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Full Length Research Paper

Bifurcation and chaos of a three-species Lotka-Volterra food-chain model with spatial diffusion and time delays

Liying Cai*, Xisheng Jia, Jianmin Zhao and Zhonghua Cheng

Department of Equipment Command and Management, Mechanical Engineering College, Shijiazhuang 050003, China.

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In this paper, a three-species Lotka-Volterra food-chain model with spatial diffusion and time delays is investigated. We first analyze the local stability of the steady states and the existence of Hopf bifurcation to this system under homogeneous Neumann boundary conditions. We consider the effects of impulses on the dynamics of the above food-chain model without spatial diffusion. Numerical simulations show that the system with constant periodic impulsive perturbations admits rich complex dynamics.

Key words: Hopf bifurcation, food chain, reaction diffusion, delay, stability, chaos.

INTRODUCTION

The dynamic relationship between predators and their preys has long been and will continue to be one of the dominant themes in both ecology and mathematical ecology due to its universal existence and importance. The classical Lotka-Volterra type systems are very important in the models of multi-species population dynamics and have been studied by many authors for example (Huang and Zou, 2002; Kuang, 1993; Liu et al., 2005; Xu et al., 2004; Yan and Chua, 2006).

Recently, the effect of spatial dispersion on population dynamics has received considerable attention. In this situation, the governing equations for the population densities are described by a system of reaction-diffusion equations for example (Cosner and Lazer, 1984; Gan et al., 2009; Pao, 2003, 2004, 2007; Tang and Zhou, 2007). On the other hand, time delays of one type or another have been incorporated into biological models by many researchers; we refer to the monographs of Gopalsamy (1992), Kuang Kuang (1993) and references cited therein for general delayed biological systems. In general, delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and cause the populations to fluctuate for example, (Beretta and Kuang, 1998; Busenberg and Huang,1996; Faria, 2001; Gan et al., 2009; Song et al., 2004). Time delay due to gestation is a common example, because generally the consumption of prey by the predator throughout its past history governs the present birth rate of the predator. Therefore, more realistic models of population interactions should take into account the effects of time delays. In this paper, motivated by the above discussions, we are concerned with the following three-species food chain model with spatial diffusion and time delays (Xu and Zhien, 2009; Kaifa et al., 2007):

$$\begin{cases} \frac{\partial u}{\partial t} = D_1 \frac{\partial_2 u}{\partial x^2} + u(t,x)(r_1 - a_{11}u(t,x) - a_{12}v(t,x)) \\ \frac{\partial v}{\partial t} = D_2 \frac{\partial^2 v}{\partial x^2} + v(t,x)(-r_2 + a_{21}u(t-\tau,x) - a_{22}v(t,x) - a_{23}w(t,x)) \\ \frac{\partial w}{\partial t} = D_3 \frac{\partial^2 w}{\partial x^2} + w(t,x)(-r_3 + a_{32}v(t-\tau,x) - a_{33}w(t,x)) \end{cases} \quad (1)$$

with initial conditions;

$$u(t,x) = \rho_1(t,x), v(t,x) = \rho_2(t,x), w(t,x) = \rho_3(t,x)$$
$$t \in [-\tau, 0], x \in \overline{\Omega} \quad (2)$$

In system (1)-(2), Ω is a bounded domain in R^n with smooth boundary $\partial\Omega$, The data $\rho_i(t,x)(i=1,2,3)$ are nonnegative and HÖlder continuous and satisfy $\partial\rho_i/\partial x = 0$ in $(-\infty,0) \times \overline{\Omega}$. $u(t,x), v(t,x)$ and $w(t,x)$ represent the densities of the prey, predator and top predator population at time t, and location x respectively. The parameters $a_{11}, a_{12}, a_{21}, a_{22}, a_{23}, a_{32}$,

*Corresponding author. E-mail: lixiaodong11111@sina.com.

a_{33}, τ D_i, $r_i (i = 1,2,3)$ are positive constants.

We note that impulsive differential equations are suitable for the mathematical simulation of evolutionary process in which the parameters undergo relatively long periods of smooth variation followed by a short-term rapid change (that is, jumps) in their values. Recently, equations with impulsive effect have been found in almost every domain of applied science. Numerous examples are given in Bainovs and his collaborator's book (Bainov and Simeonov, 1993; Lakshmikantham et al., 1989). Some impulsive differential equations have recently been introduced in population dynamics in relation to impulsive birth (Roberts and Kao, 1998; Tang and Chen, 2002), impulsive vaccination (D'Onofrio, 2002; Shulgin et al., 1998), chemotherapeutic treatment of disease (Lakmeche and Arino, 2000; Panetta, 1996), and population ecology (Ballinger and Liu, 1997). Motivated by the work above, in this paper, we further discuss the effect of impulses on the dynamics of Equation (1). To this end, we discuss the following impulsive equations:

$$\begin{cases} \left.\begin{array}{l} \dot{u}(t) = u(t,x)(r_1 - a_{11}u(t,x) - a_{12}v(t,x)) \\ \dot{v}(t) = v(t,x)(-r_2 + a_{21}u(t-\tau,x) - a_{22}v(t,x) - a_{23}w(t,x)) \\ \dot{w}(t) = w(t,x)(-r_3 + a_{32}v(t-\tau,x) - a_{33}w(t,x)) \end{array}\right\} t \neq nT \\ \left.\begin{array}{l} \Delta u(t) = u(t^+) - u(t^-) = 0 \\ \Delta v(t) = v(t^+) - v(t^-) = 0 \\ \Delta w(t) = w(t^+) - w(t^-) = \zeta w(t^+) \end{array}\right\} t = nT \end{cases} \quad (3)$$

LOCAL STABILITY AND HOPF BIFURCATION

In this section, we investigate the local stability of the steady states and the existence of Hopf bifurcation to Equation (1) with the initial conditions in Equation (2) and the homogeneous Neumann boundary conditions:

$$\frac{\partial u(t,x)}{\partial x} = \frac{\partial v(t,x)}{\partial x} = \frac{\partial w(t,x)}{\partial x} = 0, \quad t \geq 0, x \in \partial\Omega$$

where $\partial/\partial x$ denotes the outward normal derivative on $\partial\Omega$, the homogeneous Neumann boundary conditions imply that the populations do not move across the boundary $\partial\Omega$.

