Propagation of Turing patterns in a plankton model

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The paper is devoted to a reaction–diffusion system of equations describing phytoplankton and zooplankton distributions. Linear stability analysis of the model is carried out. Turing and Hopf stability boundaries are found. Emergence of two-dimensional spatial structures is illustrated by numerical simulations. Travelling waves between various stationary solutions are investigated. Transitions between homogeneous in space stationary solutions and Turing structures are studied.

Keywords: reaction–diffusion system; plankton model; Turing patterns; travelling waves

1. Introduction

Pattern formation in spatial predator–prey systems is observed in many biological applications. It has been shown that spontaneous spatio-temporal pattern formation is an intrinsic property of such systems [20,24]. As a result, different kinds of stationary and non-stationary spatio-temporal patterns are observed, such as spiral, spot, target and tip-splitting patterns [2]. Dynamics of interacting populations in connection with pattern formation and spatio-temporal chaos have recently become a focus of research in theoretical ecology. Liu et al. [11] studied a spatial phytoplankton–zooplankton system with periodic forcing and additive noise. Sun et al. [32] have presented a numerical study of pattern formation in the Holling–Tanner model with self- and cross-diffusion. They have observed only a spot-like pattern for equal value of self-diffusion. The mechanisms of spatio-temporal pattern formation such as patchiness and blooming have been studied by Segel and Jackson [29], Steele and Hunderson [31], Pascual [25], Malchow [13] and Upadhyay et al. [34,35]. The density of plankton population changes not only in time but also in space. Patchiness is affected by many factors such as temperature, nutrients and turbulence, which depend on the spatial scale [18,30]. Generally, the growth, competition, grazing and propagation of plankton population can be modelled by partial differential equations of the reaction–diffusion type. Turing spatial patterns have been observed in computer simulations of interaction–diffusion system by

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many authors [14–16,41]. Medvinsky et al. [21,22] examined plankton spatial patterns some of which were fish-free in the reaction–diffusion model with passive movement of individuals of two interacting species caused by turbulent mixing. Malchow et al. [17] studied the spatio-temporal dynamics of the plankton model under the influence of environmental noise and diffusion in horizontally two-dimensional space. Chen and Wang [3] carried out the qualitative analysis for a diffusive predator–prey model subject to the homogeneous Neumann boundary condition and established the existence of stationary patterns. The influence of heterogeneous environment on pattern formation in phytoplankton–zooplankton systems is studied in [23,27,28].

In this work, we will address the Holling–Tanner model which describes the dynamics of a generalist predator which feeds on its favourite food item as long as it is in abundant supply and grows logistically with an intrinsic growth rate and a carrying capacity proportional to the size of the prey. The dynamics of the Holling–Tanner predator–prey model is quite interesting for its mathematical properties [1,4,8,9,19,40] and for its efficacy in describing real ecological systems such as lynx and hare and sparrow and sparrow hawk [33,40]. Collings [5] have used the Holling–Tanner model to study the population interaction between the predacious mite *Metaseiulus occidentalis* (Nesbitt) and its spider mite prey *Tetranychus medanieli* (McGregor). Recently, a modification of the Holling–Tanner model by invoking the ratio-dependent functional response is suggested by Haque and Li [7]. The authors have obtained necessary conditions for the Turing instability to emerge.

The Holling–Tanner model has two Hopf-bifurcation points for certain parameters. When the two Hopf-bifurcation points nearly coalesce, the two stable periodic solution branches are connected. As a ratio of linear growth rates varies, the Hopf-bifurcation points separate further and the one limit cycle becomes unstable. This situation can correspond to an outbreak in populations [1]. The coexistence of a stable limit cycle and a stable equilibrium is observed by Gasull et al. [6]. Wang et al. [39] studied the positive steady-state solution of the diffusive Holling–Tanner model in heterogeneous environments, subject to the homogeneous Neumann boundary condition and investigated the appearance of sharp spatial patterns arising from degeneracies of the model system. The unique positive constant steady state is uniformly asymptotically stable for the dynamics of the Holling–Tanner model with diffusion; non-constant positive steady states can exist due to the emergence of cross-diffusion [26]. Maiti and Pathak [12] have formulated a stochastic version of the model by perturbing the growth rates of the prey and predator by Gaussian white noises. The criteria for non-equilibrium fluctuation and stability are derived. Comparative study of stability behaviour of the model in deterministic and stochastic environment is presented.

