

Noise-controlled relaxation oscillations in ratio-dependent predator–prey models

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Abstract: A class of $(N + 1)$ -species ratio-dependent predator–prey stochastic models, which consists of one predator population and N prey populations (or N subpopulations of a prey metapopulation), is considered. The influence of a fluctuating environment on the carrying capacities of prey populations is modeled as a dichotomous noise. The study is a follow-up of a previous investigation of the above class of models subjected to a colored-noise with low intensity [Physical Review E **74**, 021101 (2006)]. Relying, in case the growth rates of prey and predator are widely different, on the mean-field approach, the self-consistency equations for prey-populations mean abundance and predator-population abundance are derived. In some region of system parameters, the variations of noise amplitude or correlation time can cause transitions of the mean field from a globally asymptotically stable equilibrium to the stable limit cycle as well as in the opposite direction. The conditions for the occurrence of such a phenomenon are found and illustrated by a phase diagram.

Key-words: Stochastic dynamics, predator–prey models, functional response, ratio-dependent, dichotomous noise, limit cycle, slow-fast cycles, noise-induced transitions.

1 Introduction

One of the key issues in ecology is how environmental fluctuations and species interactions may determine the oscillations in population sizes displayed by many organisms in nature as well as in laboratory cultures [1]-[6]. Ecologists have mainly been interested in the dynamical consequences of population interaction, often ignoring environmental variability altogether. However, the essential role of environmental fluctuations has recently been recognized in theoretical ecology. Noise-induced effects on population dynamics have been subject to intense theoretical investigations [7]-[11]. Moreover, ecological investigations suggest that population dynamics is sensitive to noise correlation time (noise color) [11]-[16]. In spite of the obvious significance of this circumstance, the role of nonequilibrium fluctuations (colored noise) of environmental parameters has not been investigated much in the context of ecosystems [15]-[17].

The most popular (without fluctuations) model for predator–prey dynamics, in its classical form, can be written as [2],[18]

$$\begin{aligned}\frac{dx}{dt} &= x f(x) - \alpha g(x, y) y, \\ \frac{dy}{dt} &= y [\beta g(x, y) - d],\end{aligned}\quad (1)$$

where x and y are densities of prey abundance and predator abundance, respectively, $f(x)$ is the per capita rate of increase of the prey in absence of predation, and d is food-independent predator mortality, assumed to be constant. The function αg describes the amount of prey consumed per predator per unit time, while βg describes predator production per capita. The quotient of the two constants β and α is the conversion efficiency β/α .

During the past decade a lot of studies have been devoted to the understanding of the consequences of

assuming either a prey-dependent, $g = g(x)$, or ratio-dependent, $g = g(x/y)$, predator functional response (a trophic function) in predator-prey models [19]-[22]. Differing from the prey-dependent predator-prey models, the ratio-dependent predator-prey systems have two principal predictions: (i) equilibrium abundances are positively correlated along a gradient of enrichment [22] and (ii) the "paradox of enrichment" [23] either completely disappears or enrichment is linked to stability in a more complex way [24]. Based on a trophic function of the Michaelis-Menten-Holling type, the ratio-dependent predator-prey model (1) has recently been studied by several researchers and very rich dynamics has been observed [18],[24]-[28]. From the mathematical point of view, ratio-dependent models can display original dynamic properties that have never been observed in earlier simple two-dimensional predator-prey models. For example, the origin ($x = 0, y = 0$) can be a node simultaneously attractive and repulsive, thus shedding new light on ecological extinction, particularly in the context of biological control. Coexistence of several dynamic regimes with the same set of parameters can also be observed [18],[24]-[27]. These are realistic features since those behaviors have been observed experimentally [29].

Although deterministic ratio-dependent predator-prey models are useful in modeling many real ecological communities, there is almost nothing available either on qualitative analysis of multispecies interaction or on the effect of environmental fluctuations in models based on a ratio-dependent approach [17],[28]. It is of interest, both from theoretical and practical viewpoints, to know whether the transitions from equilibrium states to oscillatory regimes (and the opposite way) sometimes occurring in ecosystems [1]-[6] could be regarded as induced by environmental nonequilibrium fluctuations.