It is easy to show that Equation (1) always has a trivial steady state $E_0(0,0,0)$ and a semi-trivial steady state $E_1(r_1/a_{11},0,0)$. If $r_1 a_{21} > r_2 a_{11}$, Equation (1) has a semi-trivial steady state $E_2(s_1,s_2,0)$, where

$$s_1 = \frac{r_1 a_{22} + r_2 a_{12}}{a_{11}a_{22} + a_{12}a_{21}}, \quad s_2 = \frac{r_1 a_{21} - r_2 a_{11}}{a_{11}a_{22} + a_{12}a_{21}}$$

If the following holds:

$$(H_1) \quad a_{21}a_{32}r_1 - a_{11}a_{32}r_2 - a_{12}a_{21}r_3 - a_{11}a_{22}r_3 > 0$$

system (1) has a unique positive steady state $E^*(k_1,k_2,k_3)$, where

$$k_1 = \frac{a_{22}a_{33}r_1 + a_{23}a_{32}r_1 + a_{12}a_{33}r_2 - a_{12}a_{23}r_3}{a_{12}a_{21}a_{33} + a_{11}a_{22}a_{33} + a_{11}a_{23}a_{32}}$$

$$k_2 = \frac{a_{21}a_{33}r_1 - a_{11}a_{33}r_2 + a_{11}a_{23}r_3}{a_{12}a_{21}a_{33} + a_{11}a_{22}a_{33} + a_{11}a_{23}a_{32}}$$

$$k_3 = \frac{a_{21}a_{33}r_1 - a_{11}a_{32}r_2 - a_{12}a_{21}r_3 - a_{11}a_{22}r_3}{a_{12}a_{21}a_{33} + a_{11}a_{22}a_{33} + a_{11}a_{23}a_{32}}$$

Let $0 = \mu_1 < \mu_2 < \cdots$ be the eigenvalues of the operator $-\Delta$ on Ω with homogeneous Neumann boundary conditions, and $E(\mu_i)$ be the eigenspace corresponding to μ_i in $C^1(\Omega)$. Let $\mathrm{X} = [C^1(\Omega)]^3$, $\{\phi_{ij}; j = 1,\cdots,\dim E(\mu_i)\}$ be an orthonormal basis of $E(\mu_i)$, and $\mathrm{X}_{ij} = \{c\phi_{ij} | c \in R^3\}$. Then

$$\mathrm{X} = \mathop{\oplus}_{i=0}^{\infty} \mathrm{X}_i \text{ and } \mathrm{X} = \mathop{\oplus}_{j=0}^{\dim E(\mu_i)} \mathrm{X}_{ij}$$

Let $D = diag(D_1,D_2,D_3)$, $Z = (u,v,w)$, $LZ = D\Delta Z + \varsigma(\hat{E})Z$, where

$$\varsigma(\hat{E})Z = \begin{pmatrix} r_1 - 2a_{11}u^0 & -a_{12}u^0 & 0 \\ 0 & -r_2 + a_{21}u^0 - 2a_{22}v^0 - a_{23}w^0 & -a_{23}v^0 \\ 0 & 0 & -r_3 + a_{32}v^0 - 2a_{33}w^0 \end{pmatrix} \times \begin{pmatrix} u(t,x) \\ v(t,x) \\ w(t,x) \end{pmatrix} + \begin{pmatrix} 0 & 0 & 0 \\ a_{21}v^0 & 0 & 0 \\ 0 & a_{32}w^0 & 0 \end{pmatrix} \begin{pmatrix} u(t-\tau,x) \\ v(t-\tau,x) \\ w(t-\tau,x) \end{pmatrix}$$

And $\hat{E}(u^0,v^0,w^0)$ represents any feasible uniform steady state of Equation (1). The linearization of system (1) at $\hat{E}$ is of the form $Z_t = LZ$. For each $i \geq 1$, X_i is invariant under the operator L, and λ is an eigenvalue of L if and only if it is an eigenvalue of the matrix $-\mu_i D + \varsigma(\hat{E})$ for some $i \geq 1$, in which case, there is an eigenvector in X_i. The characteristic equation of $-\mu_i D + \varsigma(E_0)$ is of the form:

$$(\lambda + \mu_i D_1 - r_1)(\lambda + \mu_i D_2 + r_2)(\lambda + \mu_i D_3 + r_3) = 0 \quad (4)$$

Clearly, for $i = 1$, Equation (4) always has a positive real root r_1. Therefore, there is a characteristic root λ, with positive real part in the spectrum of *L*. Accordingly, the trivial uniform steady state $E_0(0,0,0)$ is always unstable. The characteristic equation of $-\mu_i D + \varsigma(E_1)$ is of the form

$$(\lambda+\mu_i D_1+r_1)(\lambda+\mu_i D_2+r_2-a_{21}r_1/a_{11})(\lambda+\mu_i D_3+r_3)=0 \quad (5)$$

Clearly, for any $i \geq 1$, Equation (5) always has two negative real roots $-\mu_i D_1 - r_1$ and $-\mu_i D_3 - r_3$. Its other root is $-\mu_i D_2 - r_2 + a_{21}r_1/a_{11}$.