Emergence of spatial patterns briefly discussed above in the context of the Holling–Tanner model is conventionally studied in bounded domains. In this case, bifurcation analysis allows us to describe non-homogeneous in space solutions when a homogeneous solution loses its stability. On the other hand, reaction–diffusion waves can describe transitions between two different equilibria in the case of unbounded spatial domains. Owing to this transition, stable homogeneous equilibrium spreads and fills the whole space [37,38]. But what happens if this equilibrium loses its stability resulting in the emergence of a spatial structure? By analogy with travelling waves, we can expect that this spatial structure will spread in space. However, bifurcation analysis is not applicable in this case since instead of a pair of isolated eigenvalues, as it happens in the case of bounded domains, it is the essential spectrum which crosses the imaginary axis. The existing theory of travelling waves does not allow us to study this question neither. The question about transitions between homogeneous solutions and spatial structures is open from the mathematical point of view and from the point of view of nonlinear dynamics. In this paper, we will study nonlinear dynamics of such transitions for the Holling–Tanner model. Similar effects can be observed for numerous other models.

The contents of the paper are as follows. The model is presented in Section 2. We begin its analysis with homogeneous in space solutions. Their stability is studied in Section 3, the instability
conditions and emergence of Turing structures are discussed in Section 4. We study travelling waves and transitions from the homogeneous state to Turing structures in Section 5.

2. The model system

We consider a reaction–diffusion model for an aquatic system with phytoplankton \( P(X, Y, T) \) and zooplankton \( Z(X, Y, T) \) populations as follows:

\[
\frac{\partial P}{\partial T} = rP \left( 1 - \frac{P}{K} \right) - \frac{mPZ}{(A + P)} + D_P \left( \frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right),
\]

\[
\frac{\partial Z}{\partial T} = sZ \left( 1 - \frac{hZ}{P} \right) + D_Z \left( \frac{\partial^2 Z}{\partial X^2} + \frac{\partial^2 Z}{\partial Y^2} \right).
\]

The parameters \( r, K, m, A, s, h, D_P \) and \( D_Z \) are positive constant. Here, \( r \) is the prey’s intrinsic rate in the absence of predation, \( K \) is the carrying capacity of the phytoplankton population, \( m \) is the maximal predator per capita consumption rate, \( A \) is the half saturation constant, \( s \) is the predator’s intrinsic growth rate, \( h \) is the number of phytoplankton required to support one zooplankton at equilibrium when \( Z \) equals to \( P/h \). The parameters \( D_P \) and \( D_Z \) represent the diffusion coefficients of phytoplankton and zooplankton, respectively.

The units of the parameters are as follows. Time \( T \) and length \( X, Y \in [0, R] \) are measured in days (d) and metres (m), respectively. Further, \( r, s, P, Z \) and \( A \) are usually measured in mg of dry weight per litre (mg \( dw \ l^{-1} \)); of \( m \) and \( h \) is \( (d^{-1}) \). The dimension of diffusion coefficients \( D_P \) and \( D_Z \) are measured in \( (m^2 d^{-1}) \).

We introduce the following notation in order to bring the system of equations to a non-dimensional form:

\[
u = \frac{P}{K}, v = \frac{mZ}{rK}, t = rT, x = \frac{X}{L}, y = \frac{Y}{L}, \alpha = \frac{A}{K}, \delta = \frac{s}{r}, \beta = \frac{hr}{m}, D_u = \frac{D_P}{rL^2}, D_v = \frac{D_Z}{rL^2}.
\]

We obtain the system

\[
\frac{\partial u}{\partial t} = u(1 - u) - \frac{uv}{(\alpha + u)} + D_u \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right),
\]

\[
\frac{\partial v}{\partial t} = v\delta \left( 1 - \frac{\beta v}{u} \right) + D_v \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right)
\]

with the initial condition

\[
u(x, y, 0) > 0, v(x, y, 0) > 0, \quad (x, y) \in \Omega
\]

and with the no-flux boundary conditions

\[
\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, \quad (x, y) \in \partial \Omega.
\]

3. Temporal model and its stability analysis

In this section, we carry out stability analysis of the model system in the absence of diffusion. We will find non-negative equilibrium states and will discuss their stability. We analyse system (2a)
and (2b) without diffusion. In this case, it reduces to the form

\[
\frac{du}{dt} = u(1 - u) - \frac{uv}{(\alpha + u)}, \quad (5a)
\]

\[
\frac{dv}{dt} = v\delta \left( 1 - \frac{\beta v}{u} \right). \quad (5b)
\]

System (5a) and (5b) has two non-negative equilibria, namely \( E_1 = (1, 0) \) and \( E^*(u^*, v^*) \). The axial equilibrium point \( E_1 \) exists and is a saddle point with stable manifold in \( u \)-direction and unstable manifold in \( v \)-direction. The interior equilibrium point \( E^*(u^*, v^*) \) is the point of intersection of two nullclines \( v = (1 - u)(\alpha + u) \) and \( v = u/\beta \), where \( v^* = u^*/\beta \) and \( u^* \) is the positive root of the equation

\[
\beta u^{*2} + (1 - \beta + \alpha\beta)u^* - \alpha\beta = 0.
\]

