zooplankton on N_1 and N_2 , respectively; β_1 and δ are the biomass ration consumed per new predator corresponding to the prey N_1 and N_2 , respectively; c is the natural mortality rate of zooplankton; D_1 , D_2 , and D_3 represent the diffusion coefficients of the N_1 , N_2 , and Z populations, respectively.

In the case of toxin-producing phytoplankton (TPP) by the population N_2 , the inhibition of zooplankton is instead represented by a highly nonlinear response function, namely

$$\frac{\theta N_2}{m + N_2}.$$

The spatial reaction-diffusion model for TPP is then

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= N_1 \left\{ r_1 \left(1 - \frac{N_1 + \psi_1 N_2}{K} \right) - \alpha_1 Z \right\} + D_1 \frac{\partial^2 N_1}{\partial x^2}, \\ \frac{\partial N_2}{\partial t} &= N_2 \left\{ r_2 \left(1 - \frac{N_2 + \psi_2 N_1}{K} \right) - \alpha_2 Z \right\} + D_2 \frac{\partial^2 N_2}{\partial x^2}, \\ \frac{\partial Z}{\partial t} &= Z \left\{ \beta_1 N_1 - \frac{\theta N_2^2}{m + N_2} - c \right\} + D_3 \frac{\partial^2 Z}{\partial x^2}.\end{aligned}\quad (2)$$

All the parameters in these models are assumed to be positive.

Let Ω represent a suitable spatial domain in one or two dimensions, as the case considered suggests. For the systems (1) and (2) in the domain Ω we take the following initial conditions

$$N_1(0, x) > 0, \quad N_2(0, x) > 0, \quad Z(0, x) > 0$$

and the zero-flux boundary condition

$$\frac{\partial N_1}{\partial x}|_{\partial\Omega} = \frac{\partial N_2}{\partial x}|_{\partial\Omega} = \frac{\partial Z}{\partial x}|_{\partial\Omega} = 0.$$

This means that across the boundary no external input for these populations can occur.

3 The non-toxic releasing model (1)

For the benefit of the reader, we report here in Table 1 the steady-states of the system (1) in absence of diffusion, as found in [14].

The boundary equilibria components are as follows:

$$\begin{aligned}\widehat{N}_2^{iii} &= \frac{c}{\delta}, \quad \widehat{Z}^{iii} = \frac{r_2}{\alpha_2} \left(1 - \frac{c}{K\delta}\right), \quad \widehat{N}_1^{iv} = \frac{c}{\beta_1}, \quad \widehat{Z}^{iv} = \frac{r_1}{\alpha_1} \left(1 - \frac{c}{K\beta_1}\right), \\ \widehat{N}_1^v &= \frac{K(1 - \psi_1)}{1 - \psi_1\psi_2}, \quad \widehat{N}_2^v = \frac{K(1 - \psi_2)}{1 - \psi_1\psi_2},\end{aligned}$$

while for the coexistence equilibrium $\widehat{E}^*$ we have the components

$$\begin{aligned}\widehat{N}_1^* &= \frac{r_1 r_2 K(1 - \psi_1) + K(r_1 \alpha_2 \psi_1 - r_2 \alpha_1) \widehat{Z}^*}{r_1 r_2 (1 - \psi_1 \psi_2)}, \\ \widehat{N}_2^* &= \frac{r_1 r_2 K(1 - \psi_2) + K(r_2 \alpha_1 \psi_2 - r_1 \alpha_2) \widehat{Z}^*}{r_1 r_2 (1 - \psi_1 \psi_2)}, \\ \widehat{Z}^* &= \frac{c(1 - \psi_1 \psi_2) - K\{\beta_1(1 - \psi_1) + \delta(1 - \psi_2)\}}{\beta_1 K(r_1 \psi_1 \alpha_2 - r_2 \alpha_1) + K\delta(r_2 \psi_2 \alpha_1 - r_1 \alpha_2)}\end{aligned}$$

Table 1 The equilibria of system (1) without diffusion, i.e., for $D_1 = D_2 = D_3 = 0$

Equilibria	Feasibility	Stability condition
$\widehat{E}_0 = (0, 0, 0)$		Unstable saddle point
$\widehat{E}_1 = (K, 0, 0)$		$\psi_2 > 1, \beta_1 < \frac{c}{K}$
$\widehat{E}_2 = (0, K, 0)$		$\psi_1 > 1, \delta < \frac{c}{K}$
$\widehat{E}_3 = (0, \widehat{N}_2^{iii}, \widehat{Z}^{iii})$	$\delta > \frac{c}{K}$	$\delta > \max\left(\delta_2^*, \frac{c}{K}\right), \alpha_1 > \frac{r_1 \alpha_2}{r_2}$
$\widehat{E}_4 = (\widehat{N}_1^{iv}, 0, \widehat{Z}^{iv})$	$\beta_1 > \frac{c}{K}$	$\beta_1 > \max\left(\beta_1^*, \frac{c}{K}\right), \alpha_1 < \frac{r_1 \alpha_2}{r_2}$
$\widehat{E}_5 = (\widehat{N}_1^v, \widehat{N}_2^v, 0)$	$\psi_1 < 1$ and $\psi_2 < 1$	$\delta < \delta_1^*, \beta_1 < \beta_2^*, \psi_1 < 1, \psi_2 < 1$
$\widehat{E}^* = (\widehat{N}_1^*, \widehat{N}_2^*, \widehat{Z}^*)$	Eq. 3	$\psi_1 < \frac{r_2 \alpha_1}{r_1 \alpha_2}, \psi_2 < \frac{r_1 \alpha_2}{r_2 \alpha_1}$