If $r_1 a_{21} > r_2 a_{11}$, $-r_2 + a_{21}r_1/a_{11} > 0$ .Hence, when $i=1$, Equation (5) has a positive real root. Therefore, there is a characteristic root λ with positive real part in the spectrum of L .Accordingly, if $r_1 a_{21} - r_2 a_{11} > 0$, $E_1(r_1/a_{11},0,0)$ is unstable.

If $r_1 a_{21} < r_2 a_{11}$, $-\mu_i D_2 - r_2 + a_{21}r_1/a_{11} < 0$ for any $i \geq 1$ .Therefore, all characteristic roots λ are negative constants in the spectrum of L. Accordingly, if $r_1 a_{21} < r_2 a_{11}$, $E_1(r_1/a_{11},0,0)$ is locally asymptotically stable. The characteristic equation of $-\mu_i D + \varsigma(E_2)$ is of the form

$$(\lambda+\mu_i D_3+r_3-a_{32}s_2)((\lambda+\mu_i D_1+a_{11}s_1)(\lambda+\mu_i D_2+a_{22}s_2)+a_{12}a_{21}s_1 s_2 e^{-\lambda\tau})=0 \quad (6)$$

If (H_1) holds, for $i=1$, $-\mu_i D_3 - r_3 + a_{32}s_2 > 0$, Equation(6) has a positive real root. Therefore, there is a characteristic root λ with positive real part in the spectrum of L .Accordingly, if (H_1) holds, $E_2(s_1,s_2,0)$ is unstable. If the following (H_2) holds: $a_{21}a_{32}r_1 - a_{11}a_{32}r_2 - a_{12}a_{21}r_3 - a_{11}a_{22}r_3 < 0$

For $i \geq 1$, Equation (6) always has a negative root $-\mu_i D_3 - r_3 + a_{32}s_2$. Its other roots are determined by the following equation:

$$\lambda^2 + a_1\lambda + a_0 + b_0 e^{-\lambda\tau} = 0 \quad (7)$$

Where $a_0 = (\mu_i D_1 + a_{11}s_1)(\mu_i D_2 + a_{22}s_2)$, $a_1 = \mu_i D_1 + a_{11}s_1 + \mu_i D_2 + a_{22}s_2$, $b_0 = a_{12}a_{21}s_1 s_2$. It is easy to see that the roots of Equation (7) are negative real constants when $\tau = 0$, then $E_2(s_1,s_2,0)$ is locally asymptotically stable when $\tau = 0$. If $i\sigma(\sigma>0)$ is a solution of Equation (7), separating real and imaginary parts, we can derive that

$$\begin{cases} \sigma^2 - a_0 = b_0\cos\sigma\tau \\ a_1\sigma = b_0\sin\sigma\tau \end{cases} \quad (8)$$

Squaring and adding the two equations of Equation (8), it follows that

$$\sigma^4 + (a_1^2 - 2a_0)\sigma^2 + a_0^2 - b_0^2 = 0 \quad (9)$$

If $a_{11}a_{22} > a_{12}a_{21}$, we have $a_1^2 - 2a_0 > 0$ and $a_0^2 - b_0^2 > 0$, then Equation (9) have no positive roots for all $i \geq 1$. Therefore, all characteristic roots λ are negative constants in the spectrum of L. Accordingly, if (H_2) holds and $a_{11}a_{22} > a_{12}a_{21}$, $E_2(S_1,S_2,0)$ is locally asymptotically stable for all $\tau > 0$.

If $a_{11}a_{22} < a_{12}a_{21}$, we have $a_1^2 - 2a_0 > 0$ and $a_0^2 - b_0^2 < 0$, then Equation (9) have one positive root σ_0 for $i=1$. From Equation (8), we obtain

$$\cos\sigma_0\tau = \frac{\sigma^2 - a_0}{b_0}$$

Thus, if we denote

$$\tau_j^* = \frac{1}{\sigma_0}\left\{\arccos\left(\frac{\sigma^2 - a_0}{b_0}\right) + 2j\pi\right\} \quad (10)$$

Where $j = 0,1,2,\cdots$, then $\pm\sigma_0$ is a pair of pure imaginary roots of Equation (8) with τ_j^*. Define $\tau^* = \tau_o^*$

When $\tau = \tau_j^*$, for $i=1$, Equation (7)has a pair of purely imaginary roots $\pm\sigma_0$ and all roots of Equation (7) have negative real parts for $i \geq 2$. Noting that if (H_2) holds, the positive uniform steady state E_2 is locally stable when $\tau = 0$, by the general theory on characteristic equations of delay differential equations from (Kuang,1993) (Theorem 4.1), E_2 remains stable for $\tau < \tau^*$.

We now claim that

$$\left.\frac{d(\mathrm{Re}\,\lambda)}{d\tau}\right|_{\tau=\tau^*} > 0$$

This will signify that there exists at least one eigenvalue with positive real part for $\tau > \tau^*$. Moreover, the conditions for the existence of a Hopf bifurcation (Hale, 1977) are then satisfied yielding a periodic solution. To this end, differentiating Equation (7) with respect τ, we obtain

$$2\lambda\frac{d\lambda}{d\tau} + a_1\frac{d\lambda}{d\tau} - b_0\tau e^{-\lambda\tau}\frac{d\lambda}{d\tau} = b_0\lambda e^{-\lambda\tau}$$

Hence, we drive that

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{a_1}{-\lambda(\lambda^2 + a_1\lambda + a_0)} - \frac{2}{\lambda^2 + a_1\lambda + a_0} - \frac{\tau}{\lambda}$$

It therefore follows that

$$sign\left\{\frac{d(\mathrm{Re}\,\lambda)}{d\tau}\right\}_{\lambda=i\sigma_0} = sign\left\{\mathrm{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right\}_{\lambda=i\sigma_0} = sign\left\{\frac{2\sigma_0^2 + a_1^2 - 2a_0}{a_1\sigma_0^2 + (\sigma_0^2 - a_0)^2}\right\} \quad (11)$$

Noting that $a_1^2 - 2a_0 > 0$, it follows that

$$\left.\frac{d(\mathrm{Re}\,\lambda)}{d\tau}\right|_{\tau=\tau^*,\sigma=\sigma_0} > 0$$

Therefore, the transversal condition holds. From Equation (11), we know that a Hopf bifurcation occurs at $\sigma = \sigma^0$, $\tau = \tau^*$.