In the following theorem, we formulate necessary and sufficient conditions for the positive equilibrium to be locally asymptotically stable. The proof of the theorem follows from the Routh–Hurwitz criteria and we do not present it here. For this purpose, we use the following notation:

\[
A = u^* \left( 1 - \frac{u^*}{\beta(\alpha + u^*)^2} \right) + \delta, \quad B = \delta u^* \left( 1 + \frac{\alpha}{\beta(\alpha + u^*)^2} \right).
\]  

**Theorem 1** The positive equilibrium \( E^* = (u^*, v^*) \) is locally asymptotically stable if and only if the following inequalities hold:

\[
A > 0, \quad B > 0. \quad (7)
\]

**Remark** Let

\[
u^* \in \mathbb{R}/[A_1, A_2],
\]

where \( A_1 \) and \( A_2 \) are the roots of the equation

\[
\beta u^{*2} + (2\alpha\beta - 1)u^* + \alpha^2\beta = 0.
\]

Then \( A > 0 \) and \( B > 0 \). Therefore, if Equation (8) holds, then \( E^* = (u^*, v^*) \) is locally asymptotically stable.

The parameter \( \delta \), the ratio between the predator and prey intrinsic growth rates, plays a significant role in determining local stability of \( E^* = (u^*, v^*) \). For critical values of the parameter \( \delta \), a small amplitude periodic solution bifurcates from the interior equilibrium point, and the system undergoes a Hopf bifurcation. The limit cycle arising from the Hopf bifurcation is unique and stable [10].

In order to study the stability of the positive equilibrium \( E^* = (u^*, v^*) \), we need the following lemma which establishes a region of attraction for system (5a) and (5b).

**Lemma 1** Solutions of system (5a) and (5b) with a positive initial condition remains positive and bounded. Furthermore, there exists \( t' \geq 0 \) such that \( u(t) < 1 \) and \( v(t) < 1/\beta \) for \( t \geq t' \).

**Theorem 2** If \( (u - u^*)[u(1 - u)/\phi(u) - v^*] < 0 \) where \( \phi(u) = u/(\alpha + u) \), then \( E^* = (u^*, v^*) \) is globally asymptotically stable with respect to all solutions with positive initial conditions.

The proof of this theorem is standard and we omit it.
4. Turing and Hopf instabilities

In order to study Turing instability of system (2a) and (2b), we consider the system linearized about $E^* = (u^*, v^*)$:

\[
\frac{\partial U}{\partial t} = a_{11} U + a_{12} V + D_u \left( \frac{\partial^2 U}{\partial x^2} + \frac{\partial^2 U}{\partial y^2} \right),
\]
\[
\frac{\partial V}{\partial t} = a_{21} U + a_{22} V + D_v \left( \frac{\partial^2 V}{\partial x^2} + \frac{\partial^2 V}{\partial y^2} \right),
\]

where
\[
a_{11} = -u^* \left( 1 - \frac{v^*}{(\alpha + u^*)^2} \right), \quad a_{12} = -\frac{u^*}{\alpha + u^*}, \quad a_{21} = \frac{\delta}{\beta}, \quad a_{22} = -\delta.
\]

The characteristic equation of the linearized system is

\[
\lambda^2 + \rho_1 \lambda + \rho_2 = 0,
\]

where
\[
\rho_1 = A + (D_u + D_v) k^2,
\]
\[
\rho_2 = B + \delta D_u k^2 + \left( u^* \left( 1 - \frac{u^*}{\beta(\alpha + u^*)^2} \right) + D_u k^2 \right) D_v k^2,
\]

$A, B$ are defined by Equation (6).

Diffusive instability holds, if at least one of the constants $\rho_1$ and $\rho_2$ is negative and condition (7) is satisfied. But it is evident that $\rho_1 > 0$, if the condition $A > 0$ holds. The condition $\rho_2 < 0$ for diffusive instability is equivalent to the inequality

\[
H(k^2) = D_u D_v k^4 + \left( u^* D_v \left( 1 - \frac{u^*}{\beta(\alpha + u^*)^2} \right) + \delta D_u \right) k^2 + B < 0.
\]

The function $H$ is a quadratic with respect to $k^2$. The minimum of $H(k^2)$ is reached at $k^2 = k_{cr}^2$, where

\[
k_{cr}^2 = \frac{1}{2D_u D_v} \left( \frac{u^* D_v}{\beta(\alpha + u^*)^2} - (\delta D_u + u^* D_v) \right).
\]

Consequently, the condition for diffusive instability is $H(k_{cr}^2) < 0$ or

\[
u^* D_v \left( 1 - \frac{u^*}{\beta(\alpha + u^*)^2} \right) + \delta D_u > 2(D_u D_v B)^{1/2}.
\]

We proved the following theorem.