Recently we have considered a broad class of $(N + 1)$ -species ratio-dependent predator-prey models that consist of one predator population and N prey populations with fluctuating carrying capacities [17]. Notably, in the framework of the mean field theory it is shown that the dynamical system for the mean prey abundance and predator abundance exhibits Hopf bifurcations with respect to the noise correlation time. However, this work is based on local stability analysis with the assumption that noise dispersion (or amplitude) is very small. As a consequence, for the existence of the phenomenon of noise-induced Hopf bifurcations the control parameter (prey capturing rate) must be located very near the bifurcation point α_{cr} of the corresponding deterministic model. Moreover, in the case considered in [17] the trivial equilibrium ($x = 0, y = 0$) has its own basin of attraction, even if

there exists a nontrivial stable or unstable equilibrium (with a stable limit cycle). Hence, the appearance of noise-induced Hopf bifurcations is very sensitive to small variations of system parameters and initial conditions. Consequently, the question (very important in an ecological context), whether environmental colored fluctuations with a finite amplitude can cause globally asymptotically stable limit cycles in ratio-dependent predator-prey systems is still open.

Thus motivated, we have written the present paper, considering the class of $(N + 1)$ -species ratio-dependent predator-prey models, represented in our previous work [17]. Differing from [17] we consider here that region of the system parameters space where the corresponding deterministic model is characterized by a nontrivial globally asymptotically stable equilibrium. Since one of the characteristic quantities of an ecosystem, perhaps the most fundamental one, is its average species density [30] ($\sum_{i=1}^N X_i/N$), where X_i is the population density of the i th species), we consider the average species density of preys as one of the two state parameters of an ecosystem, the other state parameter being the density of predator abundance. We study the model using a mean field approach, focusing on colored-noise-induced transitions. The effect of a fluctuating environment on the prey populations is modeled as colored fluctuations of the carrying capacities. For the sake of mathematical simplicity, we confine ourselves to the case where the noise is a dichotomous Markovian noise, also known as the random telegraph signal [31].

The main contribution of this paper is as follows. In predator-prey systems in which the growth rate of the predator is much smaller than the growth rates of preys, we establish colored-noise-induced transitions from a globally stable equilibrium to the stable limit cycle (with some oscillations of population abundance) as well as in the opposite direction. Furthermore, the transition is found to be reentrant, e.g., if the noise amplitude is greater than a threshold value then the limit cycle appears above a critical value of the noise correlation time, but disappears again through reentrant transition to the equilibrium state at a higher value of the noise correlation time. Particularly, in the case of the Michaelis-Menten-Holling type ratio-dependent trophic function and logistic self-regulation of preys we give the necessary and sufficient conditions for the appearance of such effects. We emphasize that contrary to the case described in [17], here the limit cycles rather occur at moderate or great noise amplitudes than at very small ones.

The structure of the paper is as follows. Section 2 presents the basic model investigated in this work. A mean-field description of the model is

given and the corresponding self-consistency equations are found. Section 3 analyzes the behavior of the self-consistently determined mean field. The phenomenon of colored-noise-induced relaxation oscillations of prey and predator densities is established, and the conditions for such an effect are illustrated with the help of a phase diagram in the noise parameters space. Section 4 contains brief concluding remarks.

2 A stochastic ratio-dependent predator-prey model

2.1 Model

As was mentioned in the introduction, the present model is based on a generalization of the ratio-dependent model for predator-prey dynamics (1) to the case of one predator population and N prey populations [17]:

$$\begin{aligned} \frac{dX_i}{d\tilde{t}} &= f_i(X_i)X_i - \tilde{\alpha}g\left(\frac{\bar{x}}{y}\right)\frac{y}{\bar{x}}X_i, \\ \frac{dy}{dt} &= \tilde{\beta}g\left(\frac{\bar{x}}{y}\right)y - \tilde{d}y, \end{aligned} \quad (2)$$

where $X_i(\tilde{t})$ ($i = 1, \dots, N$) is the density of the i th prey population at the time \tilde{t} , $y(\tilde{t})$ is the density of the predator population, and $\bar{x}(\tilde{t}) = (1/N) \sum_{i=1}^N X_i(\tilde{t})$ is the average of the prey population densities. The positive constants $\tilde{\alpha}$, $\tilde{\beta}$, and \tilde{d} stand for the prey capturing rate, maximal predator growth rate, and predator death rate, respectively. Here we have assumed that for consumers (predator), all prey populations are equivalent, so that the function $\tilde{\alpha}g(\bar{x}/y) \cdot X_i/\bar{x}$ describes the amount of the i th prey consumed per predator per unit time. Model (2) is biologically meaningful if the functional response g is bounded, non-negative and increasing, and equal to zero at zero [22]. More precisely, we assume that

$$\begin{aligned} 0 &\leq g(u) \leq 1, & dg(u)/du &> 0, \\ 0 &\leq u < \infty, & g(0) &= 0. \end{aligned} \quad (3)$$

