Habitat Complexity, Stochasticity and the Stability of Predator-Prey Interactions

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Abstract- **Numerous theoretical studies on predator-prey dynamics have been studied where the habitat is free of complexity. But empirical and experimental results suggest that habitat complexity plays significant role in the predator-prey dynamics. On the other hand, most of the theoretical models in ecology are studied under unvarying deterministic environment though the characterizing parameters of real environments exhibit random fluctuations. In this paper, we study a colour noise-induced predator-prey system where the interaction between prey and predator occurs in a habitat with structural complexity. Spectral density analysis indicates that the system is stochastically stable and lies within the tolerance interval at the intermediate degree of habitat complexity. The qualitative behaviors of the model system have been demonstrated with the data of Paramecium aurelia (prey) and Didinium nasutum (predator) interaction.**

Keywords- Habitat Complexity; Stochasticity; Colour Noise; Stability; Predator-Prey Interactions

I. INTRODUCTION

Theoretical works generally assume that interaction between prey and predator occurs in a habitat where no complexity is present [1]. However, no natural habitat (aquatic or terrestrial) is truly free of complexity. Aquatic habitat, for example, becomes structurally complex in presence of submerged vegetation or aquatic weeds. It is well established that habitat complexity reduces the predation rate [2, 3, 4] and the hypothesis is that there exists an inverse relationship between predation rate and degree of habitat complexity [5]. Therefore, it is important to incorporate the effect of habitat complexity when predator-prey interaction is studied by means of theoretical models. The most commonly mathematical expression used to represent the interaction between a prey and predator (known as predator's response function) is Holling Type II [6]. It is shown in [7] that the Type II response function,

given by $\dfrac{\alpha x}{1 + \alpha h x}$, can be modified to $\dfrac{\alpha(1-c)x}{1 + \alpha(1-c)hx}$,

where x is the prey density, α is the attack coefficient, h is the handling time and c (0 < c <1) measures the degree or strength of habitat complexity. For example, c = 0.30 implies that predator-prey interaction will be reduced by 30% due to the complexity of habitat. If c=0 then it will be the Holling Type II response function.

Most of the models proposed and studied in the ecological literature work within the framework of an unvarying deterministic environment. This means that present state of a population is uniquely determined by parameters in the model and by sets of previous states of these populations. Therefore, deterministic models always perform in the same way for a given set of initial conditions. However, the parameters characterizing real environment exhibit random fluctuations. That means, real environments are uncertain or stochastic. Due to these reasons, most natural phenomena do not follow strictly deterministic laws, rather oscillate randomly about some average so that the deterministic equilibrium is not an absolutely fixed state; instead it is a 'fuzzy' value around which the biological system fluctuates [8]. In models of biological systems, fluctuations or an external random force is typically approximated by delta-correlated random process or white noise which has a finite radius of correlation [9, 10, 11]. This is explained by the comparative mathematical simplicity of such processes. However, for most of the biological systems, white noise is not an accurate approximation of the actual fluctuations or randomness present in the system. In these cases, colour noise provides a more accurate description. In this paper, we study a colour noise-induced predator-prey model with habitat complexity. To take into account the effect of fluctuating environment, we consider perturbations in the prey's reproductive factor and predator's mortality factor in the form of colour noises [12, 13]. The study is based on the spectral density technique developed by Pugachev [14].

The organization of this chapter is as follows. Section II deals with the stochastic model formulation. Spectral density functions are deduced in Section III. Section IV deals with non-equilibrium fluctuations and stability. Solution of the noise-induced linearized system is given in Section V. Numerical study is performed in Section VI and a brief discussion is presented in Section VII.

II. THE STOCHASTIC MODEL

Assume that the prey population (x) grows logistically to environmental carrying capacity k in absence of predator (y) with intrinsic birth rate constant r. Let d be the food-independent death rate and θ be the conversion efficiency of the predator. Assume that the interaction between prey and predator occurs in a homogeneously complex habitat following modified Type II response function. Under these

assumptions, the prey-predator dynamics can be represented by the following couple of differential equations:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - \frac{\alpha(1-c)xy}{1+\alpha(1-c)hx},$$

$$\frac{dy}{dt} = \frac{\theta\alpha(1-c)xy}{1+\alpha h(1-c)x} - dy. \tag{1}$$

The coexistence equilibrium of the System (1) is given by $E^*(x^*, y^*)$ with equilibrium prey and predator densities

$$x^* = \frac{d}{\alpha(1-c)(\theta - hd)} \qquad \&$$

$$y^* = \frac{r(k-x^*)\{1+\alpha h(1-c)x^*\}}{\alpha k(1-c)} \quad, \quad \text{respectively. This}$$

equilibrium will be biologically meaningful if

$$(i)\ \ c < c_1\ \ \&$$

$$(ii)\ \ \theta > hd + \frac{d}{\alpha k},$$

where $c_1 = 1 - \dfrac{d}{\alpha k(\theta - hd)}$.

The System (1) is locally asymptotically stable around the equilibrium $E^*(x^*, y^*)$ if [6]

$$(i)\ \ \alpha > \frac{1}{kh}\left(\frac{1+hd}{1-hd}\right),$$

$$(ii)\ \ \frac{hd(1+\alpha kh)}{\alpha kh - 1} < \theta < 1, \tag{2}$$

$$(iii)\ \ c_2 < c < c_1$$

and unstable if $c < c_2$. A Hopf bifurcation exists at $c = c_2$ where $c_2 = 1 - \dfrac{\theta + hd}{\alpha kh(\theta - hd)}$. Assume that fluctuations in the environment will manifest mainly as fluctuations in the birth rate of prey and in the mortality rate of predator. Under these assumptions, the stochastic counterpart of the deterministic model System (1) will take the following form:

$$\frac{dx}{dt} = x\left(r + \eta_1(t) - \frac{rx}{k}\right) - \frac{\alpha(1-c)xy}{1+\alpha(1-c)hx},$$

$$\frac{dy}{dt} = \frac{\theta\alpha(1-c)xy}{1+\alpha(1-c)hx} + (-d + \eta_2(t))y. \tag{3}$$

Here the perturbed terms $\eta_j(t)$ $(j=1, 2)$ are uncorrelated colour noises and follow the Ornstein-Uhlenbeck process [15] which are more realistic noise than Gaussian white noise.