**Theorem 3** The criterion of diffusive instability for system (2a) and (2b) is given by conditions (7), (14) and (15), leading to the condition

\[
D_v (\beta(\alpha + u^*)^2 - u^* u^* + \delta \beta D_u (\alpha + u^*)^2) > 2\beta(\alpha + u^*)^2 (D_u D_v B)^{1/2}.
\]

Figure 1 shows the plot of $H(k^2)$ as a function of $k^2$ for different values of $D_v$ and other parameters fixed, $\alpha = 0.1, \beta = 0.25, \delta = 0.2$ and $D_u = 0.1$. The interval of negativity of the function $H(k_{cr}^2)$ becomes larger when $D_v$ increases.
Figure 1. The graph of the function $H(k^2)$ for $\alpha = 0.1, \beta = 0.25, \delta = 0.2$ and $D_u = 0.1$ and different values of $D_v = 3, 5$ and 7 (left). Stability boundaries for system (2a) and (2b) with parameters $\alpha = 0.1, \beta = 0.25$ and $D_u = 0.1$ (right). The Turing and Hopf stability boundaries intersect at $(0.184, 0.2021)$ and separate the parameter space into four domains.

The Turing bifurcation occurs when $\text{Im}(\lambda(k)) = 0$ and $\text{Re}(\lambda(k)) = 0$ at $k = k_r \neq 0, k_T$ is the critical wave number. If $\delta$ is considered as a bifurcation parameter, then its critical value equals to

$$\delta_T = \frac{-B_1 \pm \sqrt{B_1^2 - 4R_1C_1}}{2R_1},$$

where

$$R_1 = -\left(\frac{D_u}{D_u + D_v}\right)^2, \quad B_1 = a_{11}(D_u^2 + D_v^2) + u^*(1 + \frac{\alpha}{\beta(\alpha + u^*)^2}),$$

$$C_1 = -\left(\frac{a_{11}D_v}{D_u + D_v}\right)^2.$$

At the critical value $\delta_T$, a stationary oscillatory in space pattern emerges with the wavelength $\lambda_T = \frac{2\pi}{k_T}$ and

$$k_T^2 = \sqrt{\frac{u^*\delta(\alpha + \beta(\alpha + u^*))}{\beta D_u D_v(\alpha + u^*)^2}}.$$

The Hopf bifurcation occurs when $\text{Im}(\lambda(k)) \neq 0$ and $\text{Re}(\lambda(k)) = 0$ at $k = 0$. The critical value of the bifurcation parameter $\delta$ is

$$\delta_H = u^* \left(\frac{u^*}{\beta(\alpha + u^*)^2} - 1\right).$$

At the Hopf bifurcation threshold, the temporal symmetry of the system is broken and gives rise to uniform oscillations in space and periodic oscillations in time with the frequency $w_H$ and wavelength $\lambda_H$:

$$w_H = \sqrt{\delta u^* \left(1 + \frac{\alpha}{\beta(\alpha + u^*)^2}\right)}, \quad \lambda_H = 2\pi \sqrt{\frac{\beta(\alpha + u^*)^2}{\delta u^*(\alpha + \beta(\alpha + u^*)^2)}}.$$
Figure 2. Typical Turing patterns of prey (first column) and predator populations (second column) are plotted for
the parameters $\alpha = 0.1, \beta = 0.25, \delta = 0.2, D_u = 0.1$ and $D_v = 7$ (upper row), $\alpha = 0.1, \beta = 0.25, D_u = 0.1, D_v = 3$ and
$\delta = 0.194$ (lower row).

We have performed numerical simulations of system (2a) and (2b) for different sets of parameters. Figure 2 shows stationary stripes–spots mixed patterns in the distribution of phytoplankton and zooplankton density (upper row). We observe the shrinking region for stripes–spots mixed patterns as we approach the Turing stability boundary (lower row).

5. Travelling waves

5.1. Transition from a homogeneous state to a Turing structure

As discussed in Section 4, a homogeneous solution in a bounded interval can lose its stability, resulting in appearance of a Turing structure. It is a periodic in space stationary solution of system (2a) and (2b).

If we consider the same system in the whole axis, we can observe a transition from the homogeneous in space stationary solution to a Turing structure. Let us recall that $(u^*, v^*)$ is a homogeneous
in space stationary solution of system (2a) and (2b). We perturb it in a small interval and consider the functions
\[ u(x,0) = \begin{cases} u^*, & |x| \geq a, \\ u^* + \epsilon, & -a < x < a, \end{cases} \]
\[ v(x,0) = \begin{cases} v^*, & |x| \geq a, \\ v^* + \epsilon, & -a < x < a, \end{cases} \]
as an initial condition for system (2a) and (2b). Here \( a \) and \( \epsilon \) are some constants. If the homogeneous solution \((u^*, v^*)\) is not stable with respect to spatial perturbations, then we will observe emergence of a periodic in space solution which will propagate in both directions.

