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Spatiotemporal pattern induced by self and cross-diffusion in a spatial Holling-Tanner model

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Abstract

In this paper, we have made an attempt to provide a unified framework to understand the complex spatiotemporal patterns induced by self and cross diffusion in a spatial Holling–Tanner model for phytoplankton–zooplankton–fish interaction. The effect of critical wave length which can drive the system to instability is investigated. We have examined the criterion between two cross-diffusivity (constant and time-varying) on the stability of the model system and for diffusive instability to occur. Based on these conditions and by performing a series of extensive simulations, we observed the irregular patterns, stationary strips, spots, and strips-spots mixture patterns. Numerical simulation results reveal that the regular strip-spot mixture patterns prevail over the whole domain on increasing the values of self- diffusion coefficients of phytoplankton and zooplankton and the dynamics of the system do not undergo any further changes.

Keywords spatiotemporal pattern; diffusion; Holling–Tanner model; phytoplankton–zooplankton–fish interaction.

1 Introduction

During the last two decades there has been considerable interest to investigate the stability behavior of a system of interacting populations by taking into account the effect of self as well as cross-diffusion (Lou and Ni, 1999). The term self-diffusion implies the movement of individuals from a higher to lower concentration region. Cross-diffusion express the population fluxes of one species due to the presence of the other species. The value of the cross-diffusion coefficient may be positive, negative or zero. The term positive cross-diffusion coefficient denotes the movement of the species in the direction of lower concentration of another species and negative cross-diffusion coefficient denotes that one species tends to diffuse in the direction of higher concentration of another species. The dynamics of interacting population with self and cross-diffusion are investigated by several researchers (Chattopadhyay and Tapaswi, 1997; Dubey et al., 2001, 2002; Iida et al., 2006; Ko and Ryu, 2008; Sun et al., 2008, 2009; Vanag and Epstein, 2009). The special emphases have been put in pattern forming instability from ecological point of view. Segal and Jackson (1972) were the first to draw attention to the fact that Turing's idea (1952) would be applicable for pattern formation in ecological system also. McLaughlin and Roughgarden (1991) have observed the spatial pattern by introducing spatial heterogeneity to the Lotka-Volterra diffusive system. By exploring the idea of cross-diffusion, Chattopadhyay and Tapaswi (1997) have observed the two-dimensional (2D) spatial pattern in the same system without environmental heterogeneity. It has been observed that constant coefficient cross-diffusions are necessary to

maintain spatial pattern in 2D Lotka-Volterra competitive system. Raychaudhuri et al. (1996) studied the same system and observed that cross-diffusive instability is less likely to occur in this system with time varying cross-diffusivity than those with constant cross-diffusivity. Turing pattern have been observed in interaction-diffusion system by many authors (Xiao et al., 2006; Malchow, 2000). From the Turing theory, it is believed that there is no Turing pattern formation for the equal self-diffusion coefficients. Sun et al. (2008) have investigated a Holling-Tanner model with self and cross diffusion. They show that, when the self-diffusion coefficients are equal, Turing pattern can emerge due to cross-diffusion. Wang et al. studied the spatio-temporal patterns in the cross-diffusive Holling-Tanner model and finds that the model dynamics exhibits a cross-diffusion controlled formation growth not only to spots, but also to strips, holes, strips-spots mixture. Upadhyay et al. (2010) investigated the modified Holling-Tanner model with Holling type III functional response and different diffusion coefficients. Their study shows that the model system has not only Turing pattern in space but also has spiral waves. Rai et al. (2011) have studied dynamical behavior of a few two dimensional predator-prey systems in two dimensional parameter spaces to gain insight into how functional responses affect community dynamics.

The spatial continuous models formulated as reaction-diffusion equations have been intensively used to describe spatiotemporal dynamics and to investigate mechanisms for pattern formation (Huang and Diekmann, 2003; Hoyle, 2006; Haidar et al., 2011). The problems of spatial and spatiotemporal pattern formation include irregular and regular oscillation, spiral waves and stationary spiral patterns. Pattern forming instability in ecological system has received much attention in the field of ecological modeling as well as to the experimentalists. Many authors have tried to study this problem by using self-diffusive reaction-diffusion model (Segel and Jackson, 1972; Levin, 1977; Levin and Segel, 1976; Okubo, 1980). But a little attention has been paid to the effect of cross-diffusion in this direction. The idea that cross-diffusion on pattern forming instability in ecological model is not new, and have been examined by several authors (Okubo, 1980; Gurtin, 1974; Sun et al., 2008; Chen and Jungle, 2006). In this paper, we have investigated the spatiotemporal pattern induced by self and cross diffusion in a Holling-Tanner model with Holling type III functional responses. We are also interested to see what kind of criterion between two cross diffusivity do we have for diffusive instability to occur? In particular, does variable cross-diffusivity make the system more stable in comparison to constant cross-diffusivity?

Predator switching has a stabilizing effect on prey-predator systems if a predator focuses on a more available prey (Matsuda et al., 1986). In addition, the prey's antipredator efforts may promote predator switching (Abrams and Matsuda, 1993). Sigmoidal-shaped functional response, also known as Holling type III, was originally proposed as a model to represent a predator switching its preference from one specialist prey to an alternative prey at times when the specialist prey is at low densities or depleted (Holling, 1959). The characteristic feature is that at low densities of the specialist prey, the predator consumes it less proportionally than is available in the environment, relative to the predators' other prey (Kar and Matsuda, 2007). Holling type III functional response is used when one wishes to stabilize the system at low algal density (Truscott and Brindley, 1994; Scheffer and De Boer, 1996; Bazykin, 1998; Hammer and Pitchford, 2005). Since most marine mammals and boreal fish are considered to be generalist predators (including feeders, grazers, etc.), a sigmoidal functional response might be more appropriate (Magnusson and Palsson, 1991).

In this paper, we have considered a spatial Holling-Tanner model for phytoplankton-zooplankton-fish interaction with self and cross diffusion. We have investigated the effect of critical wave length on the stability of phytoplankton and zooplankton. Finally, we examine the effect of time-varying cross-diffusivity on the stability of the model system. Based on these conditions by performing a series of simulations, we observed

the stripe-spotted or stripe-like patterns. On fixed parameters space by increasing the self-diffusion coefficients, we try to understand the stabilizing behavior of the model system.

2 Model System

We consider a reaction-diffusion model for phytoplankton-zooplankton-fish system where at any point (x, y) and time t , the phytoplankton $P(x, y, t)$ and zooplankton $H(x, y, t)$ populations. The phytoplankton population $P(x, y, t)$ is predated by the zooplankton population $H(x, y, t)$ which is predated by fish population. The per capita predation rate is described by Holling type III functional response. The model system incorporating effects of fish predation satisfy the following:

$$\frac{\partial P}{\partial t} = rP - B_1 P^2 - \frac{B_2 P^2 H}{(P^2 + D^2)} + d_{11} \nabla^2 P + d_{12} \nabla^2 H, \quad (1a)$$

$$\frac{\partial H}{\partial t} = C_1 H - C_2 \frac{H^2}{P} - \frac{FH^2}{(H^2 + D_1^2)} + d_{22} \nabla^2 H + d_{21}(t) \nabla^2 P. \quad (1b)$$

$$P(x, y, 0) > 0, H(x, y, 0) > 0, (x, y) \in \Omega = [0, R] \times [0, R], \quad (2)$$

with the zero flux boundary conditions,

$$\frac{\partial P}{\partial n} = \frac{\partial H}{\partial n} = 0, (x, y) \in \partial\Omega \text{ for all } t. \quad (3)$$

where d_{11}, d_{22} are the self-diffusion coefficients and $d_{12}, d_{21}(t)$ are the cross diffusion coefficient of phytoplankton and zooplankton population respectively. The parameters $r, B_1, B_2, D, C_1, C_2, D_1$ are positive constants. We explain the meaning of each variable and constant. r is the prey's intrinsic rate in the absence of predation, B_1 is the intensity of competition among individuals of phytoplankton, B_2 is the rate at which phytoplankton is grazed by zooplankton and it follows Holling type-III functional response, C_1 is the predator's intrinsic rate of population growth, C_2 indicates the number of prey necessary to support and replace each individual predator. The rate equation for the zooplankton population is the logistic growth with carrying capacity proportional to phytoplankton density, P/C_2 . D, D_1 is the half-saturation constants for phytoplankton and zooplankton density respectively, F is the maximum value of the total loss of zooplankton due to fish predation, which follows Holling type-III functional response. The units of the parameters are as follows. Time t and length $x, y \in [0, R]$ are measured in days $[d]$ and meters $[m]$ respectively. r, P, H, D , and D_1 are usually measured in mg of dry weight per litre $[mg.dw/l]$; the dimension of B_2 and C_2 is $[d^{-1}]$, B_1 and C_1 are measured in $[(mg.dw/l)^{-1} d^{-1}]$ and $[d^{-1}]$ respectively. The diffusion coefficients d_{ij} are measured in $[m^2 d^{-1}]$. F is measured in $[(mg.dw/l) d^{-1}]$. The significance of the terms on the right hand side of Eq.(1) is explained as follows: The first term represents the density-dependent growth of prey in the absence of predators. The third term on the right of the prey equation

$B_2 P^2 / (P^2 + D^2)$ represents the action of the zooplankton. We assume that the predation rate follows a sigmoid (Type III) functional response. This assumption is suitable for plankton community where spatial mixing occur due to turbulence (Okubo, 1980). The dimensions and other values of the parameters are chosen from literatures (Malchow, 1996; Medvinsky et al., 2001, 2002; Murray, 1989), which are well established for a long time to explain the phytoplankton-zooplankton dynamics. Notably, the system (1) is a modified (Holling III instead of II) and extended (fish predation) version of a model proposed by May (1973).

