The Effect of Age Structure and Two Delays on the Predator-prey Model with Prey Fear Cost and Variable Predator Search Speed

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Abstract. The predator fertility function $\mathcal{M}(a)$ is thought to be a piecewise function related to the predator development time τ_2 , and a predator-prey model with predatorage structure and prey reaction time delay τ_1 is investigated. By calculating the stability switching curves and using the theory of integrated semigroups and the Hopf bifurcation theory for abstract Cauchy problems with non-dense domain, we obtain that oscillations are caused by τ_1 and τ_2 . Numerical simulations and a summary are presented at the end.

1. Introduction

For biology, fear is the innate psychological reaction of living things. Fear can not only improve the alertness of living things but also help living things avoid danger. At the same time, fear also has a certain impact on the reproductive ability of organisms, foraging behavior and physiological state. As shown by Zanette et al. [26], when the prey perceives predation risk, its reproductive rate decreases in the absence of direct killing. They conducted field experiments with song finches using electric pens throughout the breeding season, and experimental observations showed that red song sparrows parents under the fear produced 40% fewer offspring than those without fear. The risk of predation affects both the survival rate and the birth rate of offspring, which is the cause of this phenomenon. So fear of predators greatly reduces the prey reproduction rate in the predator-prey models. For more information, see Wang et al. [21], Creel et al. [2], Orrock and Fletcher [17], etc.

What is worth mentioning is that the search speed of predators is usually variable in nature. Experiments by Hassell and Comins [5] showed that they can adjust their search speeds based on prey density by observing their living environment. In Yu and Wang [25],

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they considered the following model

(1.1)
$$\begin{aligned} \frac{\mathrm{d}v}{\mathrm{d}t} &= \frac{rv}{1+ku} - \mu v - cv^2 - \frac{\alpha v^2}{\alpha H v^2 + v + g}u,\\ \frac{\mathrm{d}u}{\mathrm{d}t} &= \eta \frac{\alpha v^2}{\alpha H v^2 + v + g}u - mu. \end{aligned}$$

In the model (1.1), prey populations are reduced due to fear of predators, and a predator's search speed is influenced by prey density. Where the densities of the predator and prey, respectively, are u and v. r represents the birth rate of prey when there are no predators, k is the level of fear, and η is the predator's digestibility of captured prey. The natural mortality rate of prey is denoted by μ , c is the death rate due to competition between prey, α is the maximally accomplishable search rate, and H represents the time it takes for a predator to handle a single prey. When the search rate is halved, the prey density is represented by the semi-saturated constant g, m is the death rate of predator. r, k, η , μ , c, α , H, g, m are all positive constants.

In realistic biological population models, differential equations with time delays should be used. This is because there will be delays in factors such as pregnancy, reaction time, maturity, etc (see Liu and Li [11], Ruan [18], Ducrot et al. [4], Kuang [8], Wangersky and Cunningham [22], Zhang and Liu [28] and their cited references).

Furthermore, in recent years, our understanding of the dynamics of some important systems has made rapid progress, and it is observed that the real-world models of biological populations are structured. Therefore, the current age structure model has optimistic application prospects in population dynamic modeling. For more information on the age structure model, refer to Inaba [7], Magal and Ruan [14], Hoppensteadt [6], Webb [23], Zhang and Liu [27], Maynard Smith (Chapters 3 and 4) [16], Thieme [19], etc.

However, there are a few results about population biology models with both age structure and time delay, due to computational tediousness and difficulties in theoretical analysis. It was inspired by Yu and Wang [25], Liu and Li [11], Ducrot et al. [4], Wangersky and Cunningham [22], Zhang and Liu [27]. A predator-prey model containing predator age structure and the delay τ_1 in the response of the prey is considered in this paper. According to the model (1.1), we consider the following model

$$\begin{aligned} &(1.2)\\ &\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -mu(t,a), \quad a > 0,\\ &\frac{dV(t)}{dt} = \frac{rV(t)}{1 + k \int_0^{+\infty} u(t,a) \, \mathrm{d}a} - \mu V(t) - cV^2(t) - \frac{\alpha V^2(t)}{\alpha H V^2(t) + V(t) + g} \int_0^{+\infty} u(t,a) \, \mathrm{d}a,\\ &u(t,0) = \eta \frac{\alpha V^2(t-\tau_1)}{\alpha H V^2(t-\tau_1) + V(t-\tau_1) + g} \int_0^{+\infty} \mathcal{M}(a) u(t,a) \, \mathrm{d}a, \quad t > 0,\\ &u(0,\cdot) = u_0 \in L^1((0,+\infty), \mathbb{R}), \quad V_0 = z \in C([-\tau_1,0], \mathbb{R}), \end{aligned}$$

where a and t represent age and time, respectively. V(t) stands for the prey's population density at time t. u(t, a) provides the population density of the predator at time t and age a. $\mathcal{M}(a)$ indicates fertility function, which is affected by the age of the predator a. $\mathcal{M}(a)$ satisfies Assumption 1.1 below.

Assumption 1.1. Let

$$\mathcal{M}(a) := \begin{cases} \mathcal{M}^* & \text{if } a \ge \tau_2, \\ 0 & \text{if } a \in (0, \tau_2) \end{cases}$$

with $\tau_2 > 0$, $\mathcal{M}^* > 0$ and $\int_0^{+\infty} \mathcal{M}(a) e^{-ma} da = R < +\infty$.

The following is an arrangement of the sections of this paper. The age-structured model (1.2) with prey reaction time delay is rewritten as a non-densely defined Cauchy problem in Section 2. We consider the equilibrium and linearized equation of (1.2) in Section 3. In Section 4, we investigate the existence of Hopf bifurcation on the parametric plane of two delays. To demonstrate the theoretical findings presented in this paper, we do some numerical simulations of (1.2) in Section 5. In the end, we show a summary.

2. Preliminaries

First of all, we rescale the time and age of the model (1.2) by making $\hat{a} = \frac{a}{\tau_2}$, $\hat{t} = \frac{t}{\tau_2}$ and find the variable transformations $\hat{u}(\hat{t}, \hat{a}) = \tau_2 u(\tau_2 \hat{t}, \tau_2 \hat{a})$ and $\hat{V}(\hat{t}) = V(\tau_2 \hat{t})$ to normalize the parameter τ_2 in (1.2). Then, remove the superscript after variable transformations, and the following system can be obtained

$$\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\tau_2 m u(t,a),$$
(2.1)
$$\frac{dV(t)}{dt} = \tau_2 \left[\frac{rV(t)}{1 + k \int_0^{+\infty} u(t,a) \, da} - \mu V(t) - cV^2(t) - \frac{\alpha V^2(t) \int_0^{+\infty} u(t,a) \, da}{\alpha H V^2(t) + V(t) + g} \right],$$

$$u(t,0) = \frac{\tau_2 \eta \alpha V^2 \left(t - \frac{\tau_1}{\tau_2}\right) \int_0^{+\infty} \mathcal{M}(a) u(t,a) \, da}{\alpha H V^2 \left(t - \frac{\tau_1}{\tau_2}\right) + V \left(t - \frac{\tau_1}{\tau_2}\right) + g},$$

$$u(0,\cdot) = u_0 \in L^1((0,+\infty),\mathbb{R}), \quad V_0 = z \in C \left([-\tau_1/\tau_2,0],\mathbb{R} \right)$$

with the $\mathcal{M}(a)$ can be considered as follows:

$$\mathcal{M}(a) = \begin{cases} \mathcal{M}^* & \text{if } a \ge 1, \\ 0 & \text{otherwise} \end{cases} \quad \text{and} \quad \mathcal{M}^* = Rm \mathrm{e}^{m\tau_2}$$

with $\tau_2 > 0$, $\mathcal{M}^* > 0$ and $0 < R < +\infty$.

Let $V(t) := \int_0^{+\infty} \rho(t, a) \, da$ so that we can rewrite the second equation of (2.1) as

$$\frac{\partial \rho(t,a)}{\partial t} + \frac{\partial \rho(t,a)}{\partial a} = -\tau_2 \mu \rho(t,a),$$

$$\rho(t,0) = \widetilde{\Theta}(u(t,\cdot),\rho(t,\cdot)),$$

$$\rho_0 \in C([-\tau_1/\tau_2,0], L^1((0,+\infty),\mathbb{R}))$$

with

$$\widetilde{\Theta}(u(t,\cdot),\rho(t,\cdot)) = \tau_2 \left(\frac{r \int_0^{+\infty} \rho(t,a) \,\mathrm{d}a}{1+k \int_0^{+\infty} u(t,a) \,\mathrm{d}a} - c \left(\int_0^{+\infty} \rho(t,a) \,\mathrm{d}a\right)^2 - \frac{\alpha \left(\int_0^{+\infty} \rho(t,a) \,\mathrm{d}a\right)^2}{\alpha H \left(\int_0^{+\infty} \rho(t,a) \,\mathrm{d}a\right)^2 + \int_0^{+\infty} \rho(t,a) \,\mathrm{d}a + g} \int_0^{+\infty} u(t,a) \,\mathrm{d}a\right).$$

We can further find the following by letting $w(t, a) = \begin{pmatrix} u(t,a) \\ \rho(t,a) \end{pmatrix}$ and $w_t(\psi, a) = w(t + \psi, a)$ with $\psi \in [-\tau_1/\tau_2, 0]$ and $t \ge 0$:

(2.2)
$$\frac{\partial w(t,a)}{\partial t} + \frac{\partial w(t,a)}{\partial a} = -Dw(t,a),$$
$$w(t,0) = B(w_t(\psi,\cdot)),$$
$$w_0 = \begin{pmatrix} u_0\\\rho_0 \end{pmatrix} \in C\big([-\tau_1/\tau_2,0], L^1((0,+\infty), \mathbb{R}^2)\big),$$

where

$$D = \begin{pmatrix} \tau_2 m & 0\\ 0 & \tau_2 \mu \end{pmatrix} \quad \text{and} \quad B(w_t(\psi, \cdot\,)) = \begin{pmatrix} \frac{\tau_2 \eta \alpha \left(\int_0^{+\infty} \rho \left(t - \frac{\tau_1}{\tau_2}, a\right) \, \mathrm{d}a\right)^2 \int_0^{+\infty} \mathcal{M}(a) u(t, a) \, \mathrm{d}a}{\alpha H \left(\int_0^{+\infty} \rho \left(t - \frac{\tau_1}{\tau_2}, a\right) \, \mathrm{d}a\right)^2 + \int_0^{+\infty} \rho \left(t - \frac{\tau_1}{\tau_2}, a\right) \, \mathrm{d}a + g} \\ \widetilde{\Theta}(u(t, \cdot\,), \rho(t, \cdot\,)) \end{pmatrix}.$$

Let's think about the Banach space $A := \mathbb{R}^2 \times L^1((0, +\infty), \mathbb{R}^2)$ with the usual product norm

$$\begin{pmatrix} \zeta \\ \phi \end{pmatrix} = \|\zeta\|_{\mathbb{R}^2} + \|\phi\|_{L^1}, \quad \begin{pmatrix} \zeta \\ \phi \end{pmatrix} \in A$$

Define $N: D(N) \subset A \to A$ as follows:

$$N\begin{pmatrix}0\\\phi\end{pmatrix} = \begin{pmatrix}-\phi(0)\\-\phi' - D\phi\end{pmatrix} \quad \text{with } D(N) = \{0\} \times W^{1,1}((0, +\infty), \mathbb{R}^2).$$

Next $A_0 := \overline{D(N)} = \{0\} \times L^1((0, +\infty), \mathbb{R}^2)$. Let

$$C_N = \left\{ \begin{pmatrix} \zeta(\cdot) \\ z(\cdot) \end{pmatrix} \in C([-\tau_1/\tau_2, 0], A) : \zeta(0) = 0 \right\}.$$

Define $F: C_N \to A$ as

$$F\left(\begin{pmatrix}\zeta(\cdot)\\z(\cdot)\end{pmatrix}\right) = \begin{pmatrix}B(z(\cdot))\\0_{L_1}\end{pmatrix},$$

$$B(z(\cdot)) = \begin{pmatrix} \frac{\tau_2 \eta \alpha \left(\int_0^{+\infty} z_2(-\tau_1/\tau_2)(a) \, \mathrm{d}a\right)^2 \int_0^{+\infty} \mathcal{M}(a) z_1(0)(a) \, \mathrm{d}a}{\alpha H \left(\int_0^{+\infty} z_2(-\tau_1/\tau_2)(a) \, \mathrm{d}a\right)^2 + \int_0^{+\infty} z_2(-\tau_1/\tau_2)(a) \, \mathrm{d}a + g} \\ \widetilde{\Theta}(z_1(0)(\cdot), z_2(0)(\cdot)) \end{pmatrix}$$

Then (2.2) can be rephrased as

(2.3)
$$\frac{\mathrm{d}}{\mathrm{d}t}x(t) = Nx(t) + F(x_t), \quad t \ge 0, \quad x_0 = \begin{pmatrix} 0_{\mathbb{R}^2} \\ w_0 \end{pmatrix} \in C_N$$

by using w(t) to represent w(t,a) and $x(t) = \begin{pmatrix} 0_{\mathbb{R}^2} \\ w(t) \end{pmatrix}$ with $x_t \in C_N, x_t(\psi) = x(t+\psi)$ and $x_0(\psi) = \begin{pmatrix} 0_{\mathbb{R}^2} \\ w_0(\psi, \cdot) \end{pmatrix}$.

Next, we want to rewrite (2.3) as an abstract Cauchy problem of ODE. $y \in C([0, +\infty) \times [-\tau_1/\tau_2, 0]; A)$ is defined by

$$y(t,\psi) = x(t+\psi), \quad \forall t \ge 0, \ \forall \psi \in [-\tau_1/\tau_2, 0]$$

If $x \in C^1([-\tau_1/\tau_2, +\infty); A)$, then

$$\frac{\partial y(t,\psi)}{\partial t} = x'(t+\psi) = \frac{\partial y(t,\psi)}{\partial \psi}.$$

Accordingly,

$$\frac{\partial y(t,\psi)}{\partial t} - \frac{\partial y(t,\psi)}{\partial \psi} = 0, \quad \forall t \ge 0, \ \forall \psi \in [-\tau_1/\tau_2, 0],$$

If $\psi = 0$, then

$$\frac{\partial y(t,0)}{\partial \psi} = x'(t) = Nx(t) + F(x_t) = Ny(t,0) + F(y(t,\cdot)), \quad \forall t \ge 0.$$

By derivation, y should satisfy the following PDE

(2.4)

$$\frac{\partial y(t,\psi)}{\partial t} - \frac{\partial y(t,\psi)}{\partial \psi} = 0,$$

$$\frac{\partial y(t,0)}{\partial \psi} = Ny(t,0) + F(y(t,\cdot)), \quad t \ge 0,$$

$$y(0,\cdot) = x_0 \in C_N.$$

Next, we use the state space $G = A \times C$, $C := C([-\tau_1/\tau_2, 0], A)$ together with the usual product norm

$$\binom{f}{z} = \|f\|_A + \|z\|_C,$$

and the definition of the linear operator $L: D(L) \subset G \to G$ is

$$L\binom{0_A}{z} = \binom{-z'(0) + Nz(0)}{z'}, \quad \forall \binom{0_A}{z} \in D(L),$$

$$D(L) = \{0_A\} \times \{z \in C^1([-\tau_1/\tau_2, 0], A), z(0) \in D(N)\}.$$

Due to $G_0 := \overline{D(L)} = \{0_A\} \times C_N \neq G$, the linear operator L is non-densely defined. Define $Q: G_0 \to G$ as

$$Q\binom{0_A}{z} = \binom{F(z)}{0_{C_N}}.$$

 $y(t, \cdot)$ is represented by y(t), then

$$Y(t) := \binom{0_A}{y(t)},$$

as a result, (2.4) can be reformulated as

(2.5)
$$\frac{\mathrm{d}Y(t)}{\mathrm{d}t} = LY(t) + Q(Y(t)), \quad t \ge 0, \quad Y(0) = \begin{pmatrix} 0_A \\ x_0 \end{pmatrix} \in G_0,$$

which is non-densely defined Cauchy problem and we let

$$\vartheta := \min\{\tau_2 \mu, \tau_2 m\} > 0, \quad \mathcal{L} := \{\lambda \in \mathbb{C} : \operatorname{Re}(\lambda) > -\vartheta\}$$

Thus, the following theorem can be obtained, which Ducrot et al. demonstrated in [4].

Theorem 2.1. Operators N and L are defined as above, there hold that

(i) If $\lambda \in \mathcal{L}$, thus $\lambda \in \rho(N)$ and

$$\begin{split} (\lambda I - N)^{-1} \begin{pmatrix} \varsigma \\ \varphi \end{pmatrix} &= \begin{pmatrix} 0_{\mathbb{R}^2} \\ \phi \end{pmatrix} \iff \phi(a) = \mathrm{e}^{-\int_0^a (\lambda I + D) \, \mathrm{d}l} \varsigma + \int_0^a \mathrm{e}^{-\int_s^a (\lambda I + D) \, \mathrm{d}l} \varphi(s) \, \mathrm{d}s \\ \text{with } \begin{pmatrix} \varsigma \\ \varphi \end{pmatrix} \in A \text{ and } \begin{pmatrix} 0_{\mathbb{R}^2} \\ \phi \end{pmatrix} \in D(N); \end{split}$$

(ii) $\rho(L) = \rho(N)$. Furthermore, for each $\lambda \in \rho(L)$, we have the following explicit formula for the resolvent of L:

$$(\lambda I - L)^{-1} \begin{pmatrix} f \\ \varphi \end{pmatrix} = \begin{pmatrix} 0_A \\ z \end{pmatrix} \iff z(\psi) = e^{\lambda \psi} (\lambda I - N)^{-1} [\varphi(0) + f] + \int_{\psi}^{0} e^{\lambda(\psi - s)} \varphi(s) \, \mathrm{d}s;$$

(iii) The operators L and N are Hille-Yosida operators on G and A, respectively.

Let $A_+ := \mathbb{R}^2_+ \times L^1((0, +\infty), \mathbb{R}^2_+)$, $G_+ := A_+ \times C([-\tau_1/\tau_2, 0], A_+)$ and $G_{0+} := G_0 \cap G_+$. We get the global existence, uniqueness and positive of solutions for system (2.5) by the consequences of [13, 15].

