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Research article

A consumer-resource competition model with a state-dependent delay and stage-structured consumer species

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Abstract: In this paper, a new consumer-resource competition model with a state-dependent maturity delay is developed, which incorporates one resource species and two stage-structured consumer species. The main innovation is that the model directly manifests the relationship between resources and maturity time of consumers through a correction term, $1 - \tau'(x(t))x'(t)$. Firstly, the well-posedness of the solution is studied. At the same time, the existence and uniqueness of all equilibria are discussed. Then, the linearized stabilities of the equilibria are achieved. Finally, some sufficient conditions which ensure the global attractivity of the coexistence equilibrium are obtained.

Keywords: competition model; state-dependent maturity delay; stability; global attractivity

1. Introduction

In the evolutionary history of natural communities, ecological competition has justifiably been a significant force, which consists of exploitation and interference [1–3]. In consequence, there has been increasing studies for consumer-resource competitive models by dynamical systems theory [4–7]. Mathematically, Gopalsamy [8] developed the following resource-based competition model.

$$\begin{cases} \frac{dx}{dt} = x(t)[b - ax(t) - a_1z_1(t) - a_2z_2(t)],\\ \frac{dz_1}{dt} = z_1(t)[b_1x(t) - \beta_1z_1(t) - \mu_1z_2(t)],\\ \frac{dz_2}{dt} = z_2(t)[b_2x(t) - \beta_2z_2(t) - \mu_2z_1(t)], \end{cases}$$
(1.1)

where x(t) represents the density of a logistically self-renewing resource at time t, $z_1(t)$ and $z_2(t)$ represent the densities at time t of two species which feed on this resource alone.

For a population individual, its whole life history generally includes two or more stages, particularly, mammals show two different stages of immaturity and maturity [9–11]. Moreover, it takes some time from birth to adulthood which is considered as the maturity time delay. Thus, the competition models and stage structure population models with constant maturity delays have been studied. For example, the two-species competition model and stage-structured single population model established in [12, 13] respectively have a constant maturity delay.

Later, people noticed the biological fact about the maturity time of Antarctic whales and seals around the Second World War. Subsequent to the introduction of factory ships and with it a depletion of the large whale population, there has been a substantial increase in krill for seals and whales. It was then noted that seals took 3 to 4 years to mature and small whales only took 5 years [14]. Hence, their maturation time varies with the number of krill available, which implies that the maturity time delay is state-dependent, not a constant.

Due to this, Aiello and Freedman [15] formulated the following stage-structured state-dependent delay model, in which the delay $\tau(z(t))$ is a bounded increasing function of the total population z(t) = x(t) + y(t).

$$\begin{cases} \frac{dx(t)}{dt} = \alpha y(t) - \gamma x(t) - \alpha y(t - \tau(z(t)))e^{-\gamma \tau(z(t))}, \\ \frac{dy(t)}{dt} = \alpha y(t - \tau(z(t)))e^{-\gamma \tau(z(t))} - \beta y^{2}(t). \end{cases}$$

Subsequently, the stage-structured and competitive models with state-dependent delays were developed [16–26]. In 2017, Lv and Yuan [27] proposed the competitive model with state-dependent delays:

$$\begin{cases} \frac{dz_1}{dt} = b_1 z_1 (t - \tau(z_1)) e^{-\gamma_1 \tau(z_1)} - \beta_1 z_1^2(t) - \mu_1 z_1(t) z_2(t), \\ \frac{dz_2}{dt} = b_2 z_2 (t - \tau(z_2)) e^{-\gamma_2 \tau(z_2)} - \beta_2 z_2^2(t) - \mu_2 z_1(t) z_2(t), \end{cases}$$

where the delays $\tau(z_i(t))$ are bounded increasing functions of the populations $z_i(t)$, i = 1, 2, respectively.

