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Limit cycles in a food-chain with inhibition responses

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ABSTRACT

In this paper, by constructing a Lyapunov function, we show the global asymptotical stability of a three-dimensional food-chain model with inhibition response. We then using a corollary to center manifold theorem to show that the system undergoes a 3-D Hopf bifurcation, and obtain the existence of limit cycles for the three-dimensional model. The methods used here can be extended to many other 3-D differential systems.

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1. Introduction

The limit cycles of a mathematical model in natural systems correspond to the nonlinear oscillation phenomena of the system. In this paper, we first construct a Lyapunov function to show the global asymptotical stability of a three-dimensional food-chain model with inhibition response. Then we use a corollary to the center manifold theorem to prove the Hopf bifurcation, and obtain the existence of limit cycles for the 3-D model analytically. This food-chain model can be considered as two predators in the chemostat competing for a single renewable prey species with the predators consuming the prey in inhibition functional response.

The three-level food-chain was first studied by Rosenzweig in the famous paper on the paradox of enrichment [1], where he wrote "Man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance". Rosenzweig's analysis is based on a three-level food-chain composed of a logistic prey x_1, a predator x_2 and a super-predator x_3 with saturating functional response. The model which is called Rosenzweig–MacArthur takes the form:

$$\begin{aligned}
\frac{dx_1}{dt} &= \gamma x_1\left(1-\frac{x_1}{K}\right)-\frac{m_1x_1}{a_1+x_1}x_2,\\
\frac{dx_2}{dt} &= \left(\frac{m_1x_1}{a_1+x_1}-d_1\right)x_2-\frac{m_2x_2}{a_2+x_2}x_3,\\
\frac{dx_3}{dt} &= \left(\frac{m_2x_2}{a_2+x_2}-d_2\right)x_3,
\end{aligned}\tag{1.1}$$

where, γ is prey growth rate, K the prey carrying capacity; m_i, a_i, and d_i, $i = 1, 2$, are maximum predation rate, half saturation constant, and death rate of predator ($i = 1$), and super-predator ($i = 2$). The predators consume the prey with the functional response of Michaelis–Menten type $m_ix_i/(a_i + x_i)$, $i = 1, 2$, respectively.

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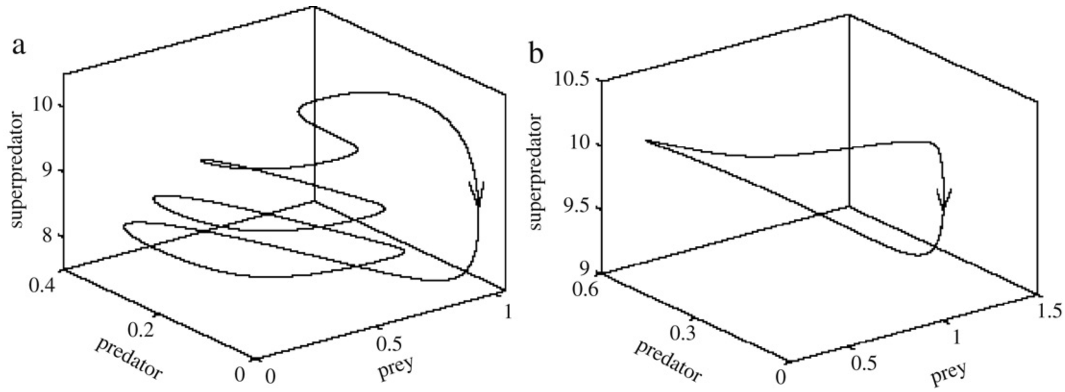

Fig. 1. Limit cycles of Rosenzweig–MacArthur three-level food-chain (x_1 is the prey, x_2, the predator, and x_3 the super-predator).

It has been shown by May [2], and Gilpin [3] that for low prey carrying capacities such food-chains settle to a positive equilibrium, while for higher carrying capacities the asymptotic regime is cyclic. The critical value K^* of the carrying capacity separating stationary from cyclic regimes corresponds to a supercritical Hopf bifurcation (Sarkar et al., [4]). In other words, the positive equilibrium loses stability when the carrying capacity is increased and, when it becomes unstable, the attractor becomes a stable limit cycle. For the Rosenzweig–MacArthur three-level food-chain model, numerical simulation for the limit cycles was provided by Gragnani, et al. [5] (see Fig. 1).

The three-level food-chain model has been studied extensively by many authors (see, for example, Chiu and Hsu [6], Hsu [7], Hsu and Huang [8], Hogeweg and Hesper [9], Scheffer [10], Hastings and Powell [11], McCann and Yodzis [12], Abrams and Roth [13], and Kuznetsov and Rinaldi [14], etc.). Such food chains have a very rich behavior, covering the whole spectrum of dynamic regimes, including chaos and nonlinear oscillation. Moreover, food chains with time responses increasing from bottom to top have cyclic regimes which are either low-frequency or high-frequency regimes. The first figure of Fig. 1 shows the low-frequency limit cycles which are characterized by large and slow variations of the super-predator and by high-frequency bursts of the prey and predator communities. By contrast, high-frequency limit cycles (as in the second figure of Fig. 1) are characterized by almost steady super-predator populations. Therefore, in conclusion, Rosenzweig–MacArthur food chains can be classified into five groups: those for which coexistence is not possible and those for which coexistence is stationary, cyclic at low-frequency, cyclic at high-frequency, and chaotic. (see Gragnani, et al., 1997 [5]).

Usually, the results of the three-level food-chain have been derived by analyzing the models in which the prey is logistic. It is of interest to see if such results hold also in the case where the prey feeds on a limiting nutrient S available in a pool. For this reason, the Rosenzweig–MacArthur food-chain can be complemented by an extra differential equation for the nutrient. Such an equation is simply the balance of the various flows regulating the nutrient concentration: inflow and outflow rates, nutrient recycling due to decomposition of dead individuals of the three populations, and nutrient uptake rate of the prey population. Assuming that the nutrient uptake per unit of prey is a Monod function of the nutrient, the model turns out to be a natural extension of the prey–predator chemostat model proposed by Canale [15] and later used in many studies of protozoan predation on bacteria and of aquatic ecosystems (see, for example, [5]). The three-level food-chain embedded in a chemostat by adding an extra state variable S denoting the concentration of the nutrient in the chemostat has the form:

$$\begin{aligned} \frac{dS}{dt} &= F_1(S, x_1, x_2, x_3), \\ \frac{dx_1}{dt} &= F_2(S, x_1, x_2, x_3), \\ \frac{dx_2}{dt} &= F_3(S, x_1, x_2, x_3), \\ \frac{dx_3}{dt} &= F_4(S, x_1, x_2, x_3). \end{aligned} \tag{1.2}$$

It is proved that the Rosenzweig–MacArthur model of three-level food-chain (1.1) is the limit system of the chemostat model (1.2) (see [5]). Therefore, the asymptotic behavior of the fourth order system (1.2) has a strong similarity. In order to analyze the four-order system (1.2), one can investigate the third order Rosenzweig–MacArthur model (1.1).

Since the limit cycles of the model correspond to the oscillatory or cyclic phenomena in natural system, an analytic proof of the existence of limit cycles for the model is necessary. However, to prove the existence of periodic solutions of an n-dimensional differential system when $n \geq 3$ is not easy. This is because the powerful tools in the plane system like Poincare–Bendixson theorem cannot be applied directly to the case of $n \geq 3$, in general. Moreover, in most of the food-chain models, the predators consume the prey with the functional response of monotonic type functions such as the Monod, or

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