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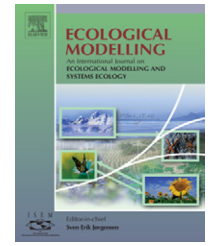

Modeling the dynamics of inhomogeneous natural rotifer populations under toxicant exposure

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ABSTRACT

Most population models assume that individuals within a given population are identical, that is, the fundamental role of variation is ignored. Here we develop a general approach to modeling heterogeneous populations with discrete evolutionary time step. The theory is applied to models of natural rotifer population dynamics. We show that under particular conditions the behavior of the inhomogeneous model possesses complex transition regimes, which depends both on the mean and the variance of the initial parameter distribution; the final state of the population depends on the least possible value from the domain of the parameter. The question of population persistence is discussed.

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1. Introduction

Due to ecological importance of zooplankton, a substantial amount of data exists on the abundance of natural populations in lakes, estuaries and coastal marine environments. A variety of mathematical models have been applied for modeling the dynamics of zooplankton populations (e.g., McCauley et al., 1996; Snell and Serra, 1998). Recently a particular class of mathematical models, extracted as deterministic dynamics components from noisy ecological time series was studied systematically (Berezovskaya et al., 2005). These models, which are discrete time maps by construction, were primarily developed to analyze the dynamics of natural rotifer populations and evaluate the ecological consequences of toxicant exposure.

Modeling population dynamics often involves balancing the competing requirements of realism and simplicity. On the side of simplicity, one has classical population models with discrete time, which have been extensively studied for decades (e.g., the pioneer works of Shapiro (1972) and May (1975), among many others). It is a well-known fact that these models can possess various dynamical behaviors varying from stable steady states and cycles to chaotic oscillations. These models keep track of the total population size and treat all individuals as identical. That is, the fundamental role of variation is ignored, and parameter values represent some averaged values while the information on variance and other characteristics are not taken into account. This, of course, simplifies the computation, albeit at the cost of realism. In recent years, several researchers have focused on generalizing continuous time population models in a way to allow for different individuals or subpopulations to have different growth or mortality rates (Karev, 2005, 2008; more abstract approach was developed earlier in works of Semenov, Okhonin, Gorban, see survey of Gorban (2005) for details and references). It was shown that recognition of heterogeneity may lead to unexpected and even counter-intuitive effects. Here we present a general framework to analyze the dynamics of inhomogeneous populations with discrete time steps, and apply it to the study of dynamical behavior of heterogeneous rotifer populations.

The paper is organized as follows. In Section 2 we summarize main results from Berezovskaya et al. (2005), which

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include parametric portrait of the model for population dynamics of rotifer populations, and discuss questions on population persistence and extinction. In Section 3 we formulate general framework for analyzing heterogeneous models with discrete time. In Section 4 we apply the theory of inhomogeneous maps to the model of rotifer population dynamics. In particular, we show that the knowledge of mean values of parameters is not sufficient for predicting the evolution and eventual fate of the population. Moreover, the behavior of populations with the same initial mean values of parameters and different variances can differ dramatically: one of the populations can go extinct while other can reach a stable stationary regime. Section 5 is devoted to discussion and conclusions.

2. The Consensus model

Methods developed to extract deterministic dynamics components from short noisy time series (Aksakaya et al., 1999) were applied to data from natural populations of nine rotifer species (Snell and Serra, 1998). Time series of a population density N_t (a number of organisms per liter at time t with time unit equals to 2 days) have been received. Using these series several phenomenological models have been checked for fitting. The best-fit model for 5 of 9 data sets (named the Consensus model) has the following scaled form:

$$N_{t+1} = N_t \exp\left\{-a + \frac{1}{N_t} - \frac{\gamma}{N_t^2}\right\} \tag{1}$$

where $a \geq 0$ is the parameter characterizing density-independent effects on the reproduction rate, which can be interpreted as an environmental press to rotifers (poor water quality, extreme temperature or toxicant exposure), and γ is the species-specific parameter. Berezovskaya et al. (2005) showed that depending on parameter values the asymptotic behavior of (1) can vary from equilibrium points to chaotic oscillations with usual period-doubling route to chaos. Moreover, model (1) possesses the property of bistability (strong Allee effect, e.g., Wang and Kot, 2001). This means that there exists a threshold level of population size such that if the total size of the population is less than this quantity the extinction of the population is certain. The diversity of behaviors of model (1) is associated with the complex form of the map. The main results of the analysis of (1) are summarized in its parametric portrait (Fig. 1a).