It is obvious that the above-mentioned models with state-dependent delays straight change the constant delays into the state-dependent delays, which is not appropriate to population modeling. Therefore, Wang, Liu and Wei [28] proposed the following new single population model with a state-dependent delay and a correction factor.

$$\begin{cases} \frac{dx(t)}{dt} = \alpha y(t) - \gamma x(t) - \alpha [1 - \tau'(z(t))\dot{z}(t)]y(t - \tau(z(t)))e^{-\gamma \tau(z(t))}, \\ \frac{dy(t)}{dt} = \alpha [1 - \tau'(z(t))\dot{z}(t)]y(t - \tau(z(t)))e^{-\gamma \tau(z(t))} - \beta y^{2}(t), \end{cases}$$

where the delay $\tau(z(t))$ is a function of the total population z(t) = x(t) + y(t).

However, the aforementioned state-dependent delays are functions of populations, not resources. A worthwhile thought is how to reflect the direct relationship between the resources and maturity time? In view of the biological background above, the time varies with the resources available, that is, the species must spend enough time in the immature stage to accumulate a certain amount of food to reach maturity. To address the question raised above, we consider a stage-structured consumer-resource competition model with a state-dependent maturity time delay, in which the delay involves a correction term, $1 - \tau'(x)x'(t)$, related to resource changes.

The paper is organized as follows. In section 2, we formulate a resource-based competition model with a state-dependent maturity delay. In section 3, we study the well-posedness properties for the model and prove the existence and uniqueness of all equilibria. In section 4, we analyze the local stabilities of equilibria. In section 5, we discuss the global behaviors of the coexistence equilibrium. Finally, section 6 gives the conclusions of the paper.

2. Model formulation

Based on model (1.1), we will formulate the competition model with a state-dependent maturity delay. For each i = 1, 2, let $y_i(t)$ and $z_i(t)$ be the densities at time t of the immature and mature consumer species, respectively. Let x(t) be the density at time t of a logistically self-renewing resource which is necessary for two consumer species. Motivated by [28–31], we introduce a threshold age $\tau(x(t))$ to distinguish the immature and mature individuals, which depends on the density of the same resource. Suppose that $\rho_i(t, a)$ is the population density of age a at time t, then the densities of $y_i(t)$ and $z_i(t)$, respectively, are given by

$$y_i(t) = \int_0^{\tau(x(t))} \rho_i(t, a) da \quad \text{and} \quad z_i(t) = \int_{\tau(x(t))}^{\infty} \rho_i(t, a) da.$$

By virtue of [32, 33], we have the following age structure partial differential equations to represent the development of the consumer species.

$$\frac{\partial \rho_1(t,a)}{\partial t} + \frac{\partial \rho_1(t,a)}{\partial a} = -\gamma_1 \rho_1(t,a), \quad \text{if} \quad a \le \tau(x(t)),$$

$$\frac{\partial \rho_1(t,a)}{\partial t} + \frac{\partial \rho_1(t,a)}{\partial a} = -\left(\beta_1 z_1(t) + \mu_1 z_2(t)\right) \rho_1(t,a), \quad \text{if} \quad a > \tau(x(t)),$$

$$\frac{\partial \rho_2(t,a)}{\partial t} + \frac{\partial \rho_2(t,a)}{\partial a} = -\gamma_2 \rho_2(t,a), \quad \text{if} \quad a \le \tau(x(t)),$$

$$\frac{\partial \rho_2(t,a)}{\partial t} + \frac{\partial \rho_2(t,a)}{\partial a} = -\left(\beta_2 z_2(t) + \mu_2 z_1(t)\right) \rho_2(t,a), \quad \text{if} \quad a > \tau(x(t)).$$
(2.1)

We suppose that $y_1(t)$ and $y_2(t)$ die at the constant rate γ_i (i = 1, 2). The parameters β_i (i = 1, 2) represent the mature natural death and overcrowding rate for $z_i(t)$, respectively. The parameters μ_i (i = 1, 2) represent interspecific competition for $z_i(t)$, respectively.