The mathematical expectation and correlation functions of the process $\eta_j(t)$ $(j=1, 2)$ are given by :

$$\langle \eta_j(t) \rangle = 0$$
$$\&$$
$$\langle \eta_j(t_1)\eta_j(t_2) \rangle = \varepsilon_j \delta_j \exp(-\delta_j |t_1 - t_2|), (j=1,2) \tag{4}$$

where $\varepsilon_j, \delta_j^{-1} > 0$ are, respectively, the intensity and the correlation time of the noise $\eta_j(t)$ and ‹.› represents the average over the ensemble of the stochastic process. $\eta_j(t)$ are the solutions of the stochastic differential equation

$$\frac{d\eta_j}{dt} = -\delta_j \eta_j + \delta_j \sqrt{2\varepsilon_j} \frac{d\omega_j}{dt}, \tag{5}$$

where $\xi_j(t) = \dfrac{d\omega_j}{dt}$ are independent standard zero mean Gaussian white noises characterized by :

$$\langle \xi_j(t) \rangle = 0$$
$$\&$$
$$\langle \xi_j(t_1)\xi_j(t_2) \rangle = \delta(t_1 - t_2), \ \ j = 1, 2 \tag{6}$$

where $\delta(t)$ denotes the Dirac delta function [16].

III. DEDUCTION OF SPECTRAL DENSITY FUNCTION

Substituting $X = \log x$ and $Y = \log y$ in Equation (3) and using the transformation $u = X - X^*$ and $v = Y - Y^*$, where $(X^*, Y^*) = (\log x^*, \log y^*)$ and (x^*, y^*) is the coexistence equilibrium of the System (1), we obtain the linearized system as

$$\frac{du}{dt} = -\gamma_1 u - \beta_1 v + \eta_1(t),$$

$$\frac{dv}{dt} = \beta_2 u + \eta_2(t), \tag{7}$$

where

$$\gamma_1 = \frac{rdh}{\theta(1-c)}\left[c - \left\{1 - \frac{\theta + hd}{\alpha kh(\theta - hd)}\right\}\right],$$

$$\beta_1 = \frac{rk}{(1-c)}\left[\left\{1 - \frac{d}{\alpha k(\theta - hd)}\right\} - c\right], \tag{8}$$

$$\& \ \beta_2 = \frac{d(\theta - hd)}{\theta}.$$

It is to be noted that γ_1, β_1 and β_2 are all positive following the deterministic stability Conditions (2).

By eliminating v from the first equation of (7) and u from the second equation of (7), we get

$$\frac{d^2u}{dt^2} + \gamma_1 \frac{du}{dt} + \beta_1\beta_2 u = F_1(t),$$

$$\frac{d^2v}{dt^2} + \gamma_1 \frac{dv}{dt} + \beta_1\beta_2 v = F_2(t), \tag{9}$$

where,

$$F_1(t) = -\delta_1 \eta_1(t) + \delta_1\sqrt{2\varepsilon_1}\xi_1(t) - \beta_1\eta_2(t),$$
$$F_2(t) = (\gamma_1 - \delta_2)\eta_2(t) + \delta_2\sqrt{2\varepsilon_2}\xi_2(t) + \beta_2\eta_1(t). \tag{10}$$

Here it is assumed that

$$\gamma_1 < 2\sqrt{\beta_1\beta_2}. \tag{11}$$

Since η_1 and η_2 are independent, the correlation function K_{F_1} of the driving force $F_1(t)$ is given by

$$K_{F_1}(t_1 - t_2) = \langle (F_1(t_1) - \langle F_1(t_1)\rangle)(F_1(t_2) - \langle F_1(t_2)\rangle)\rangle$$
$$= \langle F_1(t_1)F_1(t_2)\rangle \quad (\because \langle F_1(t)\rangle = 0)$$
$$= \delta_1^2\langle \eta_1(t_1)\eta_1(t_2)\rangle + 2\delta_1^2\varepsilon_1\langle \xi_1(t_1)\xi_1(t_2)\rangle$$
$$+ \beta_1^2\langle \eta_2(t_1)\eta_2(t_2)\rangle - \delta_1^2\sqrt{2\varepsilon_1}\{\langle \eta_1(t_1)\xi_1(t_2)\rangle$$
$$+ \langle \eta_1(t_2)\xi_1(t_1)\rangle\}. \tag{12}$$

From Equation (5),

$$\frac{d\eta_1}{dt} = -\delta_1\eta_1(t) + \delta_1\sqrt{2\varepsilon_1}\xi_1(t),$$
$$\langle \xi_1(t)\rangle = 0 \ \& \ \langle \xi_1(t_1)\xi_1(t_2)\rangle = \delta(t_1 - t_2).$$

Therefore, the correlation function K_Y of the random function $Y(t) = \frac{d\eta_1}{dt}$ is given by,

$$K_Y(\mu) = \langle Y(t_1)Y(t_2)\rangle \ (\because \langle Y(t)\rangle = 0)$$
$$= \varepsilon_1\delta_1^3 e^{-\delta|\mu|} + 2\delta_1^2\varepsilon_1\delta(\mu)$$
$$- \delta_1^2\sqrt{2\varepsilon_1}\{\langle \eta_1(t_1)\xi_1(t_2)\rangle$$
$$+ \langle \eta_1(t_2)\xi_1(t_1)\rangle\}, \ (\mu = t_1 - t_2). \tag{13}$$

Again,

$$K_Y(\mu) = -\varepsilon_1\delta_1\frac{d^2}{d\mu^2}\exp(-\delta_1|\mu|)$$
$$= \varepsilon_1\delta_1^2\exp(-\delta_1|\mu|)\left[\frac{d^2}{d\mu^2}|\mu| - \delta_1(\frac{d}{d\mu}|\mu|^2)\right] \tag{14}$$
$$= \varepsilon_1\delta_1^2\exp(-\delta_1|\mu|)\left[2\delta(\mu) - \delta_1(\mathrm{sign}\,\mu)\right],$$

where

$$\mathrm{sign}\,\mu = \begin{cases} 1, & \text{for } \mu > 0 \\ 0, & \text{for } \mu = 0 \\ -1, & \text{for } \mu < 0. \end{cases} \tag{15}$$