In Fig. 1a there are two domains (II and III) where persistence of the population is possible, though it should be noted that zero is a stable stationary point in these domains, i.e., if the total size of the population is lower than some threshold level, the extinction is certain. In domains I and IV any initial values of the population size lead to zero stable state, the population cannot survive. Different possible ways of population extinction if the parameters are varied were analyzed (see Berezovskaya et al., 2005, for details). What is important, model (1) has a density independent parameter a, which can be also interpreted as an average ability of an individual to reproduce under given toxicant exposure (compare with the above interpretation). If the population is highly heterogeneous, i.e., there are some individuals that can stand and reproduce under the conditions, and there are some for which pollution is mortal, one has to adjust the model in such a way to allow for different individuals have different reproduction rates.

3. Inhomogeneous maps theory

Let us assume that a population consists of individuals, each of those is characterized by its own parameter value $\mathbf{a} = (a_l, \ldots, a_k)$. These parameter values can take any particular value from set A. Let $n_t(a)$ be the density of the population at the moment t. Then the number of individuals having parameter values in set $\tilde{A} \subseteq A$ is given by $\tilde{N}_t = \int_{\tilde{A}} n_t(\mathbf{a})\,d\mathbf{a}$, and the total population size is $N_t = \int_A n_t(\mathbf{a})\,d\mathbf{a}$.

If a model with discrete time steps is applicable to the population, then in the next time instant $t+1$, we should have $n_{t+1}(\mathbf{a}) = W n_t(\mathbf{a})$, where $W \geq 0$ is the reproduction rate. In what follows we assume that the reproduction rate depends on the specific parameter value $\mathbf{a}$, and the total size of the population, i.e., $W = W(N_t, \mathbf{a})$. It means that we do not take into account possible mutations. The population dynamics is hence gov-

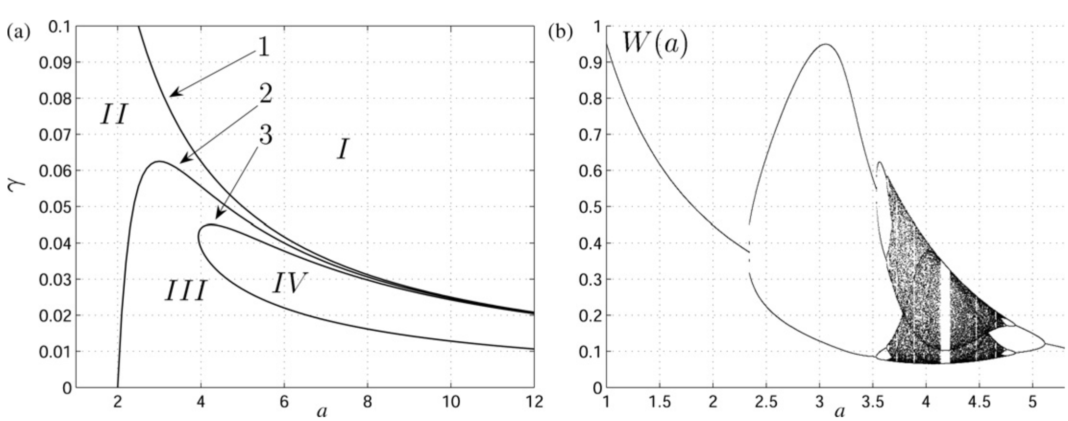

Fig. 1 – (a) Parametric portrait of model (1). The boundaries of the domains: $\gamma = 0$; (1) $\{\gamma | \gamma = 1/(4a)\}$; (2) $\{\gamma | \gamma = (a-2)/(4(a-1)^2)\}$; (3) the boundary of the 0-attracting domain. The domains are I—total extinction; II—bistability; III—oscillations and chaos and zero stable; IV—total extinction through aperiodic oscillations, zero stable (the 0-attracting domain). (b) Bifurcation diagram of (1) for $\gamma = 0.046$. W(a) is the set of observed states of the population for the given parameter values.