Taking the derivatives of $y_i(t)$ and $z_i(t)$, respectively, and combining system (2.1), it then follows that

$$\begin{aligned} \frac{dy_1(t)}{dt} &= \rho_1(t,0) - \gamma_1 y_1(t) - [1 - \tau'(x)x'(t)]\rho_1(t,\tau(x(t))), \\ \frac{dz_1(t)}{dt} &= [1 - \tau'(x)x'(t)]\rho_1(t,\tau(x(t))) - \rho_1(t,\infty) - \beta_1 z_1^2(t) - \mu_1 z_1(t)z_2(t), \\ \frac{dy_2(t)}{dt} &= \rho_2(t,0) - \gamma_2 y_2(t) - [1 - \tau'(x)x'(t)]\rho_2(t,\tau(x(t))), \\ \frac{dz_2(t)}{dt} &= [1 - \tau'(x)x'(t)]\rho_2(t,\tau(x(t))) - \rho_2(t,\infty) - \beta_2 z_2^2(t) - \mu_2 z_1(t)z_2(t). \end{aligned}$$

Note that the two primes refer to differentiation with respect to x and time t, respectively, namely, $\dot{\tau}(x(t)) = d\tau(x(t))/dt = \tau'(x)x'(t)$.

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Because of the finitude of individual life span, $\rho_i(t, \infty)$ is considered as zero. Assume that the immature consumers' functional response is Holling type I, that is, $b_i x(t)$, then the term $\rho_i(t,0) = b_i x(t) z_i(t)$ represents the number of immature individuals born at time *t*. Therefore, for $t \ge \tilde{\tau} = \max\{\tau(x(t))\}$, we have

$$\rho_i(t,\tau(x(t))) = \rho_i(t-\tau(x(t)),0) = b_i x(t-\tau(x(t))) z_i(t-\tau(x(t))) e^{-\gamma_i \tau(x(t))}, \quad i = 1, 2.$$

Consequently, we obtain the following stage-structured consumer-resource competition model with a state-dependent delay.

$$\begin{aligned} \frac{dx}{dt} &= rx(t)\left(1 - \frac{x(t)}{K}\right) - a_1 x(t) z_1(t) - a_2 x(t) z_2(t), \\ \frac{dy_1}{dt} &= b_1 x(t) z_1(t) - b_1 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_1(t - \tau(x)) e^{-\gamma_1 \tau(x)} - \gamma_1 y_1(t), \\ \frac{dz_1}{dt} &= b_1 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_1(t - \tau(x)) e^{-\gamma_1 \tau(x)} - \beta_1 z_1^2(t) - \mu_1 z_1(t) z_2(t), \\ \frac{dy_2}{dt} &= b_2 x(t) z_2(t) - b_2 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_2(t - \tau(x)) e^{-\gamma_2 \tau(x)} - \gamma_2 y_2(t), \\ \frac{dz_2}{dt} &= b_2 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_2(t - \tau(x)) e^{-\gamma_2 \tau(x)} - \beta_2 z_2^2(t) - \mu_2 z_1(t) z_2(t), \end{aligned}$$
(2.2)

where *r* and *K* represent the growth rate of the resource and its carrying capacity, respectively. The parameters a_1 and a_2 represent the capture rate of z_1 and z_2 , respectively. By [28], the inequality, $1 - \tau'(x)x'(t) > 0$, holds true, which implies that $t - \tau(x(t))$ is a strictly increasing function in *t*. This shows that mature individuals become immature only by birth.

For system (2.2), there are the following basic hypotheses:

 (\mathcal{A}_1) The constant parameters r, K, a_1 , a_2 , b_1 , b_2 , γ_1 , γ_2 , β_1 , β_2 , μ_1 , μ_2 are all positive;

 (\mathcal{A}_2) The state-dependent time delay $\tau(x)$ is a decreasing differentiable bounded function of the resource *x*, where $\tau'(x) \le 0$, and $0 \le \tau_m \le \tau(x) \le \tau_M$ with $\tau(+\infty) = \tau_m$, $\tau(0) = \tau_M$.

