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DIFFUSIVE INSTABILITY IN A PREY-PREDATOR SYSTEM WITH TIME-DEPENDENT DIFFUSIVITY

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An ecological model for prey-predator planktonic species has been considered, in which the growth of prey has been assumed to follow a Holling type II function. The model consists of two reaction-diffusion equations and we extend it to time-varying diffusivity for plankton population. A comparative study of local stability in case of constant diffusivity and time varying diffusivity has been performed. It has been found that the system would be more stable with time varying diffusivity depending upon the values of system parameter.

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1. Introduction. In 1952, Turing [10] proposed a diffusion-reaction theory of morphogenesis on the basis of well-known laws of physical chemistry. This concept has been extended to develop the theory of biological pattern formation. In an ecological context, Segel and Jackson [8] were the first to apply Turing's model to predator-prey system. Since then, diffusive instability has been playing an important role in the study of ecosystem [4, 5, 6]. In the above-mentioned studies, the considered system parameters are all time-independent and the ratio of diffusivities of predator and prey beyond a critical value determines the diffusive instability of the system. In case of oceanic diffusion, the diffusivities can vary with time. Horizontal currents in the sea depend upon the depth of the sea. Due to the mixing process of these horizontal currents with the vertical currents, horizontal dispersion occurs [2]. As a result, the horizontal diffusivities of phytoplankton (prey) and zooplankton (predator) are not only to be different but also to vary with time [1].

In the present paper, we consider an ecological model for prey-predator, where the population size of prey is not very large. The growth of prey population is assumed to follow a Holling Type-II function. In this case, the diffusive instability of the system may occur and mortality resulting from intraspecies competition among prey is assumed to be negligible. In many real situations, due to severe intraspecies competition, the natural mortality of the predator may be ignored. We consider a basic prey-predator model, taking into account all the above situations with time-varying diffusivities and analyze its stability near equilibrium. We will also describe a general approach to

the amplitude equations for perturbations and relate this to Hill's equation. Section 5 presents the stability analysis of the amplitude equation for small values of a parameter representing a level of variation in diffusivity.

2. Model system : diffusive instability with constant diffusion coefficients. We consider a prey-predator system described by the system of equations (see [9])

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= N_1\left[\frac{\varepsilon N_1}{1+N_1} - N_2\right] + D_1\frac{\partial^2 N_1}{\partial x^2},\\ \frac{\partial N_2}{\partial t} &= N_2[N_1 - \gamma N_2] + D_2\frac{\partial^2 N_2}{\partial x^2},\end{aligned} \tag{2.1}$$

where $N_1(x,t)$ and $N_2(x,t)$ are the concentrations of prey and predator at a position x and at time t and D_1 and D_2 are their diffusion coefficients, respectively.

In the absence of diffusion, the prey-predator system has spatially uniform steady states given by

$$E_1 = (0,0), \qquad E_2 = \left(\varepsilon\gamma - 1, \frac{\varepsilon\gamma - 1}{\gamma}\right). \tag{2.2}$$

For the existence of the second stationary point, namely, E_2, we must have $\varepsilon\gamma > 1$ or $\gamma > 1/\varepsilon$.

We now consider the effect of small inhomogeneous perturbations of the steady state E_2. Let $x_1(x,t)$ and $x_2(x,t)$ be the perturbations such that

$$N_1(x,t) = {N_1}^* + x_1(x,t), \qquad N_2(x,t) = {N_2}^* + x_2(x,t). \tag{2.3}$$

Assuming x_1 and x_2 to be sufficiently small and linearizing (2.1) about E_2, we get

$$\begin{aligned}\frac{\partial x_1}{\partial t} &= a_{11}x_1 + a_{12}x_2 + D_1\frac{\partial^2 x_1}{\partial x^2},\\ \frac{\partial x_2}{\partial t} &= a_{21}x_1 + a_{22}x_2 + D_2\frac{\partial^2 x_2}{\partial x^2},\end{aligned} \tag{2.4}$$

where

$$a_{11} = \frac{\varepsilon\gamma - 1}{\varepsilon\gamma^2} \qquad a_{12} = 1 - \varepsilon\gamma \qquad a_{21} = \frac{\varepsilon\gamma - 1}{\gamma} \qquad a_{22} = 1 - \varepsilon\gamma. \tag{2.5}$$