An example of numerical simulations is shown in Figure 3. We consider bounded, but a sufficiently large interval with the initial condition described above. A periodic solution emerges in the centre of the interval and propagates to the left and to the right. We can conjecture that it is a periodic travelling wave, that is a solution of system (2a) and (2b) of the form
\[ u(x,t) = u^* + \phi(x-ct,t)(u_p(x) - u^*), \]
\[ v(x,t) = v^* + \psi(x-ct,t)(v_p(x) - v^*), \]
where \((u_p(x), v_p(x))\) is a periodic in space stationary solution of system (2a) and (2b), \( \phi(x,t) \) and \( \psi(x,t) \) are periodic in time functions with the limits
\[ \lim_{x \to -\infty} \phi(x,t), \psi(x,t) = 0, \]
\[ \lim_{x \to +\infty} \phi(x,t), \psi(x,t) = 1 \]
(the limits can be opposite depending on the direction of propagation), \( c \) is the speed of propagation.

5.2. Transitions between homogeneous states

Along with the homogeneous in space stationary solution \( E^* = (u^*, v^*) \), we will consider two other solution \( E_0 = (0,0) \) and \( E_1 = (1,0) \). Both of them are unstable. The point \( E^* \) can be stable or unstable depending on the values of parameters. Let us consider the case where it is stable. We can expect the existence of a travelling wave connecting the points \( E_0 \) and \( E^* \). This is a solution of system (2a) and (2b) of the form
\[ u(x,t) = U(x - ct), \quad v(x,t) = V(x - ct) \]
with the limits
\[ \lim_{x \to -\infty} (U,V) = E^*, \quad \lim_{x \to +\infty} (U,V) = E_0. \]
It satisfies the system

\[ D_u U'' + cU' + F(U, V) = 0, \]  
\[ D_v V'' + cV' + G(U, V) = 0, \]

where

\[ F(U, V) = U(1 - U) - \frac{UV}{\alpha + U}, \quad G(U, V) = \delta V \left( 1 - \frac{\beta V}{U} \right). \]

We note that the functions \( U(x) \) and \( V(x) \) decay exponentially at \(+\infty\). Therefore, their ratio in Equation (2b) is well defined. Another remark concerns the multiplicity of waves. In the monostable case, conventionally the wave is not unique. They exist for all speeds from some interval. By analogy with the scalar reaction–diffusion equation, we can expect that the solution with an initial condition with a finite support converges to the wave with the minimal speed.

Numerical simulations of wave propagation are shown in Figures 4 and 5. There are also waves connecting the points \( E_0 \) and \( E_1 \) with \( v = 0 \). They correspond to the scalar reaction–diffusion equations, and they are well studied in the literature [38].

Figure 4. Travelling wave between the points \( E_0 \) and \( E^* \). The same parameters as in Figure 3 except for \( D_u = 1.5 \). Functions \( u(x, t) \) (left) and \( v(x, t) \) (right) for \( t = 5, 10 \) and 15.

Figure 5. Travelling wave between the points \( E_1 \) and \( E^* \). Functions \( u(x, t) \) (left) and \( v(x, t) \) (right) for \( t = 4, 7 \) and 10.
5.3. **Essential spectrum**

The wave is a solution of the system (16) and (17). Stability of waves is related to the spectrum of the problem linearized about the wave

\[
D_u u'' + cu' + F'_u(U(x), V(x))u + F'_v(U(x), V(x))v = \lambda u, \quad (18)
\]

\[
D_v V'' + cv' + G'_u(U(x), V(x))u + G'_v(U(x), V(x))v = \lambda v. \quad (19)
\]

It can be easily verified that the derivative \((U'(x), V'(x))\) of the wave is the eigenfunction corresponding to the zero eigenvalue. If all other spectrum of the linearized system lies in the left half-plane, then the wave is asymptotically stable with shift [38]. If a simple real eigenvalue crosses the origin, then the wave loses its stability and some other stationary waves will bifurcate. Another possible situation is when a pair of complex conjugate eigenvalues crosses the imaginary axis. Then, a Hopf-like bifurcation occurs resulting in appearance of periodic in time solutions. These bifurcations of travelling waves are well known and intensively studied in relation with flame propagation and with numerous other applications [38].

We will discuss here another situation where a part of the essential spectrum crosses the imaginary axis. This type of bifurcations cannot be studied by conventional bifurcation analysis. We will see that behaviour of solutions is quite different in comparison with the case where a single eigenvalue or a couple of complex conjugate eigenvalues cross the imaginary axis.