To simplify system (2.2), we can readily scale off r and K by proper rescaling of t and x. Accordingly, system (2.2) becomes

$$\begin{cases}
\frac{dx}{dt} = x(t)(1 - x(t) - a_1z_1(t) - a_2z_2(t)), \\
\frac{dy_1}{dt} = b_1x(t)z_1(t) - b_1[1 - \tau'(x)x'(t)]x(t - \tau(x))z_1(t - \tau(x))e^{-\gamma_1\tau(x)} - \gamma_1y_1(t), \\
\frac{dz_1}{dt} = b_1[1 - \tau'(x)x'(t)]x(t - \tau(x))z_1(t - \tau(x))e^{-\gamma_1\tau(x)} - \beta_1z_1^2(t) - \mu_1z_1(t)z_2(t), \\
\frac{dy_2}{dt} = b_2x(t)z_2(t) - b_2[1 - \tau'(x)x'(t)]x(t - \tau(x))z_2(t - \tau(x))e^{-\gamma_2\tau(x)} - \gamma_2y_2(t), \\
\frac{dz_2}{dt} = b_2[1 - \tau'(x)x'(t)]x(t - \tau(x))z_2(t - \tau(x))e^{-\gamma_2\tau(x)} - \beta_2z_2^2(t) - \mu_2z_1(t)z_2(t).
\end{cases}$$
(2.3)

In this paper, we will study the dynamics of system (2.3). The initial data for system (2.3) are

$$x(s) = \Upsilon(s) \ge 0,$$

 $z_1(s) = \Phi_1(s) \ge 0, y_1(s) = \Psi_1(s) \ge 0$ for all $s \in [-\tau_M, 0],$

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$$z_2(s) = \Phi_2(s) \ge 0, \ y_2(s) = \Psi_2(s) \ge 0 \text{ for all } s \in [-\tau_M, 0],$$

with

$$\Psi_1(0) = \int_{-\tau(x(0))}^0 b_1 x(s) z_1(s) e^{\gamma_1 s} ds \quad \text{and} \quad \Psi_2(0) = \int_{-\tau(x(0))}^0 b_2 x(s) z_2(s) e^{\gamma_2 s} ds,$$

which represent the number of immature consumers who survived to time t = 0.

3. Preliminary results

In this section, we first study the well-posedness properties of the solution for system (2.3) and then prove the existence and uniqueness of all equilibria.

Theorem 3.1. Let $\Upsilon(t) \ge 0$, $\Phi_1(t) \ge 0$ and $\Phi_2(t) \ge 0$ for $-\tau_M \le t \le 0$, then the solution $(x(t), y_1(t), z_1(t), y_2(t), z_2(t))$ of system (2.3) is nonnegative and uniformly ultimate bounded for all $t \ge 0$.

Proof. Consider the first equation in system (2.3).

$$\frac{dx}{dt} = x(t)(1 - x(t) - a_1 z_1(t) - a_2 z_2(t)),$$

with $x(0) = \Upsilon(0) \ge 0$. Then

$$x(t) = x(0) \exp \int_0^t [1 - x(s) - a_1 z_1(s) - a_2 z_2(s)] ds \ge 0, \ t \ge 0.$$

Suppose that there exists t > 0 such that $z_1(t) = 0$. Let $t^* = \inf\{t : t > 0, z_1(t) = 0\}$, then

$$z_1'(t^*) = b_1[1 - \tau'(x(t^*))x'(t^*)]x(t - \tau(x(t^*)))z_1(t^* - \tau(x(t^*)))e^{-\gamma_1\tau(x(t^*))}$$

Since $\tau(x) > 0$, $1 - \tau'(x(t^*))x'(t^*) > 0$, $t^* - \tau(x(t^*)) < t^*$, it follows from the definition of t^* that $z_1(t^* - \tau(x(t^*))) > 0$, which implies that $z'_1(t^*) > 0$ and is a contradiction. Therefore, there does not exist t^* and $z_1(t) > 0$ for all t > 0.

Integrating the second equation of system (2.3), we have the following integral expression for $y_1(t)$.

$$y_{1}(t) = e^{-\gamma_{1}t} \left(\Phi_{1}(0) + \int_{0}^{t} b_{1}x(s)z_{1}(s)e^{\gamma_{1}s}ds - \int_{-\tau(x(0))}^{t-\tau(x(t))} b_{1}x(s)z_{1}(s)e^{\gamma_{1}s}ds \right)$$
$$= \int_{t-\tau(x(t))}^{t} b_{1}x(s)z_{1}(s)e^{-\gamma_{1}(t-s)}ds.$$

It is easy to see that $y_1(t) \ge 0$ by the nonnegativity x(t), $z_1(t)$ and $\tau(x)$. In a similar way, we can prove the nonnegativity of $z_2(t)$ and $y_2(t)$. Hence, the solution $(x(t), y_1(t), z_1(t), y_2(t), z_2(t))$ of system (2.3) is nonnegative. Especially, when $\Upsilon(0) > 0$, $\Psi_1(0) > 0$, $\Phi_1(0) > 0$, the solution of system (2.3) is positive.