In the absence of diffusion, the conditions for the stability of the system are (see [8])

$$a_{11} + a_{22} < 0, \qquad a_{11}a_{22} > a_{12}a_{21}. \tag{2.6}$$

Now, the first inequality in (2.6) implies that

$$\frac{\varepsilon\gamma - 1}{\varepsilon\gamma^2}(1 - \varepsilon\gamma^2) < 0 \tag{2.7}$$

or

$$\gamma > \frac{1}{\sqrt{\varepsilon}}. \tag{2.8}$$

But for the existence of E_2, we should have $\varepsilon\gamma > 1$ or

$$\gamma > \frac{1}{\varepsilon}. \tag{2.9}$$

Again for $\varepsilon < 1$,

$$\frac{1}{\varepsilon} > \frac{1}{\sqrt{\varepsilon}}. \tag{2.10}$$

Inequalities (2.9) and (2.10) together imply that for $\varepsilon < 1$,

$$\gamma > \frac{1}{\sqrt{\varepsilon}}. \tag{2.11}$$

Thus,

$$a_{11}a_{22} - a_{12}a_{21} = \frac{(\varepsilon\gamma - 1)^3}{\varepsilon\gamma^2} \tag{2.12}$$

is obviously positive as $\varepsilon\gamma > 1$.

Therefore, it follows that for $\varepsilon < 1$, the system will become stable. The system may be unstable for $\varepsilon > 1$.

We now consider the system with diffusion. We take the solution of the system in this case as

$$x_i(x,t) = \phi_i(t)\exp(ikx) \quad i = 1,2, \tag{2.13}$$

where k is the wave number. Let

$$\phi_i(t) = \alpha_i \exp\lambda t, \tag{2.14}$$

where λ is the growth rate of perturbation in time t and α_i is the amplitude at time t.

The characteristic equation of the system is

$$\lambda^2 + \{(D_1 + D_2)k^2 - (a_{11} + a_{22})\}\lambda + (a_{11} - k^2D_1)(a_{22} - k^2D_2) - a_{12}a_{21} = 0. \tag{2.15}$$

The system will not be stable if at least one of the roots of the above equation is positive, that is, the condition for diffusive instability is (see [3])

$$H = (a_{11} - k^2D_1)(a_{22} - k^2D_2) - a_{12}a_{21} < 0. \tag{2.16}$$

Now, H is a quadratic in k^2 and we suppose that D_1 and D_2 are constants. Then $H(k^2)$ has a minimum for the value ${k_m}^2 = k^2$, where

$$ {k_m}^2 = \frac{1}{2}\left[\frac{\varepsilon\gamma - 1}{\varepsilon\gamma^2}\left(\frac{1}{D_1} - \frac{\varepsilon\gamma^2}{D_2}\right)\right]. \tag{2.17} $$

Then the inequality $H({k_m}^2) < 0$ gives

$$ \left(D_2 + D_1\varepsilon\gamma^2\right)^2 > 4D_1D_2\varepsilon^2\gamma^3. \tag{2.18} $$

Thus $H({k_m}^2)$ will be negative when (2.18) is satisfied, and for the wave numbers close to ${k_m}^2$, the growth rate of perturbations λ can be positive. This criterion is equivalent to the dimensionless form

$$ \beta^{1/2} + p\beta^{-1/2} > 2(p+\xi)^{1/2} > 0, \tag{2.19} $$

where

$$ \beta = \frac{D_2}{D_1}, \qquad p = \frac{a_{22}}{a_{11}} = -\varepsilon\gamma^2, \qquad \xi = \varepsilon^2\gamma^3. \tag{2.20} $$

The second inequality in (2.19) is automatically satisfied as $\varepsilon\gamma^2(\varepsilon\gamma - 1) > 0$ is true from the condition of existence of the second stationary point E_2.