The constants used have been introduced in [14]: $\beta_1^* = \frac{c(r_1 \alpha_2 - r_2 \alpha_1 \psi_2)}{K(r_1 \alpha_2 - r_2 \alpha_1)}$, $\beta_2^* = \frac{c(1 - \psi_1 \psi_2)}{K(1 - \psi_1)}$, $\delta_1^* = \frac{c(1 - \psi_1 \psi_2) - \beta_1 K(1 - \psi_1)}{K(1 - \psi_2)}$, $\delta_2^* = \frac{c(r_2 \alpha_1 - r_1 \alpha_2 \psi_1)}{K(r_2 \alpha_1 - r_1 \alpha_2)}$

and the sufficient conditions for its feasibility are

$$\alpha_1 > \frac{r_1 \alpha_2}{r_2}, \quad \psi_1 < \min \left\{ \frac{r_2 \alpha_1}{r_1 \alpha_2}, 1 \right\}, \quad \psi_2 < \min \left\{ \frac{r_1 \alpha_2}{r_2 \alpha_1}, 1 \right\}, \quad \delta_1^* < \delta < \delta_2^*, \quad (3)$$

where

$$\delta_1^* = \frac{c(1 - \psi_1 \psi_2) - \beta_1 K(1 - \psi_1)}{K(1 - \psi_2)}, \quad \delta_2^* = \frac{c(r_2 \alpha_1 - r_1 \alpha_2 \psi_1)}{K(r_2 \alpha_1 - r_1 \alpha_2)}.$$

Denoting the general uniform steady state (USS) of the spatial model (1) by $(\widehat{N}_1, \widehat{N}_2, \widehat{Z})$, we now investigate perturbations of the following form

$$\begin{pmatrix} N_1(t, x) \\ N_2(t, x) \\ Z(t, x) \end{pmatrix} = \begin{pmatrix} \widehat{N}_1 \\ \widehat{N}_2 \\ \widehat{Z} \end{pmatrix} + \begin{pmatrix} N_{1d}(t) \\ N_{2d}(t) \\ Z_d(t) \end{pmatrix} \cos(lx) \exp(\lambda t),$$

where $l > 0$ is the wave number of the spatial perturbation and $\lambda > 0$ is the time evolution rate. By substituting these expressions into Eq. 1, and differentiating, we see that the exponential factors out. Eliminating it, and using the fact that $(\widehat{N}_1, \widehat{N}_2, \widehat{Z})$ is a steady state for Eq. 1, we obtain the following system of ordinary differential equations

$$\begin{aligned} \frac{dN_{1d}}{dt} &= -\lambda N_{1d} + N_{1d} \left\{ r_1 \left(1 - \frac{\widehat{N}_1 + \psi_1 \widehat{N}_2}{K} \right) - r_1 \frac{N_{1d}}{K} \cos(lx) \exp(\lambda t) \right. \\ &\quad \left. - r_1 \frac{\Psi_1}{K} N_{2d} \cos(lx) \exp(\lambda t) - \alpha_1 \widehat{Z} - \alpha_1 Z_d \cos(lx) \exp(\lambda t) \right\} \\ &\quad - \widehat{N}_1 \left[r_1 \frac{N_{1d}}{K} + r_1 \frac{\Psi_1}{K} N_{2d} + \alpha_1 Z_d \right] - D_1 l^2 N_{1d}, \\ \frac{dN_{2d}}{dt} &= -\lambda N_{2d} + N_{2d} \left\{ r_2 \left(1 - \frac{\widehat{N}_2 + \psi_2 \widehat{N}_1}{K} \right) - r_2 \frac{N_{2d}}{K} \cos(lx) \exp(\lambda t) \right. \\ &\quad \left. - r_2 \frac{\Psi_2}{K} N_{1d} \cos(lx) \exp(\lambda t) - \alpha_2 \widehat{Z} - \alpha_2 Z_d \cos(lx) \exp(\lambda t) \right\} \\ &\quad - \widehat{N}_2 \left[r_2 \frac{N_{2d}}{K} + r_2 \frac{\Psi_2}{K} N_{1d} + \alpha_2 Z_d \right] - D_2 l^2 N_{2d}, \\ \frac{dZ_d}{dt} &= -\lambda Z_d + \widehat{Z} [\beta_1 N_{1d} + \delta N_{2d}] \\ &\quad + Z_d [\beta_1 N_{1d} \cos(lx) \exp(\lambda t) + \delta N_{2d} \cos(lx) \exp(\lambda t)] - D_3 l^2 Z_d. \end{aligned}$$

After linearization we seek the system's equilibria. The problem is then reduced to an eigenvalue problem in the parameter λ for the following matrix at the generic USS $(\widehat{N}_1, \widehat{N}_2, \widehat{Z})$,

$$J \equiv (\widehat{J}_{ij}) = \begin{pmatrix} \widehat{J}_{11} - l^2 D_1 & -\frac{r_1 \psi_1}{K} \widehat{N}_1 & -\alpha_1 \widehat{N}_1 \\ -\frac{r_2 \psi_2}{K} \widehat{N}_2 & \widehat{J}_{22} - l^2 D_2 & -\alpha_2 \widehat{N}_2 \\ \beta_1 \widehat{Z} & \delta \widehat{Z} & \widehat{J}_{33} - l^2 D_3 \end{pmatrix}, \quad (4)$$

with $\widehat{J}_{33} = \beta_1 \widehat{N}_1 + \delta \widehat{N}_2 - c$ and

$$\begin{aligned}\widehat{J}_{11} &= r_1 - \frac{2r_1}{K} \widehat{N}_1 - \frac{r_1 \psi_1}{K} \widehat{N}_2 - \alpha_1 \widehat{Z}, \\ \widehat{J}_{22} &= r_2 - \frac{2r_2}{K} \widehat{N}_2 - \frac{r_2 \psi_2}{K} \widehat{N}_1 - \alpha_2 \widehat{Z}.\end{aligned}\quad (5)$$

Its eigenvalues will thus provide the needed time dependency λ .

The eigenvalues for the plankton-free USS, $\widehat{E}_0$, are $r_1 - l^2 D_1$, $r_2 - l^2 D_2$ and $-c - l^2 D_3$. Hence, in presence of diffusion $\widehat{E}_0$ is uniformly stable if

$$D_1 > D_1^{(1)} \equiv \frac{r_1}{l^2}, \quad D_2 > D_1^{(2)} \equiv \frac{r_2}{l^2}, \quad (6)$$

i.e., when the prey diffusion coefficients exceed a threshold, the system can collapse, wiping out all the populations.

