Global stability and Hopf bifurcation of a diffusive predator–prey model with hyperbolic mortality and prey harvesting*

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Abstract. This paper is concerned with a predator–prey model with hyperbolic mortality and prey harvesting. The parameter regions for the stability and instability of the unique positive constant solution of ODE and PDE are derived, respectively. Especially, the global asymptotical stability of positive constant equilibrium of the diffusive model is obtained by iterative technique. The stability and direction of periodic solutions of ODE and PDE are investigated by center manifold theorem and normal form theory, respectively. Numerical simulations are carried out to depict our theoretical analysis.

Keywords: predator–prey model, Hopf bifurcation, global asymptotical stability, iterative technique, center manifold theorem.

1 Introduction

Predator–prey models are basic differential equation models for describing the interactions between two species and are of great interest to researchers in mathematics and ecology. Both the functional response and harvesting can affect dynamical properties of biological and mathematical models. There are many different kinds of functional response for different kinds of species to model the phenomena of predation such as Holling I–III type (see [7]), Ivlev type (see [9, 14]), Beddington–DeAngelis type (see [2, 4]), the Crowley–Martin type (see [3]), and the recent well-known ratio dependence type, which was first proposed by Arditi and Ginzburg (see [1]). For different species, constant

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harvesting, proportional harvesting, and nonlinear harvesting are currently investigated by many authors, see [5, 8, 13].

In paper [17], the authors performed the following predator–prey model with hyperbolic mortality:

$$u_t = \alpha u \left(1 - u - \frac{v}{1 + \beta u} \right), \quad t > 0,$$

$$v_t = v \left(\frac{\beta u}{1 + \beta u} - \frac{h(v)}{v} \right), \quad t > 0,$$

where u,v represent the populations of the prey and predator, respectively, all parameters are positive, and h(v) is given by

$$h(v) = \frac{rv^2}{e + \eta v}$$

for hyperbolic mortality, where r is the death rate of the predator, e and η are coefficients of light attenuation by water and self-shading in the context of plankton mortality. Please refer to [17] for the more background of the model. Here notice that when $\eta=0$ and $e\neq 0$, it is quadratic mortality; when $\eta\neq 0$ and e=0, it gives the linear mortality; and when both η and e are not zero, it is a mortality of the hyperbolic type, see [17]. The authors studied the reaction–diffusion model and mainly focused on the formation of some elementary two-dimensional patterns such as hexagonal spots and stripe patterns.

In paper [11], the authors also considered a predator–prey model with hyperbolic mortality as follows:

$$u_t = u(1 - u) - \frac{suv}{\beta + u}, \quad t > 0,$$

$$v_t = \alpha \left(\frac{uv}{\beta + u} - \frac{rv^2}{1 + rv}\right), \quad t > 0.$$

For the ordinary differential equations and partial differential equations, the authors did the stability and Hopf bifurcation analysis with α as the bifurcation parameter.

In our another paper [10], we considered the delayed differential equation

$$u_{t} = u(1 - u) - \frac{suv}{\beta + u}, \quad t > 0,$$

$$v_{t} = \alpha \left(\frac{u(t - \tau)v}{\beta + u(t - \tau)} - \frac{rv^{2}}{1 + rv} \right), \quad t > 0,$$

$$u(t) = u_{0}(t) \ge 0, \quad t \in [-\tau, 0],$$

$$v(t) = v_{0}(t) \ge 0, \quad t \in [-\tau, 0],$$
(1)

where τ is a time delay due to gestation period of predations. We regarded τ as the bifurcation parameter and did Hopf bifurcation analysis. Our conclusions declared that time delay can enrich the dynamics of model. Stationary pattern of the corresponding diffusive model without time delay is also considered.

Unlike (1), in this paper, we incorporate a prey harvesting and develop the following model:

$$u_{t} = u(1 - u) - \frac{suv}{\beta + u} - hu, \quad t > 0,$$

$$v_{t} = \alpha \left(\frac{uv}{\beta + u} - \frac{rv^{2}}{1 + rv}\right), \quad t > 0,$$

$$u(0) = u_{0} \ge 0, \qquad v(0) = v_{0} \ge 0,$$

$$(2)$$

where h is the prey harvesting coefficient.

It is easy to see that when h < 1, problem (2) has three constant equilibria (0,0), (1,0), and $(\lambda, \lambda/(\beta r))$, where

$$\lambda = \frac{1}{2} \bigg(1 - h - \beta - \frac{s}{\beta r} + \sqrt{\bigg(1 - h - \beta - \frac{s}{\beta r} \bigg)^2 - 4\beta (h - 1)} \bigg) < 1.$$

The corresponding partial differential equations of (2) with homogeneous Neumann boundary condition is as follows:

$$\frac{\partial u}{\partial t} - d_1 \Delta u = u(1 - u) - \frac{suv}{\beta + u} - hu, \quad (x, t) \in (0, l\pi) \times (0, \infty),$$

$$\frac{\partial v}{\partial t} - d_2 \Delta v = \alpha \left(\frac{uv}{\beta + u} - \frac{rv^2}{1 + rv} \right), \quad (x, t) \in (0, l\pi) \times (0, \infty),$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, \quad x = 0, l\pi, \ t \in (0, \infty),$$

$$u(x, 0) = u_0(x) \geqslant 0, \quad v(x, 0) = v_0(x) \geqslant 0, \quad x \in (0, l\pi),$$
(3)

where n is the outward unit normal vector of the boundary x = 0, $l\pi$. The homogeneous Neumann boundary conditions means that this system is self-contained with zero population flux across the boundary. Parameters d_1 , d_2 , called self-diffusion, are positive.

In this paper, we treat λ (or equivalently h) as Hopf bifurcation parameter and do analysis of stability and Hopf bifurcation to demonstrate the important role of prey harvesting in the model. Compared with (1), problem (3) is a special case that the growth function with harvesting is the combined term $u(1-h)-u^2$ and $\tau=0$. We focus on the important role of the prey harvesting, while paper [10] is concerned with the role of the time delay, and we also obtain the global asymptotical stability of the unique positive constant equilibrium of the diffusive model in term of the iteration technique.