3. Equilibria and linearized equation

Let $\overline{Y} = \begin{pmatrix} 0_A \\ \overline{\varphi} \end{pmatrix} \in D(L)$ be the equilibrium of system (2.5) with $\overline{\varphi} = \begin{pmatrix} \overline{\zeta}(\cdot) \\ \overline{z}(\cdot) \end{pmatrix} \in C^1 \left([-\tau_1/\tau_2, 0], A \right), \overline{\varphi}(0) \in D(N)$ and $\overline{z}(\cdot) = \begin{pmatrix} \overline{z}_1(\cdot) \\ \overline{z}_2(\cdot) \end{pmatrix}$. Next $L\overline{Y} + Q(\overline{Y}) = 0$ is equivalent to $-\overline{\varphi}'(0) + N\overline{\varphi}(0) + F(\overline{\varphi}) = 0, \quad \overline{\varphi}' = 0.$

Hence

$$\overline{z}(a) = \begin{pmatrix} \overline{z}_1(a) \\ \overline{z}_2(a) \end{pmatrix} = \begin{pmatrix} \frac{\tau_2 \eta \alpha \overline{V}^2 \int_0^{+\infty} \mathcal{M}(a) \overline{z}_1(a) \, \mathrm{d}a}{\alpha H \overline{V}^2 + \overline{V} + g} \mathrm{e}^{-\tau_2 m a} \\ \tau_2 \left(\frac{r \overline{V}}{1 + k \int_0^{+\infty} \overline{z}_1(a) \, \mathrm{d}a} - c \overline{V}^2 - \frac{\alpha \overline{V}^2 \int_0^{+\infty} \overline{z}_1(a) \, \mathrm{d}a}{\alpha H \overline{V}^2 + \overline{V} + g} \right) \mathrm{e}^{-\tau_2 \mu a} \end{pmatrix},$$

where $\overline{V} = \int_0^{+\infty} \overline{z}_2(a) \, \mathrm{d}a.$

(1) If $\overline{z}_1(a) \neq 0$, then $\int_0^{+\infty} \mathcal{M}(a)\overline{z}_1(a) \, \mathrm{d}a \neq 0$ and

$$1 = \frac{\tau_2 \eta \alpha \overline{V}^2 \int_0^{+\infty} \mathcal{M}(a) \mathrm{e}^{-\tau_2 m a} \,\mathrm{d}a}{\alpha H \overline{V}^2 + \overline{V} + g}$$

that is,

$$(\alpha H - \alpha \eta R)\overline{V}^2 + \overline{V} + g = 0.$$

Analysis shows that the above formula has a unique positive root only when $H < \eta R$. As a result, we obtain

$$\overline{V} = \frac{-1 - \sqrt{1 - 4\alpha(H - \eta R)g}}{2\alpha(H - \eta R)}$$

and

$$\overline{V} = \tau_2 \left(\frac{r\overline{V}}{1 + k \int_0^{+\infty} \overline{z}_1(a) \, \mathrm{d}a} - c\overline{V}^2 - \frac{\alpha \overline{V}^2 \int_0^{+\infty} \overline{z}_1(a) \, \mathrm{d}a}{\alpha H \overline{V}^2 + \overline{V} + g} \right) \int_0^{+\infty} \mathrm{e}^{-\tau_2 \mu a} \, \mathrm{d}a.$$

Hence

$$A_1\left(\int_0^{+\infty} \mathcal{M}(a)\overline{z}_1(a) \,\mathrm{d}a\right)^2 + A_2 \int_0^{+\infty} \mathcal{M}(a)\overline{z}_1(a) \,\mathrm{d}a + A_3 = 0,$$

that is,

$$\int_{0}^{+\infty} \mathcal{M}(a)\overline{z}_{1}(a) = \frac{-A_{2} + \sqrt{A_{2}^{2} - 4A_{1}A_{3}}}{2A_{1}},$$

where

$$\begin{split} A_1 &= k\eta^2 \alpha^3 \overline{V}^6 > 0, \\ A_2 &= \eta m \alpha \overline{V}^3 (\alpha H \overline{V}^2 + \overline{V} + g) \left[k (c \overline{V} + \mu) (\alpha H \overline{V}^2 + \overline{V} + g) + \alpha \overline{V} \right] > 0, \\ A_3 &= -\overline{V} m^2 (\alpha H \overline{V}^2 + \overline{V} + g)^3 (r - \mu - c \overline{V}). \end{split}$$

Then

$$\overline{z}_1(a) = \frac{\tau_2 \eta \alpha \overline{V}^2 \left(-A_2 + \sqrt{A_2^2 - 4A_1 A_3} \right) \mathrm{e}^{-\tau_2 m a}}{2A_1 (\alpha H \overline{V}^2 + \overline{V} + g)}$$

The above shows that $\overline{z}_1(a)$ is positive only if $A_3 < 0$. As a result, we have

 $r > \mu + c\overline{V}.$

(2) If $\overline{z}_1(a) \equiv 0$, then $\int_0^{+\infty} \mathcal{M}(a)\overline{z}_1(a) \, \mathrm{d}a = 0$, we obtain that

$$\begin{cases} \overline{z}_{01}(a) = 0, \\ \overline{z}_{02}(a) = 0 \end{cases} \text{ and } \begin{cases} \overline{z}_{03}(a) = 0, \\ \overline{z}_{04}(a) = \frac{\tau_2 \mu (r - \mu) e^{-\tau_2 \mu a}}{c} \end{cases}$$

are always present.

Lemma 3.1. The system (2.5) always has the following two equilibriums

$$\overline{Y}_{01} = \begin{pmatrix} 0_A \\ \left(\overline{\zeta}_{01}(\cdot) \\ \left(\overline{z}_{01}(\cdot) \\ \overline{z}_{02}(\cdot) \right) \end{pmatrix} \end{pmatrix} \quad and \quad \overline{Y}_{02} = \begin{pmatrix} 0_A \\ \left(\overline{\zeta}_{02}(\cdot) \\ \left(\overline{z}_{03}(\cdot) \\ \overline{z}_{04}(\cdot) \right) \right) \end{pmatrix},$$

where $\overline{\zeta}_{01}(\theta) = \overline{\zeta}_{02}(\theta) = 0_{\mathbb{R}^2}$. Furthermore, the system (2.5) has a unique positive equilibrium

$$\overline{Y} = \begin{pmatrix} 0_A \\ \overline{\zeta}(\cdot) \\ \begin{pmatrix} \overline{z}_1(\cdot) \\ \overline{z}_2(\cdot) \end{pmatrix} \end{pmatrix}$$

with $\overline{\zeta}(\theta) = 0_{\mathbb{R}^2}$, if and only if

$$(3.1) r > \mu + c\overline{V} \quad and \quad H < \eta R.$$

For the rest of this article, assume that condition (3.1) holds. Taking the variable transformation $\tilde{Y}(t) := Y(t) - \overline{Y}$, (2.5) can be rewritten as

$$(3.2) \quad \frac{\mathrm{d}\widetilde{Y}(t)}{\mathrm{d}t} = L\widetilde{Y}(t) + Q(\widetilde{Y}(t) + \overline{Y}) - Q(\overline{Y}), \quad t \ge 0, \quad \widetilde{Y}(0) = \begin{pmatrix} 0_A \\ x_0 - \overline{\varphi} \end{pmatrix} =: \widetilde{Y}_0 \in \overline{D(L)}.$$

The linearized equation of system (3.2) at equilibrium 0 is

$$\frac{\mathrm{d}Y(t)}{\mathrm{d}t} = L\widetilde{Y}(t) + DQ(\overline{Y})\widetilde{Y}(t) \quad \text{for } t \ge 0, \ \widetilde{Y}(0) \in D(L),$$

and

where

$$DQ(\overline{Y}) \begin{pmatrix} 0_A \\ \varphi \end{pmatrix} = \begin{pmatrix} DF(\overline{\varphi})(\varphi) \\ 0_{C_N} \end{pmatrix}, \quad \forall \begin{pmatrix} 0_A \\ \varphi \end{pmatrix} \in D(L), \ \varphi = \begin{pmatrix} \zeta(\cdot) \\ z(\cdot) \end{pmatrix}$$
$$DF(\overline{\varphi})(\varphi) = \begin{pmatrix} DB(\overline{z})(z) \\ 0_{L^1((0,+\infty),\mathbb{R}^2)} \end{pmatrix}$$

and

$$\begin{aligned} DB(\overline{z})(z) \\ &= \begin{pmatrix} 0 & 0 \\ \frac{-\tau_2 r k \overline{V}}{\left(1 + k \int_0^{+\infty} \overline{u}(a) \, \mathrm{d}a\right)^2} - \frac{\tau_2 \alpha \overline{V}^2}{\alpha H \overline{V}^2 + \overline{V} + g} & \tau_2 \left(\frac{r}{1 + k \int_0^{+\infty} \overline{u}(a) \, \mathrm{d}a} - 2c \overline{V} - \frac{\alpha \overline{V}(\overline{V} + 2g) \int_0^{+\infty} \overline{u}(a) \, \mathrm{d}a}{\left(\alpha H \overline{V}^2 + \overline{V} + g\right)^2} \right) \end{pmatrix} \\ &\times \int_0^{+\infty} z(0)(a) \, \mathrm{d}a \\ &+ \left(\frac{\tau_2 \eta \alpha \overline{V}^2}{\alpha H \overline{V}^2 + \overline{V} + g} & 0 \\ 0 & 0 \right) \times \int_0^{+\infty} \mathcal{M}(a) z(0)(a) \, \mathrm{d}a \\ &+ \left(0 & \frac{\tau_2 \eta \alpha \overline{V}(\overline{V} + 2g) \int_0^{+\infty} \mathcal{M}(a) \overline{u}(a) \, \mathrm{d}a}{\left(\alpha H \overline{V}^2 + \overline{V} + g\right)^2} \right) \times \int_0^{+\infty} z(-\tau_1/\tau_2)(a) \, \mathrm{d}a. \end{aligned}$$

Therefore, system (3.2) can be rewritten as

$$\frac{\mathrm{d}Y(t)}{\mathrm{d}t} = \widetilde{L}\widetilde{Y}(t) + \widetilde{Q}(\widetilde{Y}(t)) \quad \text{for } t \ge 0$$

with the definition of the linear operator \widetilde{L} being $\widetilde{L} := L + DQ(\overline{Y})$ and

$$\widetilde{Q}(\widetilde{Y}(t)) = Q(\widetilde{Y}(t) + \overline{Y}) - Q(\overline{Y}) - DQ(\overline{Y})\widetilde{Y}(t)$$

satisfying $\widetilde{Q}(0) = 0$ and $D\widetilde{Q}(0) = 0$. Next

$$||T_{N_0}(t)|| \le e^{-\vartheta t}, \quad \forall t \ge 0.$$

Therefore

$$\omega_{0,\mathrm{ess}}(L_0) \le \omega_0(L_0) \le -\vartheta$$

Using the resulting perturbations from Ducrot et al. [4] or Thieme [20], we can get

$$\omega_{0,\text{ess}}((L+DQ(\overline{Y}))_0) \le -\vartheta < 0$$

since $DQ(\overline{Y})$ is a compact bounded linear operator. Thus, we can arrive at the proposition below.