Combining (13) and (14), we get

$$\sqrt{2\varepsilon_1}\{\langle \eta_1(t_1)\xi_1(t_2)\rangle + \langle \eta_1(t_2)\xi_1(t_1)\rangle\}$$
$$= \varepsilon_1[\delta_1\exp(-\delta_1|\mu|)$$
$$+ 2\delta(\mu) + \exp(-\delta_1|\mu|)\{\delta_1(\mathrm{sign}\,\mu)^2 - 2\delta(\mu)\}]. \tag{16}$$

From Equations (4), (6), (12) and (16), we have

$$K_{F_1}(\mu) = \delta_1^3\varepsilon_1\exp(-\delta_1|\mu|) + 2\delta_1^2\varepsilon_1\delta(\mu)$$
$$+ \beta_1^2\varepsilon_2\delta_2\exp(-\delta_2|\mu|)$$
$$- \delta_1^2\varepsilon_1[\delta_1\exp(-\delta_1|\mu|) + 2\delta(\mu)$$
$$+ \exp(-\delta_1|\mu|)\{\delta_1(\mathrm{sign}\,\mu)^2 - 2\delta(\mu)\}]. \tag{17}$$

Similarly, the correlation function K_{F_2} of the driving force $F_2(t)$ is given by

$$K_{F_2}(\mu) = (\gamma_1 - \delta_2)^2\delta_2\varepsilon_2\exp(-\delta_2|\mu|)$$
$$+ 2\delta_2^2\varepsilon_2\delta(\mu) + \beta_2^2\varepsilon_1\delta_1\exp(-\delta_1|\mu|)$$
$$+ (\gamma_1 - \delta_2)^2\delta_2\varepsilon_2[\delta_2\exp(-\delta_2|\mu|)$$
$$+ 2\delta(\mu) + \exp(-\delta_2|\mu|)\{\delta_2(\mathrm{sign}\,\mu)^2 - 2\delta(\mu)\}]. \tag{18}$$

The spectral density function of $F_1(t)$ is given by (after some simplification) :

$$S_{F_1}(\omega) = \frac{1}{2\pi}\int_{-\infty}^{\infty} K_{F_1}(\mu)e^{-i\omega\mu}d\mu \quad (i = \sqrt{-1})$$
$$= \frac{1}{\pi}\left[\frac{\varepsilon_1\delta_1^2\omega^2}{\omega^2 + \delta_1^2} + \frac{\beta_1^2\delta_2^2\varepsilon_2}{\omega^2 + \delta_2^2}\right]. \tag{19}$$

Similarly, the spectral density function of $F_2(t)$ is given by :

$$S_{F_2}(\omega) = \frac{1}{2\pi}\int_{-\infty}^{\infty} K_{F_2}(\mu)e^{-i\omega\mu}d\mu \quad (i = \sqrt{-1})$$
$$= \frac{1}{\pi}\left[\frac{\varepsilon_2\delta_2^2(\omega^2 + \gamma_1^2)}{\omega^2 + \delta_2^2} + \frac{\beta_2^2\delta_1^2\varepsilon_1}{\omega^2 + \delta_1^2}\right]. \tag{20}$$

IV. NON-EQUILIBRIUM FLUCTUATION AND STABILITY

The mean square deviation of u and v at any arbitrary instant t satisfying the stochastic differential Equation (9) are given by

$$D_u(t) = \int_{-\infty}^{\infty} S_{F_1}(\omega)|y(t,\omega)|^2 d\omega,$$
$$D_v(t) = \int_{-\infty}^{\infty} S_{F_2}(\omega)|y(t,\omega)|^2 d\omega, \tag{21}$$

where $y(t,\omega)$ is the coordinate function which is given by the solution of Equation (10) with $F_j(t) = e^{i\omega t}$, $(j=1, 2)$, $u(t) = v(t)$ and $y(0,\omega) = 0$. Therefore,

$$y(t,\omega) = \frac{e^{i\omega t}}{\beta_1\beta_2 + i\gamma_1\omega - \omega^2}$$
$$+ \frac{(\lambda_2 - i\omega)e^{\lambda_1 t} - (\lambda_1 - i\omega)e^{\lambda_2 t}}{(\lambda_1 - \lambda_2)(\beta_1\beta_2 + i\gamma_1\omega - \omega^2)}, \tag{22}$$

where

$$\lambda_1 = -\frac{\gamma_1}{2} + i\gamma, \ \lambda_2 = -\frac{\gamma_1}{2} - i\gamma$$
$$\& \ \gamma = \frac{1}{2}\sqrt{4\beta_1\beta_2 - \gamma_1^2}. \tag{23}$$

Thus,

$$D_u(t) = \frac{\varepsilon_1\delta_1^2}{\pi}\left\{\int_{-\infty}^{\infty}|y(t,\omega)|^2 d\omega\right.$$
$$\left. -\delta_1^2\int_{-\infty}^{\infty}\frac{|y(t,\omega)|^2}{\omega^2 + \delta_1^2}d\omega\right\}$$
$$+ \frac{2\beta_1^2\delta_2^2\varepsilon_2}{\pi}\int_{-\infty}^{\infty}\frac{|y(t,\omega)|^2}{\omega^2 + \delta_2^2}d\omega \tag{24}$$

and

$$D_v(t) = \frac{\varepsilon_2\delta_2^2}{\pi}\left\{\int_{-\infty}^{\infty}|y(t,\omega)|^2 d\omega\right.$$
$$\left. + (\gamma_1^2 - \delta_2^2)\int_{-\infty}^{\infty}\frac{|y(t,\omega)|^2}{\omega^2 + \delta_2^2}d\omega\right\}$$
$$+ \frac{2\beta_2^2\delta_1^2\varepsilon_1}{\pi}\int_{-\infty}^{\infty}\frac{|y(t,\omega)|^2}{\omega^2 + \delta_1^2}d\omega. \tag{25}$$

