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Top-predator interference and gestation delay as determinants of the dynamics of a realistic model food chain

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ABSTRACT

An attempt has been made to understand the role of top predator interference and gestation delay on the dynamics of a three species food chain model involving intermediate and top predator populations. Interaction between the prey and an intermediate predator follows the Volterra scheme (with Holling type IV functional response), while that between the top predator and its prey depends on Beddington–DeAngelis type functional response. Stability switches and Hopf-bifurcation occurs when the delay crosses some critical value. Model system exhibits irregular behavior when the interference is high or gestation period is larger than its critical value. Furthermore, the direction of Hopf-bifurcation and the stability of the bifurcating periodic solutions are determined using the center manifold theorem and normal form theory. Computer simulations have been carried out to illustrate the analytical findings. Different diagnostic tests, like, initial sensitivity, Lyapunov exponent, recurrence plot tests ensure the complex dynamical behavior of the model system. Finally, we observed the subcritical Hopf-bifurcation phenomena in the designed model system and the bifurcating periodic solution is unstable for the considered set of parameter values.

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1. Introduction

Time delays play important role on the dynamics of food chain model systems. They could cause a stable equilibrium to become unstable and also cause population to fluctuate. It often represents gestation times, incubation periods, transport delays or can simply lump complicated biological processes together, accounting only for the time required for these processes to occur. Kuang [1] mentioned that animals must take time to digest their food before further activities and responses take place. Freedman and Ruan [2] determined the stability of bifurcating solutions and Hopf-bifurcation in three species delayed food chain models, in which the prey exhibits group defense. Gopalsamy [3] and Kuang [1] studied the stability and oscillations in delay differential equations and its

application to population dynamics. Ma et al. [4] studied the stability and Hopf-bifurcation for a delayed three species Lotka–Volterra food chain model with time delay and spatial diffusion.

Food chain models incorporating mutual interference were first proposed by Hassell [5] and Rogers and Hassell [6] and mutual interference among predators and time delay due to gestation were proposed by Freedman and Rao [7] and Erbe and Freedman [8]. They observed that time delay do not necessarily destabilize the model system if there is other stabilizing effect (mutual interference) acting on the system and increasing delay may cause a bifurcation into periodic solutions. Multiple periodic solutions of delayed predator–prey system with Holling type IV functional response was first obtained by Chen [9] using the theory of coincidence degree. Dynamical complexities of a three species food chain model with Holling type IV predator response is investigated analytically as well as

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numerically in Upadhyay and Raw [10]. Also, Zhuang [11] demonstrates a three species food chain model on time scales with Monod–Haldane functional response and time delay. With the help of coincidence degree theory, Zhuang [11] establishes the existence of periodic solutions. Xu and Wang [12] investigated a delayed discrete three species food chain model with Beddington–DeAngelis (BD) type functional response. Liu et al. [13] studied the combined effect of two delays (maturation and gestation) and degree of predator interference on the dynamical behaviors of a BD type model. It has been shown that predator interference can stabilize the solution and multiperiodic and chaotic solutions may occur with the introduction of gestation delay. Also it is known from many previous work that predator's interference makes a system irregular from its regular state or vice versa [14–16].

A time delayed predator–prey model with prey dispersal and BD type functional response is investigated by Xu et al. [17]. Li and Wang [18] studied the Hopf-bifurcation for a delayed three species food chain model with BD type functional response and shown that Hopf-bifurcation occurs as the delay τ passes through a sequence of critical values. Ruan [19] presented a brief review on predator–prey models with discrete delay for both Kolmogorov and Non-Kolmogorov type model system. Meng et al. [20] investigated the stability and global Hopf-bifurcation consisting of a prey and two predators. Do et al. [21] proposed and analyzed a three species food chain model with Holling type II and BD type functional response. Zhang et al. [22] studied the bifurcation analysis of a delayed food chain model with hybrid type functional responses (Holling type II and BD type) proposed by Do et al. [21] and investigated the effect of time delay due to gestation of the middle predator and the top predator on the system. We have extended the model studied by Zhang et al. [22] by replacing the Holling type II functional response by Holling type IV and considering the Kolmogorov type system whereas Zhang et al. [22] has taken the Non-Kolmogorov type model system.