Proposition 3.2. The linear operator \widetilde{L} is a Hille–Yosida operator whose part \widetilde{L}_0 in G_0 satisfies

$$\omega_{0,\mathrm{ess}}(\widetilde{L}_0) < 0.$$

Set $\lambda \in \mathcal{L}$. $(\lambda I - L)$ is invertible, as we can observed. Notice that $\lambda I - \tilde{L}$ is invertible if and only if $I - DQ(\overline{Y})(\lambda I - L)^{-1}$ is invertible. Furthermore

$$(\lambda I - \widetilde{L})^{-1} = (\lambda I - (L + DQ(\overline{Y})))^{-1}$$
$$= (\lambda I - L)^{-1} (I - DQ(\overline{Y})(\lambda I - L)^{-1})^{-1}.$$

Let

$$(I - DQ(\overline{Y})(\lambda I - L)^{-1}) \begin{pmatrix} \varsigma_A \\ \phi_{C_N} \end{pmatrix} = \begin{pmatrix} \gamma_A \\ \varphi_{C_N} \end{pmatrix}$$

with

$$\varsigma_A = \begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix}, \quad \gamma_A = \begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix} \text{ and } \varphi_{C_N} = \begin{pmatrix} \varphi_1(\cdot) \\ \varphi_2(\cdot) \end{pmatrix} \in C^1([-\tau_1/\tau_2, 0], A),$$

namely

$$\varsigma_A - DF(\overline{\varphi}) \left(e^{\lambda \psi} (\lambda I - N)^{-1} [\phi_{C_N}(0) + \varsigma_A] + \int_{\psi}^0 e^{\lambda(\psi - s)} \phi_{C_N}(s) \, \mathrm{d}s \right) = \gamma_A, \ \phi_{C_N} = \varphi_{C_N}$$

Hence

$$\begin{split} & \left[I - DF(\overline{\varphi}) \left(\mathrm{e}^{\lambda \psi} (\lambda I - N)^{-1} \right) \right] \varsigma_A \\ &= \gamma_A + DF(\overline{\varphi}) \left(\mathrm{e}^{\lambda \psi} (\lambda I - N)^{-1} \varphi_{C_N}(0) + \int_{\psi}^0 \mathrm{e}^{\lambda(\psi - s)} \varphi_{C_N}(s) \, \mathrm{d}s \right), \\ & \phi_{C_N} = \varphi_{C_N}. \end{split}$$

Set

$$\begin{pmatrix} \overline{\varsigma}_1\\ \overline{\varsigma}_2 \end{pmatrix} := \left[I - DF(\overline{\varphi}) \left(e^{\lambda \psi} (\lambda I - N)^{-1} \right) \right] \varsigma_A,$$

that is

$$\varsigma_A - \begin{pmatrix} DB(\overline{z}) \left[e^{\lambda \psi} \left(e^{-\int_0^a (\lambda I + D) \, \mathrm{d}l} \varsigma_1 + \int_0^a e^{-\int_s^a (\lambda I + D) \, \mathrm{d}l} \varsigma_2(s) \, \mathrm{d}s \right) \right] \\ 0_{L^1((0, +\infty), \mathbb{R}^2)} \end{pmatrix} = \begin{pmatrix} \overline{\varsigma}_1 \\ \overline{\varsigma}_2 \end{pmatrix},$$

or

$$\left[I - DB(\overline{z})\left(\mathrm{e}^{\lambda\psi}\mathrm{e}^{-\int_0^a(\lambda I + D)\,\mathrm{d}l}\right)\right]\varsigma_1 = \overline{\varsigma}_1 + DB(\overline{z})\left(\mathrm{e}^{\lambda\psi}\int_0^a\mathrm{e}^{-\int_s^a(\lambda I + D)\,\mathrm{d}l}\varsigma_2(s)\,\mathrm{d}s\right), \quad \varsigma_2 = \overline{\varsigma}_2.$$

Set

(3.3)
$$\Delta(\lambda) = I - DB(\overline{z}) \left(e^{\lambda \psi} e^{-\int_0^a (\lambda I + D) \, dI} \right)$$

,

and

$$\Theta(\lambda, \overline{\varsigma}_2) = DB(\overline{z}) \left[e^{\lambda \psi} \int_0^a e^{-\int_s^a (\lambda I + D) \, \mathrm{d}l} \overline{\varsigma}_2(s) \, \mathrm{d}s \right].$$

Hence

$$\Delta(\lambda)\varsigma_1 = \overline{\varsigma}_1 + \Theta(\lambda, \overline{\varsigma}_2).$$

Since $\Delta(\lambda)$ is invertible, there is

$$\varsigma_1 = (\Delta(\lambda))^{-1}(\overline{\varsigma}_1 + \Theta(\lambda, \overline{\varsigma}_2)).$$

We get the following lemma from the previous analysis.

Lemma 3.3. We have $\sigma(L+DQ(\overline{Y}))\cap \mathcal{L} = \sigma_p(L+DQ(\overline{Y}))\cap \mathcal{L} = \{\lambda \in \mathcal{L} : \det(\Delta(\lambda)) = 0\},\$ and the formula for each $\lambda \in \rho(L+DQ(\overline{Y}))\cap \mathcal{L}$ in the resolvent of $L+DQ(\overline{Y})$ is as follows

$$\begin{split} &[\lambda I - (L + DQ(\overline{Y}))]^{-1} \begin{pmatrix} \gamma_A \\ \varphi_{C_N} \end{pmatrix} \\ &= \begin{pmatrix} 0_A \\ e^{\lambda \psi} (\lambda I - N)^{-1} [\varphi_{C_N}(0) + \varsigma_A] + \int_{\psi}^{0} e^{\lambda(\psi - s)} \varphi_{C_A}(s) \, \mathrm{d}s \end{pmatrix}, \end{split}$$

where $\gamma_A = \begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix}$ and $\varsigma_A = \begin{pmatrix} \tilde{\gamma} \\ \gamma_2 \end{pmatrix}$ with

$$\widetilde{\gamma} = (\Delta(\lambda))^{-1} \left[\gamma_1 + DB(\overline{z}) \left(\int_{\psi}^0 e^{\lambda(\psi - s)} \varphi_2(s) \, \mathrm{d}s + e^{\lambda\psi} (\lambda I - A)^{-1} \varphi_2(0) \right) \right] + \Theta(\lambda, \gamma_2).$$

The proof of the above lemma can be seen in Lemma 3.3 of Liu and Li [11]. It can be obtained from Assumption 1.1 and (3.3):

$$\int_{0}^{+\infty} z(0)(a) \, \mathrm{d}a = \begin{pmatrix} \frac{1}{\lambda + \tau_2 m} & 0\\ 0 & \frac{1}{\lambda + \tau_2 \mu} \end{pmatrix},$$
$$\int_{0}^{+\infty} \mathcal{M}(a) z(0)(a) \, \mathrm{d}a = \begin{pmatrix} \frac{Rme^{-\lambda}}{\lambda + \tau_2 m} & 0\\ 0 & \frac{\mathcal{M}^* e^{-(\lambda + \tau_2 \mu)}}{\lambda + \tau_2 \mu} \end{pmatrix}$$

and

$$\int_0^{+\infty} z(-\tau_1/\tau_2)(a) \,\mathrm{d}a = \mathrm{e}^{-\frac{\tau_1}{\tau_2}\lambda} \begin{pmatrix} \frac{1}{\lambda+\tau_2m} & 0\\ 0 & \frac{1}{\lambda+\tau_2\mu} \end{pmatrix}.$$

Therefore, the characteristic equation in \overline{Y} is

$$(3.4) \det(\Delta(\lambda)) = \begin{vmatrix} 1 - \frac{\tau_2 \eta \alpha \overline{V}^2 R m e^{-\lambda}}{(\alpha H \overline{V}^2 + \overline{V} + g)(\lambda + \tau_2 m)} & \frac{-\frac{\tau_2 \eta \alpha \overline{V} (\overline{V} + 2g)\xi}{(\alpha H \overline{V}^2 + \overline{V} + g)^2} e^{-\frac{\tau_1}{\tau_2}\lambda}}{\lambda + \tau_2 \mu} \\ \frac{\frac{\tau_2 r k \overline{V}}{(1 + k \overline{U})^2} + \frac{\tau_2 \alpha \overline{V}^2}{\alpha H \overline{V}^2 + \overline{V}^2 + g}}{\lambda + \tau_2 m} & 1 - \frac{\tau_2 \left(\frac{r}{1 + k \overline{U}} - 2c \overline{V} - \frac{\alpha \overline{V} (\overline{V} + 2g) \overline{U}}{(\alpha H \overline{V}^2 + \overline{V} + g)^2}\right)}{\lambda + \tau_2 \mu} \end{vmatrix}$$
$$= \frac{\lambda^2 + \tau_2 p_1 \lambda + \tau_2^2 p_0 + \left(\tau_2^2 r_0 + \tau_2 r_1 \lambda\right) e^{-\lambda} + \tau_2^2 q_1 e^{-\frac{\tau_1}{\tau_2}\lambda}}{(\lambda + \tau_2 m)(\lambda + \tau_2 \mu)}$$
$$\triangleq \frac{\widetilde{f}(\lambda)}{\widetilde{g}(\lambda)},$$

$$\begin{split} \overline{U} &= \int_{0}^{+\infty} \overline{u}(a) \, \mathrm{d}a, \qquad p_1 = m - \frac{r}{1 + k\overline{U}} + \mu + 2c\overline{V} + \frac{\alpha\overline{V}(\overline{V} + 2g)\overline{U}}{(\alpha H\overline{V}^2 + \overline{V} + g)^2}, \\ \overline{V} &= \int_{0}^{+\infty} \overline{v}(a) \, \mathrm{d}a, \qquad p_0 = \mu m - \frac{mr}{1 + k\overline{U}} + 2cm\overline{V} + \frac{m\alpha\overline{V}(\overline{V} + 2g)\overline{U}}{(\alpha H\overline{V}^2 + \overline{V} + g)^2}, \\ \xi &= \int_{0}^{+\infty} \mathcal{M}(a)\overline{u}(a) \, \mathrm{d}a, \qquad r_0 = \frac{\eta\alpha\overline{V}^2 Rm}{\alpha H\overline{V}^2 + \overline{V} + g} \left[\frac{r}{1 + k\overline{U}} - \mu - 2c\overline{V} - \frac{\alpha\overline{V}(\overline{V} + 2g)\overline{U}}{(\alpha H\overline{V}^2 + \overline{V} + g)^2} \right], \\ r_1 &= -\frac{\eta\alpha\overline{V}^2 Rm}{\alpha H\overline{V}^2 + \overline{V} + g}, \qquad q_1 = \frac{\eta\alpha\overline{V}(\overline{V} + 2g)\xi}{(\alpha H\overline{V}^2 + \overline{V} + g)^2} \left(\frac{rk\overline{V}}{(1 + k\overline{U})^2} + \frac{\alpha\overline{V}^2}{\alpha H\overline{V}^2 + \overline{V} + g} \right), \\ \widetilde{g}(\lambda) &= (\lambda + \tau_2 m)(\lambda + \tau_2 \mu), \quad \widetilde{f}(\lambda) = \lambda^2 + \tau_2 p_1 \lambda + \tau_2^2 p_0 + (\tau_2 r_1 \lambda + \tau_2^2 r_0) \mathrm{e}^{-\lambda} + \tau_2^2 q_1 \mathrm{e}^{-\frac{\tau_1}{\tau_2}\lambda}. \end{split}$$