The characteristic equation of $-\mu_i D + \varsigma(E^*)$ is of the form

$$\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + (q_1\lambda + q_0)e^{-\lambda\tau} = 0 \quad (12)$$

where

$$p_0 = (\mu_i D_1 + a_{11}k_1)(\mu_i D_2 + a_{22}k_2)(\mu_i D_3 + a_{33}k_3)$$

$$p_1 = (\mu_i D_1 + a_{11}k_1)(\mu_i D_2 + a_{22}k_2) + (\mu_i D_2 + a_{22}k_2)(\mu_i D_3 + a_{33}k_3) + (\mu_i D_1 + a_{11}k_1)(\mu_i D_3 + a_{33}k_3)$$

$$p_2 = (\mu_i D_1 + a_{11}k_1) + (\mu_i D_2 + a_{22}k_2) + (\mu_i D_3 + a_{33}k_3)$$

$$q_0 = a_{12}a_{21}k_1k_2(\mu_i D_3 + a_{33}k_3) + a_{23}a_{32}k_2k_3(\mu_i D_1 + a_{11}k_1)$$

$$q_0 = a_{12}a_{21}k_1k_2 + a_{23}a_{32}k_2k_3$$

When $\tau = 0$, Equation (12) becomes

$$\lambda^3 + p_2\lambda^2 + (p_1 + q_1)\lambda + p_0 + q_0 = 0 \quad (13)$$

It is easy to verify that $p_2 > 0$, $p_0 + q_0 > 0$ and $(p_1 + q_1)p_2 > p_0 + q_0$. Then it follows from Hurwitz criterions that all roots of Equation (13) have negative parts. Hence, the positive uniform steady state E^* is locally asymptotically stable when $\tau = 0$.

If $i\omega(\omega > 0)$ is a solution of Equation (12), separating real and imaginary parts, we derive that:

$$\begin{cases} -\omega^3 + p_1\omega = q_0 \sin\omega\tau - q_1\omega\cos\omega\tau \\ p_2\omega^2 - p_0 = q_0\cos\omega\tau + q_1\omega\sin\omega\tau \end{cases} \quad (14)$$

Squaring and adding Equations(14), it follows that

$$\omega^6 + (p_2^2 - 2p_1)\omega^4 + (p_1^2 - 2p_0p_2 - q_1^2)\omega^2 + p_0^2 - q_0^2 = 0 \quad (15)$$

Let $z = \omega^2$, Equation (15) becomes

$$z^3 + (p_2^2 - 2p_1)z^2 + (p_1^2 - 2p_0p_2 - q_1^2)z + p_0^2 - q_0^2 = 0 \quad (16)$$

In the following, we need to seek conditions under which Equation (16) has at least one positive root. Denote

$$h(z) = z^3 + (p_2^2 - 2p_1)z^2 + (p_1^2 - 2p_0p_2 - 2q_1^2)z + p_0^2 - q_0^2 \quad (17)$$

If the following holds:

(H_3) $a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{11}a_{23}a_{32} > 0$

It is easy to verify that $p_2^2 - 2p_1 > 0, p_0^2 - q_0^2 > 0$ and $p_1^2 - 2p_0p_2 - q_1^2 > 0$ for all $i \geq 1$. Hence, Equation (15) has no positive roots in this case.

If the following holds:

(H_4) $a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{11}a_{23}a_{32} < 0$ we have $p_0^2 - q_0^2 = k_1k_2k_3(a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{11}a_{23}a_{32})(p_0 + q_0) < 0$ and $\lim_{t\to\infty} h(z) = \infty$ for $i = 1$, then Equation (15) has at least one positive root. Hence, Equation (12) has a pair of purely imaginary roots $\pm i\omega_0$, and all roots of Equation (12)have negative real parts for $i \geq 2$.

Suppose that Equation (16)has positive roots. Without loss of generality, we assume that it has three positive roots, defined by z_1, z_2 and z_3 respectively. Then Equation (15) has three positive roots $\omega_1 = \sqrt{z_1}$, $\omega_2 = \sqrt{z_2}$ and $\omega_3 = \sqrt{z_3}$. From (14), we have

$$\cos\omega\tau = \frac{q_0(p_2\omega^2 - p_0) + q_1(\omega^2 - p_1)\omega^2}{q_0^2 + q_1^2\omega^2}$$

Thus, if we denote

$$\tau_k^{(j)} = \frac{1}{\omega_k}\left\{\arccos\left(\frac{q_0(p_2\omega^2 - p_0) + q_1(\omega^2 - p_1)\omega^2}{q_0^2 + q_1^2\omega^2}\right) + 2j\pi\right\} \quad (18)$$

Where $k = 1,2,3; j = 0,1,\cdots$, then $\pm\omega_k$ is a pair of pure imaginary roots of Equation (14) with $\tau_k^{(j)}$. Define

$$\tau_0 = \tau_{k_0}^{(0)} = \min_{k\in\{1,2,3\}}\left\{\tau_k^{(0)}\right\}, \quad \tau < \tau_0 \quad (19)$$