Now we prove uniform ultimate boundedness of the solution. Define the following Lyapunov functional.

$$V = \left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) x(t) + z_1(t) + z_2(t) + \int_{t-\tau(x(t))}^t b_1 x(s) z_1(s) e^{-\gamma_1(t-s)} ds$$

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$$+\int_{t-\tau(x(t))}^t b_2 x(s) z_2(s) e^{-\gamma_2(t-s)} ds.$$

Calculating the time derivative of V(t) along the solutions of system (2.3), we have

$$\begin{split} V'(t) &= \left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) x(t) [1 - x(t) - a_1 z_1(t) - a_2 z_2(t)] + b_1 x(t) z_1(t) + b_2 x(t) z_2(t) \\ &- \gamma_1 \int_{t - \tau(x(t))}^t b_1 x(s) z_1(s) e^{-\gamma_1(t-s)} ds - \beta_1 z_1^2(t) - \mu_1 z_1(t) z_2(t) \\ &- \gamma_2 \int_{t - \tau(x(t))}^t b_2 x(s) z_2(s) e^{-\gamma_2(t-s)} ds - \beta_2 z_2^2(t) - \mu_2 z_1(t) z_2(t) \\ &< -\gamma V + \left(\frac{b_1}{a_1} + \frac{b_2}{a_2}\right) [(1 + \gamma) x(t) - x^2(t)] + \gamma z_1(t) - \beta_1 z_1^2(t) + \gamma z_2(t) - \beta_2 z_2^2(t) \\ &\leq -\gamma V + M_1 + M_2 + M_3, \end{split}$$

where $\gamma = \min\{\gamma_1, \gamma_2\}$, M_1 , M_2 and M_3 are the maximum values of quadratic function $(b_1/a_1 + b_2/a_2)[(1 + \gamma)x(t) - x^2(t)]$, $\gamma z_1(t) - \beta_1 z_1^2(t)$ and $\gamma z_2(t) - \beta_2 z_2^2(t)$, respectively. Obviously, M_1 , M_2 and M_3 are positive. Thus, $\limsup_{t\to\infty} V(t) \leq (M_1 + M_2 + M_3)/\gamma$ and the solution of system (3.1) is uniformly ultimate bounded. It then follows that the solution of system (2.3) is uniformly ultimate bounded.

Since variables $y_1(t)$ and $y_2(t)$ of system (2.3) are decoupled from the other equations, we study the following reduced system:

$$\begin{pmatrix}
\frac{dx}{dt} = x(t)(1 - x(t)) - a_1 x(t) z_1(t) - a_2 x(t) z_2(t), \\
\frac{dz_1}{dt} = b_1 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_1(t - \tau(x)) e^{-\gamma_1 \tau(x)} - \beta_1 z_1^2(t) - \mu_1 z_1(t) z_2(t), \\
\frac{dz_2}{dt} = b_2 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_2(t - \tau(x)) e^{-\gamma_2 \tau(x)} - \beta_2 z_2^2(t) - \mu_2 z_1(t) z_2(t).
\end{cases}$$
(3.1)

In the rest of this section, we will discuss the existence and patterns of equilibria (x, z_1, z_2) of system (3.1). The equilibria satisfy the following equations:

$$\begin{cases} x(1 - x - a_1 z_1 - a_2 z_2) = 0, \\ b_1 x z_1 e^{-\gamma_1 \tau(x)} - \beta_1 z_1^2 - \mu_1 z_1 z_2 = 0, \\ b_2 x z_2 e^{-\gamma_2 \tau(x)} - \beta_2 z_2^2 - \mu_2 z_1 z_2 = 0. \end{cases}$$
(3.2)

It is easy to see that system (3.1) has one trivial equilibrium $E_0 = (0, 0, 0)$ and one semitrivial equilibrium $E_1 = (1, 0, 0)$. And we obtain the following result for nontrivial equilibria.