Holling type III functional responses are rarely used in complex multispecies model, since they are difficult to implement (Turchin, 2002; Liermann and Hilborn, 2001). This response function is sigmoid, rising slowly when prey are rare, accelerating when they become more abundant, and finally reaching a saturated upper limit. Type III functional response also levels off at some prey density. Keeping the above mentioned properties in mind, we have considered the zooplankton grazing rate on phytoplankton and the zooplankton predation by fish follows a sigmoidal functional response.

3 Stability Analysis of the Spatial Model System

Upadhyay et al., (2010) have studied the stability analysis of non-spatial model system (1a)-(1b). In this section, we have studied the stability analysis of spatial model for one dimensional and two dimensional cases. We study the effect of diffusion on the model system about the interior equilibrium point $E^*(P^*, H^*)$. Complex marine ecosystems exhibit patterns that are bound to each other yet observed over different spatial and time scales (Grimm et al., 2005). Turing instability can occur for the model system because the equation for predator is nonlinear with respect to predator population, H and unequal values of diffusive constants.

To study the effect of diffusion on the model system (1a)-(1b), we derive conditions for stability analysis in one and two dimensions cases.

3.1 One dimensional case and constant diffusivity

In this section, we consider the model equation (1a)-(1b) together with initial and boundary conditions (2) and (3). We also assume that $d_{21}(t) = d'_{21}$. As a consequence of initial-boundary conditions, $E^*(P^*, H^*)$ is a uniform steady state for the system.

The model system (1) in the presence of one dimensional diffusion has the following form:

$$\frac{\partial P}{\partial t} = rP - B_1 P^2 - \frac{B_2 P^2 H}{(P^2 + D^2)} + d_{11} \frac{\partial^2 P}{\partial x^2} + d_{12} \frac{\partial^2 H}{\partial x^2}, \quad (4a)$$

$$\frac{\partial H}{\partial t} = C_1 H - C_2 \frac{H^2}{P} - \frac{F H^2}{(H^2 + D_1^2)} + d_{22} \frac{\partial^2 H}{\partial x^2} + d'_{21} \frac{\partial^2 P}{\partial x^2}. \quad (4b)$$

The model is to be analyzed under the following non-zero initial condition and no-flux boundary condition:

$$P(x, 0) > 0, H(x, 0) > 0, \text{ for } x \in [0, R], \quad (5)$$

$$\left. \frac{\partial P}{\partial x} \right|_{(0,t)} = \left. \frac{\partial P}{\partial x} \right|_{(R,t)} = \left. \frac{\partial H}{\partial x} \right|_{(0,t)} = \left. \frac{\partial H}{\partial x} \right|_{(R,t)} = 0. \quad (6)$$

The zero-flux boundary conditions (6) imply that no external input is imposed from outside. To study the effect of diffusion on the model system, we have considered the linearized form of model system (4a)- (4b) about $E^*(P^*, H^*)$ as follows:

$$\frac{\partial U}{\partial t} = b_{11}U + b_{12}V + d_{11} \frac{\partial^2 U}{\partial x^2} + d_{12} \frac{\partial^2 V}{\partial x^2}, \tag{7a}$$

$$\frac{\partial V}{\partial t} = b_{21}U + b_{22}V + d_{22} \frac{\partial^2 V}{\partial x^2} + d_{21} \frac{\partial^2 U}{\partial x^2}, \tag{7b}$$

where $P = P^* + U$, $H = H^* + V$ and

$$b_{11} = -P^* (B_1 - B_2 H^* f_1(P^*, D)), \quad b_{12} = -B_2 P^{*2} / (P^{*2} + D^2),$$

$$b_{21} = C_2 H^{*2} / P^{*2}, \quad b_{22} = H^* (F f_2(H^*, D_1) - C_2 / P^*).$$

where $f_1(P^*, D) = (P^{*2} - D^2) / (P^{*2} + D^2)^2$ and $f_2(H^*, D_1) = (H^{*2} - D_1^2) / (H^{*2} + D_1^2)^2$.

It may be noted that (U, V) are small perturbations of (P, H) about the equilibrium point (P^*, H^*) .

In this case, we look for eigenfunctions of the form

$$\sum_{n=0}^{\infty} \begin{pmatrix} a_n \\ b_n \end{pmatrix} \exp(\lambda t) \cos \frac{n\pi x}{R},$$

and thus solutions of system (7) is of the form

$$\begin{pmatrix} U \\ V \end{pmatrix} = \begin{pmatrix} a \\ b \end{pmatrix} \exp(\lambda t) \cos \frac{n\pi x}{R},$$

where λ and $R/n\pi$ are the frequency and critical wave length respectively, R is the length of the system. We now investigate the stability condition for the system (7a) and (7b) in different environmental consequences and show that the critical wave length plays a crucial role for instability. The characteristic equation of the linearized system (7) is given by

$$\lambda^2 + \sigma_1 \lambda + \sigma_2 + r_1 \rho_1 - s_1 \rho_2 - \rho_1 \rho_2 = 0, \tag{8}$$

where,

$$\left. \begin{aligned}
 \sigma_1 &= A + (d_{11} + d_{22}) \frac{n^2 \pi^2}{R^2} > 0, \\
 \sigma_2 &= B - (b_{11}d_{22} + b_{22}d_{11}) \frac{n^2 \pi^2}{R^2} + d_{11}d_{22} \frac{n^4 \pi^4}{R^4} > 0, \\
 A &= P^* (B_1 - B_2 H^* f_1(P^*, D)) + H^* (C_2/P^* - Ff_2(H^*, D_1)), \\
 B &= P^* H^* (B_1 - B_2 H^* f_1(P^*, D)) (C_2/P^* - Ff_2(H^*, D_1)) + (B_2 C_2 H^{*2}) / (P^{*2} + D^2)^2, \\
 r_1 &= b_{21} > 0, \\
 s_1 &= -b_{12} > 0, \\
 \rho_1 &= d_{12} \frac{n^2 \pi^2}{R^2}, \\
 \rho_2 &= d'_{21} \frac{n^2 \pi^2}{R^2}.
 \end{aligned} \right\} \quad (9)$$

Now we assume that $A > 0$, $B > 0$. In such case $E^*(P^*, H^*)$ is locally asymptotically stable in the absence of diffusion.

Then from Routh-Hurwitz criteria, the stability of the equilibrium point E^* in the presence of diffusion depends on

$$\sigma_2 + r_1 \rho_1 - s_1 \rho_2 - \rho_1 \rho_2 \quad (10)$$

We shall discuss the following cases under the assumption that $A > 0$, $B > 0$.

Case 1.

If $d_{11} = d_{12} = d_{22} = d'_{21} = 0$.

Then the characteristic equation (8) becomes

$$\lambda^2 + A\lambda + B = 0, \quad (11)$$

which is same as, when no diffusion occurs. Thus the equilibrium point $E^*(P^*, H^*)$ is locally asymptotically stable iff $A > 0$, $B > 0$.

Case 2.

Let $d_{12} = 0$, $d'_{21} \neq 0$, then $\rho_1 = 0$ and equation (8) becomes

$$\lambda^2 + \sigma_1 \lambda + \sigma_2 - s_1 \rho_2 = 0, \quad (12)$$

In this case $E^*(P^*, H^*)$ is locally stable if

$$\sigma_2 - s_1 d'_{21} \frac{n^2 \pi^2}{R^2} > 0 \tag{13}$$

i.e.,

$$\frac{R^2}{n^2 \pi^2} > \frac{s_1 d'_{21}}{\sigma_2} \quad \forall n > 0. \tag{14}$$

We note that if, $d'_{21} < 0$ then Eq. (14) is automatically satisfied. This shows that if the predator species tends to diffuse in the direction of higher concentration of the prey species and the prey species moves along its own concentration gradient, then the equilibrium E^* remains locally asymptotically stable. This situation is a usual phenomena in nature.