4. The existence of Hopf bifurcation and stability switching curves

In this section, the existence of the Hopf bifurcation of (2.5) is considered by using the stability switching curves method of Lin and Wang [10] when τ_1 and τ_2 varies independently in \mathbb{R}_+ . First, to apply the stability switching curves method, we should examine Assumptions (I)–(IV) in [10]. Then, we provide the explicit expression of the stability switching curves in the plane (τ_1, τ_2) by trying to find pure imaginary roots. By calculating the stable switching curves, we investigate the stable region of the positive constant steady state. Finally, the crossing directions of the stability switching curves is used to support the Hopf bifurcation theorem on the two-parameter plane. The stability switching curves method has been applied and extended by some scholars, see [1,3,9,24]. Next, to obtain more results, we apply the Hopf bifurcation theory in Liu et al. [12] to the Cauchy problem (2.5) to investigate the existence of Hopf bifurcation when τ_1 and τ_2 are equal.

4.1. Stability switching curves

Let $\lambda := \tau_2 \widetilde{\lambda}$, and then remove the superscript after the variable transformation of (3.4). We have

$$\widetilde{f}(\lambda) := \tau_2^2 \mathcal{G}(\lambda; \tau_1, \tau_2),$$

where

(4.1)
$$\mathcal{G}(\lambda;\tau_1,\tau_2) = \kappa_0(\lambda) + \kappa_1(\lambda) e^{-\tau_1 \lambda} + \kappa_2(\lambda) e^{-\tau_2 \lambda} = 0,$$

and

$$\kappa_0(\lambda) = \lambda^2 + p_1\lambda + p_0, \quad \kappa_1(\lambda) = q_1, \quad \kappa_2(\lambda) = r_1\lambda + r_0.$$

Notice that when $p_1 + r_1 > 0$, the real part of all roots of (4.1) are negative for $\tau_1 = \tau_2 = 0$. Next, from the reference [10], the polynomial $\kappa_0(\lambda)$, $\kappa_1(\lambda)$ and $\kappa_2(\lambda)$ must satisfy the four assumptions below.

- (I) deg[$\kappa_0(\lambda)$] $\geq \max \{ deg[\kappa_1(\lambda)], deg[\kappa_2(\lambda)] \}$ is true, there are a finite number of characteristic roots on $\mathbb{C}_+ = \{ \lambda \in \mathbb{C} : \operatorname{Re} \lambda > 0 \}.$
- (II) $\kappa_0(0) + \kappa_1(0) + \kappa_2(0) \neq 0.$
- (III) $\kappa_0(\lambda)$, $\kappa_1(\lambda)$, $\kappa_2(\lambda)$ are coprime polynomials.
- (IV) $\lim_{\lambda \to \infty} \left(\left| \frac{\kappa_1(\lambda)}{\kappa_0(\lambda)} \right| + \left| \frac{\kappa_2(\lambda)}{\kappa_0(\lambda)} \right| \right) < 1.$

Conditions (I)–(IV) are clearly satisfied. For further analysis, similar to [24], we introduce the following lemma.

Lemma 4.1. When the delays (τ_1, τ_2) change continuously on \mathbb{R}^2_+ , the number of characteristic roots (computational multiplicity) of $\mathcal{G}(\lambda; \tau_1, \tau_2)$ on \mathbb{C}_+ change only when a characteristic root appears on or crosses the imaginary axis.

Next, we should suppose that $\lambda = i\omega$ ($\omega > 0$) is the zero in (4.1). We get

$$\kappa_0(i\omega) + \kappa_1(i\omega)e^{-i\omega\tau_1} + \kappa_2(i\omega)e^{-i\omega\tau_2} = 0,$$

then

$$|\kappa_0(i\omega)|^2 + |\kappa_1(i\omega)|^2 - |\kappa_2(i\omega)|^2 = 2\left[\Lambda_1(\omega)\cos(\omega\tau_1) - \Upsilon_1(\omega)\sin(\omega\tau_1)\right]$$

with $\Lambda_1(\omega) = \operatorname{Re}(-\kappa_0(i\omega)\overline{\kappa}_1(i\omega))$ and $\Upsilon_1(\omega) = \operatorname{Im}(-\kappa_0(i\omega)\overline{\kappa}_1(i\omega))$. Assume $\Lambda_1^2(\omega) + \Upsilon_1^2(\omega) > 0$, then

(4.2)
$$|\kappa_0(i\omega)|^2 + |\kappa_1(i\omega)|^2 - |\kappa_2(i\omega)|^2 = 2\sqrt{\Lambda_1^2(\omega) + \Upsilon_1^2(\omega)}\cos(\omega\tau_1 + \widetilde{\beta}_1(\omega)),$$

where $\widetilde{\beta}_1(\omega) = \operatorname{Arg}\{-\kappa_0(i\omega)\overline{\kappa}_1(i\omega)\} \in (-\pi,\pi]$, thus, there exists a $\tau_1 \in \mathbb{R}_+$ satisfies (4.2) if and only if

(4.3)
$$\left| |\kappa_0(i\omega)|^2 + |\kappa_1(i\omega)|^2 - |\kappa_2(i\omega)|^2 \right| \le 2\sqrt{\Lambda_1^2(\omega) + \Upsilon_1^2(\omega)}.$$

Special case $\Lambda_1^2(\omega) + \Upsilon_1^2(\omega) = 0$ is already included in (4.3). Set

$$\cos[\theta_1(\omega)] = \frac{|\kappa_0(i\omega)|^2 + |\kappa_1(i\omega)|^2 - |\kappa_2(i\omega)|^2}{2\sqrt{\Lambda_1^2(\omega) + \Upsilon_1^2(\omega)}}, \quad \theta_1 \in [0, \pi],$$

then

(4.4)
$$\tau_{1,j_1}^{\pm}(\omega) = \frac{\pm \theta_1(\omega) - \widetilde{\beta}_1(\omega) + 2j_1\pi}{\omega}, \quad j_1 \in \mathbb{Z},$$

similarly, we can get

(4.5)
$$\tau_{2,j_2}^{\pm}(\omega) = \frac{\pm \theta_2(\omega) - \bar{\beta}_2(\omega) + 2j_2\pi}{\omega}, \quad j_2 \in \mathbb{Z},$$
$$\cos(\theta_2(\omega)) = \frac{|\kappa_0(i\omega)|^2 - |\kappa_1(i\omega)|^2 + |\kappa_2(i\omega)|^2}{2\sqrt{\Lambda_2^2(\omega) + \Upsilon_2^2(\omega)}},$$

$$\Lambda_2(\omega) = \operatorname{Re}(-\kappa_0(i\omega)\overline{\kappa}_2(i\omega)), \quad \Upsilon_2(\omega) = \operatorname{Im}(-\kappa_0(i\omega)\overline{\kappa}_2(i\omega)),$$
$$\widetilde{\beta}_2(\omega) = \operatorname{Arg}\{-\kappa_0(i\omega)\overline{\kappa}_2(i\omega)\} \in (-\pi,\pi].$$

The following inequality is satisfied by ω :

(4.6)
$$\left| |\kappa_0(i\omega)|^2 - |\kappa_1(i\omega)|^2 + |\kappa_2(i\omega)|^2 \right| \le 2\sqrt{\Lambda_2^2(\omega) + \Upsilon_2^2(\omega)}.$$

We can assume that the sets of $\omega \in \mathbb{R}_+$ satisfying (4.3) and (4.6) are Ω^1 and Ω^2 , respectively. It is easy to verify $\Omega^1 = \Omega^2$. Thus, denote $\Omega^1 = \Omega^2 \triangleq \Omega$.

From the reference [10], the following lemma on ω can be obtained.

Lemma 4.2. Ω consists of a finite number of intervals of finite length.

According to (4.4) and (4.5), when $\tau_1 = \tau_{1,j_1}^+(\omega)$, there is $\tau_2 = \tau_{2,j_2}^-(\omega)$, and when $\tau_1 = \tau_{1,j_1}^-(\omega)$, then $\tau_2 = \tau_{2,j_2}^+(\omega)$. Hence

$$\begin{aligned} \mathcal{T}_{j_1,j_2}^{\pm j} &= \left\{ (\tau_1^{\pm}(\omega), \tau_2^{\mp}(\omega)) \mid \omega \in \Omega_j \right\} \\ &= \left\{ \left(\frac{\pm \theta_1(\omega) - \widetilde{\beta}_1(\omega) + 2j_1\pi}{\omega}, \frac{\mp \theta_2(\omega) - \widetilde{\beta}_2(\omega) + 2j_2\pi}{\omega} \right) \mid \omega \in \Omega_j \right\}, \\ \mathcal{T}^j &= \bigcup_{j_1 = -\infty}^{\infty} \bigcup_{j_2 = -\infty}^{\infty} \left(\mathcal{T}_{j_1,j_2}^{+j} \cup \mathcal{T}_{j_1,j_2}^{-j} \right) \cap \mathbb{R}^2_+, \quad \text{and} \quad \mathcal{T} = \bigcup_{j=1}^N \mathcal{T}^j. \end{aligned}$$

So we have the following proposition.