The first inequality in (2.19) gives the criterion of diffusive instability and from the first equation in (2.20), we get $D_2 = \beta D_1$. Therefore, (2.18) gives $(\beta + \varepsilon\gamma^2)^2 > 4\beta\varepsilon^2\gamma^3$ or

$$ \beta^2 + 2\beta\varepsilon\gamma^2(1 - 2\varepsilon\gamma) + \varepsilon^2\gamma^4 > 0. \tag{2.21} $$

Therefore, the critical values of β are given by

$$ \beta_{cr} = \varepsilon\gamma^2\left(2\varepsilon\gamma - 1 \pm \sqrt{4\varepsilon^2\gamma^2 - 4\varepsilon\gamma}\right). \tag{2.22} $$

So the diffusive system given by (2.1) will be stable if

$$ \varepsilon\gamma^2\left(2\varepsilon\gamma - 1 - \sqrt{4\varepsilon^2\gamma^2 - 4\varepsilon\gamma}\right) < \frac{D_2}{D_1} < \varepsilon\gamma^2\left(2\varepsilon\gamma - 1 + \sqrt{4\varepsilon^2\gamma^2 - 4\varepsilon\gamma}\right). \tag{2.23} $$

The condition for diffusive instability can also be written as

$$ \varepsilon^2(4\beta\gamma^3 - \gamma^4) - 2\beta\varepsilon\gamma^2 - \beta^2 < 0, \tag{2.24} $$

that is,

$$ \frac{\beta(1 - 2\gamma^{3/2})}{\gamma^2(4\beta - \gamma)} < \varepsilon < \frac{\beta(1 + 2\gamma^{3/2})}{\gamma^2(4\beta - \gamma)}. \tag{2.25} $$

3. Variable diffusivities and amplitude equations. To examine the stability of the uniform steady state to spatial and temporal perturbations in the presence of diffusion, we consider the system of (2.4) and define dimensionless time $\omega t = \tau$, where $\omega > 0$ is the frequency of variation in D_2. Here we consider D_1 as a constant and D_2 as a function of time. We now express the solutions of (2.4) in the form

$$x_1(t) = \phi_1(t)\exp(ikx), \qquad x_2(t) = \phi_2(t)\exp(ikx). \tag{3.1}$$

Then we obtain the system of equations for ϕ_i as

$$\begin{aligned} \frac{d\phi_1}{d\tau} &= (a_{11} - k^2 D_1)\omega^{-1}\phi_1 + a_{12}\omega^{-1}\phi_2, \\ \frac{d\phi_2}{d\tau} &= a_{21}\omega^{-1}\phi_1 + \{a_{22} - k^2 D_2(\tau)\}\omega^{-1}\phi_2. \end{aligned} \tag{3.2}$$

For simplicity, we consider the time-varying diffusivity D_2 in τ as

$$D_2(\tau) = D_1(\beta_1 + \alpha\sin\tau) > 0, \tag{3.3}$$

where $\beta_1 > 1$ and $\beta_1 > |\alpha|$.

The system of (3.2) can be rewritten as

$$\frac{d\phi_1}{d\tau} = \hat{a}_{11}\phi_1 + \hat{a}_{12}\phi_2, \qquad \frac{d\phi_2}{d\tau} = \hat{a}_{21}\phi_1 + \hat{a}_{22}\phi_2, \tag{3.4}$$

where

$$\begin{aligned} &\hat{a}_{11} = \frac{a_{11} - k^2 D_1}{\omega}, \qquad \hat{a}_{12} = \frac{a_{12}}{\omega}, \qquad \hat{a}_{21} = \frac{a_{21}}{\omega}, \\ &\hat{a}_{22} = \hat{a}_{22}^* - \frac{k^2 D_1 \alpha \sin\tau}{\omega} \quad \text{with } \hat{a}_{22}^* = \frac{a_{22} - k^2 D_1 \beta_1}{\omega}. \end{aligned} \tag{3.5}$$

As a reference state we take $\alpha = 0$, that is, the case with constant diffusivities.