The outline of this paper is as follows. In Section 2, after analyzing the characteristic equations of (2) and (3), we conclude the stability of positive constant solutions and the existence, stability, and direction of periodic solutions, respectively. Section 3 is devoted to the global asymptotical stability of the unique positive constant equilibrium of the diffusive model. Numerical simulations are adopted to depict our theoretical analysis in Section 4.

2 Hopf bifurcation

In this section, we analyze the characteristic equations, derive the stability/instability of $(\lambda, \lambda/(\beta r))$ and do Hopf bifurcation analysis treating λ as a Hopf bifurcation parameter.

2.1 Hopf bifurcation of ODE

Some computations show that the Jacobian matrix of (2) at $(\lambda, \lambda/(\beta r))$ can be written as

$$A = \begin{pmatrix} \frac{s\lambda^2}{r\beta(\beta+\lambda)^2} - \lambda & -\frac{s\lambda}{\beta+\lambda} \\ \frac{\alpha\lambda}{r(\beta+\lambda)^2} & -\frac{\alpha\beta\lambda}{(\beta+\lambda)^2} \end{pmatrix},$$

and the two eigenvalues of A satisfy

$$\lambda_1 + \lambda_2 = T(\lambda) = \frac{\lambda \left[\frac{s\lambda}{\beta r} - (\beta + \lambda)^2 - \alpha \beta \right]}{(\beta + \lambda)^2},$$

$$\lambda_1 \lambda_2 = D(\lambda) = \frac{\alpha \beta \lambda^2 (s + r(\beta + \lambda)^2)}{r(\beta + \lambda)^4} > 0.$$

Let

$$F(\lambda) = \frac{s\lambda}{\beta r} - (\beta + \lambda)^2 - \alpha\beta. \tag{4}$$

If

$$\frac{s}{\beta r} > 2\beta + \beta^2 + \alpha\beta + 1,\tag{5}$$

that is, F(1) > 0, there exits a λ_0 such that $T(\lambda) < 0$ when $0 < \lambda < \lambda_0$, and $T(\lambda) > 0$ when $\lambda_0 < \lambda < 1$, where

$$\lambda_0 = \frac{\frac{s}{\beta r} - 2\beta - \sqrt{(\frac{s}{\beta r} - 2\beta)^2 - 4\beta(\alpha + \beta)}}{2},$$

which indicates that when $0 < \lambda < \lambda_0$, $(\lambda, \lambda/(\beta r))$ is locally asymptotically stable.

In what follows, we do Hopf bifurcation analysis choosing λ as a bifurcation parameter.

When $\lambda=\lambda_0$, we have $T(\lambda)=0$, which implies that Jacobian matrix A has a pair of imaginary eigenvalues. Let $p(\lambda)\pm \mathrm{i} q(\lambda)$ be the eigenvalues of Jacobian matrix A, then

$$p(\lambda) = \frac{T(\lambda)}{2}, \qquad q(\lambda) = \frac{\sqrt{4D(\lambda) - T^2(\lambda)}}{2},$$

and

$$p'(\lambda)|_{\lambda=\lambda_0} = \frac{\lambda_0}{\beta + \lambda_0} \left(-2\lambda_0 - 2\beta + \frac{s}{\beta r} \right)$$
$$= \frac{\lambda_0}{\beta + \lambda_0} \sqrt{\left(\frac{s}{\beta r} - 2\beta\right)^2 - 4\beta(\alpha + \beta)} > 0.$$

Collecting the above analysis, we have the following theorem.

Theorem 1. Assume that h < 1 and (5) hold.

- (i) If $0 < \lambda < \lambda_0$, $(\lambda, \lambda/(\beta r))$ of problem (2) is locally asymptotically stable;
- (ii) If $\lambda_0 < \lambda < 1$, $(\lambda, \lambda/(\beta r))$ of problem (2) is unstable;
- (iii) Problem (2) undergoes a Hopf bifurcation at $(\lambda, \lambda/(\beta r))$ when $\lambda = \lambda_0$.

In what follows, we further analyse the stability and direction of Hopf bifurcation. To this end, similar to the computations in [15], by virtue of translation $\hat{u}=u-\lambda$, $\hat{v}=v-\lambda/(\beta r)$ and denoting \hat{u} and \hat{v} by u and v, respectively, we translate problem (2) into

$$u_{t} = (u+\lambda)(1-\lambda-u) - \frac{s(u+\lambda)(v+\frac{\lambda}{\beta r})}{\beta+u+\lambda} - hu - h\lambda, \quad t > 0,$$

$$v_{t} = \alpha \left(\frac{(u+\lambda)(v+\frac{\lambda}{\beta r})}{\beta+u+\lambda} - \frac{r(v+\frac{\lambda}{\beta r})^{2}}{1+r(v+\frac{\lambda}{\beta r})}\right), \quad t > 0.$$
(6)

Rewrite (6) as

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = A \begin{pmatrix} u \\ v \end{pmatrix} \begin{pmatrix} f(u, v, \lambda) \\ g(u, v, \lambda) \end{pmatrix},$$
 (7)

where

$$\begin{split} f(u,v,\lambda) &= \left(\frac{s\lambda}{r(\beta+\lambda)^3} - 1\right) u^2 - \frac{s\beta}{(\beta+\lambda)^2} uv - \frac{s\lambda}{r(\beta+\lambda)^4} u^3 \\ &\quad + \frac{s\beta}{(\beta+\lambda)^3} u^2 v + \cdots, \\ g(u,v,\lambda) &= \frac{\alpha r}{(\beta+\lambda)^3} u^2 + \frac{\alpha\beta}{(\beta+\lambda)^2} uv - \frac{\alpha r\beta^3}{(\beta+\lambda)^3} v^2 + \frac{\alpha\lambda}{r(\beta+\lambda)^4} u^3 \\ &\quad + \frac{\alpha r^2\beta^4}{(\beta+\lambda)^4} v^3 - \frac{\alpha\beta}{(\beta+\lambda)^3} u^2 v + \cdots. \end{split}$$

Set

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

where

$$M = \frac{\beta + \lambda}{s\lambda} q(\lambda), \qquad N = \frac{(p(\lambda) + \frac{\alpha\beta\lambda}{(\beta + \lambda)^2})(\beta + \lambda)}{s\lambda}.$$