Proposition 4.3. A crossing point is any $(\tau_1, \tau_2) \in \mathcal{T}$ such that $\mathcal{G}(\lambda; \tau_1, \tau_2) = 0$ has at least one root $i\omega$ with $\omega \in \Omega$. The set \mathcal{T} of all crossing points is called the stability switching curves.

Next, we set

$$\mathcal{F}(\omega) := \left(|\kappa_0(i\omega)|^2 + |\kappa_1(i\omega)|^2 - |\kappa_2(i\omega)|^2\right)^2 - 4(\Lambda_1^2(\omega) + \Upsilon_1^2(\omega)), \quad \omega \ge 0.$$

Since $\mathcal{F}(a_j) = \mathcal{F}(b_j) = 0$, we have

$$\theta_i(a_j) = \delta_i^a \pi, \quad \theta_i(b_j) = \delta_i^b \pi,$$

where δ_i^a , $\delta_i^b = 0, 1, i = 1, 2$. By (4.4) and (4.5), we can easily prove that

$$\begin{bmatrix} \tau_{1,j_1}^{+j}(a_j), \tau_{2,j_2}^{-j}(a_j) \end{bmatrix} = \begin{bmatrix} \tau_{1,j_1+\delta_1^a}^{-j}(a_j), \tau_{2,j_2-\delta_2^a}^{+j}(a_j) \end{bmatrix}, \\ \begin{bmatrix} \tau_{1,j_1}^{+j}(b_j), \tau_{2,j_2}^{-j}(b_j) \end{bmatrix} = \begin{bmatrix} \tau_{1,j_1+\delta_1^b}^{-j}(b_j), \tau_{2,j_2-\delta_2^b}^{+j}(b_j) \end{bmatrix}.$$

It can be seen that, one end of $\mathcal{T}_{j_1,j_2}^{+j}$ is connected to $\mathcal{T}_{j_1+\delta_1^a,j_2-\delta_2^a}^{-j}$ at one end a_j , and the other end is connected to $\mathcal{T}_{j_1+\delta_1^b,j_2-\delta_2^b}^{-j}$ at b_j .

4.2. Crossing directions

Let $\lambda = \tilde{\sigma} + i\omega$, we have

$$R_0 := \frac{\operatorname{Re}(\partial \mathcal{G}(\lambda; \tau_1, \tau_2))}{\partial \widetilde{\sigma}} \Big|_{\lambda = i\omega}, \quad I_0 := \frac{\operatorname{Im}(\partial \mathcal{G}(\lambda; \tau_1, \tau_2))}{\partial \widetilde{\sigma}} \Big|_{\lambda = i\omega},$$

then

$$R_{i} := \frac{\operatorname{Re}(\partial \mathcal{G}(\lambda; \tau_{1}, \tau_{2}))}{\partial \tau_{i}}\Big|_{\lambda=i\omega}, \quad I_{i} := \frac{\operatorname{Im}(\partial \mathcal{G}(\lambda; \tau_{1}, \tau_{2}))}{\partial \tau_{i}}\Big|_{\lambda=i\omega},$$

where i = 1, 2. It's easy for us to prove

$$\frac{\operatorname{Re}(\partial \mathcal{G}(\lambda;\tau_1,\tau_2))}{\partial \omega}\Big|_{\lambda=i\omega} = -I_0, \quad \frac{\operatorname{Im}(\partial \mathcal{G}(\lambda;\tau_1,\tau_2))}{\partial \omega}\Big|_{\lambda=i\omega} = R_0$$

According to the implicit function theory if and only if the condition $R_1I_2 - R_2I_1 \neq 0$ holds, there is

$$\delta(\omega) := \begin{pmatrix} \frac{\partial \tau_1}{\partial \tilde{\sigma}} & \frac{\partial \tau_1}{\partial \omega} \\ \frac{\partial \tau_2}{\partial \tilde{\sigma}} & \frac{\partial \tau_2}{\partial \omega} \end{pmatrix} \Big|_{\substack{\tilde{\sigma}=0\\\omega \in \Omega}} = - \begin{pmatrix} R_1 & R_2 \\ I_1 & I_2 \end{pmatrix}^{-1} \begin{pmatrix} R_0 & -I_0 \\ I_0 & R_0 \end{pmatrix}$$

Next, we need to define the positive direction of $\mathcal{T}_{j_1,j_2}^{\pm j}$. For convenience, we align its positive direction with the increasing direction of $\omega \in \Omega_j$. The region on the right (left) is referred to as the region on the right-hand (left-hand) when we proceed in the positive direction of the curve. Moreover, it is established that $(\partial \tau_2/\partial \omega, -\partial \tau_1/\partial \omega)$ is the normal vector of $\mathcal{T}_{j_1,j_2}^{\pm j}$ in the right region and that $(\partial \tau_1/\partial \omega, \partial \tau_2/\partial \omega)$ is the tangent vector of $\mathcal{T}_{j_1,j_2}^{\pm j}$ in the positive direction. In addition, a pair of complex characteristic roots also move from left to right on the imaginary axis of the complex plane as the $\tilde{\sigma}$ changes from negative to positive, which leads (τ_1, τ_2) to move along $(\partial \tau_1/\partial \tilde{\sigma}, \partial \tau_2/\partial \tilde{\sigma})$. Denote

$$\widetilde{d}(\omega) := \left(\frac{\partial \tau_1}{\partial \widetilde{\sigma}}, \frac{\partial \tau_2}{\partial \widetilde{\sigma}}\right) \cdot \left(\frac{\partial \tau_2}{\partial \omega}, -\frac{\partial \tau_1}{\partial \omega}\right) = \frac{\partial \tau_1}{\partial \widetilde{\sigma}} \frac{\partial \tau_2}{\partial \omega} - \frac{\partial \tau_2}{\partial \widetilde{\sigma}} \frac{\partial \tau_1}{\partial \omega} = \det \delta(\omega).$$

Therefore, we may conclude from the preceding that $\mathcal{T}_{j_1,j_2}^{\pm j}$ has two characteristic roots with positive real portions in the left region if $\tilde{d}(\omega) < 0$. On the other hand, if $\tilde{d}(\omega) > 0$, $\mathcal{T}_{j_1,j_2}^{\pm j}$ has two characteristic roots in the right region with positive real parts.

 \mathbf{As}

$$\det \begin{pmatrix} R_0 & -I_0 \\ I_0 & R_0 \end{pmatrix} = R_0^2 + I_0^2 \ge 0,$$

we obtain that if $R_0^2 + I_0^2 \neq 0$, sign $\widetilde{d}(\omega) = \text{sign}\{R_1I_2 - R_2I_1\}$. Thus

$$R_1I_2 - R_2I_1 = \pm \omega^2 \big| - \kappa_0 \overline{\kappa}_1 \big| \sin(\theta_1)$$

can be verified.

Denote by $\overset{\circ}{\Omega}_{j}$ the interior of Ω_{j} . Then

sign
$$\widetilde{d}(\omega \in \overset{\circ}{\Omega}_j) = \pm \operatorname{sign}(\omega^2 | -\kappa_0 \overline{\kappa}_1 | \sin(\theta_1)).$$

Through the preceding analysis, we obtain the following lemma.

Lemma 4.4. For any $j = 1, 2, \ldots, N$, it can be obtained

$$\widetilde{d}(\omega \in \overset{\circ}{\Omega}_{j}) \begin{cases} > 0 & \text{for all } [\tau_{1}(\omega), \tau_{2}(\omega)] \in \mathcal{T}_{j_{1}, j_{2}}^{+j}, \\ < 0 & \text{for all } [\tau_{1}(\omega), \tau_{2}(\omega)] \in \mathcal{T}_{j_{1}, j_{2}}^{-j}. \end{cases}$$

As a result, the right (left) area of the crossing curve $\mathcal{T}_{j_1,j_2}^{+j}$ ($\mathcal{T}_{j_1,j_2}^{-j}$) contains two more characteristic roots with positive real parts.

4.3. Theorem of Hopf bifurcation

The following Hopf bifurcation theorem on the two-parameter plane was first presented by Du et al. [3].

Theorem 4.5. [3] For any j = 1, 2, ..., N, \mathcal{T}^j is a Hopf bifurcation curve in the following sense: for any $q \in \mathcal{T}^j$ and for any smooth curve Γ intersecting with \mathcal{T}^j transversely at q, we define the tangent of Γ at q by \vec{l} (shown in Figure 4.1). If $\frac{\partial \operatorname{Re}\lambda}{\partial \vec{l}}\Big|_q \neq 0$ and the other eigenvalues of (4.1) at q have nonzero real parts, then system (1.2) undergoes a Hopf bifurcation at q when parameters (τ_1, τ_2) cross \mathcal{T}^j at q along Γ .



Figure 4.1: A sketch of the (τ_1, τ_2) plane.

Remark 4.6. Theorem 4.5 provides sufficient conditions for the existence of Hopf bifurcation on the two-parameter plane and defines Hopf bifurcation curves \mathcal{T}^{j} on the plane (τ_1, τ_2) . If $(\tau_1, \tau_2) \in \mathcal{T}^{j}$, then $\mathcal{G}(\lambda; \tau_1, \tau_2) = 0$ has a pair of pure imaginary roots $\pm i\omega_q$ with $\omega_q \in \Omega_j$. The transversality condition for the Hopf bifurcation is $\frac{\partial \operatorname{Re}\lambda}{\partial l}\Big|_q \neq 0$. System (1.2) undergoes a Hopf bifurcation at q when parameters (τ_1, τ_2) cross \mathcal{T}^j at q along Γ . A detailed proof of Theorem 4.5 can be found in [3].