After some simplification [23], it is obtained

$$D_u(t) = -\varepsilon_1 \delta_1^4 A_1(t) + \varepsilon_1 \delta_1^2 B(t) + 2\beta_1^2 \delta_2^2 \varepsilon_2 A_2(t), \quad (26)$$

and

$$D_v(t) = \varepsilon_2 \delta_2^2 (\gamma_1^2 - \delta_2^2) A_2(t) \\ + \varepsilon_2 \delta_2^2 B(t) + 2\beta_2^2 \delta_1^2 \varepsilon_1 A_1(t). \quad (27)$$

Here,

$$A_j(t) = \frac{1}{\gamma_1} \left[\frac{\delta_j + \gamma_1}{\delta_j \beta_1 \beta_2 (\delta_j^2 + \gamma_1 \delta_j + \beta_1 \beta_2)} \right. \\
\times \left\{ 1 + \left(\frac{\gamma_1}{2\gamma} \sin \gamma t + \cos \gamma t \right)^2 e^{-\gamma_1 t} \right\} \\
- 2 \left(\frac{\gamma_1}{2\gamma} \sin \gamma t + \cos \gamma t \right) e^{-\left(\frac{\gamma_1}{2}\right)t} (\beta_1 \beta_2 - \gamma_1 \delta_j + \delta_j^2)^{-1} \\
\times (\beta_1 \beta_2 + \gamma_1 \delta_j + \delta_j^2)^{-1} \left\{ \frac{\gamma_1}{\delta_j} e^{-\delta_j t} - \frac{2\sqrt{\beta_1 \beta_2}}{\sqrt{4\beta_1 \beta_2 - \gamma_1^2}} \right. \\
\times \exp\left(-t\sqrt{\beta_1 \beta_2} \cos\phi\right) \sin\left(\phi - t\sqrt{\beta_1 \beta_2} \sin\phi\right) \\
+ \frac{2(2\beta_1 \beta_2 - \gamma_1^2 + \delta_j^2)}{\sqrt{\beta_1 \beta_2 (4\beta_1 \beta_2 - \gamma_1^2)}} \\
\left. \times \exp\left(-t\sqrt{\beta_1 \beta_2} \cos\phi\right) \sin\left(\phi - t\sqrt{\beta_1 \beta_2} \sin\phi\right) \right\} \\
- \frac{2}{\gamma} e^{-\left(\frac{\gamma_1}{2}\right)t} (\beta_1 \beta_2 - \gamma_1 \delta_j + \delta_j^2)^{-1} (\beta_1 \beta_2 + \gamma_1 \delta_j + \delta_j^2)^{-1} \sin \gamma t \\
\times \left\{ \gamma_1 e^{-\delta_j t} - \frac{2\beta_1 \beta_2}{\sqrt{4\beta_1 \beta_2 - \gamma_1^2}} \right. \\
\times \exp\left(-t\sqrt{\beta_1 \beta_2} \cos\phi\right) \sin\left(\phi - t\sqrt{\beta_1 \beta_2} \sin\phi\right) \\
+ \frac{2(2\beta_1 \beta_2 - \gamma_1^2 + \delta_j)}{\sqrt{4\beta_1 \beta_2 - \gamma_1^2}} \\
\left. \times \exp\left(-t\sqrt{\beta_1 \beta_2} \cos\phi\right) \sin\left(\phi - t\sqrt{\beta_1 \beta_2} \sin\phi\right) \right\} \\
\left. + \frac{e^{-\gamma_1 t} \sin^2 \gamma t}{(\beta_1 \beta_2 + \gamma_1 \delta_j + \delta_j^2)} \right], \quad (j = 1, 2) \quad (28)$$

$$B(t) = \frac{1}{\beta_1 \beta_2 \gamma_1} \left\{ 1 + \left(\frac{\gamma_1}{2\gamma} \sin \gamma t + \cos \gamma t \right)^2 e^{-\gamma_1 t} \right\} \\
- 2 \left(\frac{\gamma_1}{2\gamma} \sin \gamma t + \cos \gamma t \right) e^{-\left(\frac{\gamma_1}{2}\right)t} \\
\times \exp\left(-t\sqrt{\beta_1 \beta_2} \cos\phi\right) \frac{\sin\left(\phi + t\sqrt{\beta_1 \beta_2} \sin\phi\right)}{(\beta_1 \beta_2)^{\frac{3}{2}} \sin 2\phi}$$

$$- \frac{2}{\beta_1 \beta_2 \gamma} e^{-\left(\frac{\gamma_1}{2}\right)t} \sin \gamma t \, \exp\left(-t\beta_1 \beta_2 \cos\phi\right) \frac{\sin\left(t\sqrt{\beta_1 \beta_2} \sin\phi\right)}{\sin 2\phi} \\
\times \frac{\sin\left(t\sqrt{\beta_1 \beta_2} \sin\phi\right)}{\sin 2\phi} + \frac{1}{\gamma_1 \gamma^2} e^{-\left(\frac{\gamma_1}{2}\right)t} \sin^2 \gamma t$$

$$(29)$$

and

$$\cos 2\phi = \frac{\gamma_1^2 - 2\beta_1 \beta_2}{2\beta_1 \beta_2}, \quad |\phi| < \frac{\pi}{2}. \quad (30)$$

Now as $t \to \infty$, $D_u(t) \to D_u(\infty)$ and $D_v(t) \to D_v(\infty)$, ($\because \gamma_1 > 0$), where

$$D_u(\infty) = \frac{\varepsilon_1 \delta_1^2}{\gamma_1 (\delta_1^2 + \gamma_1 \delta_1 + \beta_1 \beta_2)} \\
+ \frac{2\beta_1 \delta_2 \varepsilon_2 (\delta_2 + \gamma_1)}{\beta_2 \gamma_1 (\delta_2^2 + \gamma_1 \delta_2 + \beta_1 \beta_2)} \quad (31)$$

and

$$D_v(\infty) = \frac{\varepsilon_2 \delta_2 \{\gamma_1^2 (\delta_2 + \gamma_1) + \beta_1 \beta_2 \delta_2\}}{\beta_1 \beta_2 \gamma_1 (\delta_2^2 + \gamma_1 \delta_2 + \beta_1 \beta_2)} \\
+ \frac{2\beta_2 \delta_1 \varepsilon_1 (\delta_1 + \gamma_1)}{\beta_1 \gamma_1 (\delta_1^2 + \gamma_1 \delta_1 + \beta_1 \beta_2)}. \quad (32)$$