The following analysis applies to concave increasing functions $g(u)$ with

$$\frac{g(u)}{u} \leq 1, \quad 0 \leq u < \infty. \quad (4)$$

Convex functions (e.g. sigmoid or with a threshold) require a specific analysis but they do not lead to any important property qualitatively different from those that will be examined in the rest of the paper.

The function $f_i(X_i)$ describes the development of the i th species without any interaction with other

species. A typical mechanism for self-regulation in ecosystems includes, for example, territorial breeding requirements and the crowding effect caused by competition for resources [30]. These are taken into account by applying the generalized Verhulst model

$$f_i(X_i) = \delta \left[1 - \left(\frac{X_i}{K_i} \right)^c \right], \quad (5)$$

where $c > 0$ and δ are constants, and K_i is the carrying capacity of the i th species.

Random interaction with the environment (climate, diseases, etc.) is taken into account by introducing a colored noise in $f_i(X_i)$. From now on we shall use fluctuations of the carrying capacity

$$K_i = K[1 + a_0 Z_i(\tilde{t})], \quad (6)$$

where colored noise $Z_i(\tilde{t})$ is assumed to be a dichotomous Markovian stochastic process [31]. A dichotomous process is a random stationary Markovian process consisting of jumps between two values $z = -1, 1$. The jumps follow in time according to a Poisson process, while the values occur with the stationary probability $1/2$. The mean values of $Z_i(\tilde{t})$ and the correlation function are

$$\langle Z_i(\tilde{t}) \rangle = 0, \quad \langle Z_i(\tilde{t}) Z_j(\tilde{t}') \rangle = \delta_{ij} \exp(-\nu|\tilde{t} - \tilde{t}'|), \quad (7)$$

where δ_{ij} is the Kronecker symbol and the switching rate ν is the reciprocal of the noise correlation time $\nu = 1/\tau_c$.

Obviously, model (2) with Eqs. (5) and (6) is biologically meaningful only if

$$a_0 < 1. \quad (8)$$

It is practicable, by applying the properties of the dichotomous process, to convert the term K_i^{-c} in Eq. (5) to the form

$$K_i^{-c} = \gamma[1 + aZ_i(\tilde{t})] \quad (9)$$

in which we have introduced

$$\gamma = \frac{1}{2K^c(1 - a_0^2)^c} [(1 + a_0)^c + (1 - a_0)^c], \quad (10)$$

and the amplitude of the fluctuations

$$a = \frac{(1 + a_0)^c - (1 - a_0)^c}{(1 + a_0)^c + (1 - a_0)^c}. \quad (11)$$

By substituting identity (9) into Eqs. (5) and (2) and applying a scaling of the form

$$t = \delta\tilde{t}, \quad \nu = \frac{\tilde{\nu}}{\delta}, \quad \alpha = \frac{\tilde{\alpha}}{\delta}, \quad \beta = \frac{\tilde{\beta}}{\delta}, \quad d = \frac{\tilde{d}}{\delta} \quad (12)$$

we get a dimensionless formulation of the dynamics

$$\begin{aligned} \frac{dX_i(t)}{dt} &= X_i(t) \left\{ 1 - \gamma [1 + aZ_i(t)] X_i^c(t) \right. \\ &\quad \left. - \alpha g\left(\frac{\bar{x}}{y}\right) \frac{y}{\bar{x}} \right\}, \\ \frac{dy}{dt} &= y \left[\beta g\left(\frac{\bar{x}}{y}\right) - d \right], \quad i = 1, \dots, N, \end{aligned} \quad (13)$$

where $Z_i(t)$ is a dichotomous noise with an amplitude 1 and a switching rate ν . We emphasize that Eqs. (13) are mathematically equivalent to the initial system (2), (5), and (6) and have been derived without any approximation. Note that if noise is absent and the distribution of the initial prey–population abundances is uniform, $x_i(0) = x_0$, then model (13) can be reduced to the deterministic ratio-dependent model (1) for \bar{x} and y , i.e.

$$\begin{aligned} \frac{d\bar{x}}{dt} &= \bar{x} \left[1 - \gamma \bar{x}^c - \alpha g\left(\frac{\bar{x}}{y}\right) \frac{y}{\bar{x}} \right], \\ \frac{dy}{dt} &= y \beta \left[g\left(\frac{\bar{x}}{y}\right) - s \right], \quad s = \frac{d}{\beta}. \end{aligned} \quad (14)$$

Thus, in this case, the results described in [18],[24]-[28] are immediately applicable.