But, if $d'_{21} > 0$, then $E^*(P^*, H^*)$ is unstable, since there always exists values of n such that

$$\frac{R^2}{n^2 \pi^2} < \frac{s_1 d'_{21}}{\sigma_2}. \tag{15}$$

This shows that when the critical wave length is too small that the predator species tends to diffuse in the direction of lower concentration of the prey species and the prey species moves along its own concentration gradient, then the equilibrium state E^* becomes unstable. Such a case arises in nature where the predator prefers to avoid group defense by a large number of prey and chooses to catch its prey from a smaller group unable to sufficiently resist (Dubey *et al.*, 2001).

Remark 1.

Let $A < 0$, then E^* is unstable. We assume that $d_{12} = 0$, $d'_{21} \neq 0$, then unstable equilibrium E^* will be stable if the following inequalities hold

$$\left. \begin{array}{l} \sigma_1 > 0 \\ \sigma_2 - s_1 \rho_2 > 0 \end{array} \right\} \tag{16}$$

It may be noted that if $d'_{21} < 0$, then by increasing d_{11} and d_{22} to a large value, σ_1 and $\sigma_2 - s_1 \rho_2 > 0$ can be made positive. This shows that an unstable equilibrium E^* can be made stable by increasing self-diffusion coefficients appropriately.

Case 3.

Let $d_{12} \neq 0$, $d'_{21} = 0$, then equation (8) reduces to

$$\lambda^2 + \sigma_1 \lambda + \sigma_2 + r_1 \rho_1 = 0, \quad (17)$$

We note that E^* is locally stable if

$$\sigma_2 + r_1 \rho_1 > 0,$$

$$\text{i.e., } \frac{R^2}{n^2 \pi^2} + \frac{r_1 d_{12}}{\sigma_2} > 0 \quad \forall n \geq 0. \quad (18)$$

Further if $d_{12} > 0$, then the inequality (18) is satisfied. This implies that if the phytoplankton species moves in the direction of lower concentration of the zooplankton species and the zooplankton species moves along its own concentration gradient, then the equilibrium E^* remains locally asymptotically stable. This situation can be compared in nature where the phytoplankton moves towards the lower concentration of the zooplankton in search of new food.

It may be noted that r_1 is positive. If $d_{12} < 0$, then we can always find n such that

$$\frac{R^2}{n^2 \pi^2} < -\frac{r_1 d_{12}}{\sigma_2} \quad (19)$$

In such a case $E^*(P^*, H^*)$ will be unstable. This shows that when the critical wave length is too small that the phytoplankton species moves towards the higher concentration of the zooplankton species and the zooplankton species moves along its own concentration gradient, then the equilibrium state which is stable without self and cross-diffusion becomes unstable. This situation can be compared in nature where the zooplankton attracts the phytoplankton towards itself as a predation technique and the suicidal tendencies among the phytoplankton exist.

Remark 2.

Let $A < 0$, then the interior equilibrium E^* unstable in the absence of self and cross-diffusion. But the unstable equilibrium E^* becomes stable in the presence of self and cross-diffusion if

$$\left. \begin{array}{l} \sigma_1 > 0 \\ \sigma_2 + r_1 \rho_1 > 0 \end{array} \right\} \quad (20)$$

We note that by increasing d_{11} and d_{22} to a large value so that σ_1 can be made positive. And if $d_{12} > 0$, the inequalities (20) are satisfied.

Case 4.

If $d_{12} \neq 0$, $d_{21} \neq 0$. In this case $E^*(P^*, H^*)$ is locally stable if

$$\sigma_2 + r_1\rho_1 - s_1\rho_2 - \rho_1\rho_2 > 0, \tag{21}$$

and unstable if the inequality is reversed.

Again, we note that if $\rho_1 > 0$ and $\rho_2 < 0$, i.e., if $d_{12} > 0$ and $d'_{21} < 0$, then the condition (21) is automatically satisfied. This shows that if the phytoplankton species tends to diffuse in the direction of lower concentration of the zooplankton species, and the zooplankton species tends to diffuse in the direction of higher concentration of the phytoplankton species, then the stable equilibrium state without self and cross-diffusion remains stable. Such situations are common in nature for the survival of the prey-predator species.

Remark 3.

Let $A < 0$ then the interior equilibrium E^* is unstable

Now, if $d_{12} \neq 0, d'_{21} \neq 0$, it may be seen that the unstable equilibrium point E^* becomes stable if

$$\left. \begin{aligned} \sigma_1 &> 0 \\ \sigma_2 + r_1\rho_1 - s_1\rho_2 - \rho_1\rho_2 &> 0 \end{aligned} \right\} \tag{22}$$

In particular it may be noted that the above two inequalities are satisfied if $\rho_1 > 0$ (i.e., $d_{12} > 0$), $\rho_2 < 0$ (i.e., $d'_{21} < 0$) and d_{11} and d_{22} are increased to a large value.

In the following theorem we shall investigate the global stability behavior of the interior equilibrium E^* .

For this, we first write the following notations:

$$\left. \begin{aligned} \alpha_{11} &= d_{11} \frac{P^*(P^2 + 3D^2) - 2D^2P}{B_2P^4}, \\ \alpha_{12} &= -d_{12} \frac{P^*(P^2 + 3D^2) - 2D^2P}{B_2P^4} - d'_{21} \frac{\omega H^*}{H^2}, \\ \alpha_{22} &= d_{22} \frac{\omega H^*}{H^2}, \end{aligned} \right\} \tag{23}$$

Theorem 1.

Let $d_{12} \neq 0, d'_{21} \neq 0$. If the following condition holds

$$\alpha_{12}^2 < 4\alpha_{11}\alpha_{22} \tag{24}$$

then the uniform steady state E^* of the initial-boundary-value problems eqs. (7a)-(7b) is globally asymptotically stable with respect to all solutions initiating in the positive quadrant. (for Proof see Appendix A)

Remark 4.

If $d_{12} \neq d'_{21} \neq 0$, and if \dot{W} is positive definite, then from (A2) (Appendix A) we note that \dot{W}_1 can be made negative definite by increasing d_{11} and d_{22} to sufficiently large values. If $d_{12} = d'_{21} = 0$, then Eq. (24) is automatically satisfied. This shows that if the equilibrium point E^* is globally asymptotically stable, then the uniform steady state E^* of initial- boundary value problems without cross- diffusion remains globally asymptotically stable.

This implies that the unstable equilibrium E^* of model system (7) can be made stable by increasing self-diffusion coefficients to sufficiently large values.

3.2 Two dimensional case and constant diffusivity

In two dimensional case the model can be written as

$$\frac{\partial P}{\partial t} = rP - B_1 P^2 - \frac{B_2 P^2 H}{(P^2 + D^2)} + d_{11} \left(\frac{\partial^2 P}{\partial x^2} + \frac{\partial^2 P}{\partial y^2} \right) + d_{12} \left(\frac{\partial^2 H}{\partial x^2} + \frac{\partial^2 H}{\partial y^2} \right) \quad (25a)$$

$$\frac{\partial H}{\partial t} = C_1 H - C_2 \frac{H^2}{P} - \frac{FH^2}{(H^2 + D_1^2)} + d_{22} \left(\frac{\partial^2 H}{\partial x^2} + \frac{\partial^2 H}{\partial y^2} \right) + d'_{21} \left(\frac{\partial^2 P}{\partial x^2} + \frac{\partial^2 P}{\partial y^2} \right) \quad (25b)$$

We analyze the above model under the following initial and boundary conditions:

$$P(x, y, 0) > 0, H(x, y, 0) > 0, (x, y) \in \Omega, \quad (26)$$

with the zero flux boundary conditions,

$$\frac{\partial P}{\partial n} = \frac{\partial H}{\partial n} = 0, (x, y) \in \partial\Omega \text{ for all } t. \quad (27)$$

where n is the outward normal to $\partial\Omega$.

Now, we state the main results of this section in the following theorem:

Theorem 2.

(i) Let the following inequalities hold

$$\frac{dW}{dt} \leq 0 \quad , \quad (28)$$

and

$$\left[d_{12} \frac{P^* (P^2 + 3D^2) - 2D^2 P}{B_2 P^4} + d'_{21} \frac{\omega H^*}{H^2} \right]^2 < 4d_{11}d_{22} \frac{\omega H^* (P^* (P^2 + 3D^2) - 2D^2 P)}{B_2 P^4 H^2} \quad , \quad (29)$$

where W is given in equation (A1), (Appendix A). Then the uniform steady state of the model system (25a)-(25b) is globally asymptotically stable.