Then

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

and

$$\begin{split} M_0 &= M|_{\lambda = \lambda_0} = \frac{\sqrt{\alpha \beta r \lambda_0^2 (s + r(\beta + \lambda_0)^2)}}{s \lambda r (\beta + \lambda_0)}, \\ N_0 &= N|_{\lambda = \lambda_0} = \frac{\alpha \beta \lambda_0}{s \lambda_0 (\beta + \lambda_0)}. \end{split}$$

Set

$$\binom{u}{v} = P\binom{x}{y},$$

then (7) can be rewritten as

$$\begin{pmatrix} x_t \\ y_t \end{pmatrix} = J \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} F^1(x, y, \lambda) \\ F^2(x, y, \lambda) \end{pmatrix},$$

where

$$J = \begin{pmatrix} p(\lambda) & -q(\lambda) \\ q(\lambda) & p(\lambda) \end{pmatrix},$$

and

$$\begin{split} F^1(x,y,\lambda) &= \left(\frac{s\beta N}{(\beta+\lambda)^3} - \frac{s\lambda}{r(\beta+\lambda)^4}\right) x^3 + \left(\frac{s\lambda}{r(\beta+\lambda)^3} - 1 - \frac{s\beta N}{(\beta+\lambda)^2}\right) x^2 \\ &+ \frac{s\beta M}{(\beta+\lambda)^3} x^2 y - \frac{s\beta M}{(\beta+\lambda)^2} xy, \end{split}$$

$$F^{2}(x,y,\lambda) = A_{30}x^{3} + A_{20}x^{2} + A_{21}x^{2}y + A_{11}xy + A_{02}y^{2} + A_{03}y^{3} + A_{12}xy^{2},$$

where

$$\begin{split} A_{30} &= -\frac{N}{M} \bigg(\frac{s\beta N}{(\beta + \lambda)^3} - \frac{s\lambda}{r(\beta + \lambda)^4} \bigg) \\ &+ \frac{1}{M} \bigg(\frac{\alpha\lambda}{r(\beta + \lambda)^4} + \frac{\alpha r^2 \beta^4 n^3}{(\beta + \lambda)^4} - \frac{\alpha\beta N}{(\beta + \lambda)^3} \bigg), \\ A_{20} &= -\frac{N}{M} \bigg(\frac{s\lambda}{r(\beta + \lambda)^3} - 1 - \frac{s\beta N}{(\beta + \lambda)^2} \bigg) \\ &+ \frac{1}{M} \bigg(\frac{\alpha\beta N}{(\beta + \lambda)^2} - \frac{\alpha r}{(\beta + \lambda)^3} - \frac{\alpha r\beta^3 N^2}{(\beta + \lambda)^3} \bigg), \\ A_{21} &= -\frac{s\beta N}{(\beta + \lambda)^3} + \frac{1}{M} \bigg(\frac{3\alpha r^2 \beta^4 N^2 M}{(\beta + \lambda)^4} - \frac{\alpha\beta N}{(\beta + \lambda)^3} \bigg), \\ A_{11} &= \frac{s\beta N}{(\beta + \lambda)^2} + \frac{\alpha\beta}{(\beta + \lambda)^2} - \frac{2N\alpha r\beta^3}{(\beta + \lambda)^3}, \\ A_{02} &= -\frac{\alpha r\beta^3 M}{(\beta + \lambda)^3}, \qquad A_{03} &= \frac{\alpha M^2 r^2 \beta^4}{(\beta + \lambda)^4}, \qquad A_{12} &= \frac{3\alpha r^2 \beta^4 M N}{(\beta + \lambda)^4}. \end{split}$$

Rewrite (7) in the following polar coordinates form:

$$\dot{r} = p(\lambda)r + a(\lambda)r^3 + \cdots, \dot{\theta} = q(\lambda) + c(\lambda)r^2 + \cdots,$$
(8)

then the Taylor expansion of (8) at $\lambda = \lambda_0$ yields

$$\dot{r} = p'(\lambda_0)(\lambda - \lambda_0)r + a(\lambda_0)r^3 + \cdots,$$

$$\dot{\theta} = q(\lambda_0) + q'(\lambda_0)(\lambda - \lambda_0) + c(\lambda_0)r^2 + \cdots.$$

In order to determine the stability of the periodic solutions, we need to calculate the sign of the coefficient $a(\lambda_0)$, which is given by

$$a(\lambda_{0}) = \frac{1}{16} \left(F_{xxx}^{1} + F_{xyy}^{1} + F_{xxy}^{2} + F_{yyy}^{2} \right)$$

$$+ \frac{1}{16q(\lambda_{0})} \left(F_{xy}^{1} \left(F_{xx}^{1} + F_{yy}^{1} \right) - F_{xy}^{2} \left(F_{xx}^{2} + F_{yy}^{2} \right) - F_{xx}^{1} F_{xx}^{2} + F_{yy}^{1} F_{yy}^{2} \right)$$

$$= \frac{1}{16} \left\{ 6 \left(\frac{s\beta N_{0}}{(\beta + \lambda)^{3}} - \frac{s\lambda}{r(\beta + \lambda)^{4}} \right) + 2A_{21} + 6A_{03} \right\}$$

$$+ \frac{\sqrt{r}(\beta + \lambda)^{2}}{16\sqrt{\alpha\beta\lambda^{2}(s + r(\beta + \lambda)^{2})}} \left\{ - \left(\frac{s\beta M_{0}}{(\beta + \lambda)^{2}} + 2A_{20} \right) \right\}$$

$$\times \left(\frac{s\lambda}{r(\beta + \lambda)^{3}} - 1 - \frac{s\beta N}{(\beta + \lambda)^{2}} \right) - A_{11}(2A_{20} + 2A_{02}) \right\} \Big|_{\lambda = \lambda_{0}}.$$

Now from Poincaré–Andronov–Hopf bifurcation theorem, $p'(\lambda_0) > 0$, and the above calculation of $a(\lambda_0)$ we summarize our results as follows:

Theorem 2. For problem (2),

- (i) If $a(\lambda_0) > 0$, the periodic solutions bifurcating from $(\lambda, \lambda/(\beta r))$ at $\lambda = \lambda_0$ are stable, and the direction of the Hopf bifurcation is supercritical;
- (ii) If $a(\lambda_0) < 0$, the periodic solutions bifurcating from $(\lambda, \lambda/(\beta r))$ at $\lambda = \lambda_0$ are unstable, and the direction of the Hopf bifurcation is subcritical.

