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Bifurcation on diffusive Holling–Tanner predator–prey model with stoichiometric density dependence

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Abstract. This paper studies a diffusive Holling–Tanner predator–prey system with stoichiometric density dependence. The local stability of positive equilibrium, the existence of Hopf bifurcation and stability of bifurcating periodic solutions have been obtained in the absence of diffusion. We also study the spatially homogeneous and nonhomogeneous periodic solutions through all parameters of the system, which are spatially homogeneous. In order to verify our theoretical results, some numerical simulations are carried out.

Keywords: stability analysis, stoichiometry, food quality, Hopf bifurcation, predator–prey model.

1 Introduction

Nowadays, reaction–diffusion equation modeling of several different systems has attracted considerable attention in mathematical biology, especially, the predator–prey systems with many different kinds of functional responses and distinct boundary conditions. In general, one top predator species are considered feeding on other species, which make up a food web. At present, mathematical ecology along with experimental ecology represents an important tool for the evolution of a quantitative theory to describe predator–prey interactions. Predator–prey interactions play the most important role in the functioning of ecosystems. The ecological interaction between the species such as lynx and hare, spider mite and mite, sparrow and sparrow hawk, etc., are modeled through the predator–prey system by many researchers (see [25,26] to mention only some of them). May modernized a model known as the Holling–Tanner predator–prey model [14] in which he incorporated the Holling rate [5,6]. The Holling–Tanner functional is one of the prototypical model for the predator–prey interactions, which has been studied by many researchers; for more details, one can refer to May [14] and Murray [15].

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Among the most widely used mathematical models in theoretical ecology, the Holling–Tanner model plays a peculiar role in view of the interesting dynamics it possesses. The Holling–Tanner predator–prey model, stability and Hopf bifurcation analysis has been investigated extensively by many authors; see [2–4, 7, 8, 10, 12, 13, 16–24, 27]. In particular, the authors have concentrated on the study of the local and global stability of equilibrium and Hopf bifurcation. However, spatial dynamic behavior has been not well studied. Recently, Hsu and Huang [7] analyze global stability of the positive equilibrium of a predator–prey system without diffusivity along with certain conditions on the parameters. Further, the existence/nonexistence of the nonconstant positive steady state solutions with cross-diffusion and global stability of the positive constant steady state studied in [16]. Chen and Shi [4] proved that the unique constant equilibrium of a diffusive system is globally asymptotically stable under a new, simpler parameter condition, and Liu [12] studied spatiotemporal behavior of the Holling–Tanner system. Li et al. [10] studied the Hopf bifurcation and Turing instability of the Holling–Tanner predator–prey model with diffusion. In [11], authors studied the global stability of a predator–prey system with Beddington–DeAngelis and Tanner functional response by using the iteration method and comparison principle of the unique positive equilibrium solution.

Predator–prey interactions have been modeled and analyzed by various authors in different aspects. In particular, Anderson et al. [1] constructed predator (herbivore)–prey (autotroph) model using stoichiometric density dependence principles to admit predation effects on food quantity and food quality. Using this intention, we construct a predator–prey model with food quality term. We enclose that term via stoichiometry principles [1]. The main goal of this paper is to study the stability and Hopf bifurcation analysis of the positive equilibrium solution of the diffusive Holling–Tanner predator–prey model with stoichiometric density dependence.

The structure of this paper is arranged as follows: In Section 2, we introduce a mathematical predator–prey model. In Section 3, we analyze the local stability and Hopf bifurcation of that model (2). In Section 4, bifurcations of spatially homogeneous and nonhomogeneous periodic solutions are rigorously proved for system (3). To verify our theoretical results, some numerical simulations are carried out in Section 5, and some concluding comments are made in Section 6.

2 Mathematical model and analysis

The Lotka–Volterra predator–prey model has been a point of origin for much theoretical analysis of population dynamics. In recent years, a lot of predator–prey models have been proposed and analyzed widely since the innovators Lotka and Volterra's theoretical works. Population models have a long history dating back to the Malthus model formulated in the early nineteenth century and then corrected by Verhulst about 50 years later to compensate for the prediction that either a population grows or dies out exponentially fast. The logistic correction allows instead for a horizontal asymptote to which the population tends as time flows, the value of which expresses the carrying capacity of the environment for the population under scrutiny.

Predator–prey model has been developed by various authors who considered several environmental conditions. Also, food quantity and quality effects play a major role in population dynamics. Basically, stoichiometric models incorporate both food quantity and food quality effects in a single model. Since prey and predator have shared the same function in the food chain and the same nutritional relationship to the primary sources of energy, it is sensible that their population sizes both ought to be constrained by the total nutrient of the system. Stoichiometric considerations used to modify predator–prey system through both the density dependence of prey growth rate and the growth efficiency of predators.

To present the stoichiometric principles in our mathematical model, we need to concentrate on two things. First one is, individual growth and population dynamics may be directly constrained by food quality in terms of the nutrient element content. And another one implies that release and recycling of elements will be determined by the difference between ingested nutrients and those incorporated into new consumer biomass. In [1], Anderson et al. proposed the stoichiometric density dependence functional response α $(1 - Qu/(K - qv))$ instead of classical Lotka–Volterra model.

We consider a two-compartment predator–prey system with constant dilution. For both prey (u) and predator (v), total nutrient K is provided at a constant rate. If the predators have a constant nutrient content q and the preys have a minimum nutrient content Q, then the system must be confined to the triangle bounded below by the positive cone (i.e. $u \geqslant 0$ and $v \geqslant 0$) and above by $Qu + qv \leqslant K$. Notice that by this we implicitly assume that the concentration of dissolved inorganic nutrient is negligible, so that nutrient in prey is given as the difference between the total nutrient and the nutrient contained in predator. This simplifying assumption, which is very convenient for maintaining a planar phase space directly comparable to the Lotka–Volterra model.

When predator has constant stoichiometry q, the quantity of nutrient available to prey growth will be $K - qv$. In contrast to logistic density dependence (Qu/K), stoichiometric density dependence $(Qu/(K - qv))$ implies that prey growth rate becomes a decreasing function of both prey (u) and predator (v) biomasses. Introducing stoichiometric density dependence has a strong effect on the shape of the prey nullcline, and thus also on the dynamical stability properties of the system.

For this stoichiometric density dependence functional response, the predator–prey model takes the form

$$\begin{aligned} &\dot{u}(t) = \alpha u\left(1 - \frac{Qu}{K - qv}\right) - \frac{\beta uv}{u + v}, \qquad \dot{v}(t) = \gamma v\left(1 - \frac{\delta v}{u}\right), \\ &u(0) = u_0 > 0, \qquad v(0) = v_0 > 0, \end{aligned} \tag{1}$$

where the parameters α, β, γ, δ, q, Q and K are positive constants, u and v denote, respectively, the population densities of the prey and predator at time t. The prey grows logistically with intrinsic growth rate α and carrying capacity K/Q. The rate at which predator removes the prey $(\beta uv/(u + v))$ is known as a ratio dependent functional response [9]. The predator population grows logistically with intrinsic growth rate γ and carrying capacity proportional to the population size of the prey; δ is the number of preys involve to sustain one predator at equilibrium when v matches u/δ [25].

For easiness, we nondimensionalize (1) with the following scaling:

$$u \mapsto \frac{Qu}{K}, \quad v \mapsto v, \quad t \mapsto \alpha t,$$

and then obtain the form

$$\begin{aligned} &\dot{u}(t) = u\left(1 - \frac{u}{1-av}\right) - \frac{suv}{u+cv}, \qquad \dot{v}(t) = \rho v\left(1 - \frac{ev}{u}\right), \\ &u(0) = u_0 > 0, \qquad v(0) = v_0 > 0, \end{aligned} \tag{2}$$

where $a = q/K$, $s = \beta Q/(\alpha K)$, $c = Q/K$, $\rho = \gamma/\alpha$, $e = Q\delta/K$.