(ii) If the equilibrium E^* of non-diffusive model is unstable, even then the corresponding uniform steady state of model system in two dimensional cases can be made globally asymptotically stable by increasing the self-diffusion coefficient d_{11} and d_{22} to a sufficiently large value.

To proof this result we consider the following functional

$$W_2(t) = \iint_{\Omega} W(P, H) \, dA,$$

where $W = \int_{P^*}^P \frac{\xi - P^*}{\xi \phi(\xi)} d\xi + \omega \int_{H^*}^H \frac{\eta - H^*}{\eta} d\eta$

and $\phi(\xi) = \frac{B_2 \xi^2}{\xi^2 + D^2}$.

Differentiating W_2 with respect to time t along the solution model (25a)-(25b), we

$$\frac{dW_2}{dt} = I_1 + I_2$$

where,

$$I_1 = \iint_{\Omega} \frac{dW}{dt} dA$$

$$I_2 = \iint_{\Omega} (d_{11} \frac{\partial W}{\partial P} + d'_{21} \frac{\partial W}{\partial H}) \nabla^2 P \, dA + \iint_{\Omega} (d_{12} \frac{\partial W}{\partial P} + d_{22} \frac{\partial W}{\partial H}) \nabla^2 H \, dA$$

Using Green's first identity in the plane

$$\iint_{\Omega} F \nabla^2 G dA = \int_{\partial\Omega} F \frac{\partial G}{\partial n} ds - \iint_{\Omega} (\nabla F \cdot \nabla G) dA,$$

Solving I_2 , we get

$$I_2 = \iint_{\Omega} \left[\begin{aligned} & -d_{11} \left(\frac{P^* (P^2 + 3D^2) - 2D^2 P}{B_2 P^4} \right) \left(\frac{\partial P}{\partial x} \right)^2 - d_{22} \frac{\omega H^*}{H^2} \left(\frac{\partial H}{\partial x} \right)^2 + \\ & \left(-d_{12} \frac{P^* (P^2 + 3D^2) - 2D^2 P}{B_2 P^4} - d'_{21} \frac{\omega H^*}{H^2} \right) \frac{\partial P}{\partial x} \frac{\partial H}{\partial x} \end{aligned} \right] dA$$

$$+ \iint_{\Omega} \left[\begin{aligned} & -d_{11} \left(\frac{P^* (P^2 + 3D^2) - 2D^2 P}{B_2 P^4} \right) \left(\frac{\partial P}{\partial y} \right)^2 - d_{22} \frac{\omega H^*}{H^2} \left(\frac{\partial H}{\partial y} \right)^2 + \\ & \left(-d_{12} \frac{P^* (P^2 + 3D^2) - 2D^2 P}{B_2 P^4} - d'_{21} \frac{\omega H^*}{H^2} \right) \frac{\partial P}{\partial y} \frac{\partial H}{\partial y} \end{aligned} \right] dA$$

We note that (28) implies $I_1 \leq 0$ and (29) implies that $I_2 \leq 0$. This shows that under conditions (28) and (29) $\frac{dW_2}{dt} \leq 0$.

This implies that if in the absence of diffusion E^* is globally asymptotically stable, then in the presence of diffusion E^* will remain globally asymptotically stable. This proves the first part of the Theorem.

We also note that if $\frac{dW}{dt} > 0$, then $I_1 > 0$. In such case E^* will be unstable in the absence of diffusion.

Even in this by increasing d_{11} and d_{22} to a sufficiently large value dW_2 / dt can be made negative definite.

This proves the second part of the Theorem.

Remark 5.

If $d_{12} \neq 0$, $d'_{21} \neq 0$, and if \dot{W} is positive definite, then we note that \dot{W}_2 can be made negative definite by increasing d_{11} and d_{22} to sufficiently large values. This implies that the unstable equilibrium E^* of model equation (25a)-(25b) can be made stable by increasing self-diffusion coefficient to sufficiently large values. In this case, the number of negative term is more than one-dimensional case. This implies that the rate of convergence towards its equilibrium in two-dimension is faster in comparison to one-dimension case.

4 Model With Time Varying Cross-diffusivity

In this section, we consider model equation (7a)-(7b) together with the initial and boundary conditions. In order to investigate the stability behavior of the uniform steady state, we linearized the system equation (7a)-(7b) by substituting $P = P^* + U$ and $H = H^* + V$ where U, V are assumed to be small. Thus, the linearized equation (7a)-(7b) is given by

$$\frac{\partial U}{\partial t} = b_{11}U + b_{12}V + d_{11} \frac{\partial^2 U}{\partial x^2} + d_{12} \frac{\partial^2 V}{\partial x^2} \tag{30a}$$

$$\frac{\partial V}{\partial t} = b_{21}U + b_{22}V + d_{22} \frac{\partial^2 V}{\partial x^2} + d_{21}(t) \frac{\partial^2 U}{\partial x^2} \tag{30b}$$

Now we define the dimensionless time by $\omega t = \tau$ ($\omega > 0$), and we express the solution in the form:

$$U = \Phi_1(t) e^{ikx},$$

$$V = \Phi_2(t) e^{ikx}.$$

Then equation for $\Phi_1(t)$ and $\Phi_2(t)$ are given by

$$\left. \begin{aligned} \frac{d\Phi_1}{d\tau} &= B_{11}\Phi_1(t) + B_{12}\Phi_2(t) \\ \frac{d\Phi_2}{d\tau} &= B_{21}\Phi_1(t) + B_{22}\Phi_2(t) \end{aligned} \right\} \tag{31}$$

where,

$$\left. \begin{aligned} B_{11} &= \frac{b_{11} - k^2 d_{11}}{\omega}, & B_{12} &= \frac{b_{12} - k^2 d_{12}}{\omega}, \\ B_{21} &= \frac{b_{21} - k^2 d_{21}(\tau)}{\omega}, & B_{22} &= \frac{b_{22} - k^2 d_{22}}{\omega}. \end{aligned} \right\} \tag{32}$$

Now, we assume that a particular form of $d_{21}(\tau)$ as $d_{21}(\tau) = d_{21}(a + b \sin \tau) > 0$ with $a > 1$,

$$a > |b|.$$

Now, using the following transformation

$$\psi_1 = \exp\left[-\frac{1}{2}(B_{11} + B_{22})\tau\right] \Phi_1$$

and assuming $\psi_1 = \exp(\mu\tau) \sum_r a_r \exp(r\tau i)$, where the sum runs from $-\infty$ to ∞ and under an analysis similar to Timm and Okubo (1992), it can be shown that

$$\mu < \frac{1}{2} |B_{11} + B_{22}|,$$

$$\Phi_1 = \exp\left\{\left(\mu - \frac{1}{2}|B_{11} + B_{22}|\right)\tau\right\} \sum_r a_r \exp(r\tau i),$$

Since $\sum_r a_r \exp(r\tau i) \leq \sum_r |a_r \exp(r\tau i)| \leq \sum_r |a_r|$ which implies that $\Phi_1 \rightarrow 0$ as $\tau \rightarrow \infty$.

This shows that if the variability of cross-diffusivity is small, then the variable cross-diffusivity tends to make the system more stable in comparison to constant cross-diffusivity.

5 Numerical Simulations

In this section, we perform numerical simulations to illustrate the results obtained in previous sections. The dynamics of the model systems (1a)-(1b) is studied with the help of numerical simulation both in one and two dimensions. To investigate the spatiotemporal dynamics of the model system (1a)-(1b), we solved it numerically using semi-implicit (in time) finite difference method. The step lengths Δx and Δt of the numerical grid are chosen sufficiently small so that the results are independent of step size and numerically stable. Application of the finite difference method gives rise to a sparse, banded linear system of algebraic equations. The resulting linear system is solved by using the *LU* factorization method for the one-dimensional case and by GMRES algorithm (Garvie, 2007, Garvie and Golinski, 2010) for the two-dimensional case.

For one dimensional case, the plots (space vs. population densities) are obtained to study the spatial dynamics of the model systems for constant and time varying diffusivity. For the two-dimensional case, the spatial snapshots of phytoplankton and zooplankton densities are obtained by increasing the self and cross diffusion coefficients of phytoplankton and zooplankton respectively. Turing and spiral wave patterns for the model system (25) obtained.