In order to determine the essential spectrum of this system, we substitute the limits \((u^*, v^*)\) of the functions \((U(x), V(x))\) at \(-\infty\) and consider the spectral problem

\[
D_u u'' + cu' + F'_u(u^*, v^*)u + F'_v(u^*, v^*)v = \lambda u, \quad (20)
\]

\[
D_v V'' + cv' + G'_u(u^*, v^*)u + G'_v(u^*, v^*)v = \lambda v. \quad (21)
\]

![Figure 6. Schematic representation of the essential spectrum for the critical values of the parameters.](image)

Figure 6. Schematic representation of the essential spectrum for the critical values of the parameters.
By definition, the essential spectrum of the linear system in the left-hand side of Equations (18) and (19) is the set of all complex \( \lambda \) for which system (20) and (21) has a non-zero bounded solution [36]. In fact, it is only the part of the essential spectrum, which corresponds to minus infinity. A similar construction should be done at plus infinity.

Since system (20) and (21) has constant coefficients, we can apply the Fourier transform. Therefore, the essential spectrum is given by the eigenvalues of the matrix

\[
B(\xi) = \begin{pmatrix}
F_u'(u^*, v^*) - D_u \xi^2 + ci\xi, & F_v'(u^*, v^*) \\
G_u'(u^*, v^*), & G_v'(u^*, v^*) - D_v \xi^2 + ci\xi
\end{pmatrix}
\]

for all real \( \xi \). Denote the eigenvalues by \( \lambda_j(\xi), j = 1, 2 \).

The eigenvalues of the matrix \( B(\xi) \) can be expressed through the eigenvalues \( \mu_j(\xi) \) of the matrix \( A(\xi) \):

\[
A(\xi) = \begin{pmatrix}
F_u'(u^*, v^*) - D_u \xi^2, & F_v'(u^*, v^*) \\
G_u'(u^*, v^*), & G_v'(u^*, v^*) - D_v \xi^2
\end{pmatrix}
\]

which determines the emergence of Turing structures (Section 4)

\[
\lambda_j(\xi) = \mu_j(\xi) + ci\xi, \quad j = 1, 2.
\]

The curve \( \lambda_1(\xi) \) for the critical values of the parameters is schematically shown in Figure 6. It touches the imaginary axis at two points, \( \lambda(\xi_0) = \pm ic\xi_0 \). For the value of the parameter exceeding the critical one, the essential spectrum is partially in the right-half plane. Therefore, the wave \((U(x), V(x))\) can lose its stability. However, the usual bifurcation analysis is not applicable here since these are not isolated eigenvalues. In the next paragraph, we illustrate the behaviour of solutions with numerical simulations.

Figure 7. The first component \( u(x, t) \) of the solution as a function of two variables, \( x \) and \( t \), for \( D_u = 0.43 \). A Turing structure emerges behind a periodic travelling wave.
5.4. Travelling waves and Turing structures

We carry out numerical simulations of system (2a) and (2b) with the initial condition

\[ u(x,0) = \begin{cases} 
\epsilon, & 0 < x < a, \\
0, & x > a,
\end{cases} \quad v(x,0) = \begin{cases} 
\epsilon, & x < a, \\
0, & x > a,
\end{cases} \]

where \( a \) and \( \epsilon \) are some positive constants. Their exact values are not essential. In the case where point \( E^* \) is stable, we observe the propagation of the wave connecting \( E_0 \) with \( E^* \) (see above). Let us now consider the values of parameters for which the point \( E^* \) is unstable and a Turing structure emerges around it. Thus, we can expect a transition between the homogeneous solution \( E_0 \) and a Turing structure.

Figure 7 shows an example of numerical simulations. The picks in the front of the image correspond to a periodic travelling wave which connects the homogeneous states \( E_0 \) and \( E^* \). Since the latter is unstable, there is a spatial structure which emerges after some time. It forms parallel hills whose height is not constant but oscillates periodically in time. It can be considered as a time-periodic Turing structure. Thus, it is a spatio-temporal structure which spreads in space also as a travelling wave. Since the speed of the \( E_0 - E^* \) wave is greater than the speed of the wave between the constant equilibrium \( E^* \) and the periodic structure, the former runs away from the latter leaving the homogeneous state \( E^* \) between them. Another representation of the same simulation is shown in Figure 8. We clearly see here the propagation of two wave fronts with different speeds.

Let us now decrease the value of \( D_u \) (Figure 9). As we can expect, the speed of the periodic \( E_0 - E^* \) wave decreases while the speed of spreading of the structure behind it increases. In fact, this spatio-temporal structure fills the whole space behind the wave. After some time, there is a reorganization of this structure into a time-periodic Turing structure.