2.2 Hopf bifurcation of PDE

In this subsection, we do Hopf bifurcation analysis of problem (3).

Theorem 3. For problem (3),

- (i) Assume that h < 1 and (9) hold. If $\lambda \in (0, \lambda_*]$, $(\lambda, \lambda/(\beta r))$ is locally asymptotically stable; If $\lambda \in (\lambda_*, 1)$, $(\lambda, \lambda/(\beta r))$ is unstable, where λ_* is determined in (10).
- (ii) Assume that h < 1, $s/r > 4\beta^2 + \alpha\beta$ and (11) hold. Let Ω be a bounded smooth domain so that the spectral set $S = \{\mu_i\}$ satisfies
 - (S) All the eigenvalues μ_i are simple for $i \ge 0$;

then there exists a n_0 such that $\lambda_* \in (\lambda(n_0), \lambda(n_0 + 1))$, and there are $(n_0 + 1)$ Hopf bifurcation points satisfying

$$\lambda_0 = \lambda_H(0) > \lambda_H(1) > \cdots > \lambda_H(n_0) > \lambda_*$$

For every Hopf bifurcation point $\lambda_H(k)$, problem (3) undergoes a Hopf bifurcation, and the bifurcation periodic orbits near $(\lambda, \lambda/(\beta r))$ can be parameterized in the form $\lambda(s) = \lambda_H(j) + o(s)$, $s \in (0, \delta)$ for some small δ , and

$$u(s)(x,t) = \lambda_{H}(j) + sa_{j}\cos(\omega(\lambda_{H}(j))t)\phi_{j}(x) + o(s),$$

$$v(s)(x,t) = \frac{\lambda_{\rm H}(j)}{\beta r} + sb_j \cos(\omega(\lambda_{\rm H}(j))t)\phi_j(x) + o(s),$$

where $\omega(\lambda_{\rm H}(j)) = \sqrt{D_j(\lambda_{\rm H}(j))}$ is the corresponding time frequency, $\phi_j(x)$ is the corresponding spatial eigenfunction, and (a_j,b_j) is the corresponding eigenvector, that is to say,

$$[L(\lambda_{\mathbf{H}}(j)) - \mathrm{i}\omega(\lambda_{\mathbf{H}}(j))I][(a_j, b_j)^{\mathrm{T}}\phi_j(x)] = (0, 0)^{\mathrm{T}}.$$

Moreover,

- (i) The periodic orbits bifurcating from $\lambda = \lambda_{\rm H}(0)$ are spatially homogeneous, which coincide with the periodic orbits of the corresponding ODE system;
- (ii) The periodic orbits bifurcating from $\lambda = \lambda_H(j)$ are spatially nonhomogeneous, $1 \le j \le n_0$.

Proof. Some calculations show that the Jacobian matrix of (3) at $(\lambda, \lambda/(\beta r))$ can be written as

$$A_n(\lambda) = \begin{pmatrix} \frac{s\lambda^2}{\beta r(\beta+\lambda)^2} - \lambda - d_1 \frac{n^2}{l^2} & -\frac{s\lambda}{\beta+\lambda} \\ \frac{\alpha\lambda}{r(\beta+\lambda)^2} & -\frac{\alpha\beta\lambda}{(\beta+\lambda)^2} - d_2 \frac{n^2}{l^2} \end{pmatrix},$$

and the eigenvalues of $A_n(\lambda)$ satisfy

$$\lambda_{1n} + \lambda_{2n} = T_n(\lambda) = \frac{\lambda \left[\frac{s\lambda}{\beta r} - (\beta + \lambda)^2 - \alpha\beta\right]}{(\beta + \lambda)^2} - (d_1 + d_2) \frac{n^2}{l^2},$$

$$\lambda_{1n} \lambda_{2n} = D_n(\lambda)$$

$$= \frac{\alpha \beta \lambda^2 (s + r(\beta + \lambda)^2)}{r(\beta + \lambda)^4} - d_2 \frac{n^2}{l^2} \left(\frac{s\lambda^2}{r\beta(\beta + \lambda)^2} - \lambda\right)$$

$$+ d_1 d_2 \frac{n^4}{l^4} + d_1 \frac{n^2}{l^2} \frac{\alpha \beta \lambda}{(\beta + \lambda)^2}.$$

It is easy to see that when $\lambda < \lambda_0$, $T_n(\lambda) < 0$ always holds.

Ιf

$$r\beta^3 + r\beta\lambda_0^2 + (2\beta^2 r - s)\lambda_0 < 0, (9)$$

there exists

$$\lambda_* = \frac{s - 2r\beta^2 - \sqrt{(s - 2r\beta^2)^2 - 4r^2\beta^4}}{2r\beta} \tag{10}$$

such that when $\lambda \in (0, \lambda_*]$, $D_n(\lambda) > 0$ holds for all n, which implies that $(\lambda, \lambda/(\beta r))$ is locally asymptotically stable. Then the interval of emergence of Hopf bifurcation lies

in $(\lambda_*, 1)$. $T_n(\lambda) = 0$ means that $(d_1 + d_2)n^2/l^2 = (\lambda/(\beta + \lambda)^2)F(\lambda)$, where $F(\lambda)$ is defined in (4).

Let λ_H be possible Hopf bifurcation value, by [6, 16], to identify λ_H be the Hopf bifurcation point, we recall the following sufficient conditions:

(A_H) There exists $i \in \mathbb{N}_0 := \mathbb{N} \cup \{0\}$ such that $T_i(\lambda_{\mathrm{H}}) = 0$ and $D_i(\lambda_{\mathrm{H}}) > 0$ hold, and as $i \neq j$, $T_j(\lambda_{\mathrm{H}}) \neq 0$ and $D_j(\lambda_{\mathrm{H}}) \neq 0$. And the unique pair of complex eigenvalues $\tau(\lambda) \pm \mathrm{i}\omega(\lambda)$ near the imaginary axis satisfy $\tau'(\lambda_{\mathrm{H}}) \neq 0$, $\omega(\lambda_{\mathrm{H}}) > 0$.