In fact, living beings are distributed in space and regularly interface with the physical environment and different living beings in their spatial neighborhood. Numerous physical aspects of the earth, for example, atmosphere, substance creation or physical structure can differ from place to place. So, we need to consider the population dynamic changes depends upon both space and time (spatial movement) also.

As the predator–prey with their density confined to a fixed open bounded domain Ω in $\mathbb{R}^N$ with smooth boundary, system (2) is expressed as the following reaction–diffusion system (spatial system):

$$\begin{aligned} &u_t = d_1\Delta u + u\left(1 - \frac{u}{1-av}\right) - \frac{suv}{u+cv}, \quad x \in \Omega,\ t > 0, \\ &v_t = d_2\Delta v + \rho v\left(1 - \frac{ev}{u}\right), \qquad x \in \Omega,\ t > 0, \\ &\partial_\nu u = \partial_\nu v = 0, \quad x \in \partial\Omega,\ t > 0, \\ &u(x,0) = u_0(x) \geqslant 0, \quad v(x,0) = v_0(x) \geqslant 0, \quad x \in \Omega. \end{aligned} \tag{3}$$

In the above, Δ is the Laplacian operator on $\Omega \in \mathbb{R}^N$, where d_1 and d_2 denote, respectively, diffusivity of prey and predator are kept independent of space and time. The no-flux boundary condition means that the spatial environment Ω is isolated, and ν is the outward unit normal to $\partial\Omega$. The initial values $u_0(x)$, $v_0(x)$ are assumed to be positive and bounded in Ω.

3 Existence of stability and Hopf bifurcation

In this section, we study mainly the local stability of the equilibria and the existence of the Hopf bifurcation of constant periodic solutions surrounding the positive equilibrium of system (2).

3.1 Steady states

System (2) has a boundary equilibrium point E^1 and a nontrivial positive equilibrium point E^*, where

(i) $E^1 = (1, 0)$ – the prey only survives or extinct of the predator.
(ii) $E^* = (u^*, v^*)$ is a nontrivial stationary state (coexistence of prey and predator), where

$$u^* = \frac{e(c+e-s)}{(c+e)(e-a)-as} > 0 \quad \text{and} \quad v^* = \frac{u^*}{e} > 0.$$

The dynamical behavior of the equilibrium points can be studied by computing the eigenvalues of the Jacobian matrix J of system (2), namely,

$$J = \begin{pmatrix} 1 - \frac{2u}{1-av} - \frac{csv^2}{(u+cv)^2} & -\frac{au^2}{(1-av)^2} - \frac{su^2}{(u+cv)^2} \\ \frac{\rho e v^2}{u^2} & \rho(1 - \frac{2ev}{u}) \end{pmatrix}. \tag{4}$$

The existence and local stability of the equilibrium solutions can be stated as follows:

Theorem 1. *The boundary equilibrium point $E^1 = (1, 0)$ is always a saddle point.*

Proof. The Jacobian matrix of system (2) evaluated at the equilibrium point $E^1 = (1, 0)$ is given by

$$J|_{E^1} = \begin{pmatrix} -1 & -(a+s) \\ 0 & \rho \end{pmatrix}$$

$\operatorname{tr} J|_{E^1} = \rho - 1$ and $\det J|_{E^1} = -\rho < 0$. Therefore $E^1 = (1, 0)$ is saddle point. □

3.2 Interior equilibrium

The Jacobian evaluated at the coexistence equilibrium $E^*(u^*, v^*)$ is

$$J|_{E^*} = \begin{pmatrix} \frac{-u^*}{1-av^*} + \frac{su^*v^*}{(u^*+cv^*)^2} & -\frac{au^{*2}}{(1-av^*)^2} - \frac{su^{*2}}{(u^*+cv^*)^2} \\ \frac{\rho}{e} & -\rho \end{pmatrix}. \tag{5}$$

Then trace and determinant of the Jacobian matrix (5) is

$$T = \operatorname{tr} J|_{E^*} = \frac{u^*}{av^*-1} + \frac{su^*v^*}{(u^*+cv^*)^2} - \rho$$

and

$$D = \det J|_{E^*} = \rho u^* \biggl(\frac{1}{av^*-1} \biggl(\frac{au^*}{e(av^*-1)} - 1 \biggr) \biggr).$$

Therefore the characteristic equation of the linearized system of (5) at $E^* = (u^*, v^*)$ is

$$\lambda^2 - T\lambda + D = 0. \tag{6}$$

The two roots are given as $\lambda_{1,2} = T \pm \sqrt{(T)^2 - 4D}/2$. Therefore if $D > 0$, then the real part of the eigenvalues $(\lambda_{1,2})$ have the same sign. Therefore local stability of E^* entirely depend upon the sign of T, that is, E^* is stable when $T < 0$ and unstable when $T > 0$.

So for our convenience, consider the condition

(H) $v^* < 1/a$ holds.

It is clear that if (H) holds, then $D > 0$. Therefore equilibrium point E^* is locally asymptotically stable when

$$u^*(u^* + cv^*)^2 < (av^* - 1)\left[\rho(u^* + cv^*)^2 - su^*v^*\right].$$

Further, we analyze the Hopf bifurcation occurring at E^*. For the sake of convenience, let $\rho_0 = u^*/(av^* - 1) + su^*v^*/(u^* + cv^*)^2$. We note that the parameter ρ represents predation efficiency, and we analyze the Hopf bifurcation occurring at (u^*, v^*) by choosing ρ as the bifurcation parameter.

When $\rho > \rho_0$ (i.e. $T = \rho_0 - \rho < 0$), the roots of characteristic equation (6) have negative real part, then the positive equilibrium E^* is asymptotically stable. When $\rho_0 > \rho$ (i.e. $T = \rho_0 - \rho > 0$), the roots of (6) have positive real part, then the positive equilibrium E^* is unstable.

When $\rho = \rho_0$ (i.e. $T = \rho_0 - \rho = 0$), the Jacobian matrix $J|_{E^*}$ has a pair of imaginary eigenvalues. Let $\lambda_{1,2} = p(\rho) \pm \mathrm{i}\omega(\rho)$ be the roots of (6), where

$$p(\rho) = \frac{\rho_0 - \rho}{2} = \frac{T}{2}, \qquad \omega(\rho) = \frac{1}{2}\sqrt{4D - (\rho_0 - \rho)^2} = \frac{1}{2}\sqrt{4D - (T)^2}$$

and we get

$$\left.\frac{\mathrm{d}p}{\mathrm{d}\rho}\right|_{\rho=\rho_0} = -\frac{1}{2} < 0.$$

This shows that the transversality condition holds. By the Poincaré–Andronov–Hopf bifurcation theorem, we know that system (2) undergoes a Hopf bifurcation at E^* when $\rho = \rho_0$.

Theorem 2. *Assume that condition* (H) *holds. The equilibrium* (u^*, v^*) *of system* (2) *is locally asymptotically stable when* $\rho > \rho_0$ *and unstable when* $\rho < \rho_0$; *system* (2) *undergoes a Hopf bifurcation at the positive equilibrium* (u^*, v^*) *when* $\rho = \rho_0$.