From a realistic biological point of view, we consider a non-monotonic form of initial condition which determines the initial spatial distribution of the species in the real community as

$$\begin{aligned} P(x, 0) &= P^* + \varepsilon (x - x_1) (x - x_2) \\ H(x, 0) &= H^* \end{aligned} \tag{33}$$

where $(P^*, H^*) = (1.8789, 1.3984)$ is the non-trivial equilibrium point of non-spatial model with fixed parameter set $r = 1, B_1 = 0.2, B_2 = 0.91, D^2 = 0.3, C_1 = 0.22, C_2 = 0.2, F = 0.1, D_1 = 0.1$ and $\varepsilon = 10^{-8}, x_1 = 1200, x_2 = 2800$ is the parameter affecting the system dynamics. At the boundary, we assume the zero-flux boundary conditions as given in Eq. (6). This type of boundary conditions is specifically used for modeling the dynamics of spatially bounded aquatic ecosystems.

The dynamics of the model system (4) in one dimensional case is observed for the set of parameter values given in Eq. (34) at the time level $t = 1000$ and for different values of self diffusion coefficient i.e., $d_{11} = 0.28, 0.286, 0.29$ and 0.3 as shown in Fig. 1.

$$\begin{aligned} r &= 1, B_1 = 0.2, B_2 = 0.91, D^2 = 0.3, C_1 = 0.22, C_2 = 0.2, D_1^2 = 0.01, F = 0.001 \\ h &= 1, \Delta t = 0.1. \end{aligned} \tag{34}$$

From Fig. 1, we observed the stabilizing effect of self-diffusion coefficient (d_{11}) on the dynamics of the model system (4) by increasing its values from 0.28 (cf. Fig. (1a), where we observed the chaotic dynamics) to 0.3 (cf. Fig. (1d), where we observed the stable focus) for both the population. Fig. 2 shows the effect of time varying cross-diffusivity on the dynamics of the model system. We observed that if the variability in the cross-diffusivity is small, then the variable cross diffusivity make the system more stable in comparison to the constant cross-diffusivity. It is observed that the fluctuation in the phytoplankton population decreasing rapidly for time varying cross diffusivity in comparison to the constant cross diffusivity in the spatial domain (400, 3600).

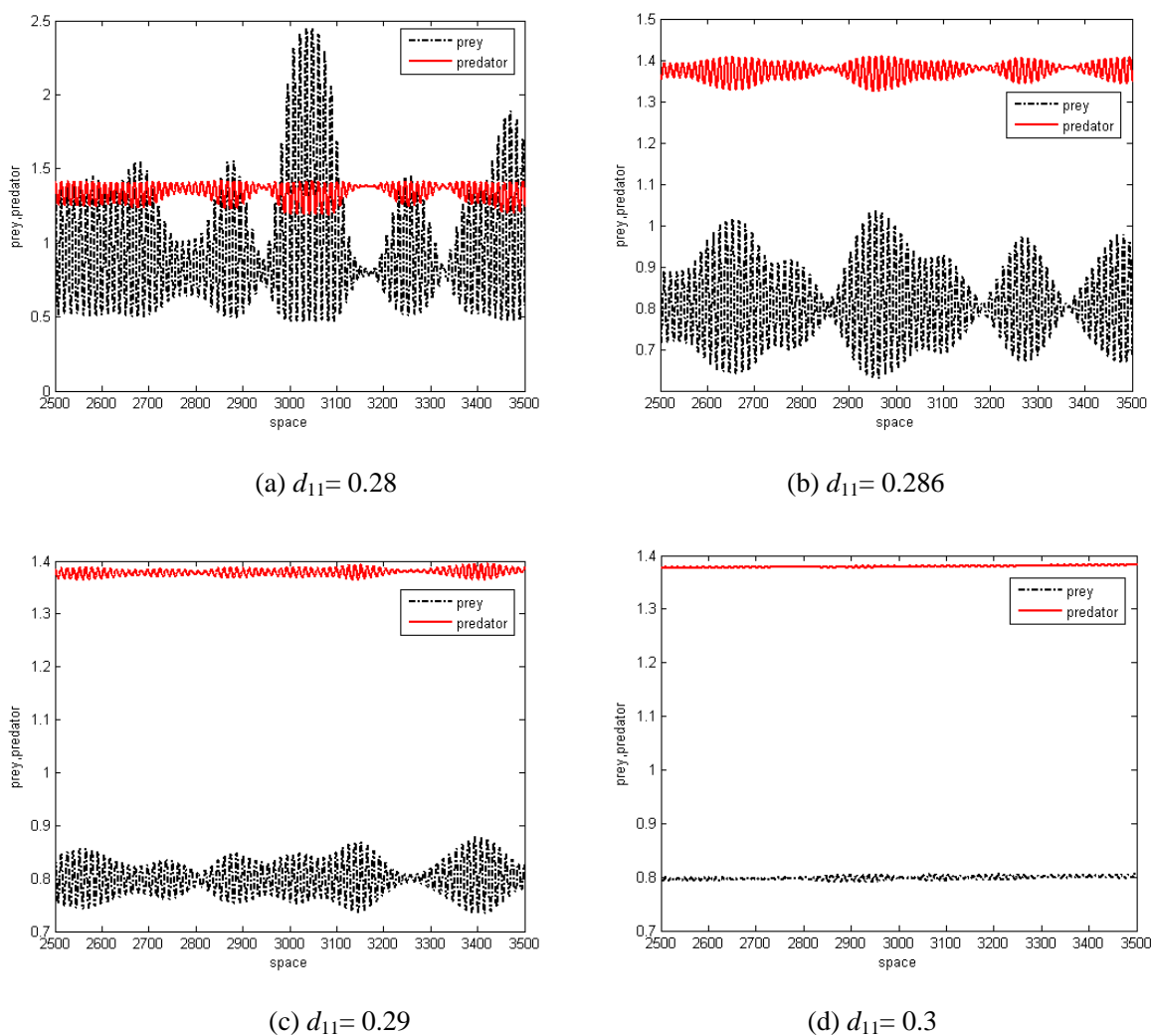


Fig. 1 Spatial distribution of plankton population showing the effect of self-diffusion on the dynamics of the model systems (4a)-(4b) for the fixed values of diffusivity constant $d_{12}=0.01$, $d_{21}=0.01$, $d_{22}=10$ at $t=1000$ and for different values of self-diffusivity constants at (a) $d_{11}=0.28$, (b) $d_{11}=0.286$, (c) $d_{11}=0.29$ and (d) $d_{11}=0.3$.

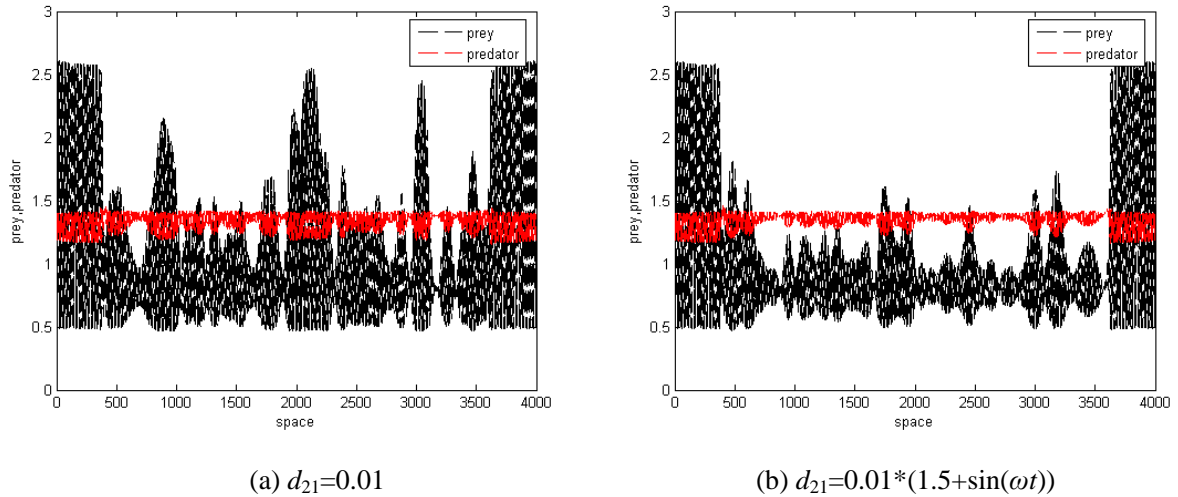


Fig. 2 Spatial distribution of plankton population showing the effect of time varying cross- diffusion on the dynamics of the model system (30) for the fixed values of diffusivity constant $d_{11}= 0.08$, $d_{12}= 0.01$, $d_{22}=10$ at $t=1000$ and for (a) $d_{21}=0.01$, (b) $d_{21}=0.01*(1.5+\sin(\omega t))$ with $\omega=0.337$.