4.4. Hopf bifurcation of $\tau_1 = \tau_2$

Let $\tau_1 = \tau_2 := \tau$. From (3.4), we can get

$$\tilde{f}(\lambda) = \lambda^2 + \tau_2 p_1 \lambda + \tau_2^2 p_0 + (\tau_2 r_1 \lambda + \tau_2^2 r_0) e^{-\lambda} + \tau_2^2 q_1 e^{-\lambda}$$

We consider τ as a bifurcation parameter and let $\lambda = \tau \tilde{\xi}$, then we can obtain

$$\widetilde{f}(\lambda) = \widetilde{f}(\tau \widetilde{\xi}) := \tau^2 S(\widetilde{\xi}),$$

where

(4.7)
$$S(\tilde{\xi}) = \tilde{\xi}^2 + p_1 \tilde{\xi} + p_0 + (r_0 + q_1 + r_1 \tilde{\xi}) e^{-\tau \tilde{\xi}}.$$

Thus $\{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\} = \{\lambda = \tau \tilde{\xi} \in \Omega : S(\tilde{\xi}) = 0\}$ and $p_0 + r_0 + q_1 > 0$. Through the above analysis, we can know that $\xi = 0$ is not an eigenvalue of $S(\tilde{\xi}) = 0$, and then it should be assumed that the zero of $S(\tilde{\xi}) = 0$ is $\lambda = i\omega$ ($\omega > 0$). We have

$$-\omega^{2} + ip_{1}\omega + p_{0} + (r_{0} + q_{1})e^{-i\omega\tau} + ir_{1}\omega e^{-i\omega\tau} = 0.$$

Thus

(4.8)
$$-\omega^2 + p_0 = -r_1\omega\sin(\omega\tau) - (r_0 + q_1)\cos(\omega\tau), \quad p_1\omega = (r_0 + q_1)\sin(\omega\tau) - r_1\omega\cos(\omega\tau).$$

So $(p_0 - \omega^2)^2 + (p_1\omega)^2 = (r_0 + q_1)^2 + (r_1\omega)^2, \text{ or}$
(4.9) $\omega^4 + (p_1^2 - 2p_0 - r_1^2)\omega^2 + p_0^2 - (r_0 + q_1)^2 = 0.$

Setting $\sigma = \omega^2$, (4.9) becomes

(4.10)
$$\sigma^2 + (p_1^2 - 2p_0 - r_1^2)\sigma + p_0^2 - (r_0 + q_1)^2 = 0.$$

Notice that $p_0 + r_0 + q_1 > 0$. If $p_0 - (r_0 + q_1) < 0$, there is only one positive root of (4.10), denoted by σ_0 . Thus, the only one positive root of (4.9) is $\omega_0 = \sqrt{\sigma_0}$. From (4.8), we obtain that when $\tau = \tau_{\iota}, \pm i\omega_0$ is a pair of pure imaginary roots with $S(\tilde{\xi}) = 0$, where

$$\omega_0^2 = \frac{1}{2} \left(-(p_1^2 - 2p_0 - r_1^2) + \sqrt{(p_1^2 - 2p_0 - r_1^2)^2 - 4(p_0^2 - (r_0 + q_1)^2)} \right)$$

and

$$\begin{aligned} (4.11) \\ \tau_{\iota} &= \begin{cases} \frac{1}{\omega_{0}} \left[\arccos \frac{(r_{0}+q_{1}-p_{1}r_{1})\omega_{0}^{2}-p_{0}(r_{0}+q_{1})}{(r_{0}+q_{1})^{2}+r_{1}^{2}\omega_{0}^{2}} + 2\iota\pi \right] & \text{if } \frac{p_{1}(r_{0}+q_{1})\omega_{0}+r_{1}\omega_{0}(\omega_{0}^{2}-p_{0})}{(r_{0}+q_{1})^{2}+r_{1}^{2}\omega_{0}^{2}} \geq 0, \\ \frac{1}{\omega_{0}} \left[2\pi - \arccos \frac{(r_{0}+q_{1}-p_{1}r_{1})\omega_{0}^{2}-p_{0}(r_{0}+q_{1})}{(r_{0}+q_{1})^{2}+r_{1}^{2}\omega_{0}^{2}} + 2\iota\pi \right] & \text{if } \frac{p_{1}(r_{0}+q_{1})\omega_{0}+r_{1}\omega_{0}(\omega_{0}^{2}-p_{0})}{(r_{0}+q_{1})^{2}+r_{1}^{2}\omega_{0}^{2}} < 0. \end{aligned}$$

with $\iota = 0, 1, 2, ...$

Lemma 4.7. Let Assumption 1.1, (3.1) and $p_0 - (r_0 + q_1) < 0$ hold. Then we have

$$\frac{\mathrm{d}S(\tilde{\xi})}{\mathrm{d}\tilde{\xi}}\Big|_{\tilde{\xi}=i\omega_0}\neq 0$$

Consequently, $\tilde{\xi} = i\omega_0$ is a simple root of $S(\tilde{\xi}) = 0$.

Proof. According to (4.7), we obtain

$$\frac{\mathrm{d}S(\xi)}{\mathrm{d}\tilde{\xi}}\Big|_{\tilde{\xi}=i\omega_0} = i2\omega_0 + p_1 + r_1\mathrm{e}^{-i\omega_0\tau_\iota} - (r_0 + q_1)\tau_\iota\mathrm{e}^{-i\omega_0\tau_\iota} - ir_1\omega_0\tau_\iota\mathrm{e}^{-i\omega_0\tau_\iota}$$

Due to $S(\widetilde{\xi}) = 0$, we have

$$\left(2\widetilde{\xi} + p_1 + r_1 \mathrm{e}^{-\widetilde{\xi}\tau} - \tau (r_0 + q_1 + r_1\widetilde{\xi})\mathrm{e}^{-\widetilde{\xi}\tau}\right) \frac{\mathrm{d}\xi(\tau)}{\mathrm{d}\tau} = \widetilde{\xi}(r_0 + q_1 + r_1\widetilde{\xi})\mathrm{e}^{-\widetilde{\xi}\tau}.$$

Suppose $\frac{\mathrm{d}S(\tilde{\xi})}{\mathrm{d}\tilde{\xi}}|_{\tilde{\xi}=i\omega_0}=0$, thus

 $i\omega_0(r_0 + q_1 + r_1i\omega_0)\mathrm{e}^{-i\omega_0\tau} = 0.$

Since $\omega_0 > 0$, $r_0 + q_1 + r_1 i \omega_0 = 0$, this means that

$$r_0 + q_1 = r_1 = 0$$

Notice that $r_1 = -\frac{\eta \alpha \overline{V}^2 Rm}{\alpha H \overline{V}^2 + \overline{V} + g} < 0$, thus we conclude that

$$\frac{\mathrm{d}S(\zeta)}{\mathrm{d}\widetilde{\zeta}}\Big|_{\widetilde{\zeta}=i\omega_0}\neq 0.$$

Lemma 4.8. Let Assumption 1.1, (3.1) and $p_0 - (r_0 + q_1) < 0$ hold. $S(\tilde{\xi}) = 0$ has the root $\tilde{\xi}(\tau) = \varrho(\tau) + i\omega(\tau)$ that satisfies $\varrho(\tau_{\iota}) = 0$ and $\omega(\tau_{\iota}) = \omega_0$, τ_{ι} is given by (4.11). Thus

$$\frac{\mathrm{dRe}(\tilde{\xi})}{\mathrm{d}\tau}\Big|_{\tau=\tau_{\iota}}=\varrho'(\tau_{\iota})>0.$$

Proof. We replace $\frac{d\tilde{\xi}}{d\tau}$ by discussing $\frac{d\tau}{d\tilde{\xi}}$. We get it first

$$\begin{split} \frac{\mathrm{d}\tau}{\mathrm{d}\tilde{\xi}}\Big|_{\tilde{\xi}=i\omega_{0}} &= \frac{2\tilde{\xi}+p_{1}+r_{1}\mathrm{e}^{-\tau\tilde{\xi}}-\tau(r_{0}+q_{1}+r_{1}\tilde{\xi})\mathrm{e}^{-\tau\tilde{\xi}}}{\tilde{\xi}(r_{0}+q_{1}+r_{1}\tilde{\xi})\mathrm{e}^{-\tau\tilde{\xi}}}\Big|_{\tilde{\xi}=i\omega_{0}} \\ &= \left(-\frac{2\tilde{\xi}+p_{1}}{\tilde{\xi}(\tilde{\xi}^{2}+p_{1}\tilde{\zeta}+p_{0})}+\frac{r_{1}}{\tilde{\xi}(r_{0}+q_{1}+r_{1}\tilde{\xi})}-\frac{\tau}{\tilde{\xi}}\right)\Big|_{\tilde{\xi}=i\omega_{0}} \\ &= \frac{1}{\omega_{0}}\frac{(i2\omega_{0}+p_{1})[p_{1}\omega_{0}+i(p_{0}-\omega_{0}^{2})]}{(p_{1}\omega_{0})^{2}+(p_{0}-\omega_{0}^{2})^{2}}-\frac{1}{\omega_{0}}\frac{r_{1}[r_{1}\omega_{0}+i(r_{0}+q_{1})]}{(r_{1}\omega_{0})^{2}+(r_{0}+q_{1})^{2}}+\frac{i\tau}{\omega_{0}}. \end{split}$$

Hence, we have

$$\operatorname{Re}\left(\frac{\mathrm{d}\tau}{\mathrm{d}\tilde{\xi}}\Big|_{\xi=i\omega_0}\right) = \frac{2\omega_0^2 + p_1^2 - 2p_0}{(p_1\omega_0)^2 + (p_0 - \omega_0^2)^2} - \frac{r_1^2}{(r_1\omega_0)^2 + (r_0 + q_1)^2} = \frac{2\omega_0^2 + p_1^2 - 2p_0 - r_1^2}{(r_1\omega_0)^2 + (r_0 + q_1)^2}.$$

Since

$$\omega_0^2 = \frac{1}{2} \left(-(p_1^2 - 2p_0 - r_1^2) + \sqrt{(p_1^2 - 2p_0 - r_1^2)^2 - 4(p_0^2 - (r_0 + q_1)^2)} \right)$$

we can get

$$\operatorname{sign}\left(\frac{\mathrm{d}\operatorname{Re}(\widetilde{\xi})}{\mathrm{d}\tau}\Big|_{\tau=\tau_k}\right) = \operatorname{sign}\left(\operatorname{Re}\frac{\mathrm{d}\tau}{\mathrm{d}\widetilde{\xi}}\right)\Big|_{\widetilde{\xi}=i\omega_0} = \operatorname{sign}\left(\frac{2\omega_0^2 + p_1^2 - 2p_0 - r_1^2}{(r_1\omega_0)^2 + (r_0 + q_1)^2}\right) > 0. \quad \Box$$

Thus, we can get the following important results of this section.