In contrast, the eigenvalues for phytoplankton (N_2) and zooplankton (Z) free USS, $\widehat{E}_1$, are $-(r_1 + l^2 D_1)$, $r_2(1 - \psi_2) - l^2 D_2$ and $\beta_1 K - c - l^2 D_3$. In the absence of diffusion, all the eigenvalues are negative when $\psi_2 > 1$ and $\beta_1 < \frac{c}{K}$. For these conditions, all the eigenvalues remain negative also in the presence of diffusion, and therefore $\widehat{E}_1$ is spatially stable.

By a similar argument, $\widehat{E}_2$ is also spatially stable when $\psi_1 > 1$ and $\delta_1 < \frac{c}{K}$.

At $\widehat{E}_3$, the characteristic equation factors to give the eigenvalue $\widehat{A} - l^2 D_1$ with $\widehat{A} = r_1 \left(1 - \frac{\psi_1}{K} \widehat{N}_2^{iii}\right) - \alpha_1 \widehat{Z}^{iii}$ and λ can be obtained from the quadratic

$$\lambda^2 + \lambda \left[l^2 D_3 + l^4 D_2 D_3 + \frac{r_2 c}{K \delta} \right] + \alpha_2 \lambda \widehat{N}_2^{iii} \widehat{Z}^{iii} + l^4 D_2 D_3 + l^2 D_3 \frac{r_2 c}{K \delta} = 0.$$

In the absence of diffusion, $\widehat{E}_3$ is locally asymptotically stable (LAS) if $\delta > \max(\delta_2^*, \frac{c}{K})$, $\alpha_1 > \frac{r_1 \alpha_2}{r_2}$. Clearly, the presence of diffusion does not alter the sign of the eigenvalues, so that the equilibrium $\widehat{E}_3$ in the presence of diffusion is uniformly stable when it is LAS in absence of diffusion.

Similarly, if $\widehat{E}_4$ is LAS in absence of diffusion it remains uniformly spatially stable when diffusion is also considered.

The characteristic equation for $\widehat{E}_5$ again factors to give the eigenvalue $-C_3 + l^2 D_3$ with $C_3 = \beta_1 \widehat{N}_1^v + \delta \widehat{N}_2^v - c$ and the quadratic

$$\begin{aligned}\lambda^2 + \lambda[l^2(D_1 + D_2) - (A_1 + B_2)] + l^4 D_1 D_2 - l^2(D_1 B_2 + D_2 A_1) \\ + A_1 B_2 - A_2 B_1 = 0\end{aligned}\quad (7)$$

where

$$A_1 = -\frac{r_1}{K} \widehat{N}_1^v, \quad B_1 = -\frac{r_1 \psi_1}{K} \widehat{N}_1^v, \quad A_2 = -\frac{r_2 \psi_2}{K} \widehat{N}_2^v, \quad B_2 = -\frac{r_2}{K} \widehat{N}_2^v.$$

Now, in view of the feasibility condition $\psi_1 \psi_2 < 1$ we find

$$A_1 B_2 - A_2 B_1 = \frac{r_1 r_2}{K^2} \widehat{N}_1^v \widehat{N}_2^v (1 - \psi_1 \psi_2) > 0.$$

Moreover, for $A_1 < 0$ and $B_2 < 0$, both the linear and the constant terms in Eq. 7 are positive. In the absence of diffusion, $\widehat{E}_5$ is LAS if $C_3 < 0$. Hence, in the presence of diffusion, all the eigenvalues retain the negative real part. Thus the zooplankton-free equilibrium $\widehat{E}_5$ is also spatially stable.

The characteristic equation for $\widehat{E}^*$ is

$$\lambda^3 + \widehat{a}_1 \lambda^2 + \widehat{a}_2 \lambda + \widehat{a}_3 = 0, \quad (8)$$

with

$$\begin{aligned} \widehat{a}_1 &= a_1 + l^2(D_1 + D_2 + D_3), \\ \widehat{a}_2 &= a_2 + l^4(D_1 D_2 + D_1 D_3 + D_2 D_3) \\ &\quad - l^2 D_2 \widehat{J}_{11} - l^2 D_3 \widehat{J}_{11} - l^2 D_1 \widehat{J}_{22} - l^2 D_3 \widehat{J}_{22}, \\ \widehat{a}_3 &= a_3 + l^6 D_1 D_2 D_3 - l^4(D_2 D_3 \widehat{J}_{11} + D_1 D_3 \widehat{J}_{22}) \\ &\quad + l^2(-D_3 \widehat{J}_{12} \widehat{J}_{21} + D_3 \widehat{J}_{11} \widehat{J}_{22} - D_2 \widehat{J}_{13} \widehat{J}_{31} - D_1 \widehat{J}_{23} \widehat{J}_{32}), \end{aligned}$$

where a_1 , a_2 , and a_3 are the coefficients of the characteristic equation in the absence of diffusion, which satisfy the Routh-Hurwitz criteria: $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 - a_3 > 0$ for local asymptotic stability.

Now diffusive instability occurs if one of the Routh-Hurwitz criteria fails: but both $\widehat{a}_1 > 0$ and $\widehat{a}_3 > 0$ will hold always, since the latter can be rewritten as follows:

$$\widehat{a}_3 = l^6 \widehat{H}_0 + l^4 \widehat{H}_1 + l^2 \widehat{H}_2 + a_3, \quad (9)$$

where $\widehat{H}_0 = D_1 D_2 D_3 > 0$ and

$$\begin{aligned} \widehat{H}_1 &= -D_2 D_3 \widehat{J}_{11} - D_1 D_3 \widehat{J}_{22} = D_3 \left(\frac{r_1 D_2}{K} \widehat{N}_1^* + \frac{r_2 D_1}{K} \widehat{N}_2^* \right) > 0, \\ \widehat{H}_2 &= -D_3 \widehat{J}_{12} \widehat{J}_{21} + D_3 \widehat{J}_{11} \widehat{J}_{22} - D_2 \widehat{J}_{13} \widehat{J}_{31} - D_1 \widehat{J}_{23} \widehat{J}_{32} \\ &= D_3 \widehat{N}_1^* \widehat{N}_2^* (1 - \psi_1 \psi_2) \frac{r_1 r_2}{K^2} + D_2 \alpha_1 \beta_1 \widehat{N}_1^* \widehat{Z}^* + D_1 \alpha_2 \delta \widehat{N}_2^* \widehat{Z}^* > 0, \end{aligned}$$

the last inequality following from $\psi_1 \psi_2 < 1$.