Noting that the positive uniform steady state E^* is locally stable when $\tau = 0$, by the general theory on characteristic equations of delay differential equations from (Theorem 4.1), E^* remains stable for $\tau < \tau_0$. We now claim that

$$\left.\frac{d(\mathrm{Re}\,\lambda)}{d\tau}\right|_{\tau=\tau_0} > 0$$

Differentiating Equation (12) with respect τ, it follows that\

$$(3\lambda^2 + 2p_2\lambda + p_1)\frac{d\lambda}{d\tau} + q_1e^{-\lambda\tau}\frac{d\lambda}{d\tau} - \tau(q_1\lambda + q_0)e^{-\lambda\tau}\frac{d\lambda}{d\tau} = \lambda(q_1\lambda + q_0)e^{-\lambda\tau}$$

Hence, we drive that

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{3\lambda^2 + 2p_2\lambda + p_1}{\lambda(q_1\lambda + q_0)e^{-\lambda\tau}} + \frac{q_1}{(q_1\lambda + q_0)} - \frac{\tau}{\lambda}$$

$$= \frac{3\lambda^2 + 2p_2\lambda + p_1}{-\lambda(\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} + \frac{q_1}{\lambda(q_1\lambda + q_0)} - \frac{\tau}{\lambda}$$ It therefore follows that

$$sign\left\{\frac{d(\mathrm{Re}\lambda)}{d\tau}\right\}_{\lambda=i\omega_0} = sign\left\{\mathrm{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right\}_{\lambda=i\omega_0}$$

$$= sign\left\{\frac{3\omega_0^4 + 2(p_2^2 - 2p_1^2)\omega_0^2 + p_1^2 - 2p_0p_2 - q_1^2}{q_0^2 + q_1^2\omega_0^2}\right\}$$

Noting that $p_2^2 - 2p_1 > 0$ and $p_1^2 - 2p_0p_2 - q_1^2 > 0$, it follows that

$$\frac{d(\mathrm{Re}\,\lambda)}{d\tau}\Big|_{\tau=\tau_0,\omega=\omega_0} > 0$$

Therefore, the transversal condition holds and a Hopf bifurcation occurs at E^* when $\omega = \omega_0$, $\tau = \tau_0$. We therefore obtain the following results.

RESULTS

Theorem 2.1

Let τ^* and τ_0 *be* defined by Equation (11) and Equation(19)*,* respectively. For Equation (1) we have

(i) The trivial uniform steady state $E_0(0,0,0)$ is always unstable*.*

(ii) If $r_1a_{21} < r_2a_{11}$,the semi-trivial steady state $E_1(r_1/a_{11},0,0)$ is locally asymptotically stable*; if* $r_1a_{21} > r_2a_{11}$, E_1 is unstable*.*

(iii) Let $r_1a_{21} > r_2a_{11}$. If (H_2) holds and $a_{11}a_{22} > a_{12}a_{21}$ the semi-trivial steady state $E_2(s_1,s_2,0)$ is locally asymptotically stable for all $\tau \geq 0$ *; if* (H_1) holds, E_2 is unstable for all $\tau \geq 0$; *if* (H_2) *holds and* $a_{11}a_{22} < a_{12}a_{21}$, E_2 *is* locally asymptotically stable *when* $0 \leq \tau < \tau^*$ and is unstable when $\tau > \tau^*$; further, Equation (1) undergoes a Hopf bifurcation at E_2 *when* $\tau = \tau^*$.

(iv) Let (H_1) hold. If (H_3) holds, the positive uniform steady state $E^*(k_1,k_2,k_3)$ is locally asymptotically stable for all $\tau \geq 0$ *;* if (H_4) holds, the positive uniform steady state E^* is asymptotically stable when $0 \leq \tau < \tau_0$ and is unstable when $\tau > \tau_0$ *;* further, Equation (1) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$. We now give two examples to illustrate the main results.

Example 1

In Equation (1), we set $D_1 = D_2 = D_3 = 1$, $r_1 = 2, r_2 = r_3 = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{12} = 3$, $a_{23} = 0.5$, $a_{21} = 0.6$, $a_{32} = 0.7$. It is easy to show that Equation (1) has three steady states $E_0(0,0,0), E_1(20/3,0,0)$ and $E_2(10/9, 5/9, 0)$. By Theorem 2.1 we see that E_0 and E_1 are unstable for all $\tau > 0$, E_2 is asymptotically stable when $0 \leq \tau < \tau^* = 0.4676$ and the bifurcation occurs when τ crosses τ^* to the right ($\tau > \tau^*$). These facts are illustrated by the numerical simulations in Figures 1 and 2.

Example 2

In Equation (1), we let $D_1 = D_2 = D_3 = 1$, $r_1 = 2$, $r_2 = r_3 = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{12} = a_{23} = 0.5$, $a_{21} = 0.6$, $a_{32} = 0.7$ .It is easy to show that system (1.1) has four steady states $E_0(0,0,0)$, $E_1(20/3,0,0)$, $E_2(85/39, 35/13, 0)$ and $E^*(415/111, 65/37, 90/37)$. It follows from Theorem 2*:*1 that E_0 , E_1 , E_2 are unstable for all $\tau > 0$, E^* is asymptotically stable when $0 \leq \tau < \tau_0 = 0.4749$ and the bifurcation takes place when τ crosses $\tau^*$to the right ($\tau > \tau_0$). These facts are illustrated by the numerical simulations in Figures 3 and 4.

Chaotic behavior in Equation (3)

The influences of τ may be documented by stroboscopically sampling some of the variables over a range of τ values.