The spatiotemporal dynamics of the system depends to a large extent on the choice of initial conditions. In a real aquatic ecosystem, the details of the initial spatial distribution of the species can be caused by spatially homogenous initial conditions. However, in this case, the distribution of species would stay homogenous for any time, and no spatial pattern can emerge. To get a nontrivial spatiotemporal dynamics, we have perturbed the homogenous initial distribution. For this purpose, we consider the following initial condition (Medvinsky et al., 2002)

$$\begin{aligned}
 P(x, y, 0) &= P^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{S}\right) + \varepsilon_1 \sin\left(\frac{2\pi(y-y_0)}{S}\right), \\
 H(x, y, 0) &= H^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{S}\right) + \varepsilon_1 \sin\left(\frac{2\pi(y-y_0)}{S}\right),
 \end{aligned} \tag{35}$$

where, $\varepsilon_1 = 5 \times 10^{-4}$, $x_0 = y_0 = 0.1$, $S = 0.2$.

We observed the Turing pattern for the model system (25) obtained by performing numerical simulations with initial condition given in (35) and the parameter values given in Eq. (34) with domain size 200×200 and for different values of self-diffusion coefficient d_{11} and d_{22} at time level $t=10000$.

From Fig.3, we observed the evolution of spatial pattern of phytoplankton and zooplankton population with small random perturbation of stationary point P^* and H^* of the spatially homogenous system. In this case one can notice that for the model system (25), the random initial distribution leads to the formation of a strongly irregular transient pattern in the domain. After the irregular pattern forms, stationary stripe and spotted patterns emerge mixed in the distribution of phytoplankton and zooplankton population density. Finally, the regular stripe patterns prevail over the whole domain by increasing the self-diffusion coefficient of phytoplankton, and the dynamics of the system do not undergo any further changes. In Fig. 4, we observed that the stationary stripe and spotted mixed patterns in the distribution of phytoplankton and zooplankton density leads to regular stripe patterns over the whole domain by increasing the self diffusion coefficient of

zooplankton. In Fig.5 we have presented the Turing pattern for different values of self-diffusion coefficient of phytoplankton population with time varying cross diffusivity.

We have also studied the spiral wave pattern of the model system (25). We have chosen the initial conditions of the form (Upadhyay et al., 2010)

$$\begin{aligned} P(x, y, 0) &= P^* - \varepsilon_2 (x - 180)(x - 720) - \varepsilon_3 (y - 90)(y - 210), \\ H(x, y, 0) &= H^* - \varepsilon_4 (x - 450) - \varepsilon_5 (y - 135), \end{aligned} \quad (36)$$

where $\varepsilon_2 = 2 \times 10^{-7}$, $\varepsilon_3 = 6 \times 10^{-7}$, $\varepsilon_4 = 3 \times 10^{-5}$, $\varepsilon_5 = 6 \times 10^{-5}$ with fixed parameter set $r = 1$, $B_1 = 0.2$

$B_2 = 0.91$, $D^2 = 0.3$, $C_1 = 0.22$, $C_2 = 0.2$, $F = 0.1$, $D_1 = 0.1$, $d_{11} = 0.05$, $d_{12} = 0.1$, $d_{22} = 1$, $d_{21} = 0.01$.

Fig.6 shows that for the system (25) with initial conditions (36), the formation of the irregular patchy structure can be preceded by the evolution of a regular spiral spatial pattern. The center of spiral is situated in a critical point (x_{cr}, y_{cr}) , where $P(x_{cr}, y_{cr}) = P^*$, $H(x_{cr}, y_{cr}) = H^*$. The distribution (36) contains two such points; the number of spirals increases for increasing time $t = 1000, 2000, 3000$. After spirals form (Fig. 6a), they grow slightly for a certain time. (Fig. 6b and 6c).

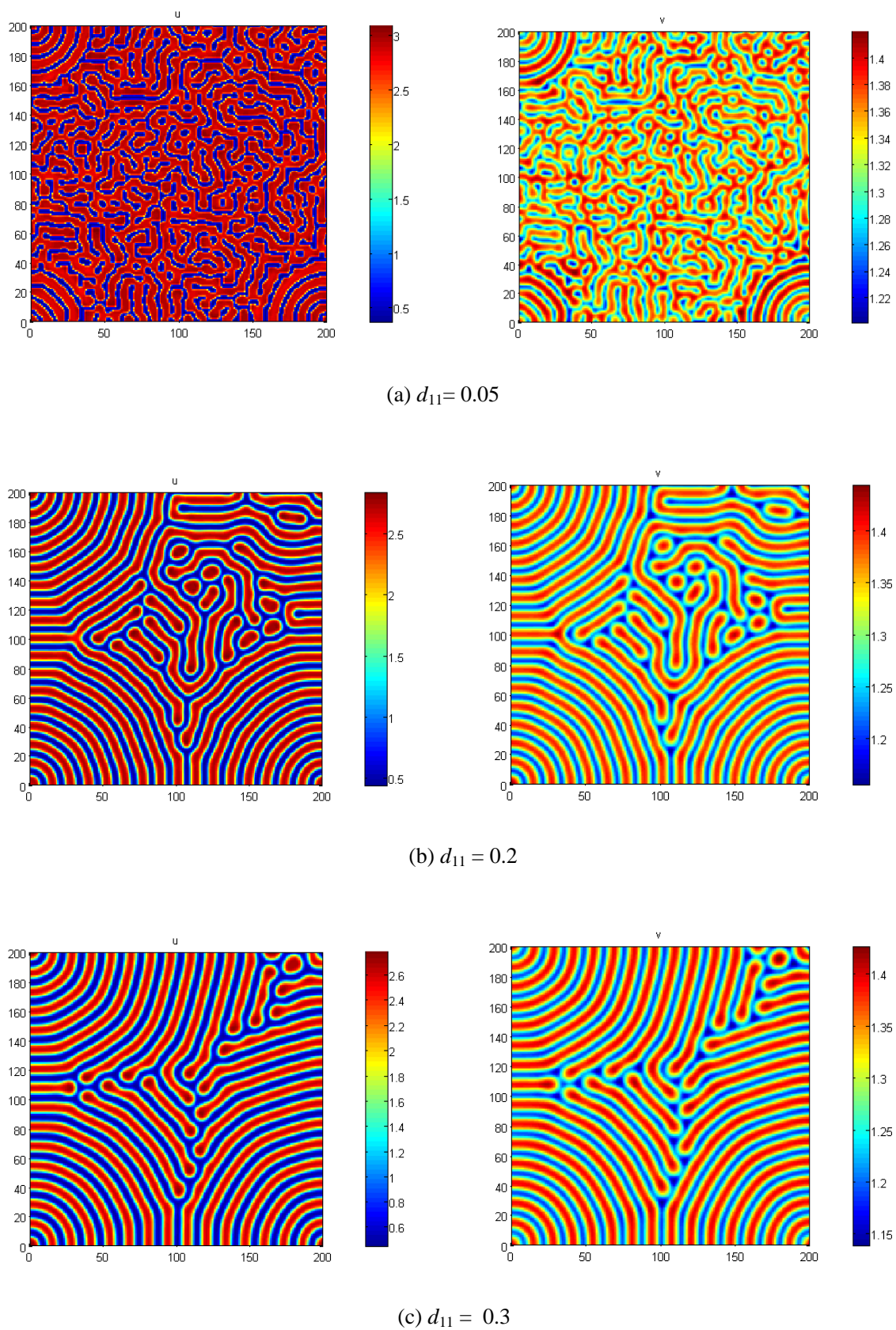
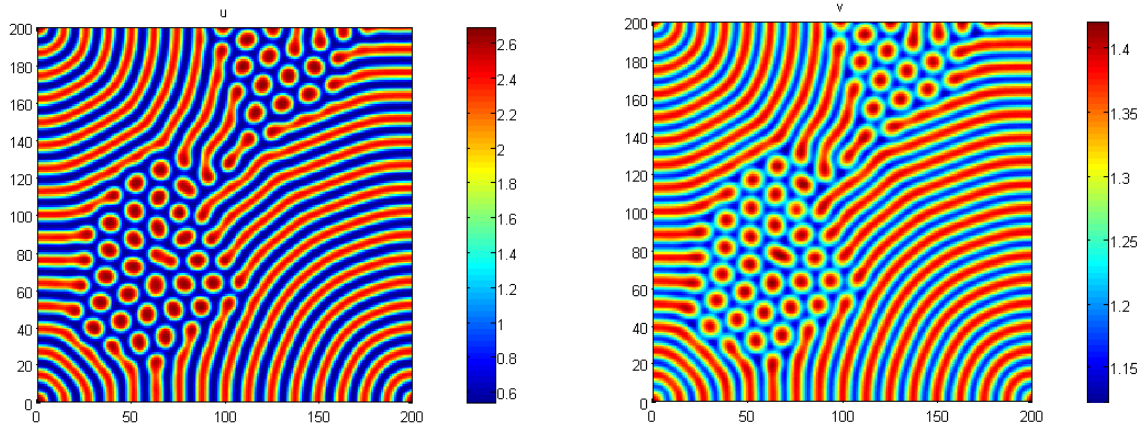
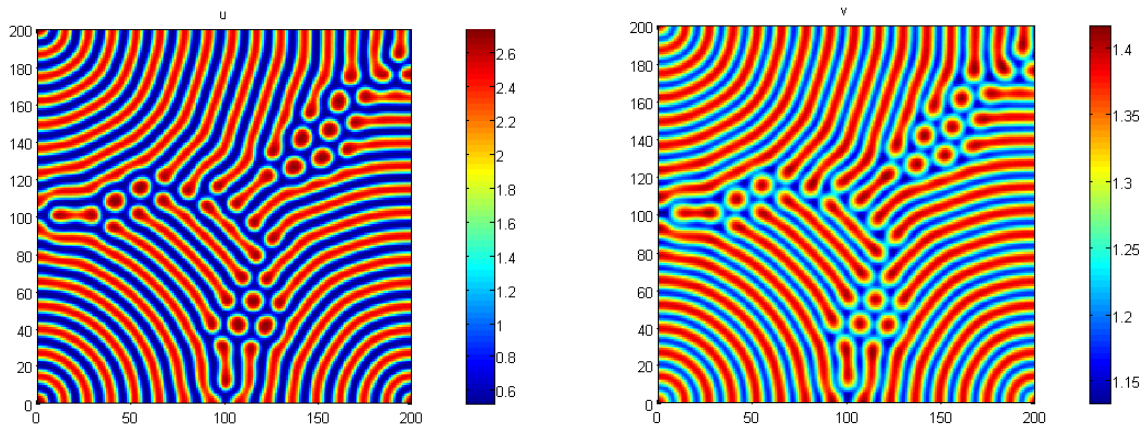