Let

$$\begin{aligned} \widehat{M}_2 &= D_1 + D_2 + D_3 > 0, \quad \widehat{L}_1 = D_1 D_3 + D_2 D_3 + D_1 D_2 > 0, \\ \widehat{L}_2 &= -(D_2 + D_3) \widehat{J}_{11} - (D_1 + D_3) \widehat{J}_{22} > 0. \end{aligned}$$

The signs of $\widehat{J}_{11}$ and $\widehat{J}_{12}$ are negative, in view of equations (5), so that

$$\begin{aligned} \widehat{a}_1 \widehat{a}_2 - \widehat{a}_3 &= l^6 (\widehat{M}_2 \widehat{L}_1 - \widehat{H}_0) + l^4 (a_1 \widehat{L}_1 + \widehat{M}_2 \widehat{L}_2 - \widehat{H}_1) + l^2 (a_1 \widehat{L}_2 \\ &\quad + a_2 \widehat{M}_2 - \widehat{H}_2) + a_1 a_2 - a_3. \end{aligned}$$

Fig. 1 Biomass distribution of species N_1 over time and space of the model (1) for the parameter values: $r_1 = 4$, $r_2 = 5$, $\alpha_1 = .6$, $\alpha_2 = .7$, $\psi_1 = .6$, $\psi_2 = .8$, $K = 56$, $\delta = .08$, $\beta_1 = .4$, $c = 3$, $D_1 = 100$, $D_2 = .50$, $D_3 = .10$

The coefficients in the above expression are positive, and in fact we have

$$\begin{aligned}\widehat{M}_2\widehat{L}_1 - \widehat{H}_0 &= (D_1 + D_2)(D_1D_3 + D_2D_3 + D_1D_2 + D_3^2) > 0, \\ a_1\widehat{L}_1 + \widehat{M}_2\widehat{L}_2 - \widehat{H}_1 &= \frac{1}{K}D_1D_2(r_1\widehat{N}_1^* + r_2\widehat{N}_2^*) + \frac{D_3}{K}(r_1D_1\widehat{N}_1^* + r_2D_2\widehat{N}_2^*) \\ &\quad + \frac{1}{K}(D_1 + D_2 + D_3)[(D_2 + D_3)r_1\widehat{N}_1^* + (D_1 + D_3)r_2\widehat{N}_2^*] > 0, \\ a_1\widehat{L}_2 + a_2\widehat{M}_2 - \widehat{H}_2 &= \frac{1}{K^2}(r_1\widehat{N}_1^* + r_2\widehat{N}_2^*)[r_1\widehat{N}_1^*(D_2 + D_3) + r_2\widehat{N}_2^*(D_1 + D_3)] \\ &\quad + D_3(\alpha_1\beta_1\widehat{N}_1^*\widehat{Z}^* + \alpha_2\delta\widehat{N}_2^*\widehat{Z}^*) + D_2\alpha_2\delta\widehat{N}_2^*\widehat{Z}^* + D_1\alpha_1\beta_1\widehat{N}_1^*\widehat{Z}^* \\ &\quad + \frac{r_1r_2\widehat{N}_1^*\widehat{N}_2^*}{K^2}(D_1 + D_2)(1 - \psi_1\psi_2) > 0.\end{aligned}$$

From the signs of the above coefficients, the condition $\widehat{a}_1\widehat{a}_2 - \widehat{a}_3 > 0$ cannot be violated. Therefore system (1) does not show diffusive instability around the USS $\widehat{E}^*$, as seen in Figs. 1, 2 and 3. Our findings are summarized in the following result.

Fig. 2 Biomass distribution of species N_2 over time and space of the model (1) for the same parameter values as in Fig. 1

Fig. 3 Biomass distribution of species Z over time and space of the model (1) for the same parameter values as in Fig. 1

Theorem 1 *All the USS of the system (1) remain spatially stable when diffusion is also considered in the system.*

4 The toxin-releasing system (2)

In Table 2 we list the equilibria and their feasibility and stability conditions as found in [14] for the model (2).

The specific components of the more involved boundary equilibria are

$$\bar{N}_1^v = \frac{c}{\beta_1}, \quad \bar{Z}^{iv} = \frac{r_1}{\alpha_1} \left(1 - \frac{c}{K\beta_1} \right), \quad \bar{N}_1^v = \frac{K(1 - \psi_1)}{1 - \psi_1\psi_2}, \quad \bar{N}_2^v = \frac{K(1 - \psi_2)}{1 - \psi_1\psi_2}.$$

Table 2 Equilibria for the model (2) without diffusion

Equilibria	Feasibility	Stability condition
$\bar{E}_0 = (0, 0, 0)$		Unstable saddle point
$\bar{E}_1 = (K, 0, 0)$		$\psi_2 > 1, \beta_1 < \frac{c}{K}$
$\bar{E}_2 = (0, K, 0)$		$\psi_1 > 1, \delta_1 < \frac{c}{K}$
$\bar{E}_3$	Does not exist	-----
$\bar{E}_4 = (\bar{N}_1^{iv}, 0, \bar{Z}^{iv})$	$\beta_1 > \frac{c}{K}$	$\beta_1 > \max\left(\beta_1^*, \frac{c}{K}\right), \alpha_1 < \frac{r_1\alpha_2}{r_2}$
$\bar{E}_5 = (\bar{N}_1^v, \bar{N}_2^v, 0)$	$\psi_1 < 1$ and $\psi_2 < 1$.	$\theta > \theta_3, \psi_1 < 1, \psi_2 < 1$
$\bar{E}^* = (\bar{N}_1^*, \bar{N}_2^*, \bar{Z}^*)$		$\psi_1 < \frac{r_2\alpha_1}{r_1\alpha_2}, \psi_2 < \frac{r_1\alpha_2}{r_2\alpha_1},$ $\theta < \min\{\theta_1, \theta_5\}$