3.3 Stability of bifurcated solutions

However, the detailed nature of the Hopf bifurcation needs further analysis of the normal form of the system. Now we investigate the direction of Hopf bifurcation and stability of bifurcated solutions arising through Hopf bifurcation. We translate the positive equilibrium $E^* = (u^*, v^*)$ to the origin by the translation $\hat{u} = u - u^*$, $\hat{v} = v - v^*$. For convenience, we denote $\hat{u}$ and $\hat{v}$ again by u and v, respectively. Thus the local system (2) becomes

$$\begin{aligned}\dot{u}(t) &= (u + u^*)\left(1 - \frac{u + u^*}{1 - a(v + v^*)}\right) - \frac{s(u + u^*)(v + v^*)}{(u + u^*) + c(v + v^*)},\\ \dot{v}(t) &= \rho(v + v^*)\left(1 - \frac{e(v + v^*)}{(u + u^*)}\right).\end{aligned} \tag{7}$$

Rewrite (7) as

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = J(\rho)\begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} f(u,v,\rho) \\ g(u,v,\rho) \end{pmatrix}, \tag{8}$$

where $J(\rho)$ is defined as in (5)

$$\begin{aligned} f(u,v,\rho) &= (a_1 - b_1)u^2 - (2u^*(a_1+b_2))uv + \big(a_2(2u^* - cv^*) - b_2\big)u^2 v \\ &\quad - a_2(3 - v^*)u^3 + \cdots, \\ g(u,v,\rho) &= -\frac{c_1}{e}u^2 + 2c_1 uv - 2c_2 u^2 v + \frac{c_2}{e}u^3 + \cdots, \end{aligned}$$

where

$$\begin{aligned} a_1 &= \frac{csv^*}{(u^*+cv^*)^3}, & b_1 &= \frac{1}{1-av^*}, & c_1 &= \frac{\rho}{u^*}, \\ a_2 &= \frac{csv^*}{(u^*+cv^*)^4}, & b_2 &= \frac{a}{(1-av^*)^2}, & c_2 &= \frac{\rho}{u^{*2}}. \end{aligned}$$

Therefore the characteristic roots of $J(\rho)$ are $\lambda_{1,2} = p(\rho) \pm \mathrm{i}\omega(\rho)$, where

$$p(\rho) = \frac{1}{2}\big(\operatorname{tr} J(\rho)\big), \qquad \omega(\rho) = \sqrt{\det J(\rho) - \big(p(\rho)\big)^2}.$$

The characteristic roots λ_1, λ_2 are a pair of complex conjugates when $\det J(\rho) - (p(\rho))^2$ is positive and λ_1, λ_2 are purely imaginary when $\rho = \rho_0$, that is, $p(\rho_0) = 0$, and we get $\lambda_{1,2} = \pm\mathrm{i}\omega(\rho_0)$.

Set the following matrix:

$$B = \begin{pmatrix} 1 & 0 \\ M & N \end{pmatrix},$$

where $\left(\begin{smallmatrix} 1 \\ M-\mathrm{i}N \end{smallmatrix}\right)$ is the eigenvector corresponding to $\lambda = p(\rho) + \mathrm{i}\omega(\rho)$ with

$$\begin{aligned} M &= \frac{(1-av^*)^2(u^*+cv^*)^2}{au^{*2}(u^*+cv^*)^2 + su^{*2}(1-av^*)^2}\left(\frac{-u^*}{1-av^*} + \frac{su^*v^*}{(u^*+cv^*)^2} - p(\rho)\right), \\ N &= \frac{(1-av^*)^2(u^*+cv^*)^2}{au^{*2}(u^*+cv^*)^2 + su^{*2}(1-av^*)^2}\omega(\rho). \end{aligned}$$

Clearly,

$$B^{-1} = \begin{pmatrix} 1 & 0 \\ \frac{-M}{N} & \frac{1}{N} \end{pmatrix}.$$

By the transformation

$$\begin{pmatrix} u \\ v \end{pmatrix} = B\begin{pmatrix} x \\ y \end{pmatrix}$$

system (7) becomes

$$\begin{pmatrix} \dot{x}(t) \\ \dot{y}(t) \end{pmatrix} = J_\rho\begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} F(x,y,b) \\ G(x,y,b) \end{pmatrix}, \tag{9}$$

where

$$J_\rho = \begin{pmatrix} p(\rho) & -\omega(\rho) \\ \omega(\rho) & p(\rho) \end{pmatrix}$$

with

$$\begin{aligned} F(x,y,\rho) = {} & \big((a_1-b_1) - M\big[2u^*(a_1+b_2)\big]\big)x^2 - N\big(2u^*(a_1+b_2)\big)xy \\ & + N\big(a_2(2u^*-cv^*)-b_2\big)x^2y + \big(M\big[a_2(2u^*-cv^*)-b_2\big] \\ & + a_2(3-v^*)\big)x^3 + \cdots, \\ G(x,y,\rho) = {} & \frac{-M}{N}F(x,y,\rho) + \frac{1}{N}g_1(x,y,\rho) \end{aligned}$$

and

$$\begin{aligned} g_1(x,y,\rho) = {} & \left(\frac{-c_1}{e} + 2Mc_1\right)x^2 + (2Nc_1)xy - (2Nc_2)x^2y \\ & + \left(\frac{c_2}{e} - 2Mc_2\right)x^3 + \cdots. \end{aligned}$$

Rewrite (9) in the polar coordinates as

$$\begin{aligned} \dot r &= p(\rho)r + a(\rho)r^3 + \cdots, \\ \dot\theta &= \omega(\rho) + c(\rho)r^2 + \cdots. \end{aligned} \tag{10}$$

Then the Taylor expansion of (10) at $\rho = \rho_0$ yields

$$\begin{aligned} \dot r &= p'(\rho_0)(\rho-\rho_0)r + a(\rho_0)r^3 + \ldots, \\ \dot\theta &= \omega(\rho_0) + \omega'(\rho_0)(\rho-\rho_0) + c(\rho_0)r^2 + \cdots. \end{aligned} \tag{11}$$

To find the stability of Hopf bifurcation periodic solution, we need to calculate the sign of the coefficient $a(\rho_0)$ given by

$$\begin{aligned} a(\rho_0) = {} & \frac{F_{xxx} + F_{xyy} + G_{xxy} + G_{yyy}}{16}\bigg|_{(0,0,\rho_0)} \\ & + \frac{F_{xy}(F_{xx}+F_{yy}) - G_{xy}(G_{xx}+G_{yy}) - F_{xx}G_{xx} + F_{yy}G_{yy}}{16\omega(\rho_0)}\bigg|_{(0,0,\rho_0)}, \end{aligned}$$

where

$$\begin{aligned} F_{xxx} &= 6\big(M\big[a_2(2u^*-cv^*)-b_2\big] + a_2(3-v^*)\big), \\ F_{xyy} &= G_{yyy} = F_{yy} = G_{yy} = 0, \\ F_{xx} &= 2\big((a_1-b_1) - M\big[2u^*(a_1+b_2)\big]\big), \qquad F_{xy} = -N\big(2u^*(a_1+b_2)\big), \\ G_{xxy} &= -2M\big[a_2(2u^*-cv^*)-b_2\big] - 4c_2, \qquad G_{xy} = M\big(2u^*(a_1+b_2)\big) + 2c_1, \\ G_{xx} &= 2\left(\frac{-M}{N}(a_1-b_1) + \frac{M^2}{N}\big(au^*(a_1+b_2)\big)\right) + 2\left(\frac{2M}{N}c_1 - \frac{c_1}{Ne}\right). \end{aligned}$$