In Equation (3), we let $r_1 = 2$, $r_2 = r_3 = a_{12} = a_{23} = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{21} = 0.6$, $a_{32} = 0.7$, $\varsigma = 0.8$, $T = 2$, $0.5 \leq \tau \leq 0.9$.

The influences of τ may be documented by stroboscopically sampling some of the variables over a range of τ values. We numerically integrate Equation (3) for 500 pulsing cycles at each value of τ. For each τ, we plot the last 100 measures of prey u, predator v and top predator w. Since we sample at forcing period, the *T*-periodic solutions appear as fixed points, the 2*T*-periodic solutions appear as two cycles, and so forth. The resulting bifurcation diagrams (Figure 5) clearly show that: with the increasing of τ from 0.5 to 0.9, Equation (3) experiences process of cycles $\rightarrow$ periodic doubling cascade $\rightarrow$ chaos (Figure 6). This periodic-doubling route to chaos is the hallmark of the logistic and Ricker maps

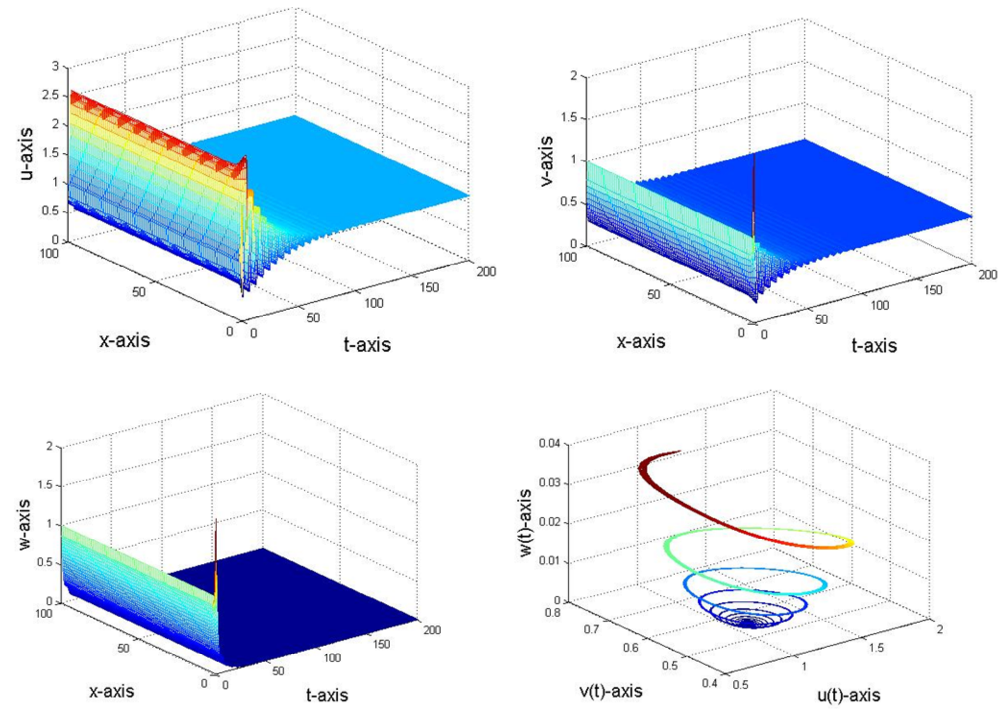

Figure 1. The temporal solution found by numerical integration of problem (1.1)-(1.2) with $D_1 = D_2 = D_3 = 1$, $r_1 = 2$, $r_2 = r_3 = a_{23} = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{12} = 3,\ a_{21} = 0.6$, $a_{32} = 0.7$, $\tau = 0.2$ and $\rho_1(t,x) = \rho_2(t,x) = \rho_3(t,x) = 1 + e^{-20x}$, $t \in [-0.2, 0]$.

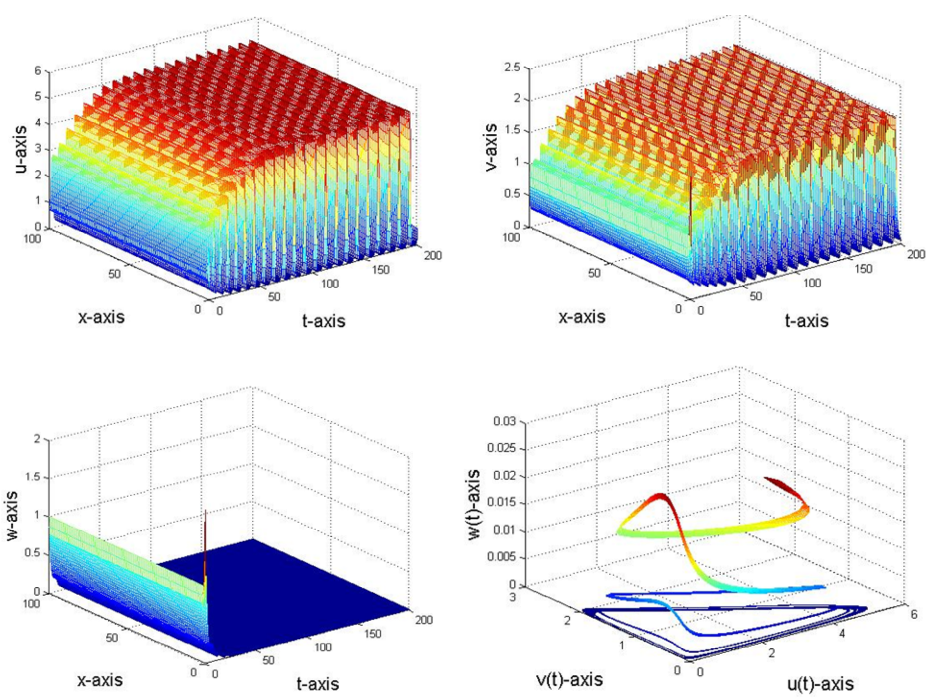

Figure 2. The temporal solution found by numerical integration of problem (1.1)-(1.2) with $D_1 = D_2 = D_3 = 1$, $r_1 = 2$, $r_2 = r_3 = a_{23} = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{12} = 3,\ a_{21} = 0.6$, $a_{32} = 0.7$, $\tau = 0.6$ and $\rho_1(t,x) = \rho_2(t,x) = \rho_3(t,x) = 1 + e^{-20x}$, $t \in [-0.6, 0]$.