For example, if we assume that

$$\begin{aligned} \alpha < \min \left\{ 1, \frac{u[c(1+d) - \beta(cg - ug')]}{(1+c)g - ug'} \mid u \in (0, \infty) \right\}, \\ d < \beta < 1 + d, \end{aligned} \quad (15)$$

where $g' = dg(u)/du$, then the system (14) has two equilibria, $E_1 = (0, 0)$ and $E_2 = (K, 0)$ on the \bar{x} axis, while the third equilibrium $E_3 = (\bar{x}_s, y_s)$ is given by

$$\bar{x}_s = K \left[1 - \frac{\alpha s}{g^{-1}(s)} \right]^{\frac{1}{c}}, \quad y_s = \frac{1}{g^{-1}(s)} \bar{x}_s, \quad (16)$$

where g^{-1} is the inverse function of g . The stability analysis of E_i , $i = 1, 2, 3$, shows that the equilibrium E_3 is globally asymptotically stable and the equilibria E_1 and E_2 are unstable (E_2 is a saddle point). The following analysis will be confined to case (15).

2.2 Mean field approximation

To proceed with the analytical examination of model (13), we follow the mean field approximation scheme. We assume that $N \rightarrow \infty$. This means that we are interested in the case of a very great number of prey populations (or subpopulations in a prey metapopulation). The mean field approximation can be reached by replacing the size average $\bar{x} = (1/N) \sum_{i=1}^N X_i(t)$ by the statistical average $\langle X(t) \rangle$ in Eqs. (13). Hence,

each stochastic differential equation for $X_i(t)$ in Eqs. (13) can be reduced to an independent and identical stochastic differential equation of the form

$$\frac{dX(t)}{dt} = X(t) \{ r(t) - \gamma X^c(t) [1 + aZ(t)] \}, \quad (17)$$

where $r(t) \equiv 1 - \alpha g(u)/u$ with $u(t) \equiv \langle X(t) \rangle / y(t)$. The corresponding composite master equation is

$$\begin{aligned} \frac{\partial}{\partial t} P_n(x, t) &= - \frac{\partial}{\partial x} \{ x [r(t) - x^c \gamma (1 + a_n)] \\ &\quad \times P_n(x, t) \} - \frac{\nu}{2} \sum_{m=1}^2 [(2\delta_{nm} - 1) P_m(x, t)], \end{aligned} \quad (18)$$

with $P_n(x, t)$ denoting the probability density for the combined process (x, a_n, t) ; $n, m = 1, 2$; $-a_1 = a_2 = a$. If the predator population density y is constant, then a significant inequality follows from Eq. (17) to characterize the stationary state of the system. For a stationary case, $x_1 = [r/\gamma(1-a)]^{1/c}$ and $x_2 = [r/\gamma(1+a)]^{1/c}$ are stable fixed points of the deterministic equations (17) with $Z(t) = -1$ and $Z(t) = 1$, respectively, and all trajectories $X(t)$ satisfy the following inequalities:

$$\left[\frac{r}{\gamma(1-a)} \right]^{1/c} > X(t) > \left[\frac{r}{\gamma(1+a)} \right]^{1/c}. \quad (19)$$

The behavior of the stationary system (17) can be analytically studied by means of a standard mean field theory procedure [32]. For a stationary state we can solve Eq. (18), taking as the boundary condition that there is no probability current at the boundary (19). This way we get the stationary probability distribution in the x space, $P(x, r) = \sum_n P_n^s(x)$, where $P_n^s(x)$ is the stationary probability density for the state (x, a_n) . After quite simple calculations one can find

$$\begin{aligned} P(x, r) &= \frac{crx^{-(1+c)}}{\gamma a B(1/2, \nu/(2rc))} \\ &\quad \times \left| 1 - \frac{r^2}{\gamma^2 a^2} \left(\frac{\gamma}{r} - \frac{1}{x^c} \right)^2 \right|^{[\nu/(2rc)]-1}, \end{aligned} \quad (20)$$

where $r = 1 - \alpha g(u)/u$, $u = \langle X \rangle / y$, $B(\lambda, \kappa) = \Gamma(\lambda)\Gamma(\kappa)/\Gamma(\lambda + \kappa)$ is the beta function, and Γ is the gamma function. The probability density $P(x, r)$ is normalized to restrict x within the interval (x_1, x_2) .