Theorem 3.2. System (3.1) has exactly two semitrivial equilibria $E_2 = (\hat{x}, \hat{z_1}, 0)$ and $E_3 = (\tilde{x}, 0, \tilde{z_2})$. Assume that

$$\min\left\{\frac{\beta_1}{\mu_2},\frac{\mu_1}{\beta_2}\right\} < \frac{b_1 e^{-\gamma_1 \tau_M}}{b_2 e^{-\gamma_2 \tau_m}} < \frac{b_1 e^{-\gamma_1 \tau_m}}{b_2 e^{-\gamma_2 \tau_M}} < \max\left\{\frac{\beta_1}{\mu_2},\frac{\mu_1}{\beta_2}\right\};$$

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$$\min\left\{\frac{\beta_1}{\mu_1}, \frac{\mu_2}{\beta_2}\right\} < \frac{a_1}{a_2} < \max\left\{\frac{\beta_1}{\mu_1}, \frac{\mu_2}{\beta_2}\right\}.$$
(3.3)

Then there exists unique coexistence equilibrium $E^* = (x^*, z_1^*, z_2^*)$.

Proof. There are three cases to prove the existence of nontrivial equilibria.

Case 1 If $z_2 = 0$, then Eq (3.2) reduces to

$$\begin{cases} x(1 - x - a_1 z_1) = 0, \\ b_1 x z_1 e^{-\gamma_1 \tau(x)} - \beta_1 z_1^2 = 0. \end{cases}$$

The inequality, $z_1 < b_1/(a_1b_1 + \beta_1)$, is valid to make sure $x = 1 - a_1z_1 > 0$, $y_1 = \gamma_1^{-1}z_1(b_1 - a_1b_1z_1 - \beta_1z_1) > 0$. Thus, we will investigate the existence and uniqueness of nontrivial equilibrium in $\Lambda = \{z_1 \in R \mid 0 < z_1 < b_1/(a_1b_1 + \beta_1)\} \subset R$. Define $f : \overline{\Lambda} \to R$ be a continuous mapping by

$$f(z_1) = b_1(1 - a_1 z_1) e^{-\gamma_1 \tau (1 - a_1 z_1)} - \beta_1 z_1.$$

Clearly, $f(0) = b_1 x e^{-\gamma_1 \tau(1)} > 0$, $f(b_1/(a_1b_1 + \beta_1)) = b_1\beta_1/(a_1b_1 + \beta_1)[e^{-\gamma_1 \tau(\beta_1/(a_1b_1 + \beta_1))} - 1] < 0$, which implies that $f(z_1)$ has at least one positive zero point $\hat{z_1}$.

Note that $f'(\hat{z_1}) = -a_1b_1e^{-\gamma_1\tau(1-a_1\hat{z_1})} + a_1b_1\gamma_1(1-a_1\hat{z_1})e^{-\gamma_1\tau(1-a_1\hat{z_1})}\tau'(1-a_1\hat{z_1}) - \beta_1 < 0$, it then follows that $f(z_1)$ has a unique positive root in the interval $(0, b_1/(a_1b_1+\beta_1))$. Hence, system (3.1) has a unique boundary equilibrium $E_2 = (\hat{x}, \hat{z_1}, 0)$.

Case 2 If $z_1 = 0$, then system (3.1) has a unique boundary equilibrium $E_3 = (\tilde{x}, 0, \tilde{z_2})$ by similar arguments in the case 1.