Thus we obtain

$$\Lambda = -\frac{a(\rho_0)}{p'(\rho_0)}.$$

Now, from the Poincaré–Andronov–Hopf bifurcation theorem $p'(\rho)|_{\rho=\rho_0} = -1/2 < 0$, and from the above calculations of $a(\rho_0)$ we have the following conclusion:

Theorem 3. *Assume that condition* (H) *holds. When* $a(\rho_0) < 0$*, the direction of Hopf bifurcation is supercritical, and the bifurcated periodic solutions are stable*; *when* $a(\rho_0) > 0$*, the direction of Hopf bifurcation is subcritical, and the bifurcated periodic solutions are unstable.*

4 Stability and direction of spatial Hopf bifurcation

Now we discuss the existence of spatially homogeneous and nonhomogeneous periodic solutions bifurcating from the Hopf bifurcation of the reaction–diffusion system

$$\begin{aligned}
&u_t = d_1 u_{xx} + u\left(1 - \frac{u}{1-av}\right) - \frac{suv}{u+cv}, \quad x \in (0, l\pi),\ t > 0,\\
&v_t = d_2 v_{xx} + \rho v\left(1 - \frac{ev}{u}\right), \quad x \in (0, l\pi),\ t > 0,\\
&\partial_\nu u = \partial_\nu v = 0, \quad x \in 0, l\pi,\ t > 0,\\
&u(x,0) = u_0(x) \geqslant 0, \quad v(x,0) = v_0(x) \geqslant 0, \quad x \in (0, l\pi).
\end{aligned} \tag{12}$$

To cast our focus into the frame work of the Hopf bifurcation theorem, by the transition $\hat{u} = u - u^*$, $\hat{v} = v - v^*$ we translate (12) into the following system. For the sake of convenience, we still indicate $\hat{u}$ and $\hat{v}$ by u and v, respectively. Thus the reaction–diffusion system (12) becomes

$$\begin{aligned}
&u_t - d_1 u_{xx} = \mathcal{F}(\rho, u, v), \quad x \in (0, l\pi),\ t > 0,\\
&v_t - d_2 v_{xx} = \mathcal{G}(\rho, u, v), \quad x \in (0, l\pi),\ t > 0,\\
&u_x(0,t) = u_x(l\pi, t) = 0, \quad v_x(0,t) = v_x(l\pi, t) = 0, \quad t > 0,\\
&u(x,0) = u_0(x), \quad v(x,0) = v_0(x), \quad x \in (0, l\pi).
\end{aligned} \tag{13}$$

Define

$$\begin{aligned}
&\mathcal{F}(\rho, u, v) = (u + u^*)\left(1 - \frac{(u+u^*)}{1 - a(v+v^*)}\right) - \frac{s(u+u^*)(v+v^*)}{(u+u^*) + c(v+v^*)},\\
&\mathcal{G}(\rho, u, v) = \rho(v + v^*)\left(1 - \frac{e(v+v^*)}{(u+u^*)}\right),
\end{aligned}$$

where $\mathcal{F}, \mathcal{G} : \mathbb{R} \times \mathbb{R}^2 \to \mathbb{R}$ are C^∞ smooth with $\mathcal{F}(\rho, 0, 0) = \mathcal{G}(\rho, 0, 0) = 0$.

Now we define the real-valued Sobolev space

$$X = \left\{(u, v) \in \left[H^2(0, l\pi)\right]^2\colon\ (u_x, v_x)|_{x=0,l\pi} = 0\right\},$$

and the complexification of X:

$$X_{\mathbb{C}} := X \oplus \mathrm{i}X = \{u_1 + \mathrm{i}u_2\colon u_1, u_2 \in X\}.$$

The linearized operator of system (12) evaluated at (u^*, v^*) is

$$L(\rho) = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + A(\rho) & B(\rho) \\ C(\rho) & d_2 \frac{\partial^2}{\partial x^2} + D(\rho) \end{pmatrix}$$

with the domain $D_{L(\rho)} = X_{\mathbb{C}}$, where

$$\begin{aligned} A(\rho) &= \mathcal{F}_u(\rho, 0, 0) = -\frac{u^*}{1 - av^*} + \frac{su^*v^*}{(u^* + cv^*)^2}, \\ B(\rho) &= \mathcal{F}_v(\rho, 0, 0) = \frac{-au^{*2}}{(1 - av^*)^2} - \frac{su^{*2}}{(u^* + cv^*)^2}, \\ C(\rho) &= \mathcal{G}_u(\rho, 0, 0) = \frac{\rho}{e}, \qquad D(\rho) = \mathcal{G}_v(\rho, 0, 0) = -\rho \end{aligned}$$

with (u^*, v^*) as defined in Section 3.1.

The following condition is necessary to ensure that the Hopf bifurcation occurs:

(H1) There exists a number $\rho^H \in \mathbb{R}$ and a neighborhood O of ρ^H such that for $\rho \in O$, $L(\rho)$ has a pair of complex, simple, conjugate eigenvalues $p(\rho) \pm \mathrm{i}\omega(\rho)$, continuously differentiable in ρ with $p(\rho^H) = 0$, $\omega_0 = \omega(\rho^H) > 0$ and $p'(\rho^H) \neq 0$; all other eigenvalues of $L(\rho)$ have nonzero real parts for $\rho \in O$.

Now we apply Hopf bifurcation result appearing in [28] to our model. It is well known that the eigenvalue problem

$$\begin{aligned} -\varphi'' &= \mu\varphi, \quad x \in (0, l\pi), \\ \varphi'(0) &= \varphi'(l\pi) = 0, \end{aligned}$$

has eigenvalues $\mu_n = n^2/l^2$ $(n = 0, 1, 2, \dots)$ with corresponding eigenfunctions $\varphi_n(x) = \cos(nx/l)$. Let

$$\begin{pmatrix} \phi \\ \psi \end{pmatrix} = \sum_{n=0}^{\infty} \begin{pmatrix} a_n \\ b_n \end{pmatrix} \cos \frac{nx}{l}$$

be an eigenfunction of $L(\rho)$ corresponding to an eigenvalue $\sigma(b)$. That is, $L(\rho)(\phi, \psi)^{\mathrm{T}} = \sigma(\rho)(\phi, \psi)^{\mathrm{T}}$. Then from a straightforward analysis we obtain the following relation:

$$L_n(\rho) \begin{pmatrix} a_n \\ b_n \end{pmatrix} = \sigma(\rho) \begin{pmatrix} a_n \\ b_n \end{pmatrix}, \quad n = 0, 1, 2, \dots,$$

where

$$L_n(\rho) = \begin{pmatrix} -d_1 \frac{n^2}{l^2} + A(\rho) & B(\rho) \\ C(\rho) & -d_2 \frac{n^2}{l^2} + D(\rho) \end{pmatrix}.$$