The convergence is rapid except when γ_1 is very large. As the correlation times of the coloured noises $\eta_j(t)$, $\mu_j^{cor} = \delta_j^{-1} \to 0^+$, $\eta_j(t) \to \sqrt{2\varepsilon_j} \xi_j(t)$, ($j = 1, 2$), where $\xi_j(t)$ are the independent zero mean standard Gaussian white noises characterized by Equation (6). In this case,

$$D_u(\infty) \to \frac{\varepsilon_1}{\gamma_1} + \frac{2\beta_1 \varepsilon_2}{\beta_2 \gamma_1}$$

and

$$D_v(\infty) \to \frac{\varepsilon_2 (\gamma_1^2 + \beta_1 \beta_2)}{\beta_1 \beta_2 \gamma_1} + \frac{2\beta_2 \varepsilon_1}{\beta_1 \gamma_1}.$$

Therefore, for high amplitude random forces, $D_u(\infty)$ and $D_v(\infty)$ are large and the system exhibits large fluctuations. The interior equilibrium, which is stable in the absence of these fluctuating environmental conditions, become unstable.

In the deterministic environment, the stability determining quantity is γ_1 and β_1 (given by (8)). If $\gamma_1 > 0$ and $\beta_1 > 0$, then the deterministic stability Criteria (2) for the coexisting equilibria are satisfied. In a rapidly fluctuating environment, however, it is no longer enough for stability. Here, in addition with γ_1 and β_1, the intensity ε_j of the noise $\eta_j(t)$ becomes a regulatory factor. We observe that if $\varepsilon_j \gg \gamma_1$, populations exhibit abnormally large fluctuations which rapidly lead to population extinction. In the intermediate region, where ε_j and γ_1 are commensurate, the populations are likely to undergo moderate fluctuations. If $\varepsilon_j \ll \gamma_1$, then population fluctuations are relatively small and the environment is effectively deterministic.

V. SOLUTION OF THE NOISE INDUCED LINEARIZED SYSTEM

The solutions of the noise induced linearized System (8), using the approach of Hoel et al. [16], are

$$u(t) = u(0)\phi_1(t) + u'(0)\phi_2(t) + \eta_1(t)$$
$$+ \beta_1\left[\frac{1}{\delta_2}\eta_2(t) - \sqrt{2\varepsilon_2}\omega_2(t)\right],$$
$$v(t) = v(0)\phi_1(t) + v'(0)\phi_2(t)$$
$$+ \left(1 - \frac{\gamma_1}{\delta_2}\right)\eta_2(t) - \frac{\beta_2}{\delta_1}\eta_1(t)$$
$$+ \left[\gamma_1\sqrt{2\varepsilon_2}\omega_2(t) + \beta_2\sqrt{2\varepsilon_1}\omega_1(t)\right].$$

$$(33)$$

Here

$$\phi_1(t) = \frac{r_1'e^{r_1't} - r_1''e^{r_1''t}}{r_1' - r_1''}, \text{ when } \gamma_1^2 - 4\beta_1\beta_2 > 0,$$
$$= e^{\alpha_1't}\left(\cos\beta_1't - \frac{\alpha_1'}{\beta_1'}\sin\beta_1't\right), \text{ when } \gamma_1^2 - 4\beta_1\beta_2 < 0,$$
$$= e^{r_1t}(1 - r_1t), \text{ when } \gamma_1^2 - 4\beta_1\beta_2 = 0,$$

and

$$\phi_2(t) = \frac{e^{r_1't} - e^{r_1''t}}{r_1' - r_1''}, \text{ when } \gamma_1^2 - 4\beta_1\beta_2 > 0,$$
$$= e^{\alpha_1't}\sin\beta_1't, \text{ when } \gamma_1^2 - 4\beta_1\beta_2 < 0,$$
$$= e^{r_1t}t, \text{ when } \gamma_1^2 - 4\beta_1\beta_2 = 0,$$

with

$$r_1' = \frac{1}{2}\left(-\gamma_1 + \sqrt{\gamma_1^2 - 4\beta_1\beta_2}\right), r_1'' = \frac{1}{2}\left(-\gamma_1 - \sqrt{\gamma_1^2 - 4\beta_1\beta_2}\right),$$
$$\alpha_1' = \frac{-\gamma_1}{2}, \beta_1' = \frac{1}{2}\sqrt{4\beta_1\beta_2 - \gamma_1^2}, r_1 = \frac{-\gamma_1}{2},$$
$$u(0) = \log\frac{x(0)}{x^*}, u'(0) = \left[r\left(1 - \frac{x(0)}{k}\right) - \frac{\alpha(1-c)y(0)}{1+\alpha(1-c)hx(0)}\right],$$

and $v(0) = \log\dfrac{y(0)}{y^*}, v'(0) = \left[\dfrac{\theta\alpha(1-c)x(0)}{1+\alpha(1-c)hx} - d\right].$

Solution without noise takes the following form

$$u(t) = u(0)\phi_1(t) + u'(0)\phi_2(t)$$
$$\& \ v(t) = v(0)\phi_1(t) + v'(0)\phi_2(t).$$

$$(34)$$

In this case, the ensemble average of the populations are given by

$$\langle u(t)\rangle = u(0)\langle\phi_1(t)\rangle + u'(0)\langle\phi_2(t)\rangle$$
$$\& \ \langle v(t)\rangle = v(0)\langle\phi_1(t)\rangle + v'(0)\langle\phi_2(t)\rangle.$$

$$(35)$$

For $t \to \infty$, $\langle\phi_1(t)\rangle, \langle\phi_2(t)\rangle \to 0$. Hence, we get ‹u(t)› = 0 and ‹v(t)› = 0. Using the inverse transformations, we obtain ‹x(t)› = x^* and ‹y(t)› = y^*; and also the variance of both populations become zero, i.e., $\sigma_x^2 = 0$ and $\sigma_y^2 = 0$ when $t \to \infty$.