Case 3 If $z_1 \neq 0$ and $z_2 \neq 0$, then the coexistence equilibrium $E^* = (x^*, z_1^*, z_2^*)$ satisfies the following equations:

$$\begin{cases} 1 - x - a_1 z_1 - a_2 z_2 = 0, \\ b_1 x e^{-\gamma_1 \tau(x)} - \beta_1 z_1 - \mu_1 z_2 = 0, \\ b_2 x e^{-\gamma_2 \tau(x)} - \beta_2 z_2 - \mu_2 z_1 = 0. \end{cases}$$
(3.4)

Solving Eq (3.4), we obtain that

$$\begin{cases} x^* = \frac{1}{1 + a_1 \Gamma_1 + a_2 \Gamma_2}; \\ z_1^* = x^* \Gamma_1, \quad \Gamma_1 = \frac{\beta_2 b_1 e^{-\gamma_1 \tau(x^*)} - \mu_1 b_2 e^{-\gamma_2 \tau(x^*)}}{\beta_1 \beta_2 - \mu_1 \mu_2}; \\ z_2^* = x^* \Gamma_2, \quad \Gamma_2 = \frac{\beta_1 b_2 e^{-\gamma_2 \tau(x^*)} - \mu_2 b_1 e^{-\gamma_1 \tau(x^*)}}{\beta_1 \beta_2 - \mu_1 \mu_2}. \end{cases}$$
(3.5)

In order to make sure the positivity of x^* , z_1^* and z_2^* , we get

$$\min\left\{\frac{\beta_1}{\mu_2},\frac{\mu_1}{\beta_2}\right\} < \frac{b_1 e^{-\gamma_1 \tau_M}}{b_2 e^{-\gamma_2 \tau_m}} < \frac{b_1 e^{-\gamma_1 \tau(x^*)}}{b_2 e^{-\gamma_2 \tau(x^*)}} < \frac{b_1 e^{-\gamma_1 \tau_m}}{b_2 e^{-\gamma_2 \tau_M}} < \max\left\{\frac{\beta_1}{\mu_2},\frac{\mu_1}{\beta_2}\right\}.$$

Now we prove the uniqueness of E^* . Suppose that $f(x) = 1 - x - a_1z_1 - a_2z_2$, combining Eq (3.5), we have

$$f(x) = 1 - x - a_1 z_1 - a_2 z_2$$

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$$= 1 - x - xb_1 e^{-\gamma_1 \tau(x)} \frac{a_1 \beta_2 - a_2 \mu_2}{\beta_1 \beta_2 - \mu_1 \mu_2} - xb_2 e^{-\gamma_2 \tau(x)} \frac{a_2 \beta_1 - a_1 \mu_1}{\beta_1 \beta_2 - \mu_1 \mu_2}$$

= 1 - x - xf_1(x) - xf_2(x),

where $f_1(x) = b_1 e^{-\gamma_1 \tau(x)} (a_1 \beta_2 - a_2 \mu_2) / (\beta_1 \beta_2 - \mu_1 \mu_2), f_2(x) = b_2 e^{-\gamma_2 \tau(x)} (a_2 \beta_1 - a_1 \mu_1) / (\beta_1 \beta_2 - \mu_1 \mu_2).$ Obviously, f(0) = 1 > 0 and

$$f(1) = \frac{-a_1(\beta_2 b_1 e^{-\gamma_1 \tau(1)} - \mu_1 b_2 e^{-\gamma_2 \tau(1)}) - a_2(\beta_1 b_2 e^{-\gamma_2 \tau(1)} - \mu_2 b_1 e^{-\gamma_1 \tau(1)})}{\beta_1 \beta_2 - \mu_1 \mu_2} < 0,$$

which implies that f(x) has at least one positive zero point x^* .

It follows from $f_1(x^*) + f_2(x^*) = 1/x^* - 1$ that

$$f'(x^*) = -1 - [f_1(x^*) + f_2(x^*)] - x^*[f'_1(x^*) + f'_2(x^*)]$$
$$= -\frac{1}{x^*} - x^*[f'_1(x^*) + f'_2(x^*)].$$

If $\min \{\beta_1/\mu_1, \mu_2/\beta_2\} < a_1/a_2 < \max \{\beta_1/\mu_1, \mu_2/\beta_2\}$, then $f'(x^*) < 0$. Thus, f(x) has a unique positive root x^* in the interval (0, 1), and system (3.1) has a unique coexistence equilibrium $E^* = (x^*, z_1^*, z_2^*)$. This completes the proof.

4. Linearized stability of equilibria

In this section, the linearized stability of equilibria will be studied. We utilize the method proposed by Cooke [34] to linearize system (3.1).