The self-consistency equation for the Weiss mean field approach, whose solution yields the dependence of $\langle X \rangle$ on the system parameters, is

$$\langle X \rangle = \int_{x_2}^{x_1} x P(x, r) dx. \quad (21)$$

With the help of the stationary probability distribution (20), one can easily calculate the moments of prey population densities

$$\langle X^k \rangle = \left(\frac{r}{\gamma} \right)^{k/c} {}_2F_1 \left(\frac{k}{2c}, \frac{k}{2c} + \frac{1}{2}; m + \frac{1}{2}; a^2 \right), \quad (22)$$

where ${}_2F_1$ is the hypergeometric function, $k = 1, 2, \dots$, and

$$m := \frac{\nu}{2c[1 - \alpha g(u)/u]}. \quad (23)$$

3 Relaxation oscillations

In this Section, we discuss a special case where $\beta \ll 1$ (relaxation oscillation limit). In this limit, the last equation in Eqs. (13) indicates that y varies very slowly. Since the dynamics of X (see Eq. (17)) is much faster than that of y , a quasi-stationary probability distribution is formed before y varies. In other words, the variable y in Eq. (17) is just a parameter for the dynamics of X . In this case, we can investigate the mean field dynamics of the system (13) using the following equations (see also Eq. (22)):

$$\begin{aligned} y &= \frac{1}{u} \left(\frac{r(u)}{\gamma} \right)^{1/c} \\ &\times {}_2F_1 \left(\frac{1}{2c}, \frac{1}{2c} + \frac{1}{2}; m(u) + \frac{1}{2}; a^2 \right), \\ \frac{dy}{dt} &= \beta y [g(u) - s], \quad u := \langle X \rangle / y. \end{aligned} \quad (24)$$

The first equation in Eqs. (24) corresponds to the prey isocline of the system. It is obvious that the predator isocline is given by

$$u = g^{-1}(s) = \text{const}. \quad (25)$$

The slow-fast approach suggests an intuitive idea why predator-prey cycles sometimes occur. This can happen if the fast system (17) can have fold bifurcations of mean field in the range of interest of the parameter y , i.e. if the self-consistency equation (see the first equation in Eqs. (24)) can have more than one stable solution $u(y)$ in some interval of values of y .

To clarify why the fluctuations of carrying capacities of preys can cause the relaxation oscillations in the system, we consider now in detail the biologically important case of logistic self-regulation, $c = 1$, and of the following Michaelis-Menten-Holling type predator functional response [24]-[27]

$$g(u) = \frac{u}{u + b} = \frac{\langle X \rangle}{\langle X \rangle + by}, \quad (26)$$

where $b > 0$ is a constant. In what follows, we will,

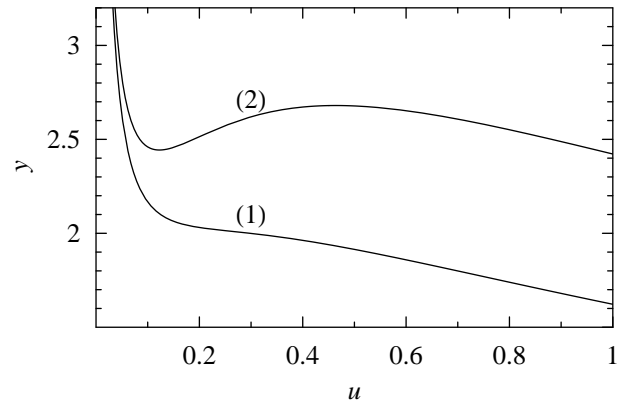


Fig.1. Two general types of prey isoclines $y(u)$ that can occur. The isoclines are computed by means of the first equation of (24) and Eq. (26), at the parameter values $c = b = \gamma = 1$, $\alpha = 0.95$, and $\nu = 0.3$. (1): The noise amplitude $a_0^2 = 0.82$ is less than the critical value a_c^2 . (2): The parameter $a_0^2 = 0.9$ is greater than a_c^2 .