If we decrease even more the value of \( D_u \), then dynamics of the solution changes. In this case, the \( E_0 - E^* \) wave is directly followed by the stationary Turing structure (Figure 10). In this case, the Turing structure spreads in space faster than the \( E_0 - E^* \) wave catches up and the two waves merge.
Figure 9. Level lines of the function $u(x,t)$ for $D_u = 0.3$. Periodic travelling wave is followed by a spatio-temporal structure.

Figure 10. Level lines of the function $u(x,t)$ for $D_u = 0.1$. Periodic travelling wave is followed by a stationary structure.

6. Conclusions

In this paper, we study spatio-temporal patterns and the periodic travelling wave observed in a spatial plankton model for phytoplankton–zooplankton interaction. We have investigated the model both analytically and numerically. The non-trivial equilibrium state $E^*$ is locally and globally asymptotically stable in the absence of diffusion. It has been observed that the instability observed in the model system is diffusion driven.

In the reaction–diffusion systems, two basic types of symmetry-breaking bifurcations are responsible for the emergence of spatio-temporal patterns. First, the space-independent Hopf-bifurcation that breaks the temporal symmetry of a model system and gives rise to oscillations that are uniform in space and periodic in time. The second one is the stationary Turing bifurcation.
that breaks spatial symmetry, leading to the formation of patterns that are stationary in time and oscillatory in space.

One of the open questions in nonlinear dynamics concerns propagation of spatial patterns. It is a generic situation which can be observed whenever such structures emerge in sufficiently large spatial domains. Conventional bifurcation analysis is not applicable here because of the essential spectrum crossing the imaginary axis. We show that there are various modes of propagation. It can be either a periodic travelling wave or a usual wave followed by a transition from a homogeneous in space solution to a periodic structure.

References

[1] P.A. Braza, The bifurcation structure of the Holling–Tanner model for predator–prey interactions using two-timing, SIAM J. Appl. Math. 63 (2003), pp. 889–904.
[2] R.S. Cantrell and C. Cosner, Spatial Ecology Via Reaction–Diffusion Equations, Wiley, Chichester, 2003.
[3] B. Chen and M. Wang, Qualitative analysis for a diffusive predator–prey model, Comput. Math. Appl. 55(3) (2008), pp. 339–355.
[4] J.B. Collings, Bifurcation and stability analysis of a temperature-dependent mite predator–prey interaction model incorporating a prey refuge, Bull. Math. Biol. 57 (1995), pp. 63–76.
[5] J.B. Collings, The effects of the functional response on the bifurcation behaviour of a mite predator–prey interaction model, Bull. Math. Biol. 36 (1997), pp. 149–168.
[6] A. Gasull, R.E. Kooij, and J. Torregrosa, Limit cycles in the Holling Tanner model, Publ. Math. 41 (1997), pp. 149–167.
[7] M. Haque and B. Li, A ratio-dependent predator–prey model with logistic growth for the predator population, Proceedings of 10th International Conference on Computer Modeling and Simulation, University of Cambridge, Cambridge, 2008, pp. 210–215.
[8] C.S. Holling, The functional response of invertebrate predators to prey density, Mem. Entomol. Soc. Can. 45 (1965), pp. 3–60.
[9] S.B. Hsu and T.W. Huang, Global stability for a class of predator–prey systems, SIAM J. Appl. Math. 55 (1995), pp. 763–783.
[10] Z. Liang and H. Pan, Qualitative analysis of a ratio-dependent Holling Tanner model, J. Math. Anal. Appl. 334 (2007), pp. 954–964.
[11] Q. Liu, B.-L. Li, and Z. Jin, Resonant patterns and frequency-locked induced by additive noise and periodically forced in phytoplankton–zooplankton system, preprint (2007). Available at arXiv: 0705.3724.
[12] A. Maiti and S. Pathak, A modified Holling–Tanner model in stochastic environment, Nonlinear Anal. Model. Control 14(1) (2009), pp. 51–71.
[13] H. Malchow, Spatio-temporal pattern formation in nonlinear nonequilibrium plankton dynamics, Proc. R. Soc. Lond. B 251 (1993), pp. 103–109.
[14] H. Malchow, Nonlinear plankton dynamics and pattern formation in an ecosystem model, J. Mar. Syst. 7(2/4) (1996), pp. 193–202.
[15] H. Malchow, Motion instabilities in predator–prey systems, J. Theoret. Biol. 204 (2000), pp. 639–647.
[16] H. Malchow, Non-equilibrium spatio-temporal patterns in models of non-linear plankton dynamics, Freshwater Biol. 45 (2000), pp. 239–251.
[17] H. Malchow, F.M. Hilker, R.R. Sarkar, and K. Brauer, Spatiotemporal patterns in an excitable plankton system with lysogenic viral infection, Math. Comput. Model. 42 (2005), pp. 1035–1048.
[18] A.P. Martin, Phytoplankton patchiness: The role of lateral stirring and mixing, Prog. Oceanogr. 57 (2003), pp. 125–174.
[19] R.M. May, Stability and Complexity in Model Ecosystems, Princeton University Press, Princeton, NJ, 1974.
[20] A.B. Medvinsky, S.V. Petrovskii, L.A. Tikhonova, H. Malchow, and B.-L. Li, Spatiotemporal complexity of plankton and fish dynamics, SIAM Rev. 44(3) (2002), pp. 311–370.
[21] A.B. Medvinsky, S.V. Petrovskii, L.A. Tikhonova, E. Venturino, and H. Malchow, Chaos and regular dynamics in a model multi-habitat plankton-fish community, J. Biosci. 26(1) (2001), pp. 109–120.
[22] A.B. Medvinsky, I.A. Tikhonova, R.R. Aliev, B.-L. Li, Z.S. Lin, and H. Malchow, Patchy environment as a factor of complex plankton dynamics, Phys. Rev. E. 64 (2001), pp. 021915–021917.
[23] A. Morozov and E.G. Arashkevich, Patterns of zooplankton functional response in communities with vertical heterogeneity: A model study, Math. Model. Nat. Phenom. 3(3) (2008), pp. 131–148.
[24] A. Okubo, Diffusion and Ecological Problems: Mathematical Models, Springer, Berlin, 1980.
[25] M. Pascual, Diffusion-induced chaos in a spatial predator–prey system, Proc. R. Soc. Lond. B 251 (1993), pp. 1–7.
[26] R. Peng, M. Wang, and G. Yang, Stationary patterns of the Holling–Tanner prey–predator model with diffusion and cross-diffusion, Appl. Math. Comput. 196 (2008), pp. 570–577.
[27] J.C. Poggiale, M. Gauduchon, and P. Auger, Enrichment paradox induced by spatial heterogeneity in a phytoplankton–zooplankton system, Math. Model. Nat. Phenom. 3(3) (2008), pp. 87–102.
[28] A.B. Ryabov and B. Blasius, Population growth and persistence in a heterogeneous environment: The role of diffusion and advection, Math. Model. Nat. Phenom. 3(3) (2008), pp. 42–86.
[29] L.A. Segel and J.L. Jackson, *Dissipative structure: An explanation and an ecological example*, J. Theoret. Biol. 37 (1972), pp. 545–559.