We have already seen that the criterion for diffusive instability with constant diffusion coefficient is $(\beta_1 + \varepsilon\gamma^2)^2 > 4\beta_1\varepsilon^2\gamma^2$.

In this case, the critical values of β_1 are

$$\beta_{cr} = \varepsilon\gamma^2\left(2\varepsilon\gamma - 1 \pm \sqrt{4\varepsilon^2\gamma^2 - 4\varepsilon\gamma}\right), \tag{3.6}$$

and the corresponding critical wave number k_{cr} for the first perturbation to grow is found by evaluating k_m from (2.17), considering $D_2 = \beta_1 D_1$ at $\beta_1 = \beta_{cr}$. This critical value of β_1 identifies the stable and unstable regions of the diffusive system (2.1).

We are now interested in finding the diffusive instability regions in the system of variable diffusivities and comparing the result with the reference system of constant diffusivities.

Substituting the first equation in (3.4) into the second equation and considering the transformation

$$\psi_1 = \exp\left[-\frac{1}{2}\int\{\hat{a}_{11}+\hat{a}_{22}(\tau)\}d\tau\right]\phi_1, \tag{3.7}$$

we get

$$\frac{d^2\psi_1}{d\tau^2}+Q(\tau)\psi_1=0, \tag{3.8}$$

where

$$Q(\tau)=\frac{1}{2}\frac{d}{d\tau}(\hat{a}_{22})-\frac{1}{4}\{\hat{a}_{11}+\hat{a}_{22}(\tau)\}^2+\{\hat{a}_{11}\hat{a}_{22}(\tau)-\hat{a}_{12}\hat{a}_{21}\}. \tag{3.9}$$

Equation (3.8) is the standard form of Hill's equation [7].

Substituting the values of $\hat{a}_{11}$, $\hat{a}_{12}$, $\hat{a}_{21}$, and $\hat{a}_{22}$ into (3.8), we get

$$\begin{aligned}\frac{d^2\psi_1}{dy^2}+[\delta+\eta\{-2\cos 2y+(2\omega)^{-1}(a_{22}-a_{11}-k^2D_1(\beta_1-1))\sin 2y\}\\ +2\eta^2\cos 4y]\psi_1=0,\end{aligned} \tag{3.10}$$

where

$$\begin{aligned}\delta=(2\omega)^{-2}\Big[2k^2D_1\Big\{(a_{22}-a_{11})(\beta_1-1)-\frac{1}{2}k^2D_1(2(\beta_1-1)^2+\alpha^2)\Big\}\\ -(a_{11}+a_{22})^2+4(a_{11}a_{22}-a_{12}a_{21})\Big],\end{aligned} \tag{3.11}$$

$$\eta=\frac{\alpha k^2D_1}{4\omega},\qquad \tau=2y.$$

The solution of (3.4) can then be written as

$$\phi_1=\exp[(2\omega)^{-1}\{(a_{11}-k^2D_1+a_{22}-k^2D_1\beta_1)\tau+k^2D_1\alpha\cos\tau\}]\psi_1. \tag{3.12}$$