After some simple computations, we get that if $s/r > 4\beta^2 + \alpha\beta$, that is, $\lambda_0 < \beta$, $\lambda'(n) < 0$ holds. Notice that $\lambda(0) = \lambda_0$. Hence, there exists a n_0 such that $\lambda_* \in (\lambda(n_0), \lambda(n_0+1))$, and there are (n_0+1) possible Hopf bifurcation points satisfying

$$\lambda_0 = \lambda_H(0) > \lambda_H(1) > \cdots > \lambda_H(n_0) > \lambda_*$$

Next, we will show that under some additional conditions, $D_j(\lambda_{\rm H}(i))>0$ for $0\leqslant i\leqslant n_0$ and $j\in\mathbb{N}_0$, then we must have $D_i(\lambda_{\rm H}(i))>0$ and $D_j(\lambda_{\rm H}(i))\neq 0$ for $0\leqslant i\leqslant n_0$ and $j\in\mathbb{N}_0$ as required in condition (A_H).

Since $T(\lambda_H(k)) = 0$, $k = 0, 1, 2, \dots, n_0$, and $\lambda'(n) < 0$, we get that when $\lambda \in (\lambda_*, \lambda_0]$,

$$\begin{split} D_n(\lambda) &= \frac{\alpha\beta\lambda^2(s+r(\beta+\lambda)^2)}{r(\beta+\lambda)^4} - d_2\frac{n^2}{l^2}\bigg(\frac{s\lambda^2}{r\beta(\beta+\lambda)^2} - \lambda\bigg) + d_1d_2\frac{n^4}{l^4} \\ &+ d_1\frac{n^2}{l^2}\frac{\alpha\beta\lambda}{(\beta+\lambda)^2} \\ &\geqslant d_1d_2\frac{n^4}{l^4} + \frac{n^2}{l^2}\bigg[\frac{d_1\alpha\beta\lambda_*}{(\beta+\lambda_*)^2} - \frac{d_2s\lambda_0^2}{r\beta(\beta+\lambda_0)^2}\bigg] + \frac{\alpha\beta\lambda_*^2(s+r(\beta+\lambda_*)^2)}{r(\beta+\lambda_*)^4} \\ &= \bigg(\sqrt{d_1d_2}\frac{n^2}{l^2} + \frac{\frac{d_1\alpha\beta\lambda_*}{(\beta+\lambda_*)^2} - \frac{d_2s\lambda_0^2}{r\beta(\beta+\lambda_0)^2}}{2\sqrt{d_1d_2}}\bigg)^2 \\ &+ \frac{\alpha\beta\lambda_*^2(s+r(\beta+\lambda_*)^2)}{r(\beta+\lambda_*)^4} - \frac{\left[\frac{d_1\alpha\beta\lambda_*}{(\beta+\lambda_*)^2} - \frac{d_2s\lambda_0^2}{r\beta(\beta+\lambda_0)^2}\right]^2}{4d_1d_2}. \end{split}$$

If

$$\frac{\alpha\beta\lambda_*^2(s+r(\beta+\lambda_*)^2)}{r(\beta+\lambda_*)^4} > \frac{\left[\frac{d_1\alpha\beta\lambda_*}{(\beta+\lambda_*)^2} - \frac{d_2s\lambda_0^2}{r\beta(\beta+\lambda_0)^2}\right]^2}{4d_1d_2},\tag{11}$$

then $D_n(\lambda) > 0$ for all n.

Let $\tau(\lambda) \pm i\omega(\lambda)$ be the pair of eigenvalue of $A_n(\lambda)$. We verify that

$$\begin{split} \tau'\big(\lambda_{\mathrm{H}}(k)\big) &= \frac{T'_n(\lambda_{\mathrm{H}}(k))}{2} = \frac{\lambda_{\mathrm{H}}(k)}{(\beta + \lambda_{\mathrm{H}}(k))^2} \bigg(-2\lambda_{\mathrm{H}}(k) - 2\beta + \frac{s}{\beta r} \bigg) \\ &+ \big(\beta - \lambda_{\mathrm{H}}(k)\big) (d_1 + d_2) \frac{n^2}{l^2} > 0, \\ \omega(\lambda_{\mathrm{H}}(k)) &= \sqrt{D_n(\lambda_{\mathrm{H}}(k))}. \end{split}$$

So the proof is accomplished by the Hopf bifurcation theorem in [6, 16].

Remark. Condition $s/r > 4\beta^2 + \alpha\beta$ implies that (9) always holds.

Adopting the framework of [6, 16], we will compute the direction of Hopf bifurcation and the stability of periodic solutions bifurcating from $(\lambda, \lambda/(\beta r))$ at $\lambda = \lambda_H(0) = \lambda_0$. We shall follow the same notations and calculations in [6, 16].

We choose

$$q = (a_0, b_0)^{\mathrm{T}} = \left(1, \frac{\frac{s\lambda_0^2}{r\beta(\beta + \lambda_0)^2} - \lambda_0 - \mathrm{i}\omega_0}{\frac{s\lambda_0}{\beta + \lambda_0}}\right)^{\mathrm{T}},$$

$$q^* = (a_0^*, b_0^*)^{\mathrm{T}} = \left(\frac{\omega_0 + \mathrm{i}(\frac{s\lambda_0^2}{r\beta(\beta + \lambda_0)^2} - \lambda_0)}{2l\pi\omega_0}, -\frac{s\lambda_0\mathrm{i}}{2l\pi\omega_0(\beta + \lambda_0)}\right)^{\mathrm{T}},$$

where

$$\omega_0 = \sqrt{\frac{\alpha\beta\lambda_0^2(s+r(\beta+\lambda_0)^2)}{r(\beta+\lambda_0)^4}}.$$