It follows that eigenvalues of $L(\rho)$ are given by the eigenvalues of $L_n(\rho)$ for $n = 0, 1, 2, \ldots$. The characteristic equation of $L_n(\rho)$ is

$$\sigma^2 - T_n(\rho)\sigma + D_n(\rho) = 0, \quad n = 0, 1, 2, \ldots,$$

where

$$\begin{aligned} T_n(\rho) &= \left(\frac{-u^*}{1-av^*} + \frac{su^*v^*}{(u^*+cv^*)^2} - \rho\right) - \frac{(d_1+d_2)n^2}{l^2}, \\ &= \left(\frac{u^*(sv^* - \frac{(u^*+cv^*)^2}{1-av^*}) - \rho(u^*+cv^*)^2}{(u^*+cv^*)^2}\right) - \frac{(d_1+d_2)n^2}{l^2} \\ D_n(\rho) &= \frac{\rho}{e}\left[\frac{u^*}{1-av^*}\left(e - \frac{au^*}{1-av^*}\right) + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)\right] \\ &\quad + d_1\frac{n^2}{l^2}\rho + d_2\frac{n^2}{l^2}\left(d_1\frac{n^2}{l^2} + \frac{u^*}{1-av^*} - \frac{su^*v^*}{(u^*+cv^*)^2}\right) \\ &= \frac{\rho}{e}\left(\frac{a{u^*}^2}{(1-av^*)^2} + \frac{s{u^*}^2}{(u^*+cv^*)^2}\right) + \rho\left(\frac{u^*}{1-av^*} - \frac{su^*v^*}{(u^*+cv^*)^2}\right) \\ &\quad + d_1\frac{n^2}{l^2}\rho + d_2\frac{n^2}{l^2}\left(d_1\frac{n^2}{l^2} + \frac{u^*}{1-av^*} - \frac{su^*v^*}{(u^*+cv^*)^2}\right). \end{aligned} \tag{14}$$

Therefore the eigenvalues are established by

$$\sigma(\rho) = \frac{T_n(\rho) \pm \sqrt{T_n^2(\rho) - 4D_n(\rho)}}{2}, \quad n = 0, 1, 2, \ldots .$$

If condition (H1) holds, we see that, at $\rho = \rho^H$, $L(\rho)$ has a pair of simple purely imaginary eigenvalues $\pm \mathrm{i}\omega_0$ if and only if there exists a unique $n \in \mathbb{N} \cup \{0\}$ such that $\pm \mathrm{i}\omega_0$ are the purely imaginary eigenvalues of $L_n(\rho)$. In such a case, denote the associated eigenvector by $q = q_n = (a_n, b_n)^{\mathrm{T}} \cos(n\pi/l)$, with $a_n, b_n \in \mathbb{C}$, such that $L_n(\rho)(a_n, b_n)^{\mathrm{T}} = \mathrm{i}\omega_0(a_n, b_n)^{\mathrm{T}}$ or $L(\rho^H)q = i\omega_0 q$.

We discover the Hopf bifurcation value ρ^H, which satisfies condition (H1) taking the following form if there exists $n \in \mathbb{N} \cup \{0\}$ such that, for any $j \neq n$,

$$T_n(\rho^H) = 0, \quad D_n(\rho^H) = 0 \quad \text{and} \quad T_j(\rho^H) \neq 0, \quad D_j(\rho^H) \neq 0, \tag{15}$$

and for the unique pair of complex eigenvalues $p(\rho) \pm \mathrm{i}\omega(\rho)$, near the imaginary axis, $p'(\rho^H) \neq 0$. It is easy to derive from (14) that $T_n(\rho) < 0$ and $D_n(\rho) > 0$ if $sv^* \leqslant (u + cv^*)^2/(1 - av^*)$, which implies that $(0, 0)$ is a locally asymptotically stable steady state of system (12).

If $sv^* > (u + cv^*)^2/(1 - av^*)$, we define

$$\rho_0^* = \frac{su^*v^* - (\frac{u^*(u^*+cv^*)^2}{1-av^*})}{(u^*+cv^*)^2} = \frac{-u^*}{1-av^*} + \frac{su^*v^*}{(u^*+cv^*)^2} > 0. \tag{16}$$

Hence the potential Hopf bifurcation point lives in the interval $(0, \rho_0^*]$. For any Hopf bifurcation ρ^H in $(0, \rho_0^*]$, $p(\rho^H) \pm \mathrm{i}\omega(\rho^H)$ are the eigenvalues of $L(\rho^H)$, where

$$(\rho^H) = \frac{T_n(\rho^H)}{2}, \qquad \omega(\rho^H) = \sqrt{D_n(\rho^H) - p^2(\rho^H)}$$

and

$$p'(\rho^H) = \frac{1}{2} T_n^{'}(\rho^H) < 0. \tag{17}$$

From the above discussion the determination of Hopf bifurcation point reduces to describing the set

$$\Lambda_1 = \{\rho^H \in (0, b_0^*]\colon \text{ for some } n \in \mathbb{N} \cup \{0\}, \text{(15) is satisfied}\}$$

when a set of parameters (d_1, d_2, a, s, c, e) are given. In the following, we fix $(d_1, d_2, a, s, c, e) > 0$ and choose l appropriately. First, for all $l > 0$, $\rho_0^H = \rho_0^*$ is always an element of Λ_1. (Since $T_0(\rho_0^H) = 0$, $T_j(\rho_0^H) < 0$ for all $j \geqslant 1$ and $D_m(\rho_0^H) > 0$ for all $m \in \mathbb{N} \cup \{0\}$.) This corresponds to the Hopf bifurcation of spatially homogeneous periodic solution. Obviously, ρ_0^H is also the unique value for the Hopf bifurcation of the spatially homogeneous periodic solution for any $l > 0$. Hence, in the following, we look for spatially nonhomogeneous Hopf bifurcation points.

Note that, when $\rho < \rho_0^*$, it is easy to show that $T_n(\rho) = 0$ is equivalent to

$$\rho = \rho_0^* - \frac{(d_1 + d_2)n^2}{l^2}.$$

Substituting it in $D_n(\rho)$ of (14), we have

$$\begin{aligned} D_n(\rho) = {} & -d_1^2\left(\frac{n^2}{l^2}\right)^2 + \frac{n^2}{l^2}\Bigg[d_1\Bigg(\rho_0^* - \frac{1}{e}\bigg[\frac{u^*}{1-av^*}\bigg(e - \frac{av^*}{1-av^*}\bigg) \\ & + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)\bigg]\Bigg) - d_2\Bigg(\frac{1}{e}\bigg[\frac{u^*}{1-av^*}\bigg(e - \frac{av^*}{1-av^*}\bigg) \\ & + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)\bigg] - \bigg(\frac{u^*}{1-av^*} - \frac{su^*v^*}{(u^*+cv^*)^2}\bigg)\Bigg)\Bigg] \\ & + \frac{\rho_0^*}{e}\bigg[\frac{u^*}{1-av^*}\bigg(e - \frac{av^*}{1-av^*}\bigg) + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)\bigg]. \end{aligned}$$

Let

$$\begin{aligned} B_0 = {} & d_1\Bigg(\rho_0^* - \frac{1}{e}\bigg[\frac{u^*}{1-av^*}\bigg(e - \frac{av^*}{1-av^*}\bigg) + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)\bigg]\Bigg) \\ & - d_2\Bigg(\frac{1}{e}\bigg[\frac{u^*}{1-av^*}\bigg(e - \frac{av^*}{1-av^*}\bigg) + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)\bigg] \\ & - \bigg(\frac{u^*}{1-av^*} - \frac{su^*v^*}{(u^*+cv^*)^2}\bigg)\Bigg), \end{aligned}$$

then $D_n(\rho) > 0$ if and only if

$$\frac{n^2}{l^2} < \frac{-B_0 + \sqrt{B_0^2 + 4d_1^2 \frac{\rho_0^*}{e}[\frac{u^*}{1-av^*}(e - \frac{av^*}{1-av^*}) + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)]}}{2d_1^2}.$$