In the present work, we have investigated the complex dynamical behavior of a hybrid three-species delayed food chain model with Holling type IV and Beddington–DeAngelis functional responses. The paper is structured as follows: In Section 2, model system and their stability analysis is described, where as in Section 3, delayed model system and their Hopf-bifurcation has been discussed. In Section 4, direction and stability of Hopf bifurcation of the delayed model system is described. In Section 5, numerical simulation results with chaotic dynamics have been presented and at last, in Section 6, conclusions and discussions have been made.

2. Three species food chain model system

The model we analyze in this paper describes a tri-trophic food chain composed of a prey, whose population density is denoted by X , a predator whose population density is denoted by Y and a superpredator (or top predator), whose population density is denoted by Z . Before we introduce the model and dip into the thick of the rigorous analysis, we would like to present a brief sketch of the

construction of the model which may indicate the biological relevance of it [30]:

1. Behavior of the entire community is assumed to arise from the coupling of these interacting species where Z prey on Y and only on Y and Y prey on X . This is an interesting practical assumption from both mathematical and biological points of view.
2. We assume that in the absence of the predators the prey population density grows according to a logistic curve with carrying capacity $K(K > 0)$, and with an intrinsic growth rate constant $a_1(a_1 > 0)$.
3. We have considered a hybrid three species model system with Holling type-IV functional response for the species $(X; Y)$, and Beddington–DeAngelis type functional response for the species $(Y; Z)$.

The above considerations motivate us to introduce a tri-trophic food chain model under the framework of the following set of non-linear ordinary differential equations:

$$\begin{aligned} \frac{dX}{dt} &= X \left[a_1 \left(1 - \frac{X}{K} \right) - \frac{wY}{\frac{x^2}{j} + X + a} \right], \\ \frac{dY}{dt} &= Y \left[-a_2 + \frac{w_1 X}{\frac{x^2}{j} + X + a} - \frac{w_2 Z}{Y + D_2 + bZ} \right], \\ \frac{dZ}{dt} &= Z \left[-c + \frac{w_3 Y}{Y + D_2 + bZ} \right], \end{aligned} \quad (2.1)$$

where a_2 is the intrinsic death rate of the intermediate predator Y in absence of the food X ; Similarly, c is the intrinsic death rate of the top predator Z in the absence of the only food Y ; as the parameter j (which is the measure of the predator's immunity from or tolerance of the prey) decreases. The parameter a can be interpreted as the half saturation constant in the absence of any inhibitory effect. D_2 and b represent the protection provided to the prey by its environment and intensity of interference between individuals of the specialist predator respectively. w, w_1, w_2, w_3 are the maximum values which per capita growth rate can attain. All the parameters are considered to be positive constants.

2.1. Equilibrium and stability analysis of non-delayed model system

Model system (2.1) has four possible non-negative equilibria, namey $E_0(0, 0, 0); E_x(K, 0, 0); E_{xy}(x_3, y_3, 0)$ and $E_{xyz}(x_4, y_4, z_4)$.

- (i) Trivial equilibrium $E_0(0, 0, 0)$ exist. The eigenvalues of the variational matrix around E_0 are $0, 0, -c$. Therefore, E_0 is a non-hyperbolic point.
- (ii) Equilibrium point $E_x(K, 0, 0)$ exist. The eigenvalues of the variational matrix around E_x are $0, -c, -a_1$. Therefore, E_x is also a non-hyperbolic point.
- (iii) Top-predator free equilibrium point $E_{xy}(x_3, y_3, 0)$ exist. From second equation of (2.1)

$$-a_2 + \frac{\omega_1 x_3}{\frac{x_3^2}{j} + x_3 + a} = 0.$$

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