It is straightforward to compute that

$$c_{0} = f_{uu} + 2f_{uv}b_{0} = \frac{s\lambda_{0}}{r(\beta + \lambda_{0})^{3}} - 1 - \frac{2\beta sb_{0}}{(\beta + \lambda_{0})^{2}},$$

$$d_{0} = g_{uu} + 2g_{uv}b_{0} + g_{vv}b_{0}^{2} = -\frac{2\alpha\lambda_{0}}{r(\beta + \lambda_{0})^{3}} + \frac{2\alpha\beta b_{0}}{(\beta + \lambda_{0})^{2}} - \frac{2\alpha r\beta^{3}b_{0}^{2}}{(\beta + \lambda_{0})^{3}},$$

$$e_{0} = f_{uu} + f_{uv}(\overline{b_{0}} + b_{0}) = \frac{s\lambda_{0}}{r(\beta + \lambda_{0})^{3}} - 1 - \frac{\beta s}{(\beta + \lambda_{0})^{2}}(\overline{b_{0}} + b_{0}),$$

$$f_{0} = g_{uu} + g_{uv}(\overline{b_{0}} + b_{0}) + g_{vv}|b_{0}|^{2}$$

$$= -\frac{2\alpha\lambda_{0}}{r(\beta + \lambda_{0})^{3}} + \frac{\alpha\beta}{(\beta + \lambda_{0})^{2}}(\overline{b_{0}} + b_{0}) - \frac{2\alpha r\beta^{3}}{(\beta + \lambda_{0})^{3}}|b_{0}|^{2},$$

$$g_{0} = f_{uuu} + f_{uuv}(2b_{0} + \overline{b_{0}}) = -\frac{6s\lambda_{0}}{r(\beta + \lambda_{0})^{4}} + \frac{2s\beta}{(\beta + \lambda_{0})^{3}}(2b_{0} + \overline{b_{0}}),$$

$$h_{0} = g_{uuu} + g_{uuv}(2b_{0} + \overline{b_{0}}) + g_{vvv}|b_{0}|^{2}b_{0}$$

$$= \frac{6\alpha\lambda_{0}}{r(\beta + \lambda_{0})^{4}} - \frac{2\alpha\beta}{(\beta + \lambda_{0})^{3}}(2b_{0} + \overline{b_{0}}) + \frac{6\alpha r^{2}\beta^{4}}{(\beta + \lambda_{0})^{4}}|b_{0}|^{2}b_{0},$$

and

$$\begin{split} \langle q^*,Q_{qq}\rangle &= l\pi(\overline{a_0^*}c_0 + \overline{b_0^*}d_0),\\ \langle q^*,Q_{q\overline{q}}\rangle &= l\pi(\overline{a_0^*}e_0 + \overline{b_0^*}f_0),\\ \langle q^*,C_{qq\overline{q}}\rangle &= l\pi(\overline{a_0^*}g_0 + \overline{b_0^*}h_0),\\ H_{11} &= Q_{q\overline{q}} - \langle q^*,Q_{q\overline{q}}\rangle q - \langle \overline{q^*},Q_{q\overline{q}}\rangle \overline{q} = 0,\\ H_{20} &= Q_{qq} - \langle q^*,Q_{qq}\rangle q - \langle \overline{q^*},Q_{qq}\rangle \overline{q} = 0, \end{split}$$

which implies that $W_{11} = W_{20} = 0$. Hence,

$$\operatorname{Re}(c_{1}(\lambda_{0})) = \operatorname{Re}\langle q^{*}, Q_{w_{11}q} \rangle + \frac{1}{2} \operatorname{Re}\langle q^{*}, C_{qq\bar{q}} \rangle + \frac{1}{2} \operatorname{Re}\langle q^{*}, Q_{w_{20}\bar{q}} \rangle$$

$$+ \operatorname{Re}\left(\frac{\mathrm{i}}{2w_{0}}\langle q^{*}, Q_{qq} \rangle \cdot \langle q^{*}, Q_{q\bar{q}} \rangle\right)$$

$$= \operatorname{Re}\left(\frac{1}{2}\langle q^{*}, C_{qq\bar{q}} \rangle + \frac{\mathrm{i}}{2w_{0}}\langle q^{*}, Q_{qq} \rangle \cdot \langle q^{*}, Q_{q\bar{q}} \rangle\right)$$

$$= \operatorname{Re}\left\{\frac{l\pi}{2}(\overline{a_{0}^{*}}g_{0} + \overline{b_{0}^{*}}h_{0}) + \frac{l^{2}\pi^{2}i}{2w_{0}}(\overline{a_{0}^{*}}c_{0} + \overline{b_{0}^{*}}d_{0})(\overline{a_{0}^{*}}e_{0} + \overline{b_{0}^{*}}f_{0})\right\}.$$

Since $\tau'(\lambda_0) > 0$, from Theorem 2.1 in [16], we have

Theorem 4. For problem (3),

- (i) If $\operatorname{Re}(c_1(\lambda_0)) < 0$, the direction of Hopf bifurcation at $\lambda = \lambda_0$ is forward, that is, the bifurcating periodic solutions exists for $\lambda > \lambda_0$, and the bifurcating periodic solutions are orbitally asymptotically stable;
- (ii) If $Re(c_1(\lambda_0)) > 0$, the direction of Hopf bifurcation at $\lambda = \lambda_0$ is backward, that is, the bifurcating periodic solutions exists for $\lambda < \lambda_0$, and the bifurcating periodic solutions are orbitally asymptotically unstable.

3 Global asymptotical stability of positive constant equilibrium of (3)

In this section, we obtain the global asymptotical stability of $(\lambda, \lambda/(\beta r))$ using the iteration technique. We first state the following lemma, which is from [12].

Lemma 1. Let f(s) be a positive C^1 function for $s \ge 0$, and let d > 0, $\beta \ge 0$ be constants. Further, let $T \in [0,\infty)$ and $w \in C^{2,1}(\Omega \times (T,\infty)) \cap C^{1,0}(\bar{\Omega} \times [T,\infty))$ be a positive function.

(i) If w satisfies

$$\begin{split} w_t - d\Delta w &\leqslant (\geqslant) \, w^{1+\beta} f(w)(\alpha - w), \quad (x,t) \in \Omega \times (T,\infty), \\ \frac{\partial w}{\partial n} &= 0, \quad (x,t) \in \partial \Omega \times [T,\infty), \end{split}$$

and the constant $\alpha > 0$, then

$$\limsup_{t\to\infty}\max_{\bar{\varOmega}}w(\cdot,t)\leqslant\alpha\Bigl(\liminf_{t\to\infty}\min_{\bar{\varOmega}}w(\cdot,t)\geqslant\alpha\Bigr).$$

(ii) If w satisfies

$$w_t - d\Delta w \le w^{1+\beta} f(w)(\alpha - w), \quad (x, t) \in \Omega \times (T, \infty),$$

$$\frac{\partial w}{\partial n} = 0, \quad (x, t) \in \partial \Omega \times [T, \infty),$$

and the constant $\alpha \leq 0$, then $\limsup_{t\to\infty} \max_{\bar{\Omega}} w(\cdot,t) \leq 0$.