So all the potential Hopf bifurcation points can be tagged as $\Lambda_1 = \{\rho_n^H\}_{n=0}^N$ for some $N \in \mathbb{N} \cup \{0\}$, where

$$\rho_n^H = \rho_0^* - \frac{(d_1 + d_2)n^2}{l^2}. \tag{18}$$

That is,

$$0 < \rho_n^H < \rho_{N-1}^H < \cdots < \rho_1^H < \rho_0^H = \rho_0^* \tag{19}$$

satisfying

$$0 \leqslant \frac{\rho_0^* - \rho_n^H}{d_1 + d_2} < \frac{-B_0 + \sqrt{B_0^2 + 4d_1^2 \frac{\rho_0^*}{e}[\frac{u^*}{1-av^*}(e - \frac{av^*}{1-av^*}) + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)]}}{2d_1^2}.$$

Now we only need to verify whether $D_i(\rho_n^H) \neq 0$ for $i \neq n$. Here we derive a condition on the parameters so that $D_i(\rho_n^H) > 0$ for each $i = 0, 1, 2, \dots$. Since

$$\begin{aligned} D_i(\rho_n^H) &= d_1 d_2 \frac{i^4}{l^4} + \frac{i^2}{l^2}(d_1 \rho_n^H - d_2 \rho_0^*) \\ &\quad + \frac{\rho_n^H}{e}\left[\frac{u^*}{1-av^*}\left(e - \frac{av^*}{1-av^*}\right) + \frac{u^*}{(u^*+cv^*)^2}(su^* - esv^*)\right], \end{aligned}$$

we choose the diffusion coefficient d_2 as small as possible so that $d_1\rho_n^H - d_2\rho_0^* > 0$, that is, given the fixed N defined by (19) for every $0 < n \leqslant N$, $d_2 < \epsilon(l, a, s, c, e, N)$, where

$$\epsilon(l, a, s, c, e, N) := \frac{b_0^* - \frac{N^2}{l^2}}{b_0^* + \frac{N^2}{l^2}} > 0. \tag{20}$$

Therefore $D_i(\rho_n^H) > 0$.

Then summarizing our analysis above and using Hopf bifurcation theorem in [28], we have the main result of this section on the existence of both spatially homogeneous and nonhomogeneous periodic solutions bifurcating from Hopf bifurcation.

Theorem 4. *Assume that* $(u + cv^*)^2/(1 - av^*) < sv^*$. *For any* ρ_n^H, *defined by* (18), *if there exists* $\epsilon = \epsilon(l, a, s, c, e, N)$ *defined by* (20) *such that* $0 < d_2 < \epsilon$, *then system* (12) *undergoes a Hopf bifurcation at each* $\rho = \rho_n^H$ $(0 \leqslant n \leqslant N)$. *With s sufficiently small, for* $\rho = \rho(s)$, $\rho(0) = \rho_n^H$, *there exists a family of* $T(s)$*-periodic continuously differentiable solutions* $(u(s)(x,t), v(s)(x,t))$, *and the bifurcating periodic solutions can be parametrized in the form*

$$\begin{aligned} u(s)(x,t) &= s\bigl(a_n \mathrm{e}^{2\pi \mathrm{i}t/T(s)} + \bar{a}_n \mathrm{e}^{-2\pi \mathrm{i}t/T(s)}\bigr)\cos\frac{nx}{l} + o(s^2), \\ v(s)(x,t) &= s\bigl(b_n \mathrm{e}^{2\pi \mathrm{i}t/T(s)} + \bar{b}_n \mathrm{e}^{-2\pi \mathrm{i}t/T(s)}\bigr)\cos\frac{nx}{l} + o(s^2), \end{aligned} \tag{21}$$

where

$$T(s) = \frac{2\pi}{\omega_0^n}\bigl(1 + \tau_2 s^2\bigr) + o\bigl(s^4\bigr),$$
$$\tau_2 = -\frac{1}{\omega_0^n}\biggl(\mathrm{Im}\bigl(c_1\bigl(\rho_n^H\bigr)\bigr) - \frac{\mathrm{Re}(c_1(\rho_n^H))}{p'(\rho_n^H)}\omega'\bigl(\rho_n^H\bigr)\biggr),$$

and

$$T''(0) = \frac{4\pi}{w_0^n}\tau_2 = -\frac{4\pi}{(\omega_0^n)^2}\biggl(\mathrm{Im}\bigl(c_1\bigl(\rho_n^H\bigr)\bigr) - \frac{\mathrm{Re}(c_1(\rho_n^H))}{p'(\rho_n^H)}\omega'\bigl(\rho_n^H\bigr)\biggr).$$

If all eigenvalues (except $\pm \mathrm{i}\omega_0^n$) of $L(\rho_n^H)$ have negative real parts, then the bifurcating periodic solutions are stable (resp., unstable) if $\mathrm{Re}(c_1(\rho_n^H)) < 0$ (resp., > 0). The bifurcation is supercritical (resp., subcritical) if $-(1/p'(\rho_n^H))\mathrm{Re}(c_1(\rho_n^H)) < 0$ (resp., > 0). Moreover

(i) *The bifurcating periodic solutions from ρ_0^H are spatially homogeneous, which coincide with the periodic solutions of the corresponding ODE system.*
(ii) *The bifurcating periodic solutions from ρ_n^H, $n > 0$, are spatially nonhomogeneous.*

Next, we follow the methods in [28] to calculate the direction of Hopf bifurcation and the stability of the bifurcating periodic orbits bifurcating from $\rho = \rho_0^*$. We have the following result.

Theorem 5. *For system (12), the bifurcating (spatially homogeneous) periodic solutions bifurcating from $\rho = \rho_0^H$ are locally asymptotically stable (resp., unstable) if $\mathrm{Re}(c_1(\rho_0^H)) < 0$ (resp. > 0). Furthermore, the direction of Hopf bifurcation at ρ_0^H is subcritical (resp., supercritical) if $\mathrm{Re}(c_1(\rho_0^H)) < 0$ (resp. > 0).*

Proof. Following the notations and calculation in [28], we set

$$\begin{aligned} q &= (a_0, b_0)^{\mathrm{T}} \\ &= \biggl(1, -\frac{(1-av^*)[u^*(u^*+cv^*)^2 - su^*v^*(1-av^*)]}{au^{*2}(u^*+cv^*)^2 + su^{*2}(1-av^*)^2} \\ &\qquad - \frac{\mathrm{i}\omega_0(1-av^*)^2(u^*+cv^*)^2}{au^{*2}(u^*+cv^*)^2 + su^{*2}(1-av^*)^2}\biggr)^{\mathrm{T}}, \\ q^* &= (a_0^*, b_0^*)^{\mathrm{T}} = \frac{A^*}{l\pi}\bigl(-\mathrm{Im}(b_0) + \mathrm{i}\mathrm{Re}(b_0), -\mathrm{i}\bigr)^{\mathrm{T}}, \end{aligned}$$

where

$$A^* = \frac{-(au^{*2}(u^*+cv^*)^2 + su^{*2}(1-av^*)^2)}{(1-av^*)^2(u^*+cv^*)^2}$$

such that $\langle q^*, q\rangle = 1$ and $\langle q^*, \bar{q}\rangle = 0$. Then, by direct computation, we get

$$c_0 = x_1 + \mathrm{i}y_1, \qquad d_0 = x_2 + \mathrm{i}y_2, \qquad e_0 = x_3,$$
$$f_0 = x_4, \qquad g_0 = x_5 + \mathrm{i}y_5, \qquad h_0 = x_6 + \mathrm{i}y_6,$$

where

$$
\begin{aligned}
&x_1 = 2(a_1 - b_1) - 4u^*(a_1 + b_2)\mathrm{Re}(b_0), \qquad y_1 = -4u^*(a_1 + b_2)\mathrm{Im}(b_0),\\
&x_2 = \frac{-2c_1}{e} + 4c_1\mathrm{Re}(b_0), \qquad y_2 = 4c_1\mathrm{Im}(b_0),\\
&x_3 = 2(a_1 - b_1) + 4u^*(a_1 + b_2)\mathrm{Re}(b_0), \qquad x_4 = \frac{-2c_1}{e} + 4c_1\mathrm{Re}(b_0),\\
&x_5 = 6\big[a_2(3 - v^*) + \big(a_2(2u^* - cv^*) - b_2\big)\mathrm{Re}(b_0)\big],\\
&y_5 = 2\big[a_2(2u^* - cv^*) - b_2\big]\mathrm{Im}(b_0),\\
&x_6 = \frac{6c_2}{e} - 12c_2\mathrm{Re}(b_0), \qquad y_6 = -4c_2\mathrm{Im}(b_0).
\end{aligned}
$$