without loss of generality, use the scaling

$$\tilde{y} = yb, \quad \tilde{\alpha} = \alpha/b. \quad (27)$$

In this case the coefficient b in Eq. (26) turns to unity and the conditions (3) are fulfilled. For convenience,

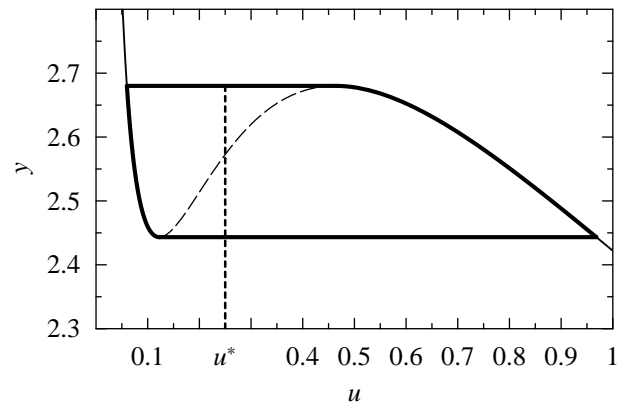


Fig.2. A noise-induced relaxation oscillation. The thick solid cycle depicts the predator population density y versus the ratio $u = \langle X \rangle / y$, computed by means of Eqs. (24) and (26). Solid lines: the stable pieces of the prey isocline determined by the first equation of (24). Dashed line: the unstable piece of the prey isocline. Dotted line: the predator isocline given by Eq. (25). Parameter values: $c = b = \gamma = 1$, $\alpha = 0.95$, $s = 0.2$, $\beta = 0.01$, $a_0^2 = 0.9$, and $\nu = 0.3$. The oscillation cycle follows a stable piece of the prey isocline and jumps to another stable branch of the isocline.

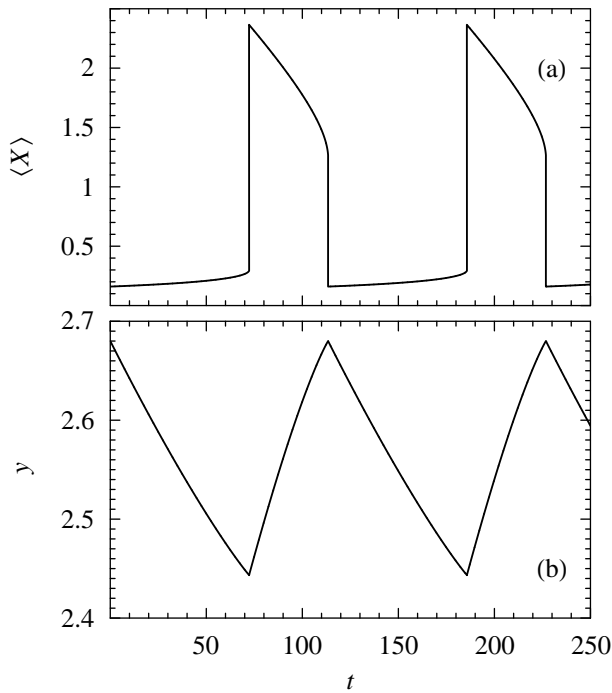


Fig.3. Time evolution of mean prey density $\langle X \rangle$ (panel (a)) and predator density y (panel (b)) obtained by numerically solving Eqs.(24) and (26) for the limit cycle displayed in Fig.2. Parameter values are $c = b = \gamma = 1$, $\alpha = 0.95$, $s = 0.2$, $\beta = 0.01$, $a_0^2 = 0.9$, and $\nu = 0.3$ (same as in Fig. 2). Note that the predator-prey cycles exhibit a delay of $\Delta t \approx 41.1$ between prey and predator maxima. The time is dimensionless as scaled by Eq.(12).