Theorem 5. If h < 1 and $s/r < \beta^2$ hold, $(\lambda, \lambda/(\beta r))$ of problem (3) is globally asymptotically stable.

Proof. By the maximum principle of parabolic equations, for any initial values $(u_0(x), v_0(x)) > (0, 0)$, solutions (u(x, t), v(x, t)) of problem (3) are positive.

From the first equation of problem (3) we have $u_t - d_1 \Delta u \leq u(1 - h - u)$. By Lemma 1, we get

$$\limsup_{t \to \infty} \max_{\bar{\Omega}} u(x, t) \leqslant 1 - h := \bar{u}_1.$$

Then for any given $\varepsilon>0$, there exists $t_1^\varepsilon\gg 1$ so that for $(x,t)\in \bar{\varOmega}\times [t_1^\varepsilon,\infty),\, u(x,t)\leqslant \bar{u}_1+\varepsilon$. In turn, for $x\in \bar{\varOmega},\, t\geqslant t_1^\varepsilon$, we have

$$v_t - d_2 \Delta v \leqslant \frac{\alpha v}{(\beta + 1 - h + \varepsilon)(1 + rv)} (1 - h + \varepsilon - \beta rv).$$

By Lemma 1 and the arbitrariness of ε , we obtain that

$$\limsup_{t \to \infty} \max_{\bar{\Omega}} v(\cdot, t) \leqslant \frac{\bar{u}_1}{\beta r} := \bar{v}_1.$$

Hence, there exists $t_2^{\varepsilon} \geqslant t_1^{\varepsilon}$ such that for $(x,t) \in \bar{\Omega} \times [t_2^{\varepsilon},\infty)$, $v(x,t) \leqslant \bar{v}_1 + \varepsilon$. Consequently, we have that

$$u_{t} - d_{1}\Delta u \geqslant u \left(1 - u - \frac{s(\bar{v}_{1} + \varepsilon)}{\beta + u} - h \right)$$

$$= \frac{u}{(\beta + u)} \left((1 - h)\beta + (1 - h - \beta)u - u^{2} - s(\bar{v}_{1} + \varepsilon) \right)$$

$$:= \frac{u}{(\beta + u)} H(u, \bar{v}_{1} + \varepsilon).$$

If $s/r < \beta^2$ holds, $H(u, \bar{v}_1 + \varepsilon) = 0$ has two roots $u_{1,2}$ satisfying

$$u_1 = \frac{1 - h - \beta - \sqrt{(1 - h - \beta)^2 + 4(1 - h)\beta - 4s\bar{v}_1}}{2} < 0,$$

$$u_2 = \frac{1 - h - \beta + \sqrt{(1 - h - \beta)^2 + 4(1 - h)\beta - 4s\bar{v}_1}}{2} > 0.$$

Then we get

$$u_t - d_1 \Delta u \geqslant \frac{u}{(\beta + u)} (u - u_1)(u_2 - u),$$

which implies that

$$\liminf_{t\to\infty} \min_{\bar{\Omega}} u(\cdot,t) \geqslant u_2 := \underline{u}_1.$$

Then for $0<\varepsilon<\underline{u}_1$, there exists $t_3^\varepsilon\geqslant t_2^\varepsilon$ such that for $(x,t)\in\bar{\varOmega}\times[t_3^\varepsilon,\infty),\,u(x,t)\geqslant\underline{u}_1-\varepsilon.$

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Therefore, $v_t - d_2 \Delta v \geqslant \alpha v((\underline{u}_1 - \varepsilon)/(\beta + \underline{u}_1 - \varepsilon) - rv/(1 + rv))$, and we have $\liminf_{t \to \infty} \min_{\underline{\Omega}} v(\cdot, t) \geqslant \frac{\underline{u}_1}{\beta r} := \underline{v}_1.$

For $0 < \varepsilon < \underline{v}_1$, there exists t_4^{ε} such that when $t \geqslant t_4^{\varepsilon} \geqslant t_3^{\varepsilon}$, $v(x,t) \geqslant \underline{v}_1 - \varepsilon$ for $x \in \bar{\Omega}$. Meanwhile,

$$u_t - d_1 \Delta u \leqslant \frac{u}{(\beta + u)} ((1 - h)\beta + (1 - h - \beta)u - u^2 - s(\underline{v}_1 - \varepsilon))$$
$$= \frac{u}{(\beta + u)} (u - u_3)(u_4 - u),$$

where

$$u_3 = \frac{1 - h - \beta - \sqrt{(1 - h - \beta)^2 + 4(1 - h)\beta - 4s\underline{v}_1}}{2} < 0,$$

$$u_4 = \frac{1 - h - \beta + \sqrt{(1 - h - \beta)^2 + 4(1 - h)\beta - 4s\underline{v}_1}}{2} > 0.$$

Hence,

$$\limsup_{t \to \infty} \max_{\bar{\Omega}} u(\cdot, t) \leqslant u_4(\underline{v}_1) := \bar{u}_2.$$

Then there exists t_5^ε such that for $(x,t)\in \bar{\Omega}\times [t_5^\varepsilon,\infty),$ $u(x,t)\leqslant \bar{u}_2+\varepsilon.$ Let

$$\varphi(\tau) = \frac{\tau}{r\beta}, \qquad \psi(\tau) = \frac{1 - h - \beta + \sqrt{(1 - h - \beta)^2 + 4(1 - h)\beta - 4s\tau}}{2},$$

then $\varphi'(\tau) > 0$, $\psi'(\tau) < 0$. Therefore, the constants \bar{u}_1 , \bar{v}_1 , \underline{u}_1 , \underline{v}_1 , \bar{u}_2 showed above satisfy

$$\begin{split} &\underline{u}_1 \leqslant \liminf_{t \to \infty} \min_{\bar{\Omega}} u(\cdot,t) \leqslant \limsup_{t \to \infty} \max_{\bar{\Omega}} u(\cdot,t) \leqslant \bar{u}_1, \\ &\underline{v}_1 \leqslant \liminf_{t \to \infty} \min_{\bar{\Omega}} v(\cdot,t) \leqslant \limsup_{t \to \infty} \max_{\bar{\Omega}} v(\cdot,t) \leqslant \bar{v}_1, \\ &\underline{u}_1 = \psi(\bar{v}_1) < \psi(\underline{v}_1) = \bar{u}_2 < \bar{u}_1, \\ &\underline{v}_1 = \varphi(\underline{u}_1) < \varphi(\bar{u}_1) = \bar{v}_1. \end{split}$$