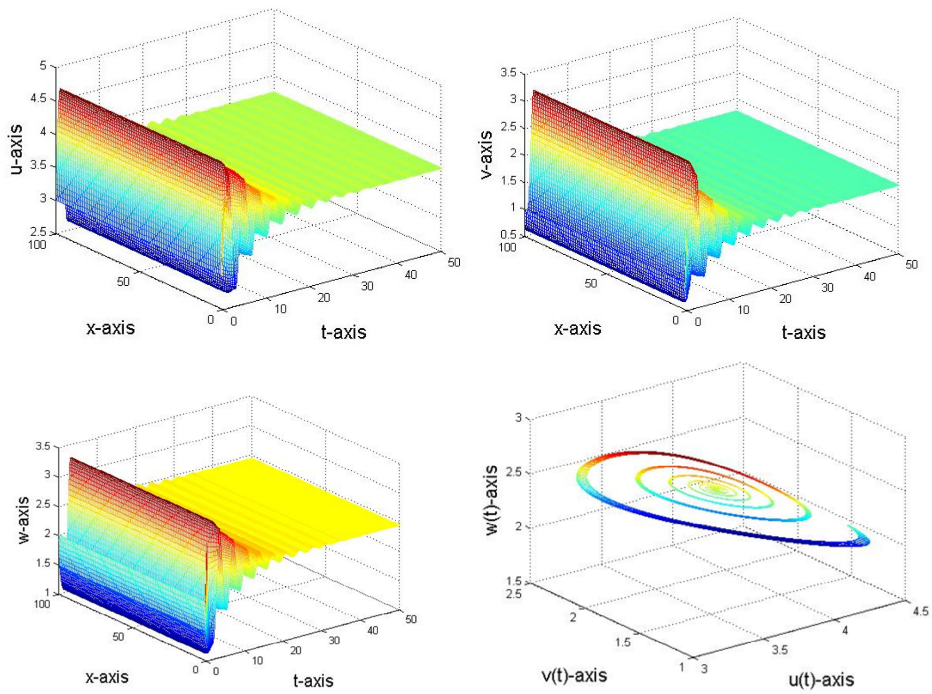

Figure 3. The temporal solution found by numerical integration of problem (1.1)-(1.2) with $D_1 = D_2 = D_3 = 1$, $r_1 = 2$, $r_2 = r_3 = a_{12} = a_{23} = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{21} = 0.6$, $a_{32} = 0.7$, $\tau = 0.3$, and $\rho_1(t,x) = 3 + e^{-20x}$, $\rho_2(t,x) = 1 + e^{-20x}$, $\rho_3(t,x) = 2 + e^{-20x}$, $t \in [-0.3, 0]$.

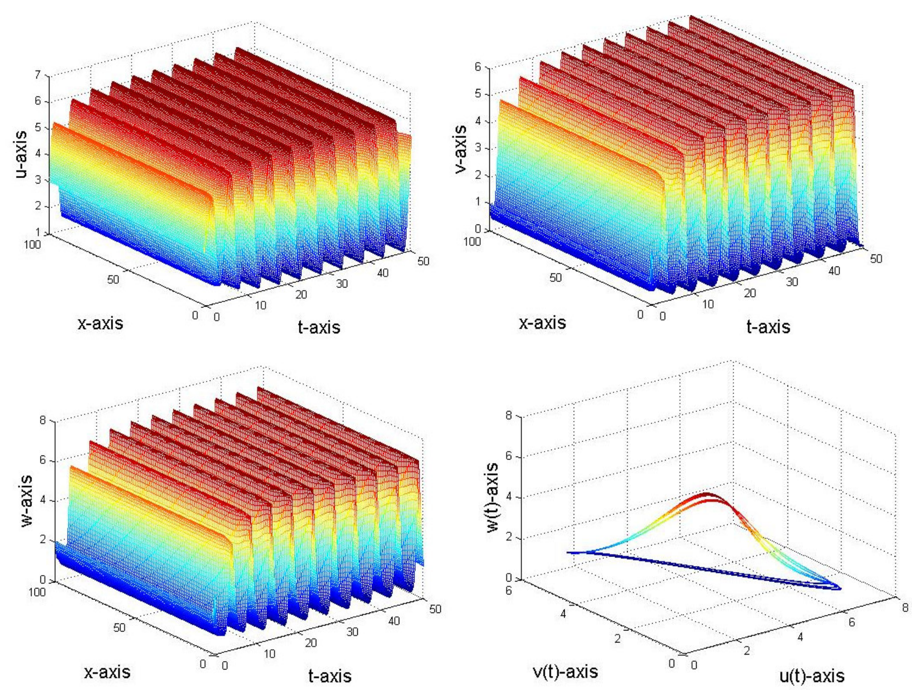

Figure 4. The temporal solution found by numerical integration of problem (1.1)-(1.2) with $D_1 = D_2 = D_3 = 1$, $r_1 = 2$, $r_2 = r_3 = a_{12} = a_{23} = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{21} = 0.6$, $a_{32} = 0.7$, $\tau = 0.6$, and $\rho_1(t,x) = 3 + e^{-20x}$, $\rho_2(t,x) = 1 + e^{-20x}$, $\rho_3(t,x) = 2 + e^{-20x}$, $t \in [-0.6, 0]$.