we shall omit the tilde. Note that in this case

$$g^{-1}(s) = \frac{s}{1-s}. \quad (28)$$

The typical forms of the prey isocline $y(u)$ are represented in Fig. 1. At the conditions of (15), one has to discern two cases. First, if the noise amplitude a_0 is lower than a threshold value $a_c(\alpha) > 0$, the curve $y(u)$ is described with a monotonically decreasing function as the variable u increases (see curve (1) in Fig. 1). Obviously the system is monostable and no relaxation cycle can occur. Second, in the case of a sufficiently large noise amplitude, $a_0 > a_c(\alpha)$, there is an interval of values of the noise correlation time $\tau_c \in (\tau_{c1}(\alpha, a_0), \tau_{c2}(\alpha, a_0))$ where there occurs a non-monotonic dependence of the prey isocline on u (see curve (2) in Fig. 1). That is, the colored noise induces two fold bifurcations of the mean field $\langle X \rangle$ of the fast system (17) with respect to y . In this case the relaxation cycles are possible and occur when the predator

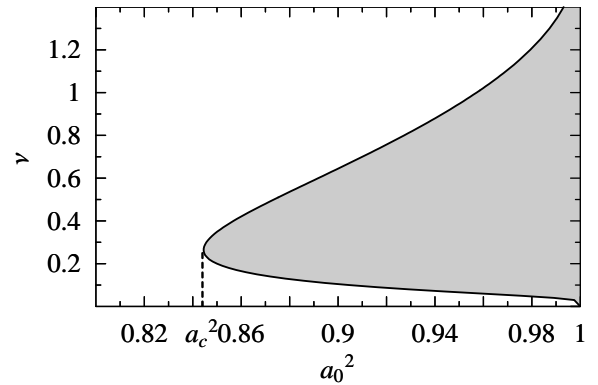


Fig.4. (ν, a_0^2) phase diagram for the occurrence of noise-induced limit cycles. The shaded domain corresponds to the region, where the relaxation oscillations are possible. The critical noise amplitude parameter $a_c^2 = 0.844$. The borders of the shaded region are computed from Eqs. (29), (24), and (26) with $c = b = \gamma = 1$, $\alpha = 0.95$.

isocline $u = s/(1-s)$ intersects the unstable piece of the prey isocline (see Fig. 2). Thus, in the last mentioned case, the system will converge to a limit cycle from any initial state (Fig. 2).

A long time series of abundances of predators and preys (Fig. 3) illustrates the fact that such cycles are characterized by periods of relatively little change, separated by rapid dramatic transitions in the ecosystem. That is why in ecological context such cycles are also called slow-fast cycles [33]. It is seen that the amplitudes of population size oscillations are relatively large. In addition the phase lag (the delay between prey and predator maxima) as a fraction of the cycle period $T = 113.4$, is 0.36, which is greater than in the case of "classical" predator-prey cycles (the quarter-cycle delay).

Figure 4 shows a phase diagram in the ν - a_0^2 plane at $\alpha = 0.95$. The shaded region in the figure corresponds to the region of noise parameters where the oscillations of population size are possible. As the noise amplitude decreases the region of oscillations narrows down and disappears at the critical value of the noise amplitude $a_c^2 = 0.844$. Hence, there is an upper limit $a_c(\alpha)$ for the noise amplitude at lower values of which the system is characterized by just one stable equilibrium (limit cycles cannot occur). The boundary of the region of the oscillatory phase and the critical noise amplitude $a_c(\alpha)$ are given by the system of transcendental equations

$$\frac{dy(u)}{du} = 0, \quad \frac{d^2y(u)}{du^2} = 0, \quad (29)$$

where $y(u)$ is given by the first equation in Eqs. (24). The dependence of $a_c^2(\alpha)$ is represented in Fig. 5.

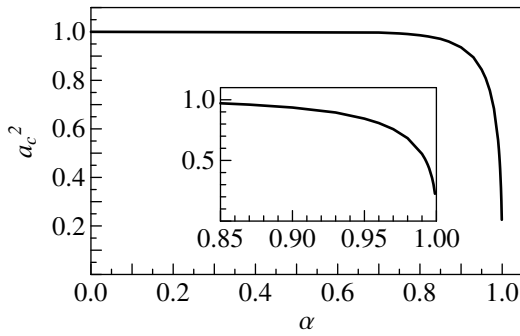


Fig.5. The critical noise amplitude parameter a_c^2 vs the prey capturing rate α . At the point $\alpha = 1$ the critical noise amplitude approaches zero.