By virtue of the inductive method, we can construct four sequences $\{\underline{u}_i\}$, $\{\bar{u}_i\}$, $\{\underline{v}_i\}$ by

$$\underline{v}_i = \varphi(\underline{u}_i), \qquad \varphi(\bar{u}_i) = \bar{v}_i, \qquad \underline{u}_i = \psi(\bar{v}_i), \qquad \psi(\underline{v}_i) = \bar{u}_{i+1}$$

such that

$$\begin{split} \underline{u}_i \leqslant \liminf_{t \to \infty} \min_{\bar{\Omega}} u(\cdot, t) \leqslant \limsup_{t \to \infty} \max_{\bar{\Omega}} u(\cdot, t) \leqslant \bar{u}_i, \\ \underline{v}_i \leqslant \liminf_{t \to \infty} \min_{\bar{\Omega}} v(\cdot, t) \leqslant \limsup_{t \to \infty} \max_{\bar{\Omega}} v(\cdot, t) \leqslant \bar{v}_i. \end{split}$$

By the monotonicity of φ , ψ , we have

$$\underline{v}_{i-1} < \underline{v}_i = \varphi(\underline{u}_i) < \varphi(\bar{u}_i) = \bar{v}_i < \bar{v}_{i-1},$$

$$\underline{u}_{i-1} < \underline{u}_i = \psi(\bar{v}_i) < \psi(\underline{v}_i) = \bar{u}_{i+1} < \bar{u}_i.$$

We may suppose that

$$\lim_{i \to \infty} \underline{u}_i = \underline{u}, \qquad \lim_{i \to \infty} \underline{v}_i = \underline{v}, \qquad \lim_{i \to \infty} \bar{u}_i = \bar{u}, \qquad \lim_{i \to \infty} \bar{v}_i = \bar{v}$$

Since problem (3) has a unique positive constant equilibrium $(\lambda, \lambda/(\beta r))$ under h < 1, then $(\underline{u}, \underline{v}) = (\bar{u}, \bar{v}) = (\lambda, \lambda/(\beta r))$ and $\lim_{t \to \infty} (u(x,t), v(x,t)) = (\lambda, \lambda/(\beta r))$. So the proof is obtained.

4 Numerical simulations

In this section, we will use mathematical software Matlab and show some numerical simulations to depict our theoretical analysis of the existence of periodic solutions and the stability of positive constant solution.

For problem (2), we choose h=0.5, $\alpha=1$, $\beta=1$, r=0.1, s=0.9, and initial value $(u_0,v_0)=(0.052,0.5)$. After some computations, we can see that $\lambda_0=0.2984$ and $(\lambda,\lambda/(\beta r))=(0.0523,0.5324)$. Then the left part of Fig. 1 shows the local stability of constant solution, while the right part of Fig. 1 shows the bifurcating periodic solutions. Here we choose h=0.1, $\alpha=0.1$, $\beta=0.65$, r=0.15, s=0.725, and initial values $(u_0,v_0)=(0.08,0.8)$. Then we can conclude that $\lambda_0=0.0805$, $(\lambda,\lambda/(\beta r))=(0.0805,0.8257)$, and $a(\lambda_0)=-0.3951<0$, which mean that the periodic solutions bifurcating near (0.0805,0.8257) are unstable and subcritical when $\lambda=0.0805$.

For problem (3), we choose $l=1, d_1=1, d_2=2, h=0.3, \alpha=0.25, \beta=0.65, r=0.2, s=0.75,$ and initial values $(u_0,v_0)=(0.0658,0.7254),$ then $\lambda_0=0.1350,$ $\lambda_*=0.0966,$ and $(\lambda,\lambda/(\beta r))=(0.0785,0.6037).$ Then the local stability is depicted in Fig. 2 when $\lambda<\lambda_0$. When we choose that $d_1=1, d_2=2, l=1, h=0.25, \alpha=0.2,$

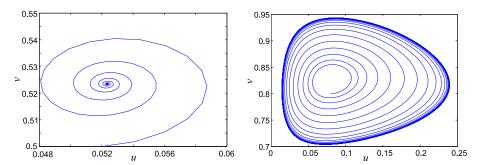


Figure 1. Convergence to the positive constant solution (0.0523, 0.5324) in the local stability region when $\lambda < \lambda_0$ (left). The periodic solutions bifurcating near (0.0805, 0.8257) are unstable and subcritical when $\lambda = 0.0805$ (right).

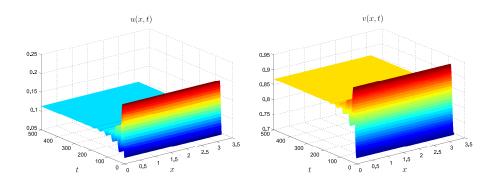


Figure 2. Convergence to the positive constant steady state solution (0.0785, 0.6037) in the local stability region: component u (left); component v (right).

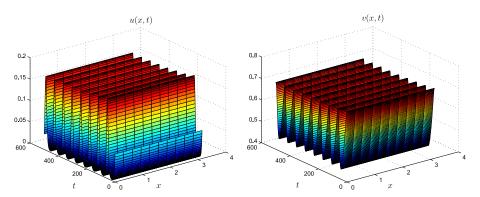


Figure 3. Convergence to the positive constant steady state solution (0.0785, 0.6037) in the local stability region: component u (left); component v (right).

 $\beta=0.5,\,r=0.15,\,s=0.9,$ and initial values $(u_0,v_0)=(0.0658,0.7254),$ then we can get $\lambda_0=0.0319,\,\lambda_*=0.0228,\,\mathrm{Re}(c_1(\lambda_0))=-1.8816<0,$ and $(\lambda,\lambda/(\beta r))=(0.0318,0.4244),$ which indicates that the homogeneous periodic solution bifurcating from (0.0318,0.4244) are forward and stable when $\lambda=\lambda_0.$ Then the periodic solutions are depicted in Fig. 3.

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