The constants used are as in Table 1, see [14]: $\theta_1 = \beta_1 b \bar{b}^{-1}$, $\theta_3 = [\beta_1 a \bar{a} + am\beta_1 r_1 r_2 (1 - \psi_1 \psi_2) - \bar{a} c r_1 r_2 (1 - \psi_1 \psi_2) - cmr_1^2 r_2^2 (1 - \psi_1 \psi_2)^2] \bar{a}^{-2}$, $\theta_5 = r_1 \alpha_2 \psi_1 \beta_1 \bar{N}_1^* (r_2 \alpha_1 \psi_2 \bar{N}_1^* + r_2 \alpha_1 \bar{N}_2^*)$

Further, for the interior equilibrium,

$$\begin{aligned}\bar{N}_1^* &= \frac{r_1 r_2 K(1 - \psi_1) + K(r_1 \alpha_2 \psi_1 - r_2 \alpha_1) \bar{Z}^*}{r_1 r_2 (1 - \psi_1 \psi_2)}, \\ \bar{N}_2^* &= \frac{r_1 r_2 K(1 - \psi_2) + K(r_2 \alpha_1 \psi_2 - r_1 \alpha_2) \bar{Z}^*}{r_1 r_2 (1 - \psi_1 \psi_2)},\end{aligned}$$

and Z^* is the positive root of the quadratic equation

$$AZ^2 + BZ + C = 0, \quad (10)$$

where, letting $a = r_1 r_2 K(1 - \psi_1)$, $\bar{a} = r_1 r_2 K(1 - \psi_2)$, $b = K(r_1 \psi_1 \alpha_2 - r_2 \alpha_1)$, $\bar{b} = K(r_2 \psi_2 \alpha_1 - r_1 \alpha_2)$, the coefficients are

$$\begin{aligned}A &= \beta_1 b \bar{b} - \theta \bar{b}^2, \\ B &= \beta_1 (\bar{a} b + a \bar{b}) - 2 \bar{a} \bar{b} \theta + r_1 r_2 \beta_1 m b (1 - \psi_1 \psi_2) - \bar{b} c r_1 r_2 (1 - \psi_1 \psi_2), \\ C &= \beta_1 a \bar{a} - \theta \bar{a}^2 + [a m \beta_1 r_1 r_2 - \bar{a} c r_1 r_2] (1 - \psi_1 \psi_2) - c m r_1^2 r_2^2 (1 - \psi_1 \psi_2)^2.\end{aligned}$$

The coexistence equilibrium, $\bar{E}^*$, is feasible when the following conditions hold

$$\alpha_1 > \frac{r_1 \alpha_2}{r_2}, \quad \psi_1 < \min \left\{ \frac{r_2 \alpha_1}{r_1 \alpha_2}, 1 \right\}, \quad \psi_2 < \min \left\{ \frac{r_1 \alpha_2}{r_2 \alpha_1}, 1 \right\}, \quad (11)$$

together with either $\theta < \min\{\theta_1, \theta_2, \theta_3\}$ and $B^2 > 4AC$, or $\theta_3 < \theta < \theta_1$, $\bar{Z}^* < L$. These new quantities are defined as follows:

$$\begin{aligned}L &= \frac{r_1 r_2 (1 - \psi_1)}{(r_2 \alpha_1 - r_1 \alpha_2 \psi_1)}, \quad \theta_1 = \frac{\beta_1 b}{\bar{b}}, \\ \theta_2 &= \frac{\beta_1 (\bar{a} b + a \bar{b}) + r_1 r_2 \beta_1 m b (1 - \psi_1 \psi_2) - \bar{b} c r_1 r_2 (1 - \psi_1 \psi_2)}{2 \bar{a} \bar{b}}, \\ \theta_3 &= \frac{\beta_1 a \bar{a} + r_1 r_2 (1 - \psi_1 \psi_2) \{a m \beta_1 - \bar{a} c - c m r_1 r_2 (1 - \psi_1 \psi_2)\}}{\bar{a}^2}.\end{aligned}$$

Considering now a spatial perturbation to the general USS $(\bar{N}_1, \bar{N}_2, \bar{Z})$ as done earlier, the matrix of the eigenvalue problem whose solution gives the time dependency is:

$$J \equiv (\bar{J}_{ij}) = \begin{pmatrix} \bar{J}_{11} - l^2 D_1 & -\frac{r_1 \psi_1}{K} \bar{N}_1 & -\alpha_1 \bar{N}_1 \\ -\frac{r_2 \psi_2}{K} \bar{N}_2 & \bar{J}_{22} - l^2 D_2 & -\alpha_2 \bar{N}_2 \\ \beta_1 \bar{Z} & -\frac{\theta(2m\bar{N}_2 + \bar{N}_2^2)\bar{Z}}{(m + \bar{N}_2)^2} & \bar{J}_{33} - l^2 D_3 \end{pmatrix}, \quad (12)$$

with

$$\begin{aligned}\bar{J}_{11} &= r_1 - \frac{2r_1}{K}\bar{N}_1 - \frac{r_1\psi_1}{K}\bar{N}_2 - \alpha_1\bar{Z} = -\frac{r_1}{K}\bar{N}_1, \\ \bar{J}_{22} &= r_2 - \frac{2r_2}{K}\bar{N}_2 - \frac{r_2\psi_2}{K}\bar{N}_1 - \alpha_2\bar{Z} = -\frac{r_2}{K}\bar{N}_2, \\ \bar{J}_{33} &= \beta_1\bar{N}_1 - \theta\frac{\bar{N}_2^2}{m + \bar{N}_2} - c.\end{aligned}$$

Since $\bar{E}_0 = \hat{E}_0$ and $\bar{E}_1 = \hat{E}_1$ and the matrix (12) for $\bar{E}_0$ and $\bar{E}_1$ is the same as for $\hat{E}_0$ and $\hat{E}_1$, the USS $\bar{E}_0$ and $\bar{E}_1$ for the system (2) are also spatially stable.

For the equilibrium $\bar{E}_2$, the eigenvalues are $r_1(1 - \psi_1) - l^2 D_1$, $-(r_2 + l^2 D_2)$ and $-\left(\frac{\theta K^2}{m+K} + c + l^2 D_3\right)$. Hence, all the eigenvalues are real negative for $\psi_1 > 1$, namely the stability condition of $\bar{E}_2$ is satisfied in the absence of diffusion. The eigenvalues remain negative also in the presence of diffusion, so that $\bar{E}_2$ is spatially stable. Furthermore, $\bar{E}_4 = \hat{E}_4$; their matrices (12) are the same, hence $\bar{E}_4$ is also spatially stable.