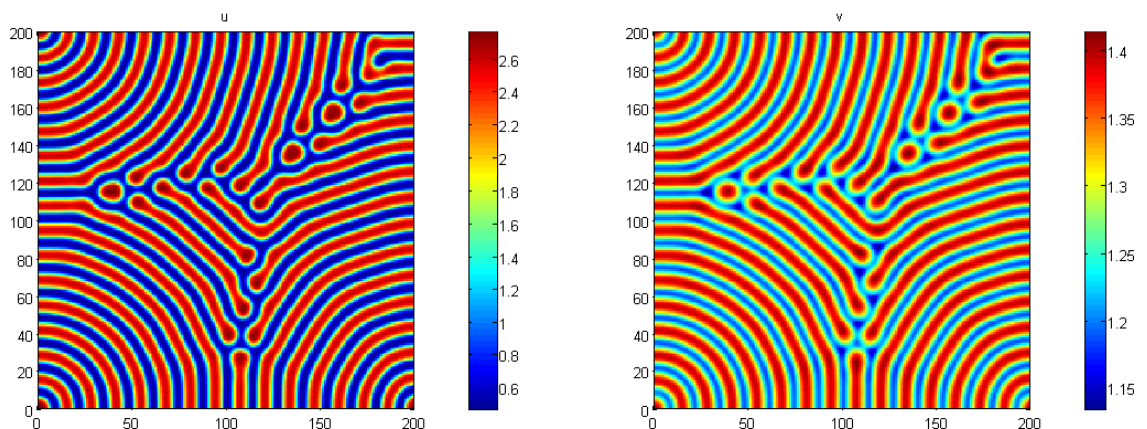
Fig. 3 Typical Turing patterns of prey [first column figures] and predator populations [second column figures] is plotted at fixed time $t=10000$ and $d_{12}=0.01$, $d_{22}=10$, $d_{21}=0.01$ at the different values of diffusivity constant (a) $d_{11} = 0.05$, (b) $d_{11} = 0.2$ and (c) $d_{11} = 0.3$.



(a) $d_{22}=7$



(b) $d_{22}=8$



(c) $d_{22}=10$

Fig. 4 Typical Turing patterns of prey [*first column figures*] and predator populations [*second column figures*] is plotted at fixed time $t=10000$ and $d_{11}=0.3$, $d_{12}=0.05$, $d_{21}=0.01$ at the different values of diffusivity constant (a) $d_{22}=7$, (b) $d_{22}=8$ and (c) $d_{22}=10$.

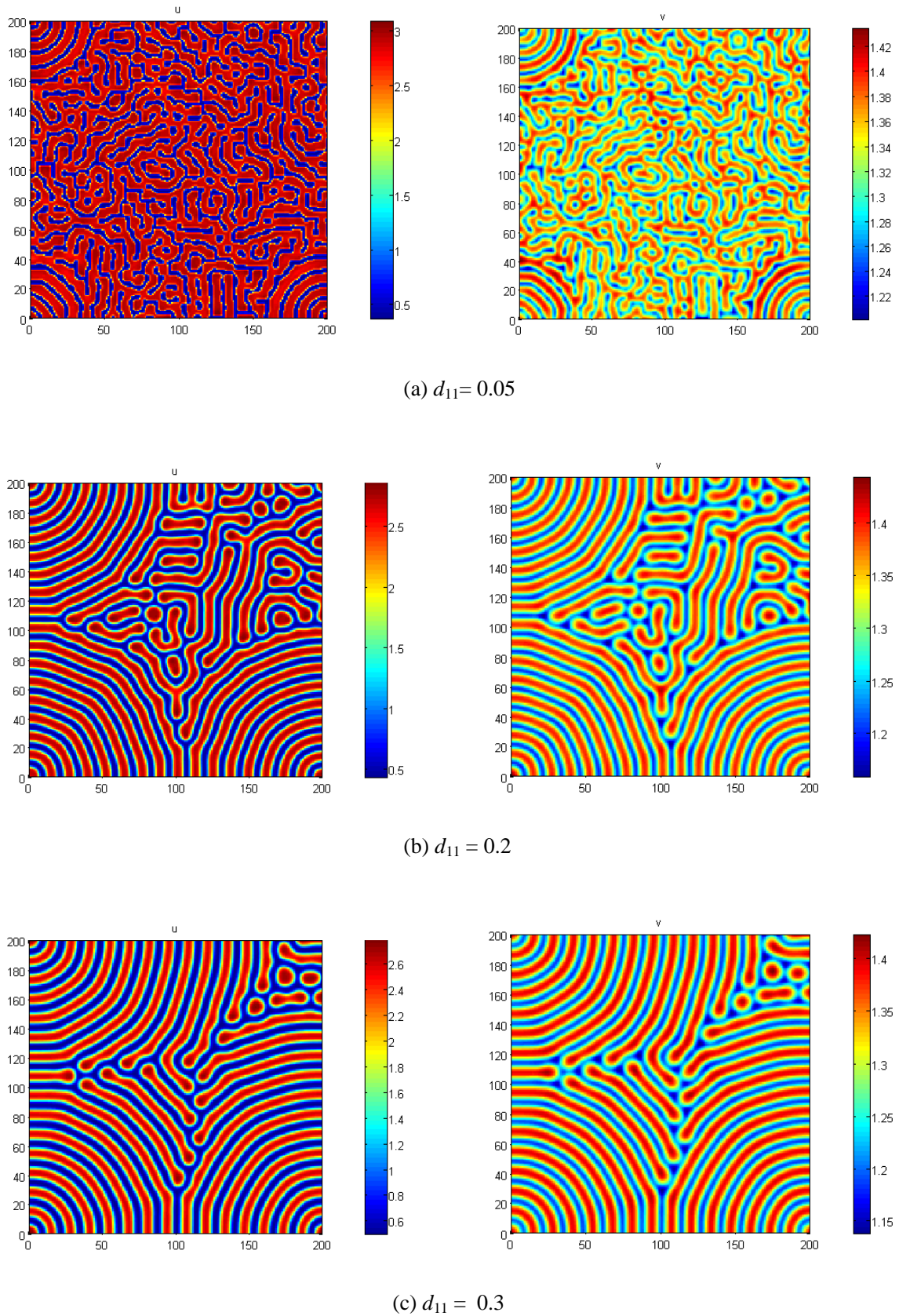
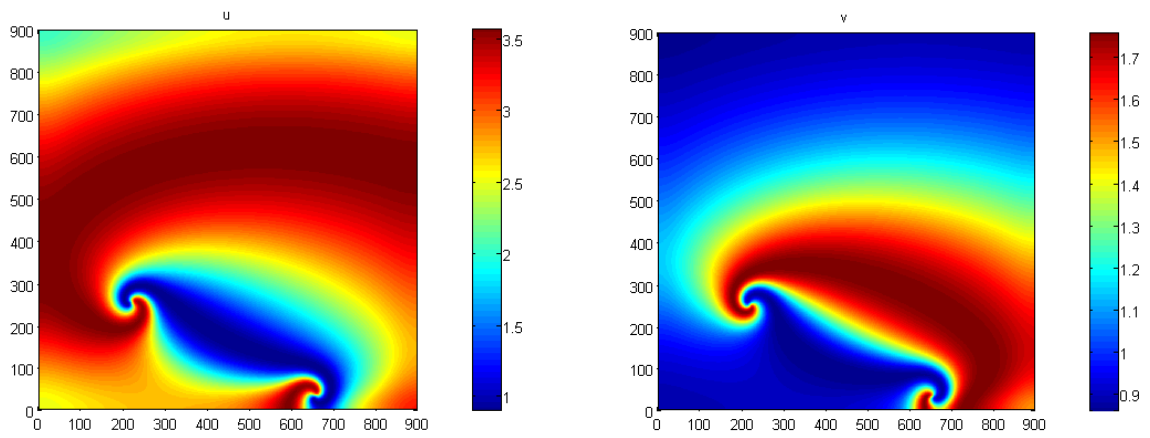
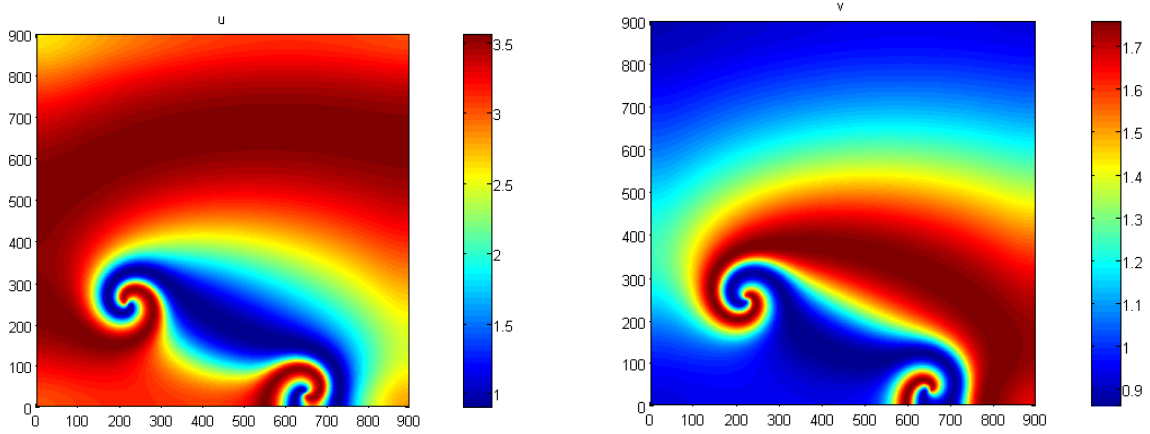