4. Linear stability for small variation in diffusion coefficient. We now study the linear stability of the system when the amplitude α of the variability in D_2 is small. For this, we first set $\beta_1=\beta_{cr}$ and $k_m=k_{cr}$ for marginal stability in the reference state and analyze the linear stability of the system when a small variation in D_2 is introduced. Equation (3.10) is then reduced to

$$\frac{d^2\psi_1}{dy^2}+\{\delta+\eta(-2\cos 2y+2m\sin 2y)\}\psi_1=0, \tag{4.1}$$

where

$$\begin{aligned}\delta&=-(\hat{a}_{11}+\hat{a}^*_{22})^2+4(\hat{a}_{11}\hat{a}^*_{22}-\hat{a}_{12}\hat{a}_{21}),\\ \eta&=\frac{{k_c}^2D_1\alpha}{\omega}\ll 1,\qquad m=\hat{a}^*_{22}-\hat{a}_{11}.\end{aligned} \tag{4.2}$$

The inequality in (4.2) holds since α is very small.

We seek a straightforward expansion for the solution of (4.1) in power series of η in the form of (see [7])

$$\psi_1(\gamma;\eta) = \psi_{10}(\gamma) + \eta\psi_{11}(\gamma) + \eta^2\psi_{12}(\gamma) + \cdots. \tag{4.3}$$

Since $\eta \ll 1$, we have

$$\psi_1(\gamma;\eta) = \psi_{10}(\gamma) + \eta\psi_{11}(\gamma). \tag{4.4}$$

Substituting from (4.4) in (4.1) and equating coefficients of like powers of η, we have

$$\ddot{\psi}_{10} + \delta\psi_{10} = 0, \tag{4.5}$$

$$\ddot{\psi}_{11} + \delta\psi_{11} - 2\psi_{10}\cos 2\gamma + 2m\psi_{10}\sin 2\gamma = 0. \tag{4.6}$$

When $\delta > 0$, say $\delta = r^2$, the solution of (4.5) can be written as

$$\psi_{10} = A\cos(r\gamma + B), \tag{4.7}$$

where A and B are constant.

Substituting from (4.7) in (4.6) and disregarding the homogeneous solution, we may write

$$\begin{aligned}\psi_{11} = \frac{A}{4}\Bigg[&-\frac{\cos(r\gamma + 2\gamma + B)}{(r+1)} + \frac{\cos(r\gamma - 2\gamma + B)}{(r-1)} \\ &-\frac{m\sin(r\gamma + 2\gamma + B)}{(r+1)} + \frac{m\sin(r\gamma - 2\gamma + B)}{(r-1)}\Bigg].\end{aligned} \tag{4.8}$$

Therefore, the solution of the first equation in (3.4) is

$$\phi_1 = \left[\exp\left\{(\hat{a}_{11} + \hat{a}_{22}^*)\gamma + \frac{1}{2}\frac{k^2 D_1\alpha}{\omega}\cos 2\gamma\right\}\right](\psi_{10} + \eta\psi_{11}). \tag{4.9}$$

Now, $(\hat{a}_{11} + \hat{a}_{22}^*) < 0$ for $\varepsilon < 1$ and consequently ϕ_1 tends to zero when γ, as well as τ, tends to infinity. Therefore, for $\delta > 0$ and $\varepsilon < 1$, the diffusive system will be asymptotically stable.

When $\delta < 0$, say $\delta = -\theta^2$, the solution of (4.5) can be written as

$$\psi_{10} = A_1\exp(\theta\gamma) + B_1\exp(-\theta\gamma), \tag{4.10}$$

where A_1 and B_1 are constants.

Consequently,

$$\begin{aligned}\psi_1 = {} & A_1 e^{\theta\gamma}\left[1 + \frac{\eta}{2(\theta^2+1)}\{\theta\sin 2\gamma - \cos 2\gamma - m\theta\cos 2\gamma - m\sin 2\gamma\}\right] \\ & + B_1 e^{-\theta\gamma}\left[1 + \frac{\eta}{2(\theta^2+1)}\{m\theta\cos 2\gamma - m\sin 2\gamma - \theta\sin 2\gamma - \cos 2\gamma\}\right].\end{aligned} \tag{4.11}$$