To determine the tolerance interval, we use the central limit theorem. Thus, we have a pre-assigned small value ε₀ > 0 for which $\lim_{t\to\infty}$ Prob($|1 - x^*| < \varepsilon_0$) = 1 (since $\sigma_x = 0$). Hence, the distribution of prey population will lie inside the tolerance interval (x^* - ε, x^* + ε₀) and predator population will also lie inside the tolerance interval (y^* - ε₀, y^* + ε₀). Now for the introduction of colour noise in the system, Equation (33) becomes (by using inverse transformations)

$$x(t) = x^*\exp[u(0)\phi_1(t) + u'(0)\phi_2(t) + \eta_1'(t)],$$
$$y(t) = y^*\exp[v(0)\phi_1(t) + v'(0)\phi_2(t) + \eta_2'(t)],$$

$$(36)$$

where,

$$\eta_1'(t) = \eta_1(t) + \beta_1\left[\frac{1}{\delta_2}\eta_2(t) - \sqrt{2\varepsilon_2}\omega_2(t)\right] \text{ and}$$
$$\eta_2'(t) = \left(1 - \frac{\gamma_1}{\delta_2}\right)\eta_2(t) - \frac{\beta_2}{\delta_1}\eta_1(t)$$
$$+ \left[\gamma_1\sqrt{2\varepsilon_2}\omega_2(t) + \beta_2\sqrt{2\varepsilon_1}\omega_1(t)\right].$$

$$(37)$$

For $t \to \infty$, we have ‹x(t)› = x^* and ‹y(t)› = y^*, but the deviations from the mean of two populations are

$$\sigma_x^2 = \left[\delta_1\varepsilon_1 + \beta_1^2\varepsilon_2(\frac{1}{\delta_2} - 2)\right]x^{*2},$$
$$\sigma_y^2 = \left[\varepsilon_2\left\{\delta_2(1 - \frac{\gamma_1}{\delta_2})^2 + 2\gamma_1^2\right\} + \varepsilon_1\beta_2^2\left(2 - \frac{1}{\delta_1}\right)\right]y^{*2}.$$

From the above results we conclude that if the deviations from means of both populations (σ_x^2 and σ_y^2) become greater than the pre-assigned value (ε₀) for different choices of parameters then both the populations will lie outside the tolerance interval and hence the system becomes unstable around the positive equilibrium. It is well known that the populations will remain stable if the variances from the equilibrium levels are minimum [17], i.e. the probability of the populations to lie inside the tolerance interval which is described previously are maximum.

VI. AN IMPORTANT OBSERVATION

In the deterministic environment, the system exhibits a Hopf-bifurcation near $E^*(x^*, y^*)$, if $c = 1 - \dfrac{\theta + hd}{\alpha kh(\theta - hd)}$.

From (8), one can observe that when $c - \left\{1 - \dfrac{\theta + hd}{\alpha kh(\theta - hd)}\right\} \to 0^+$, then $\gamma_1 \to 0^+$. After some calculations, we have

$$\lim_{\gamma_1\to 0^+} D_u(t) = \varepsilon_1\delta_1^2\left[\frac{t}{\beta_1\beta_2 + \delta_1^2} - \frac{\sin 2\sqrt{\beta_1\beta_2}t}{2\sqrt{\beta_1\beta_2}(\beta_1\beta_2 + \delta_1^2)}\right]$$
$$+ \frac{2e^{-\delta_1 t}\delta_1^2}{(\beta_1\beta_2 + \delta_1^2)^2} \times \left\{\frac{1}{\delta_1}\cos\sqrt{\beta_1\beta_2}t\right.$$

$$+ \frac{1}{\sqrt{\beta_1\beta_2}}\sin\sqrt{\beta_1\beta_2}t \Bigg\} - \frac{\delta_1\left(1+\cos^2\sqrt{\beta_1\beta_2}t\right)}{\left(\beta_1\beta_2+\delta_1^2\right)^2}$$

$$+ \frac{\delta_1^3\sin^2\sqrt{\beta_1\beta_2}t}{\beta_1\beta_2\left(\beta_1\beta_2+\delta_1^2\right)^2}\Bigg] + 2\beta_1^2\varepsilon_2\delta_2^2$$

$$\times\Bigg[\frac{t}{\beta_1\beta_2\left(\beta_1\beta_2+\delta_2^2\right)}$$

$$- \frac{\sin^2\sqrt{\beta_1\beta_2}t}{2(\beta_1\beta_2)^{\frac{3}{2}}\left(\beta_1\beta_2+\delta_2^2\right)} - \frac{2e^{-\delta_2 t}}{\left(\beta_1\beta_2+\delta_2^2\right)}$$

$$\times\Bigg\{\frac{1}{\delta_2}\cos\sqrt{\beta_1\beta_2}t + \frac{1}{\sqrt{\beta_1\beta_2}}\sin\sqrt{\beta_1\beta_2}t\Bigg\}$$

$$- \frac{\left(1+\cos^2\sqrt{\beta_1\beta_2}t\right)}{\delta_2\left(\beta_1\beta_2+\delta_1^2\right)^2} - \frac{\delta_2^3\sin^2\sqrt{\beta_1\beta_2}t}{\beta_1\beta_2\left(\beta_1\beta_2+\delta_2^2\right)^2}\Bigg],$$

$$(38)$$

$$\lim_{\gamma_1\to 0^+}D_v(t) = \varepsilon_2\delta_2^2\Bigg[\frac{t}{\beta_1\beta_2+\delta_2^2} - \frac{\sin 2\sqrt{\beta_1\beta_2}t}{2\sqrt{\beta_1\beta_2}\left(\beta_1\beta_2+\delta_2^2\right)}$$