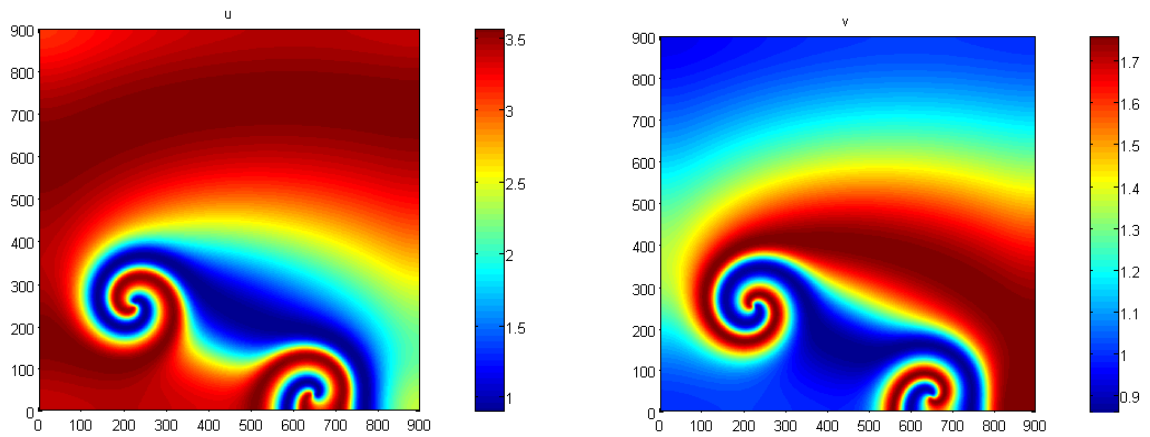
Fig. 5 Typical Turing patterns of prey [first column figures] and predator populations [second column figures] is plotted at fixed time $t=10000$, $\omega=0.377$ and $d_{12}=0.01$, $d_{22}=10$, $d_{21}=0.01*(1.5+\sin(\omega t))$ at the different values of diffusivity constant (a) $d_{11} = 0.05$, (b) 0.2 and (c) 0.3.



(a) $t=1000$



(b) $t=2000$



(c) $t=3000$

Fig. 6 Snapshots of prey [first column figures] and predator populations [second column figures] at time (a) $t=1000$, (b) $t=2000$ and (c) $t=3000$ with parameters given in eq. (36).

6 Discussion and Conclusions

In this paper, we have considered a spatial Holling –Tanner model for plankton-fish interaction with self and cross diffusion. We have studied the model system in both one and two dimensions with constant diffusivity and investigated their stability conditions. We have also analyzed the model with time- varying cross diffusivity both analytically and numerically. We have investigated the effect of critical wave length on the stability of plankton population. It has been observed that the non-trivial equilibrium state of the model system can be made globally asymptotically stable by increasing the self-diffusion coefficients to a sufficiently large value. It is also found that the solution of the spatial model converges faster to its equilibrium in case of two dimension case as compared to the one dimension case. In two dimension case, on increasing the value of self-diffusion coefficients, the irregular patterns, stationary strips-spots mixture patterns observed. As we increase the value of self-diffusion coefficients the number of spots in the strips-spots mixture pattern decreases and finally strip patterns prevail over the whole domain (see Fig. 4). For the sake of learning the wave pattern, we show the time evolution process of the pattern formation with a special initial condition and find wave pattern emerge. Our two-dimensional spatial pattern indicates the vital role of phase transient regimes in the spatiotemporal organization of the phytoplankton- zooplankton in the aquatic systems.

Diffusion of prey in the direction of lower concentration predator and the diffusion of predator in the direction of higher concentration of prey is common in nature for the survival of prey-predator species. But in real biological system, it has been observed that predator try to avoid the group defense by the large number of prey and chooses to catch its prey from a smaller group unable to sufficiently resist. Here we have considered the positive cross diffusions i.e., the movement of the species in the direction of lower concentration of another species that leads to uniform steady state unstable. It seems that cross-diffusion is able to generate many different kinds of spatiotemporal patterns. We observed that by increasing the coefficients of self diffusion the irregular pattern leads to stationary pattern. Therefore, we can predict that the interaction of self and cross-diffusion can be considered as an important mechanism for the appearance of complex spatiotemporal patterns in aquatic ecological model.

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Appendix A

Let

$$W_1 = \int_0^R W(P, H) dx,$$

where,

$$\text{where } W(P, H) = \int_{P^*}^P \frac{\xi - P^*}{\xi \phi(\xi)} d\xi + \omega \int_{H^*}^H \frac{\eta - P^*}{\eta} d\eta, \quad (\text{A1})$$

Differentiating W_1 with respect to time t along the solutions of system (4), we get

$$\frac{dW_1}{dt} = I_1 + I_2$$

where,

$$I_1 = \int_0^R \frac{dW}{dt} dx$$

$$I_2 = \int_0^R \left[\begin{aligned} & -d_{11} \left(\frac{P^* (P^2 + 3D^2) - 2D^2 P}{B_2 P^4} \right) \left(\frac{\partial P}{\partial x} \right)^2 - d_{22} \frac{\omega H^*}{H^2} \left(\frac{\partial H}{\partial x} \right)^2 + \\ & \left(-d_{12} \frac{P^* (P^2 + 3D^2) - 2D^2 P}{B_2 P^4} - d_{21} \frac{\omega H^*}{H^2} \right) \frac{\partial P}{\partial x} \frac{\partial H}{\partial x} \end{aligned} \right] dx$$

$$\Rightarrow \frac{dW_1}{dt} = \int_0^R \frac{dW}{dt} dx + \int_0^R \left[-\alpha_{11} \left(\frac{\partial P}{\partial x} \right)^2 + \alpha_{12} \frac{\partial P}{\partial x} \frac{\partial H}{\partial x} - \alpha_{22} \left(\frac{\partial H}{\partial x} \right)^2 \right] dx \tag{A2}$$

where, α_{ij} are defined in eq. (23).

From eq. (A2) we note that \dot{W}_1 is negative definite under the condition (24) that proves the theorem.

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