Then

$$
\begin{aligned}
\langle q^*, Q_{qq}\rangle &= A^*\big[-\mathrm{Im}(b_0)x_1 + \mathrm{Re}(b_0)y_1 - y_2 + \mathrm{i}\big(-\mathrm{Im}(b_0)y_1 + x_2 - \mathrm{Re}(b_0)x_1\big)\big],\\
\langle q^*, Q_{q\bar q}\rangle &= A^*\big[-\mathrm{Im}(b_0)x_3 + \mathrm{i}\big(x_4 - \mathrm{Re}(b_0)x_3\big)\big],\\
\langle \bar{q^*}, Q_{qq}\rangle &= A^*\big[-\mathrm{Im}(b_0)x_1 - \mathrm{Re}(b_0)y_1 + y_2 + \mathrm{i}\big(-\mathrm{Im}(b_0)y_1 + \mathrm{Re}(b_0)x_1 - x_2\big)\big],\\
\langle \bar{q^*}, Q_{q\bar q}\rangle &= A^*\big[-\mathrm{Im}(b_0)x_3 + \mathrm{i}\big(\mathrm{Re}(b_0)x_3 - x_4\big)\big],\\
\langle q^*, C_{qq\bar q}\rangle &= A^*\big[-\mathrm{Im}(b_0)x_5 - y_6 + \mathrm{Re}(b_0)y_5 + \mathrm{i}\big(-\mathrm{Im}g(b_0)y_5 + x_6 - \mathrm{Re}(b_0)x_5\big)\big].
\end{aligned}
$$

Direct computation gives

$$
\begin{aligned}
H_{20} &= \begin{pmatrix} c_0 \\ d_0 \end{pmatrix} - \langle q^*, Q_{qq}\rangle \begin{pmatrix} a_0 \\ b_0 \end{pmatrix} - \langle \bar{q^*}, Q_{qq}\rangle \begin{pmatrix} \bar a_0 \\ \bar b_0 \end{pmatrix} = 0,\\
H_{11} &= \begin{pmatrix} e_0 \\ f_0 \end{pmatrix} - \langle q^*, Q_{q\bar q}\rangle \begin{pmatrix} a_0 \\ b_0 \end{pmatrix} - \langle \bar{q^*}, Q_{q\bar q}\rangle \begin{pmatrix} \bar a_0 \\ \bar b_0 \end{pmatrix} = 0.
\end{aligned}
$$

Then, by Yi et al. [28], it implies that $w_{20} = w_{11} = 0$; hence

$$\langle q^*, Q_{w_{20}\bar q}\rangle = \langle q^*, Q_{w_{11}\bar q}\rangle = 0.$$

After elementary but lengthy computations, we obtain

$$
\begin{aligned}
\mathrm{Re}\big(c_1(\rho_0^H)\big) &= \mathrm{Re}\bigg\{\frac{\mathrm{i}}{2\omega_0}\langle q^*, Q_{qq}\rangle\langle q^*, Q_{q\bar q}\rangle + \frac{1}{2}\langle q^*, C_{qq\bar q}\rangle\bigg\}\\
&= \frac{-1}{2\omega_0}A^{*2}\big\{\big(-\mathrm{Im}(b_0)x_1 + \mathrm{Re}(b_0)y_1 - y_2\big)\big(x_4 - \mathrm{Re}(b_0)\big)x_3\\
&\quad + \big(-\mathrm{Im}(b_0)y_1 + x_2 - \mathrm{Re}(b_0)x_1\big)\big(-\mathrm{Im}(b_0)x_3\big)\big\}\\
&\quad + \frac{1}{2}A^*\big\{-\mathrm{Im}(b_0)x_5 - y_6 + \mathrm{Re}(b_0)y_5\big\}.
\end{aligned}
$$

It follows from (17) that $p'(\rho_0^H) < 0$, and then, by Theorem 2.1 in [28], the periodic solutions bifurcating from $\rho = \rho_0^H$ are locally asymptotically stable (resp., unstable) if $\mathrm{Re}(c_1(\rho_0^H)) < 0$ (resp., > 0). Furthermore, the direction of Hopf bifurcation at ρ_0^H is subcritical (resp., supercritical) if $\mathrm{Re}(c_1(\rho_0^H)) < 0$ (resp., > 0). □

5 Numerical example

Here we present some numerical simulation to verify our theoretical analysis by using MATLAB. We consider system (2) with $a = 1$, $s = 2.1$, $c = 0.2$, $e = 2$. We change only the predation efficiency ρ.

System (2) has unique positive equilibrium $E^*(u^*, v^*) = (0.0444, 0.0222)$. Under the set of parameters in (2), we have the critical point $\rho_0 = 0.822314$, and it follows from Theorem (2) that $E^*(u^*, v^*) = (0.0444, 0.0222)$ is locally asymptotically stable when $\rho > \rho_0 = 0.822314$ and unstable when $\rho < \rho_0 = 0.822314$. Also, when ρ passes through ρ_0 from side of ρ_0, $E^*(u^*, v^*) = (0.0444, 0.0222)$ will lose its stability, and a Hopf bifurcation occurs, that is, a family of periodic solutions bifurcate from the interior equilibrium $E^*(u^*, v^*) = (0.0444, 0.0222)$. These facts are shown by the numerical simulations; see Fig. 1.

In system (12), let $\Omega = (0, 60\pi)$, $l = 60$, $a = 1$, $s = 2.1$, $c = 0.2$, $e = 2$, $d_1 = 0.1$ and $d_2 = 0.2$. Then it follows from Theorem (5) that there exist five Hopf