[30] L. Seuront, *Microscale complexity in the ocean: Turbulence, intermittency and plankton life*, Math. Model. Nat. Phenom. 3(3) (2008), pp. 1–41.

[31] J.H. Steele and E.W. Henderson, *A simple plankton model*, Am. Nat. 117 (1981), pp. 676–691.

[32] G. Sun, Z. Jin, Q. Liu, and L. Li, *Pattern formation induced by cross-diffusion in a predator–prey system*, Chin. Phys. B 17(11) (2008), pp. 3936–3941.

[33] J.T. Tanner, *The stability and the intrinsic growth rates of prey and predator populations*, Ecology 56 (1975), pp. 855–867.

[34] R.K. Upadhyay, N.K. Thakur, and B. Dubey, *Nonlinear Non-equilibrium pattern formation in a spatial aquatic system: Effect of fish predation*, J. Biol. Syst. 18(1) (2010), pp. 129–159.

[35] R.K. Upadhyay, W. Wang, and N.K. Thakur, *Spatiotemporal dynamics in a spatial plankton system*, Math. Model. Nat. Phenom. 5(5) (2010), pp. 101–121.

[36] V. Volpert, *Elliptic Partial Differential Equations*, Fredholm Theory of Elliptic Problems in Unbounded Domains Vol. 1, Birkhäuser, Zurich, 2011.

[37] V. Volpert and S. Petrovskii, *Reaction–diffusion waves in biology*, Phys. Life Rev. 6 (2009), pp. 267–310.

[38] A. Volpert, V. Volpert, and V. Volpert, *Traveling Wave Solutions of Parabolic Systems*, Translation of Mathematical Monographs Vol. 140, American Mathematical Society, Providence, RI, 1994.

[39] M. Wang, P.Y.H. Pang, and W. Chen, *Sharp spatial patterns of the diffusive Holling–Tanner prey–predator model in heterogeneous environment*, IMA J. Appl. Math. 73 (2008), pp. 815–835.

[40] D.J. Wollkind, J.B. Collings, and J.A. Logan, *Metastability in a temperature-dependent model system for predator–prey mite outbreak interactions on fruit flies*, Bull. Math. Biol. 50 (1988), pp. 379–409.

[41] J.-H. Xiao, H.-H. Li, J.-Z. Yang, and G. Hu, *Chaotic Turing pattern formation in spatiotemporal systems*, Front. Phys. China 1 (2006), pp. 204–208.