$$+ \frac{2e^{-\delta_2 t}\delta_2^2}{\left(\beta_1\beta_2+\delta_2^2\right)^2}\times\Bigg\{\frac{1}{\delta_2}\cos\sqrt{\beta_1\beta_2}t$$

$$+ \frac{1}{\sqrt{\beta_1\beta_2}}\sin\sqrt{\beta_1\beta_2}t\Bigg\} - \frac{\delta_2\left(1+\cos^2\sqrt{\beta_1\beta_2}t\right)}{\left(\beta_1\beta_2+\delta_2^2\right)^2}$$

$$+ \frac{\delta_2^3\sin^2\sqrt{\beta_1\beta_2}t}{\beta_1\beta_2\left(\beta_1\beta_2+\delta_2^2\right)^2}\Bigg] + 2\beta_2^2\varepsilon_1\delta_1^2$$

$$\times\Bigg[\frac{t}{\beta_1\beta_2\left(\beta_1\beta_2+\delta_1^2\right)} - \frac{\sin^2\sqrt{\beta_1\beta_2}t}{2(\beta_1\beta_2)^{\frac{3}{2}}\left(\beta_1\beta_2+\delta_1^2\right)}$$

$$- \frac{2e^{-\delta_1 t}}{\left(\beta_1\beta_2+\delta_1^2\right)}\times\Bigg\{\frac{1}{\delta_1}\cos\sqrt{\beta_1\beta_2}t$$

$$+ \frac{1}{\sqrt{\beta_1\beta_2}}\sin\sqrt{\beta_1\beta_2}t\Bigg\}\times\Bigg\{\frac{1}{\delta_1}\cos\sqrt{\beta_1\beta_2}t$$

$$+ \frac{1}{\sqrt{\beta_1\beta_2}}\sin\sqrt{\beta_1\beta_2}t\Bigg\}$$

$$- \frac{\left(1+\cos^2\sqrt{\beta_1\beta_2}t\right)}{\delta_1\left(\beta_1\beta_2+\delta_2^2\right)^2} - \frac{\delta_1^3\sin^2\sqrt{\beta_1\beta_2}t}{\beta_1\beta_2\left(\beta_1\beta_2+\delta_1^2\right)^2}\Bigg].$$

$$(39)$$

It is easy to see that

$$f_j\big|_{t=0} = \frac{df_j}{dt}\bigg|_{t=0} = \frac{d^2 f_j}{dt^2}\bigg|_{t=0} = 0 \text{ and } \frac{d^3 f_j}{dt^3}\bigg|_{t=0} > 0,$$

where

$$f_j = \lim_{\gamma_1\to 0^+}D_{x_j}(t)\,(j=1,2).$$

From the above result, it follows that if c is very close to $\left\{1 - \dfrac{\theta+hd}{\alpha kh(\theta-hd)}\right\}$ (so that, $\gamma_1 \to 0^+$), the system with periodic background noise shows abnormally large fluctuations with increasing time. As the correlation time of $\eta_j(t)$, $\mu_j^{cor} = \delta_j^{-1} \to 0^+$, $\eta_j(t) \to \sqrt{2\varepsilon_j}\,\xi_j(t)$, where $\xi_j(t)$ are independent zero mean standard Gaussian white noises, so we have

$$\lim_{\delta_j\to\infty}\lim_{\gamma_1\to 0^+}D_u(t) \to \infty \text{ for all } t > 0 \text{ and}$$

$$\lim_{\delta_j\to\infty}\lim_{\gamma_1\to 0^+}D_v(t) \to \infty \text{ for all } t > 0.$$

Therefore, the system is always unstable in this case.

VII. QUANTITATIVE RESULTS

For quantitative study of the system, we consider the parameter values of much studied predator-prey system *Paramecium aurelia* (prey) and *Didinium nasutum* (predator) [18].

TABLE I DETERMINISTIC PARAMETER VALUES

Parameter	Default values
r	2.65
κ	898
α	0.045
c	…….
h	0.0437
θ	0.215
d	1.06

A single didinium may consume 12 to 48 [19, 20] paramecium per day. Thus, the handling time (h) for each prey captured varies from 0.0208 to 0.0833. We set 0.0437 as the default value for the parameter h (see Table 1). Butzel and Bolten [21] estimated that 3 to 10 paramecium are required for a binary fission of didinium. This indicates that the conversion factor θ may vary from 0.1 to 0.33. We set the average value 0.215 as the default value of θ. Harrison [22] and Jost and Ellener [23] estimated the values of r (specific growth rate of paramecium) as 3.3 and 2 per day, respectively. We consider the average value 2.65 as the default value of r. The attack coefficient (α) and the per capita death rate of didinium (d) were taken as 0.045 and 1.06 per day, respectively [23]. To explore the effects of habitat complexity on the system dynamics, we consider c as a variable parameter. For the parameter values as in the Table 1, we observe that when $c = 0.45$ then both the populations lie within the tolerance interval indicating the stable coexistence of both prey and predator populations (see Fig. 1). If the strength of the habitat complexity decreases from $c = 0.45$ to $c = 0.13$, it is observed that both populations deviate from the tolerance interval, which indicates the unstable situation of the system (see Fig. 2). These observations also resemble with the results obtained

by spectral density analysis where the deviations of both the populations decrease with increasing c (see Fig. 3).

Stability determining quantity for the coexistence equilibrium in deterministic environment is γ_1. If $\gamma_1 > 0$ then the deterministic stability criteria is satisfied. However, it is no longer enough for a fluctuating environment. In addition to γ_1, the intensity ε_j of the noise η_j is a very important factor to be considered in the later case. If $\varepsilon_j \gg \gamma_1$ then populations exhibit abnormally large fluctuations which lead population to extinction (see Fig. 4(a-b)). In the intermediate region, where ε_j and γ_1 are commensurate, the populations are likely to undergo moderate fluctuations (see Fig. 4(c-d)). Finally, if $\varepsilon_j \ll \gamma_1$ then populations fluctuations are relatively small and the environment is effectively deterministic (see Fig. 4(e-f)).