Therefore,

$$\phi_1 = \left[\exp\left\{(\hat{a}_{11}+\hat{a}_{22}^*)\gamma + \frac{1}{2}\frac{k^2 D_1 \alpha}{\omega}\cos 2\gamma\right\}\right](\psi_{10}+\eta\psi_{11}). \tag{4.12}$$

If

$$\left[\hat{a}_{11}+\hat{a}_{22}^* + \sqrt{(\hat{a}_{11}-\hat{a}_{22}^*)^2 + 4\hat{a}_{12}\hat{a}_{21}}\right] < 0, \tag{4.13}$$

then the solution ϕ_1 will be asymptotically stable. This condition can be reduced to $\hat{a}_{11}\hat{a}_{22}^* > \hat{a}_{12}\hat{a}_{21}$, that is,

$$\frac{(\varepsilon\gamma-1)^3}{\varepsilon\gamma^2} + k^2 D_1\left[k^2 D_1\beta_1 + (\varepsilon\gamma-1)\left(\frac{\varepsilon\gamma^2-\beta_1}{\varepsilon\gamma^2}\right)\right] > 0. \tag{4.14}$$

Inequality (4.14) will be satisfied if $\varepsilon\gamma^2 > \beta_1$ or

$$\frac{(\varepsilon\gamma-1)^3}{\varepsilon\gamma^2} + k^4 D_1^2\beta_1 > k^2 D_1\left(\frac{\varepsilon\gamma-1}{\varepsilon\gamma^2}\right)(\beta_1-\varepsilon\gamma^2). \tag{4.15}$$

Therefore, for $\delta < 0$ and $\varepsilon > \beta_1/\gamma^2$, ϕ_1 will be asymptotically stable.

From the analysis of Section 2, we have the condition of stability for constant diffusivity as

$$\varepsilon\gamma^2\left(2\varepsilon\gamma-1-\sqrt{(2\varepsilon\gamma-1)^2-1}\right) < \beta < \varepsilon\gamma^2\left(2\varepsilon\gamma-1+\sqrt{(2\varepsilon\gamma-1)^2-1}\right). \tag{4.16}$$

Thus, the length of the interval of β for the stability of the system is $[2\varepsilon\gamma^2\sqrt{(2\varepsilon\gamma-1)^2-1}]$.

In this section, we see that the stability criterion for variable diffusivity is $0 < \beta_1 < \varepsilon\gamma^2$, where $\varepsilon < 1$. Therefore, in this case, the length of the interval of β_1 for which stability occurs is $\varepsilon\gamma^2$. So, if $2\sqrt{(2\varepsilon\gamma-1)^2-1} < 1$ or $\varepsilon\gamma < 1.06$ (approximately), then the system will become more stable under variable diffusivity than under constant diffusivity.

5. Conclusion. In the present paper, we have considered a model of prey-predator ecosystem where the growth of prey is not directly proportional to the existing prey population and it is described by a Holling type II function. The stability analysis of the system reveals that the system without diffusion is stable when $\varepsilon < 1$, that is, the growth rate of prey is small. We have then studied the diffusive instability of the system with constant diffusion coefficient. From these studies, it follows that diffusive instability will certainly develop when

$$(D_2 + D_1\varepsilon\gamma^2)^2 > 4D_1D_2\varepsilon^2\gamma^3. \tag{5.1}$$

This condition will be satisfied when $D_2/D_1 \gg 1$. Hence, for diffusive instability of the system, the mobility of predator should be much higher than that of the prey.

When the diffusivity of the predator is driven by time-varying diffusion coefficients, the stability criterion of the system is changed. In this case, we see that, for $\varepsilon < 1$, the system will become asymptotically stable if $0 < \beta_1 < \varepsilon\gamma^2$. We also observe that, depending upon the values of ε and γ, that is, the growth rate of the prey and the competition rate of the predator, the system will become more stable with time-varying diffusivity than with constant diffusivity. If $\varepsilon\gamma < 1.06$ (approximately), then the system with varying diffusivity will be more stable.

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