For the zooplankton-free USS, $\bar{E}_5$, the characteristic equation factors to give the eigenvalue

$$\beta_1 - \theta\frac{\bar{N}_2^{v2}}{m + \bar{N}_2^v} - c - l^2 D_3. \quad (13)$$

The remaining eigenvalues are the roots of the quadratic equation

$$\begin{aligned}\lambda^2 + \lambda \left[l^2(D_1 + D_2) + \frac{1}{K}(r_1\bar{N}_1^v + r_2\bar{N}_2^v) + \frac{r_1 r_2}{K^2}(1 - \psi_1\psi_2) \right] \\ + \frac{l^2}{K}(r_1 D_2 \bar{N}_1^v + r_2 D_1 \bar{N}_2^v) + l^4 D_1 D_2 = 0.\end{aligned}$$

In the absence of diffusion, all the roots have negative real part for $\theta > \theta_3$, $\psi_1 < 1$, and $\psi_2 < 1$, where, see [14],

$$\theta_3 = \frac{\beta_1 a \bar{a} + a m \beta_1 r_1 r_2 (1 - \psi_1 \psi_2) - \bar{a} c r_1 r_2 (1 - \psi_1 \psi_2) - c m r_1^2 r_2^2 (1 - \psi_1 \psi_2)^2}{\bar{a}^2}.$$

In the presence of diffusion, all the roots retain their negative real part so that $\bar{E}_5$ is also spatially stable.

The characteristic equation for $\bar{E}^*$ is

$$\lambda^3 + \bar{c}_1 \lambda^2 + \bar{c}_2 \lambda + \bar{c}_3 = 0,$$

where

$$\begin{aligned}\bar{c}_1(l^2) &= c_1 + l^2(D_1 + D_2 + D_3), \\ \bar{c}_2(l^2) &= c_2 + l^4(D_1 D_2 + D_1 D_3 + D_2 D_3) \\ &\quad - l^2 D_2 \bar{J}_{11} - l^2 D_3 \bar{J}_{11} - l^2 D_1 \bar{J}_{22} - l^2 D_3 \bar{J}_{22}, \\ \bar{c}_3(l^2) &= c_3 + l^6 D_1 D_2 D_3 - l^4(D_2 D_3 \bar{J}_{11} + D_1 D_3 \bar{J}_{22}) \\ &\quad + l^2(-D_3 \bar{J}_{12} \bar{J}_{21} + D_3 \bar{J}_{11} \bar{J}_{22} - D_2 \bar{J}_{13} \bar{J}_{31} - D_1 \bar{J}_{23} \bar{J}_{32}).\end{aligned} \quad (14)$$

Fig. 4 Biomass distribution of species N_1 over time and space of the model (2) for the parameter values $m = 5$, $\theta = .2$, with other parameters as in Fig. 1

Now diffusive instability will occur for $\bar{E}^*$ if one of the three Routh-Hurwitz conditions is violated. Clearly, $\bar{c}_1 > 0$ always holds. By defining the quantities as follows,

$$\bar{H}_0 = D_1 D_2 D_3 > 0,$$

$$\bar{H}_1 = -D_2 D_3 \bar{J}_{11} - D_1 D_3 \bar{J}_{22} = D_3 \left(\frac{r_1 D_2}{K} \bar{N}_1^* + \frac{r_2 D_1}{K} \bar{N}_2^* \right) > 0,$$

$$\bar{H}_2 = -D_3 \bar{J}_{12} \bar{J}_{21} + D_3 \bar{J}_{11} \bar{J}_{22} - D_2 \bar{J}_{13} \bar{J}_{31} - D_1 \bar{J}_{23} \bar{J}_{32}$$

$$= D_3 \bar{N}_1^* \bar{N}_2^* (1 - \psi_1 \psi_2) \frac{r_1 r_2}{K^2} + D_2 \alpha_1 \beta_1 \bar{N}_1^* \bar{Z}^* - \theta D_1 \alpha_2 \bar{N}_2^* \bar{Z}^* \frac{2m \bar{N}_2^* + \bar{N}_2^{*2}}{(m + \bar{N}_2^*)^2},$$

we have

$$\bar{c}_3(l^2) = (l^2)^3 \bar{H}_0 + (l^2)^2 \bar{H}_1 + l^2 \bar{H}_2 + c_3. \quad (15)$$

Fig. 5 Biomass distribution of species N_2 over time and space of the model (2) for the same parameter values as in Fig. 4

Fig. 6 Biomass distribution of species Z over time and space of the model (2) for the same parameter values as in Fig. 4

Now $\bar{c}_3(0) = c_3 > 0$ and $\bar{c}_3(1) = \bar{H}_0 + \bar{H}_1 + \bar{H}_2 + \bar{c}_3$. Hence, if we impose $\bar{c}_3(1) < 0$ then we would obtain in $(0, 1)$ a root $l_{\min}^2$ of the equation

$$\bar{c}_3(l^2) = 0. \quad (16)$$

The condition $(\bar{c}_3(\alpha) < 0)$ amounts to require $\bar{H}_0 + \bar{H}_1 + \bar{H}_2 + \bar{c}_3 < 0$, explicitly yields

$$\begin{aligned} D_1 D_2 D_3 + D_3 \left(D_2 \frac{r_1}{K} \bar{N}_1^* + D_1 \frac{r_2}{K} \bar{N}_2^* \right) + D_3 \bar{N}_1^* \bar{N}_2^* (1 - \psi_1 \psi_2) \frac{r_1 r_2}{K^2} \\ + D_2 \alpha_1 \beta_1 \bar{N}_1^* \bar{Z}^* + \bar{c}_3 < \theta D_1 \alpha_2 \bar{N}_2^* \bar{Z}^* \frac{2m \bar{N}_2^* + \bar{N}_2^{*2}}{(m + \bar{N}_2^*)^2}. \end{aligned} \quad (17)$$

Therefore, as the wavelength parameter l^2 crosses the critical value $l_{\min}^2$, the Routh-Hurwitz stability criterion is violated; diffusive instability thus occurs when Eq. 17 holds. In Figs. 4, 5 and 6, we graphically report our findings. We can summarize our results as follows.