Fig. 1 Numerical solutions of equation (36) show that the maximum number of populations lie within the tolerance interval when c = 0.45, depicting the stable coexistence of system populations. Other parameters are as in the Table 1

Fig. 2 Numerical solutions of the equation (36) show that the maximum number of populations lie outside the tolerance interval for c = 0.13, depicting instability of the coexistence equilibrium. Other parameters are as in the Table 1
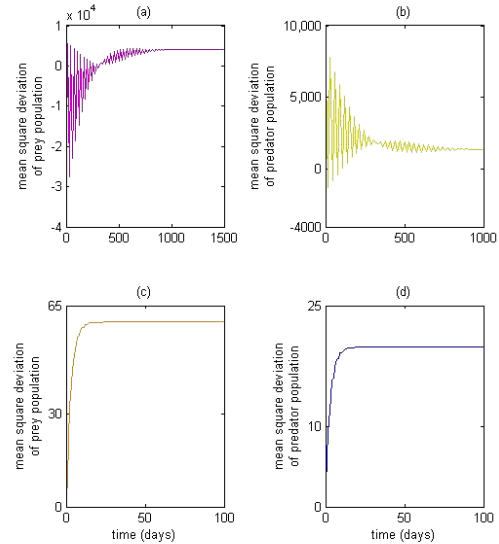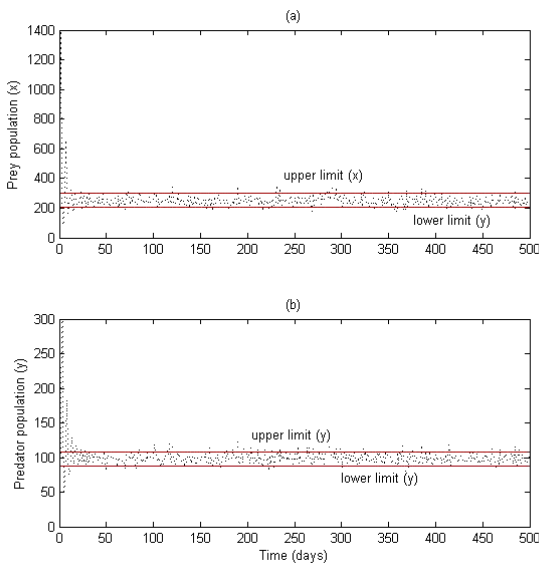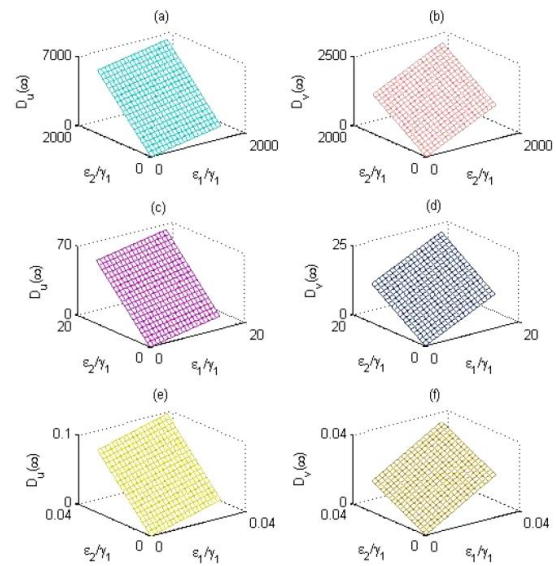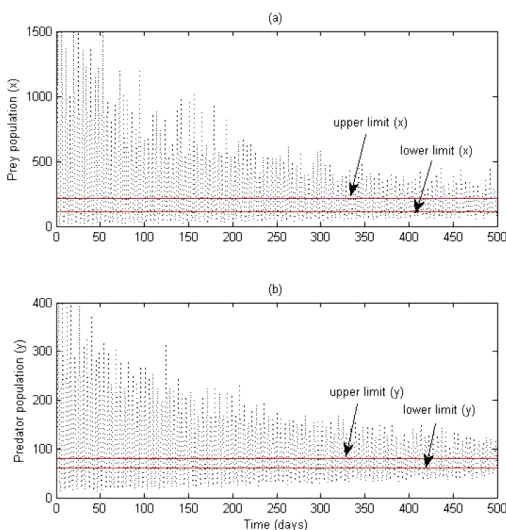

Fig. 3 Cumulative root mean square fluctuations for the prey and predator populations are evaluated by using equations (26) and (27) for different degree of habitat complexity. Figs. (a)-(b) are the cumulative root mean square fluctuations when $c=0.13$ and Figs. (c)-(d) are the same for $c=0.45$. Other parameters are as in the Table 1

VIII. DISCUSSION

Fig. 4 Fluctuations of prey and predator populations. Figs. (a) – (b) show abnormally large fluctuations when $\varepsilon j \gg \gamma_1$, Figs. (c) – (d) show moderate fluctuations when ε_j and γ_1 are commensurate. Figs. (e) – (f) show very small fluctuations when $\varepsilon j \ll \gamma_1$. Rest of the parameters are as in the Table 1

In this paper, we have studied a stochastic version of a deterministic predator-prey system that incorporates the effect of habitat complexity. To take into account the effect of fluctuating environment, we have considered random perturbations in the form of colour noise in the growth rate of prey and in the death rate of predator population. It is observed that the deterministic criteria of stability is no longer enough to guarantee the stability of the coexisting equilibrium point $E^*(x^*, y^*)$. Spectral density analysis

indicates that the system shows stochastically stable or unstable dynamics depending on the strength or degree of habitat complexity. If it is intermediate then the system is stochastically stable and lies within the tolerance interval. If the degree of habitat complexity is very low then the system is stochastically unstable and most of the solutions lie outside of the tolerance interval. This study also implies that the fluctuations of the system populations depend on the relative value of ε_j, the intensity of the noise η_j with respect to γ_1, the stability determining quantity in the deterministic environment. If ε_j is very high in comparison to γ_1 then system of populations fluctuate abnormally. If ε_j is commensurate to γ_1 then fluctuations are moderate. On the other hand, if ε_j is very low in comparison to γ_1 then fluctuation is minimum.

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