Theorem 4.9. Let Assumption 1.1, (3.1) and $p_0 - (r_0 + q_1) < 0$ hold. Thus, there is $\tau_{\iota} > 0, \, \iota = 0, 1, 2, \ldots \, (\tau_{\iota} \text{ is given by (4.11)}), \text{ if } \tau = \tau_{\iota}, \text{ the system (4.7) has a pair of purely imaginary roots <math>\pm i\omega_0$, leading to the appearance of a Hopf bifurcation near the positive equilibrium $(\overline{u}(\cdot), \overline{V})$.

5. Numerical simulation

Now, to illustrate the theoretical results shown above, let's do some numerical simulations of the system (1.2). When τ_1 and τ_2 varies independently in \mathbb{R}_+ , we choose parameters r = 1, $\mu = 0.5$, g = 0.009, c = 0.2, R = 10, $\alpha = 6.1$, k = 10, H = 10, $\eta = 5.12$, m = 0.88, thus $\overline{V} = 0.0083$, $\overline{U} = 0.0572$, $p_0 = 0.0279$, $p_1 = 0.9117$, $r_0 = -0.0279$, $r_1 = -0.8800$, $q_1 = 0.3941$.



Figure 5.1: (a) Graph of $\mathcal{F}(\omega)$. (b) Stability switching curves \mathcal{T}^{j} .

Figure 5.1(a) shows that $\mathcal{F}(\omega) = 0$ has two roots $a_1 = 0.2183$, $b_1 = 0.9497$, and $\delta_1^a = 0$, $\delta_2^a = 1$, $\delta_1^b = 0$, $\delta_2^b = 0$. With Figure 5.1(b), we take the first intercept on the τ_2 axis as an

example of the change of τ_1 and τ_2 . The area pointed by the black arrow in Figure 5.1(b) has two characteristic roots whose real part is positive. From the previous discussion and Figure 5.1(b), the internal equilibrium is stable when (τ_1, τ_2) is located in the small bottom-left region of the (τ_1, τ_2) -plane.

Figures 5.2(a) and 5.2(b) show that the system (1.2) exhibits persistent periodic oscillation behavior near the positive equilibrium as $\tau_1 = 0.5$ and $\tau_2 = 0.9$ in region A. When $\tau_1 = 0.1$ and $\tau_2 = 1$, it can be seen from Figure 5.2(c) that the positive equilibrium in region B is asymptotically stable.



Figure 5.2: (a)(c) when (a) $\tau_1 = 0.5$, $\tau_2 = 0.9$, (c) $\tau_1 = 0.1$, $\tau_2 = 1$, the trend of the solution curves of V(t) and U(t). (b) Phase portrait of $\tau_1 = 0.5$, $\tau_2 = 0.9$.

As $\tau := \tau_1 = \tau_2$, we choose parameters r = 3, $\mu = 1$, c = 0.2, g = 0.009, $\alpha = 6.1$, $k = 10, H = 2, \eta = 5.12, R = 80, m = 0.88$. Then

$$\mathcal{M}(a) := \begin{cases} 70.4 \mathrm{e}^{0.88\tau} & \text{if } a \ge \tau, \\ 0 & \text{if } a \in (0, \tau). \end{cases}$$

By calculation, select the initial value $V_0 = 0.021$, $u(0, a) = 0.013596e^{-0.044a}$. We calculate further and get that $\omega_0 = 1.1289$ and $\tau_0 = 0.1173$. The positive equilibrium $(\overline{u}_{\tau=0.1}(a), \overline{V}) = (0.013596e^{-0.088a}, 0.021)$ in Figure 5.3 is locally asymptotically stable when we choose $\tau = 0.1 < \tau_0$. Figures 5.3(a) and 5.3(b) show the solution curve behavior of predator populations and prey populations, respectively. Figure 5.3(c) describes the phase orbital behavior of V(t) and $\int_0^{+\infty} u(t, a) da$, and Figure 5.3(d) shows the distribution function u(t, a) over age and time.

In Figure 5.4, when τ is continuously increased to $0.2 > \tau_0$, the system (1.2) has a sustained periodic oscillation behavior near $(\overline{u}_{\tau=0.2}(a), \overline{V}) = (0.027192e^{-0.176a}, 0.021)$. Figures 5.4(a) and 5.4(b) show the solution curve behavior of predator populations and prey populations, separately. Figure 5.4(c) depicts the phase orbital behavior of V(t) and $\int_0^{+\infty} u(t, a) \, da$, and Figure 5.4(d) shows the distribution function u(t, a) over age and time.



Figure 5.3: $\tau = 0.1 < \tau_0$.



Figure 5.4: $\tau = 0.2 > \tau_0$.

By numerical simulation results, we can see that when the parameter τ to τ_0 is adjusted continuously, the positive equilibrium is asymptotically stable. But as τ passes τ_0 , the positive equilibrium's stability changes, and a periodic solution develops there. Combined with Theorem 4.9, it is observed that the Hopf bifurcation occurs when $\tau = \tau_0$. The above verified our conclusions.

From the above, we can get that the system with a small time delay has a stable positive equilibrium point. The appearance of a large time delay will change its stability and produce periodic oscillations near positive equilibrium.

6. Summary

In Yu and Wang [25], the authors considered a prey-predator model with variable predator search speed and prey's fear cost. By selecting k as a bifurcation parameter, Yu and Wang studied the effect of fear cost on the model (1.1). They found that the Hopf bifurcation in model (1.1) can be either subcritical or supercritical compared to models without fear effect, so that model (1.1) has two limit cycles and bi-stability. However, the effect of age structure and time delay on the predator-prey model is not considered in the reference [25].

Mainly based on the inspiration of the references Yu and Wang [25] and Liu and Li [11], we consider the model (1.2) of this paper. We introduce a predator-prey model that includes the predator age structure and the delay in prey response time. Moreover, in the model we studied, we considered that the speed of the predator's search depends on the density of the prey, and the prey's fear of predators reduces the reproduction of prey. In this model, we give the condition for the existence of a unique positive equilibrium related to age. The existence of Hopf bifurcation at the positive equilibrium $(\overline{u}(\cdot), \overline{V})$ as bifurcation parameter τ is established by the Hopf bifurcation theory of abstract Cauchy problems with non-dense domain and the integrated semigroup theory. In addition, we obtain that oscillations occur due to τ_1 and τ_2 by calculating the stability switching curves. In contrast to the model (1.1), time delay and age structure have an impact on the dynamic behavior near the positive equilibrium but not on the existence of the positive equilibrium. Our model is different in that it incorporates important factors such as age structure and delayed reaction time of predators, which may contribute to the understanding of the complex dynamic behavior of predator-prey systems. We also want to continue to discuss whether bi-stability, two limit cycles, and high codimension bifurcations can still occur in the model (1.2) that account for age structure and time delay if k is selected as the bifurcation parameter.

At the end of this section, we discuss the effect of the fear effect on predator density at the positive equilibrium $(\overline{u}(\cdot), \overline{V})$. Calculating the derivative of predator \overline{U} to k, we have

$$\frac{\mathrm{d}\overline{U}}{\mathrm{d}k} = \frac{\eta \alpha \overline{V}^2 \Big(\frac{\left(\frac{\mathrm{d}A_1}{\mathrm{d}k} A_2 - \frac{\mathrm{d}A_2}{\mathrm{d}k} A_1\right) \left(\sqrt{A_2^2 - 4A_1 A_3} - A_2\right) + 2\frac{\mathrm{d}A_1}{\mathrm{d}k} A_1 A_3}{\sqrt{A_2^2 - 4A_1 A_3}} \Big)}{2m A_1^2 (\alpha H \overline{V}^2 + \overline{V} + g)} < \frac{\eta \alpha \overline{V}^2 \Big(\frac{M_1 \sqrt{k} - M_2 k}{\sqrt{A_2^2 - 4A_1 A_3}}\Big)}{2m A_1^2 (\alpha H \overline{V}^2 + \overline{V} + g)},$$

$$M_1 = 2m^2 \eta^4 \alpha^5 \overline{V}^{10} (\alpha H \overline{V}^2 + \overline{V} + g) \sqrt{\alpha^3 \overline{V}^7 (\alpha H \overline{V}^2 + \overline{V} + g)^3 (r - \mu - c \overline{V})},$$

$$M_2 = 2m^2 \eta^4 \alpha^6 \overline{V}^{13} (\alpha H \overline{V}^2 + \overline{V} + g)^3 (r - \mu - c \overline{V}).$$

Then, when $k > \frac{M_1^2}{M_2^2}$, we can get

$$\frac{\mathrm{d}U}{\mathrm{d}k} < 0$$
 and $\lim_{k \to \infty} \frac{\mathrm{d}U}{\mathrm{d}k} = 0.$

Thus, increasing the fear effect k can reduce predator density because \overline{U} is a strictly decreasing function of k when $k > \frac{M_1^2}{M_2^2}$.

The fear effect k will cause the density of predators to decrease according to the reasoning above when there is a unique positive equilibrium in (1.2) and k increases to a certain value.

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