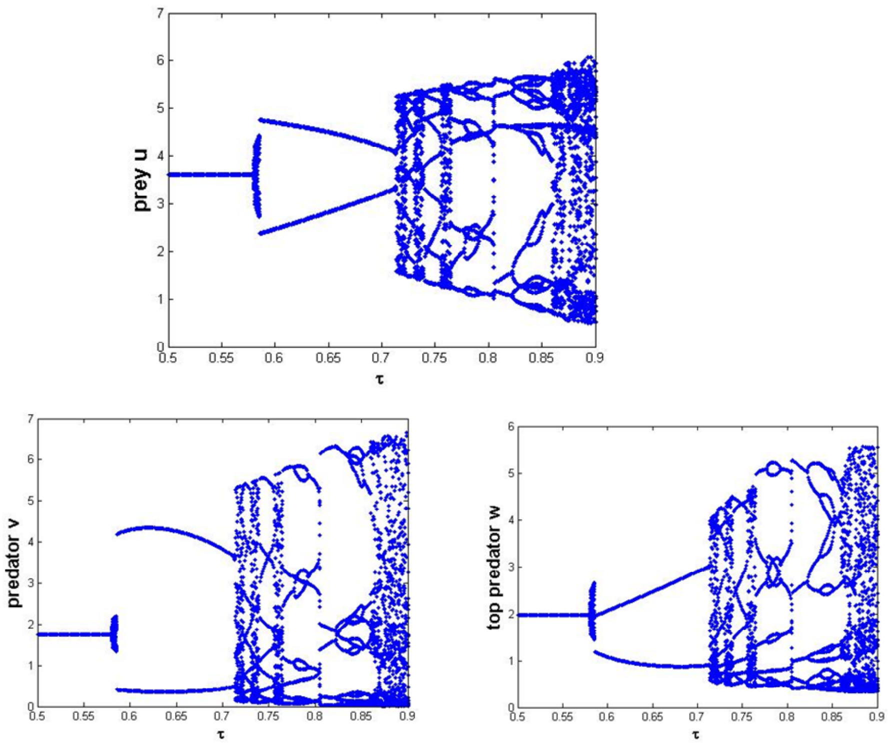

Figure 5. Bifurcation diagrams of Equation (3) showing the effect of τ with $r_1 = 2$, $r_2 = r_3 = a_{12} = a_{23} = 0.5$, $a_{11} = a_{22} = a_{33} = 0.3$, $a_{21} = 0.6$, $a_{32} = 0.7$, $\zeta = 0.8$, $T = 2$, $0.5 \le \tau \le 0.9$, and initial values $u = 2.5$, $v = 4$, $w = 6$.

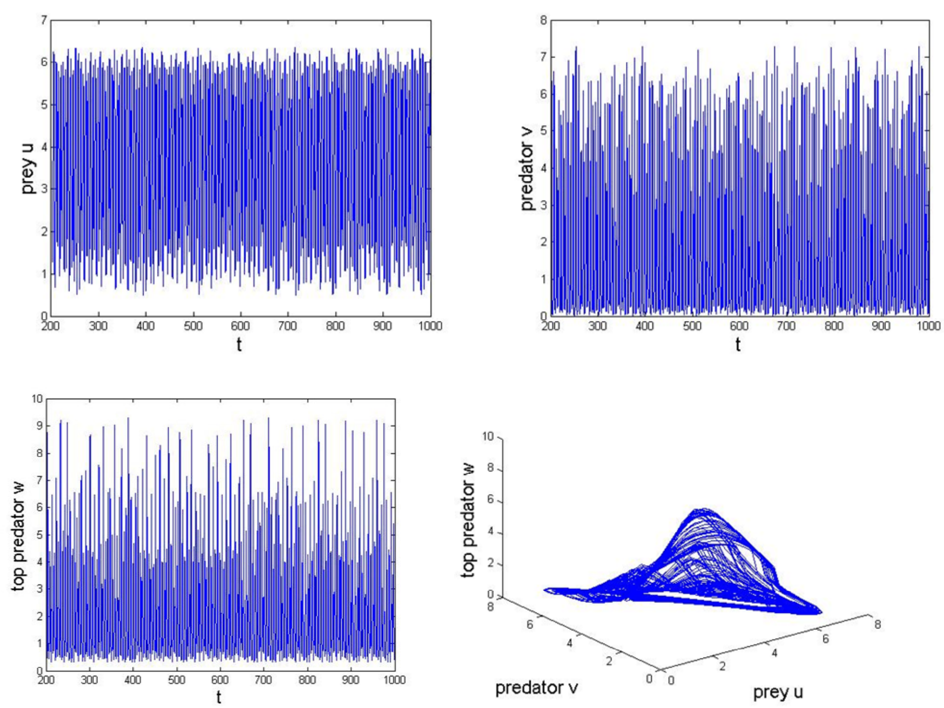

Figure 6. Chaos of Equation (3) for $\tau = 0.89$: (a) time series of prey *u*; (b) time series of predator *v*; (c) time series of top predator *w*; (d) phase portrait.

(May, 1974; May and Oster, 1976) and has been studied extensively by Mathematicians Collet and Eeckmann, 1980; Venkatesan and Parthasarathy, 2003). For the predator-prey system, chaotic behaviors are usually obtained by continuous system with periodic forcing (Vandermeer et al., 2001).

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