Theorem 2 *All the boundary USS of the system (2) are spatially stable. The coexisting steady state $(\bar{E}^*)$ is spatially unstable if the diffusive coefficients satisfy condition (17).*

5 Diffusion in two spatial dimensions

To model the plankton evolution more realistically, we also consider diffusion in two spatial dimensions, thereby replacing the second-order partial derivatives on the right-hand sides of the systems (1) and (2) by the two-dimensional diffusive Laplace operators ΔN_1 , ΔN_2 and ΔZ .

To study two-dimensional diffusion for the non-toxic phytoplankton system (1), we consider the following spatial perturbation of the general USS, $(\hat{N}_1, \hat{N}_2, \hat{Z})$:

$$\begin{pmatrix} N_1(t, x, y) \\ N_2(t, x, y) \\ Z(t, x, y) \end{pmatrix} = \begin{pmatrix} \hat{N}_1 \\ \hat{N}_2 \\ \hat{Z} \end{pmatrix} + \begin{pmatrix} N_{1d}(t) \\ N_{2d}(t) \\ Z_d(t) \end{pmatrix} \cos(lx) \cos(ny),$$

where $l > 0$, $n > 0$ are the wavenumber parameters in the directions x and y , respectively, and $\lambda > 0$ has the same meaning as before. The matrix $J \equiv (\hat{J}_{ij})$ contains only small changes in the diagonal elements as given below:

$$J = \begin{pmatrix} \hat{J}_{11} - l^2 D_1 - n^2 D_1 & -\frac{r_1 \psi_1}{K} \hat{N}_1 & -\alpha_1 \hat{N}_1 \\ -\frac{r_2 \psi_2}{K} \hat{N}_2 & \hat{J}_{22} - l^2 D_2 - n^2 D_2 & -\alpha_2 \hat{N}_2 \\ \beta_1 \hat{Z} & \delta \hat{Z} & \hat{J}_{33} - l^2 D_3 - n^2 D_3 \end{pmatrix},$$

where $\hat{J}_{11}$, $\hat{J}_{22}$ and $\hat{J}_{33}$ are the same as before.

We now investigate the stability of the USS of the system (1). For the plankton-free USS, $\hat{E}_0$, the eigenvalues are $r_1 - l^2 D_1 - n^2 D_1$, $r_2 - l^2 D_2 - n^2 D_2$, and $-c - l^2 D_3 - n^2 D_3$. All the eigenvalues are negative if

$$D_1 > D_1^{(2)} \equiv \frac{r_1}{l^2 + n^2}, \quad D_2 > D_2^{(2)} \equiv \frac{r_2}{l^2 + n^2} \quad (18)$$

both hold. Observe that $D_1^{(2)} < D_1^{(1)}$ and $D_2^{(2)} < D_2^{(1)}$. Thus, for suitable parameter values, the system can collapse under two-dimensional diffusion, while with one-dimensional diffusion the populations can still be preserved.

The eigenvalues for the equilibrium $\hat{E}_1$ are

$$-(r_1 + l^2 D_1 + n^2 D_1), \quad r_2(1 - \psi_2) - l^2 D_2 - n^2 D_2, \quad \beta_1 K - c - l^2 D_3 - n^2 D_3.$$

In the absence of diffusion, all the eigenvalues are negative when $\psi_2 > 1$ and $\beta_1 < cK^{-1}$ and remain so also in the presence of diffusion. Thus, $\hat{E}_1$ is spatially stable. In a similar way, $\hat{E}_2$ is also spatially stable when $\psi_1 > 1$ and $\delta_1 < cK^{-1}$.

The characteristic equation for $\hat{E}_3$ factors to give the eigenvalue $\hat{A} - q^2 D_1$ with $q^2 = l^2 + n^2$ and $\hat{A}$ as defined before, and the other eigenvalues are obtainable from the quadratic

$$\lambda^2 + \lambda \left(q^2 D_3 + q^4 D_2 D_3 + \frac{r_2 c}{K \delta} \right) + \alpha_2 \lambda \hat{N}_2^{iii} \hat{Z}^{iii} + q^4 D_2 D_3 + q^2 D_3 \frac{r_2 c}{K \delta} = 0.$$

Therefore, although the magnitude of the eigenvalues in the presence of two-dimensional diffusion is different from the case of one-dimensional diffusion, negativity is preserved. Therefore diffusive instability for $\hat{E}_3$ is not possible for two-dimensional diffusion.

Similarly, it is not necessary to verify the stability of the remaining boundary equilibria of the system (1). In fact, two-dimensional diffusion does not alter the sign of the eigenvalues and thus does not influence the stability condition of the corresponding equilibria in the absence of diffusion.

For the interior equilibrium, $\hat{E}^*$, the characteristic equation is

$$\lambda^3 + \hat{a}_1^{(2)} \lambda^2 + \hat{a}_2^{(2)} \lambda + \hat{a}_3^{(2)} = 0, \quad (19)$$

with $\hat{a}_1^{(2)} = \hat{a}_1(q^2)$, $\hat{a}_2^{(2)} = \hat{a}_2(q^2)$ and $\hat{a}_3^{(2)} = \hat{a}_3(q^2)$, where these right-hand sides are the same as for the one-dimensional case. As for the latter, the Routh-Hurwitz criterion is satisfied, so that in the presence of two-dimensional diffusion the system (1) near the coexistence equilibrium, $\hat{E}^*$, does not experience diffusive instability, as shown in Fig. 7.