It is remarkable that the critical parameter a_c^2 decreases monotonically from 1 to zero if the prey capturing rate $\alpha \in (0, 1)$ increases. Furthermore, from Fig. 4 it is seen that an increase of the noise correlation time, $\tau_c = 1/\nu$, can cause a transition from a stable equilibrium state to a state where both the predator-population and average prey-population densities oscillate. Notably, a further increase of τ_c causes a reentrant transition, i.e., the limit cycle disappears and the system approaches a stable equilibrium state. Therefore, in the fast-noise limit, $\tau_c \rightarrow 0$, and in the adiabatic limit, $\tau_c \rightarrow \infty$, the appearance of oscillations is impossible. Since the appearance of predator-prey cycles in model (13) with the conditions (15) and (26) is independent of the carrying capacity K (see Eqs. (10), (24) and (29)), the asymptotic behavior described above has a distinct physical meaning. In the case of the adiabatic limit, $\tau_c \rightarrow \infty$, transitions between states of nonequilibrium noise $Z(t)$ are so rare that the system has enough time to allow a deterministic dynamic to be formed between the transitions. Here we would like to remind the reader of the fact that the corresponding deterministic (the noise is absent) model (14) with conditions (15) has a globally asymptotically stable equilibrium.

At the fast-noise limit, i.e. at very high frequencies of colored fluctuations the system is under the influence of the average

$$K_{eff}^{-1} := \langle K_i^{-1} \rangle = [K(1 - a_0^2)]^{-1}. \quad (30)$$

Hence, the influence of fast fluctuations on an ecosystem can be biologically interpreted as a reduction of the carrying capacity K of a single species in Eqs. (2) and (5). Thus, our model with noise is, in the case of $\tau_c \rightarrow 0$, equivalent to a deterministic model with the carrying capacity K_{eff} .

4 Conclusion

In the present work, we analyze the behavior of the $(N + 1)$ -species ratio-dependent predator-preys stochastic model [17] in the region of the system parameters space, where the deterministic counterpart of the model is characterized by a nontrivial globally asymptotically stable equilibrium. We would like to emphasize that in our previous work [17] another parameters region where Hopf bifurcations in the corresponding deterministic model are possible, was considered.

For the sake of mathematical simplicity, we confine ourselves to the case, where the growth rate of the predator is much smaller than the growth rates of the preys. The presence of colored fluctuations of the carrying capacities of prey populations has a profound effect on a predator-prey system described by Eqs. (13), rearranging its parameter space so that in a certain region colored noise can induce quasi-bistability of the mean prey-populations density. As a consequence the colored-noise-induced relaxation oscillations of the mean prey-abundance and predator-abundance appear. This result that the fluctuations of the carrying capacities of preys can induce a stable limit cycle is somewhat surprising because, in the corresponding deterministic models (noise is absent), the qualitative behavior of the system dynamics as well as the qualitative asymptotic behavior of the solutions of the system (14) are independent of the carrying capacity K .

The results indicate that the effect of noise is not merely restricted to the shift of the critical capturing rate α_{cr} for Hopf bifurcations as in the case described in [17], but it will change the whole nature of the dynamics. Notably, transitions from an equilibrium state to a limit cycle are possible only if the noise amplitude is greater than the critical value $a_c(\alpha)$ (see Fig. 4). For sufficiently large noise amplitudes, $a_0 > a_c$, the key factor is noise correlation time. An increase of noise correlation time can cause oscillations of the mean prey-population and predator-population sizes. Moreover, the corresponding transitions are found to be reentrant, i.e. at a higher value of the correlation time the oscillations disappear and the system approaches an equilibrium state.

As the critical noise amplitude $a_c(\alpha)$ decreases if the prey capturing rate α increases (Fig. 5), it seems reasonable to assume that in predator-prey systems with a Michaelis-Menten-Holling type ratio-dependent functional response such transitions appear with a greater probability if the prey capturing rate is greater. It remains to be seen whether such a trend has a meaning in nature systems.

The phenomenon is robust enough to survive a

modification of the noise, the trophic function as well as the prey's self-regulation mechanism. For example the noise can be either a trichotomous noise [15] or a more complicated telegraph process. Although the concrete formulas are different, the general picture of the colored-noise-induced transitions is the same as that encountered in Section 3.

Finally, we believe that the results discussed here provide a possible alternative scenario for transitions from an equilibrium state to a limit cycle (and the opposite way) observed in nature. We suggest that plankton pelagic communities (preys) and fish populations (predators) might be the best candidates in order to find some empirical evidence to this scenario. Undoubtedly, an ultimate verification of the phenomenon of pure colored-noise-induced transitions in natural ecosystems lies with experimentally minded ecologists.

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