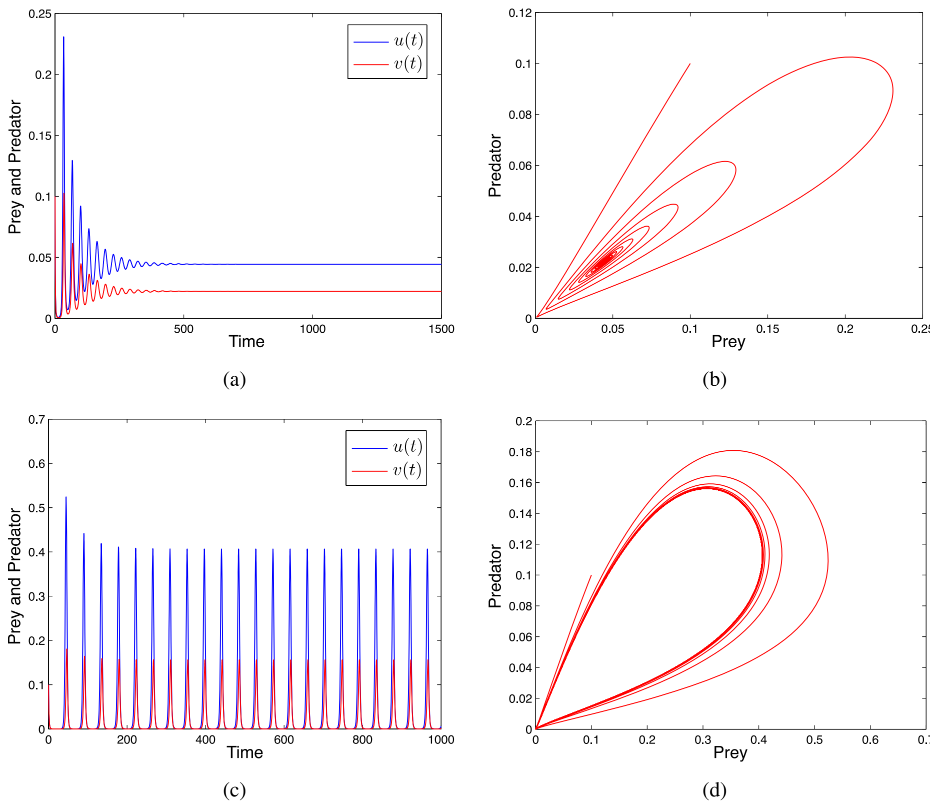

Figure 1. Time series and phase portrait of system (2) with initial data $(u_0, v_0) = (0.1, 0.1)$: (a), (b) $\rho = 0.85 > \rho_0 = 0.822314$; (c), (d) $\rho = 0.8 < \rho_0 = 0.822314$.

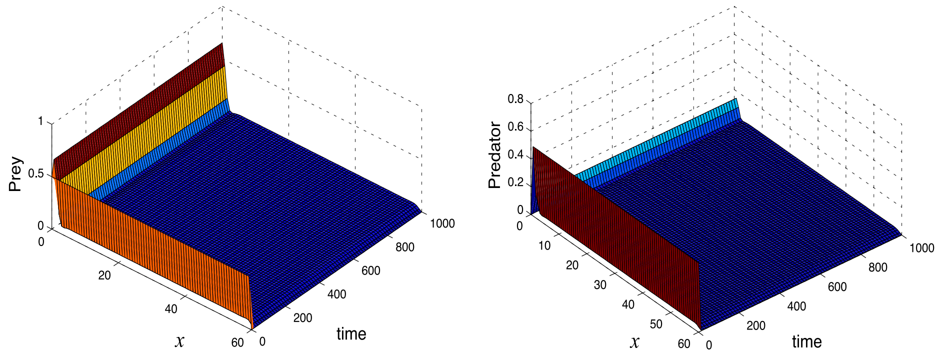

Figure 2. Numerical simulations showing the constant steady state of system (4) is locally asymptotically stable with $\rho = 0.85 > \rho_0^H$ and initial value $(0.5, 0.5)$.

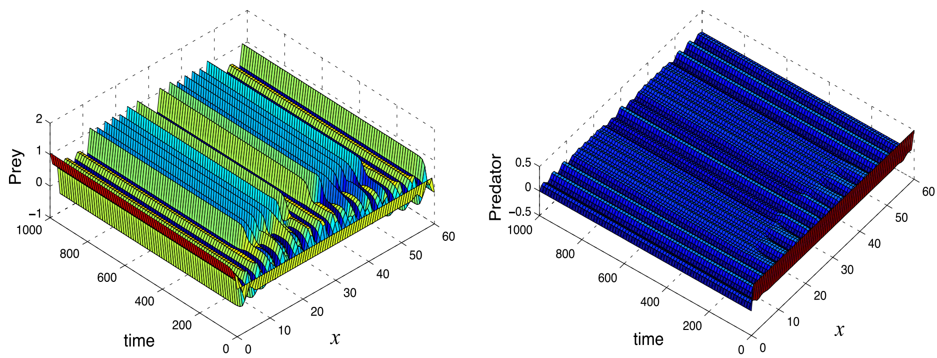

Figure 3. Numerical simulations showing a spatially homogeneous periodic of system (12) emerges when ρ across the first Hopf bifurcation point ρ_0^H with $\rho = 0.821 < \rho_0^H$ and initial value $(0.5, 0.5)$.

bifurcation points: $\rho_0^H = \rho_0^* \approx 0.8223$, $\rho_1^H \approx 0.8222$, $\rho_2^H \approx 0.8219$, $\rho_3^H \approx 0.8215$ and $\rho_4^H \approx 0.8209$. Hence we know from Theorem (5) that the bifurcating periodic solutions from ρ_0^H are locally asymptotically stable and the direction of Hopf bifurcation at ρ_0^H is supercritical. Next, we present numerical simulations near Hopf bifurcation points ρ_0^H: for $\rho = 0.85$ and $\rho = 0.821$; the solution $(u(t,x), v(t,x))$ tends to a constant steady state and spatially homogeneous periodic solution, respectively; see Figs. 2 and 3.

6 Conclusion

In this paper, we have studied a diffusive Holling–Tanner predator–prey model with stoichiometric density dependence. Last few decades, many authors have studied the predator–prey model with logistic growth instead of exponential growth term of the prey. This article encloses food quality term via stoichiometric principles. We incorporated the stoichiometric density dependence functional response in Holling–Tanner predator–prey system and discussed its stability and Hopf bifurcation.

The distribution of the roots of the characteristic equations of the local system (2) at each of the feasible equilibria and stability of the positive equilibrium point are studied. Biologically, Theorem (2) states that, whenever the ratio between the growth rate of predator and prey ($\rho = \gamma/\alpha$) is greater than the critical value ρ_0, the predator–prey population will be stable for any positive initial population. That is, when time t tending to infinity, we can predict population size precisely. That population size is nothing but converge to the positive equilibrium (u^*, v^*). Also, whenever the ratio between the growth rate of predator and prey is less than the critical value of ρ_0, the predator–prey population will be unstable. That is, when time t tending to infinity, we cannot conclude the population size exactly. Whenever the ratio between the growth rate of predator and prey is exactly equaled to the critical value ρ_0, the population dynamics change periodically. This notion is addressed by occurrence of Hopf bifurcation. That is, system (2) undergoes a Hopf bifurcation at the positive equilibrium (u^*, v^*) when $\rho = \rho_0$. Moreover, when the direction of the Hopf bifurcation is supercritical, the bifurcating periodic solution is stable, and when the direction of the Hopf bifurcation is subcritical, the bifurcating periodic solution is unstable. The main results are presented in Theorem 3.

In Section 4, we studied the dynamical changes in predator–prey population according to both space (environment atmosphere) and time movements. For this spatial movements, we considered the diffusion system (12). We analyzed stability conditions and the direction of spatial Hopf bifurcation in detail. We derived conditions for which the occurrence of Hopf bifurcation is due to the ratio between the growth rate of predator and prey and space $\Omega = (0, l\pi)$.

The positive constant steady state solutions of system (12) are locally asymptotically stable when $sv^* \leqslant (u + cv^*)^2/(1 - av^*)$. When $sv^* > (u + cv^*)^2/(1 - av^*)$, ρ_0^* is the unique homogeneous Hopf bifurcation point, where spatially homogeneous orbits bifurcate from (u^*, v^*) for any $l > 0$. Further, there exists multiple nonhomogeneous Hopf bifurcation points ρ_n^H, with $1 \leqslant n \leqslant N$, satisfying $0 < \rho_n^H < \rho_{N-1}^H < \cdots < \rho_1^H < \rho_0^H = \rho_0^*$. At these points, spatially nonhomogeneous periodic orbits bifurcate from (u^*, v^*) for suitable $l > 0$.

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