Our findings are summarized in the following theorem:

Theorem 3 *The system (1) does not show two-dimensional diffusive instability, i.e., all the USS are spatially stable in presence of two-dimensional diffusion of the species.*

Fig. 7 Biomass distribution of all the populations over space for the model (1) for the parameter values $D_1 = 0.1$, $D_2 = 0.0050$, $D_3 = 0.0010$, with other parameters as given in Fig. 1

Proceeding analytically as before, for Eq. 2 we apply the following spatial perturbation near the general USS $(\bar{N}_1, \bar{N}_2, \bar{Z})$,

$$\begin{pmatrix} N_1(t) \\ N_2(t) \\ Z(t) \end{pmatrix} = \begin{pmatrix} \bar{N}_1 \\ \bar{N}_2 \\ \bar{Z} \end{pmatrix} + \begin{pmatrix} N_{d1}(t) \\ N_{d2}(t) \\ Z_d(t) \end{pmatrix} \cos(lx) \cos(ny),$$

where l, n, λ are the same as for the unidimensional case. We obtain the following Jacobian $J \equiv (\bar{J}_{ij})$,

$$J = \begin{pmatrix} \bar{J}_{11} - l^2 D_1 - n^2 D_1 & -\frac{r_1 \psi_1}{K} \bar{N}_1 & -\alpha_1 \bar{N}_1 \\ -\frac{r_2 \psi_2}{K} \bar{N}_2 & \bar{J}_{22} - l^2 D_2 - n^2 D_2 & -\alpha_2 \bar{N}_2 \\ \beta_1 \bar{Z} & -\frac{\theta(2m\bar{N}_2 + \bar{N}_2^2)\bar{Z}}{(m + \bar{N}_2)^2} & \bar{J}_{33} - l^2 D_3 - n^2 D_3 \end{pmatrix},$$

where $\bar{J}_{11}$, $\bar{J}_{22}$, and $\bar{J}_{33}$ are the same as mentioned earlier.

The eigenvalues for the plankton-free equilibrium, $\bar{E}_0$, in the presence of two-dimensional diffusion, are identical to those of the system (1). Thus, the system may collapse in the presence of two-dimensional diffusion, while it may thrive in the presence just of one-dimensional diffusion.

For the other USS, namely, $\bar{E}_1$, $\bar{E}_2$, $\bar{E}_3$, and $\bar{E}_4$, assuming that for these equilibria the stability conditions are satisfied in the absence of diffusion, the eigenvalues in the presence of two-dimensional diffusion change their magnitude but not their sign. Diffusion thus does not alter their stability.

For the coexistence equilibrium $\bar{E}^*$, the characteristic equation is given by

$$\lambda^3 + \bar{c}_1^{(2)}\lambda^2 + \bar{c}_2^{(2)}\lambda + \bar{c}_3^{(2)} = 0,$$

where letting $q^2 = l^2 + n^2$ the coefficients $\bar{c}_1^{(2)} = \bar{c}_1(q^2)$, $\bar{c}_2^{(2)} = \bar{c}_2(q^2)$, $\bar{c}_3^{(2)} = \bar{c}_3(q^2)$ are the same as in Eq. 14.

Thus, similar to the one-dimensional case, if the condition (17) is satisfied, the Routh-Hurwitz criterion $\bar{c}_1^{(2)}\bar{c}_2^{(2)} - \bar{c}_3^{(2)} > 0$ is violated when q^2 passes through the critical value q_0^2 in $(0, 1)$. Here q_0^2 denotes the root of the cubic equation in q^2 given by $\bar{c}_3(q^2) = 0$. It therefore follows that $q_0^2 = l_0^2 + n_0^2 = l_{\min}^2$, and therefore both l_0 and n_0 , must not exceed $l_{\min}$, i.e., $l_0 < l_{\min}$ and $n_0 < l_{\min}$. The latter inequalities imply that, for two-dimensional diffusion, the system (2) will show diffusive instability with smaller wavelength parameters than for the one-dimensional case, see Figs. 8 and 9. In summary, we have the following result.

Fig. 8 Biomass distribution of all the populations over space for the model (2) for the parameter values $m = 5$, $D_1 = 0.1$, $D_2 = 0.0050$, $D_3 = 0.0010$, with $\theta = .2$, and all the other parameter values as given in Fig. 1

Fig. 9 Biomass distribution of all the populations over space for the model (2) for the parameter values $m = 5$, $D_1 = 0.1$, $D_2 = 0.0050$, $D_3 = 0.0010$, with $\theta = .75$, and all the other parameter values as given in Fig. 1

Theorem 4 *If condition (17) is satisfied, system (2) with two-dimensional diffusion shows diffusive instability near the coexistence equilibrium $\tilde{E}^*$ with smaller wavelength parameters than in the corresponding one-dimensional case.*

6 Discussion and conclusions

The precise mechanism for which coexistence and biodiversity of many species can be maintained is still partially unknown and therefore the subject of considerable interest. The reasons should be ascribed to a variety of mechanisms, both physical and biological, spatial, temporal and spatiotemporal features [9–12].

In this study, we have considered spatial interactions of two phytoplankton populations and a zooplankton grazer. Two cases have been investigated, when the two phytoplankton populations are harmless and, in contrast, when one of them is toxin-producing. Our analytic results suggest that when phytoplankton does not harm zooplankton, the biomass distribution of the plankton species is uniform in time and space. On the other hand, the presence of TPP makes the overall plankton dynamics inhomogeneous in space.

Figures 1–9 are simulated for the parameter values satisfying the sufficient condition (see Tables 1 and 2) of stable coexistence in the absence of diffusion. Note however that

with respect to [14] in model (1), the parameter value $\delta = 0.08$ has been chosen instead of the original value $\delta = 0.2$, in Figs. 1–3 and 7, while for the system (2) the same parameter values as those of [14] are used in Figs. 4–6, 8 and 9. For model (1), Figs. 1–3 and 7 show a homogeneous biomass distribution. In contrast, model (2), shown in Figs. 4–6, 8 and 9, where the presence of TPP is assumed, generates patterns over space and time. These numerical findings validate our analytic results.

In summary, our findings indicate that diffusion cannot alter the stability of the non-toxin-releasing phytoplankton model, both in one and two spatial dimensions (see Theorems 1 and 3). For the toxic-releasing phytoplankton model, the crucial condition is Eq. 17. If it holds, the coexistence equilibrium is destabilized by diffusion. In two dimensions, the wavelength of this instability will be smaller than the wavelength in one dimension (see Theorems 2 and 4). Further, independently of the type of phytoplankton considered, whether harmful to the zooplankton or not, the system can collapse, i.e., for certain parameter values the origin is stable, and the higher the spatial dimension the more likely this can be, since the ranges of these parameter values leading to system disappearance are larger for higher dimensions.

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