Let $\tilde{E} = (\tilde{x}, \tilde{z_1}, \tilde{z_2})$ be an arbitrary equilibrium. Then the linearization of system (3.1) is

$$\begin{cases} x'(t) = Ax(t) - a_1 \tilde{x} z_1(t) - a_2 \tilde{x} z_2(t), \\ z'_1(t) = A_1 x + b_1 e^{-\gamma_1 \tau(\tilde{x})} \tilde{z}_1 x(t - \tau(\tilde{x})) + b_1 e^{-\gamma_1 \tau(\tilde{x})} \tilde{x} z_1(t - \tau(\tilde{x})) + B_1 z_1 + C_1 z_2, \\ z'_2(t) = A_2 x + b_2 e^{-\gamma_2 \tau(\tilde{x})} \tilde{z}_2 x(t - \tau(\tilde{x})) + b_2 e^{-\gamma_2 \tau(\tilde{x})} \tilde{x} z_2(t - \tau(\tilde{x})) + B_2 z_1 + C_2 z_2, \end{cases}$$
(4.1)

where

$$A = 1 - 2\tilde{x} - a_{1}\tilde{z}_{1} - a_{2}\tilde{z}_{2},$$

$$A_{1} = -b_{1}\tilde{x}\tilde{z}_{1}\tau'(\tilde{x})e^{-\gamma_{1}\tau(\tilde{x})}(\gamma_{1} - A),$$

$$A_{2} = -b_{2}\tilde{x}\tilde{z}_{2}\tau'(\tilde{x})e^{-\gamma_{2}\tau(\tilde{x})}(\gamma_{2} - A),$$

$$B_{1} = a_{1}b_{1}(\tilde{x})^{2}\tilde{z}_{1}\tau'(\tilde{x})e^{-\gamma_{1}\tau(\tilde{x})} - 2\beta_{1}\tilde{z}_{1} - \mu_{1}\tilde{z}_{2},$$

$$B_{2} = a_{1}b_{2}(\tilde{x})^{2}\tilde{z}_{2}\tau'(\tilde{x})e^{-\gamma_{2}\tau(\tilde{x})} - \mu_{2}\tilde{z}_{2},$$

$$C_{1} = a_{2}b_{1}(\tilde{x})^{2}\tilde{z}_{2}\tau'(\tilde{x})e^{-\gamma_{1}\tau(\tilde{x})} - \mu_{1}\tilde{z}_{1},$$

$$C_{2} = a_{2}b_{2}(\tilde{x})^{2}\tilde{z}_{2}\tau'(\tilde{x})e^{-\gamma_{2}\tau(\tilde{x})} - 2\beta_{2}\tilde{z}_{2} - \mu_{2}\tilde{z}_{1}.$$

The corresponding characteristic equation of system (4.1) is as follows:

$$\begin{vmatrix} \lambda - A & a_1 \tilde{x} & a_2 \tilde{x} \\ -A_1 - b_1 \tilde{z_1} e^{-(\gamma_1 + \lambda)\tau(\tilde{x})} & \lambda - B_1 - b_1 \tilde{x} e^{-(\gamma_1 + \lambda)\tau(\tilde{x})} & -C_1 \\ -A_2 - b_2 \tilde{z_2} e^{-(\gamma_2 + \lambda)\tau(\tilde{x})} & -B_2 & \lambda - C_2 - b_2 \tilde{x} e^{-(\gamma_2 + \lambda)\tau(\tilde{x})} \end{vmatrix} = 0.$$

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For the extinction equilibrium $E_0 = (0, 0, 0)$, it follows that A = 1, $A_1 = 0$, $B_1 = 0$, $C_1 = 0$, $A_2 = 0$, $B_2 = 0$, $C_2 = 0$, then $(\lambda - 1)\lambda^2 = 0$, and $\lambda = 1 > 0$ is one of these eigenvalues. Thus, we have the following result.

Theorem 4.1. The extinction equilibrium $E_0 = (0, 0, 0)$ is unstable.

For the trivial equilibrium $E_1 = (1, 0, 0)$, the characteristic equation is as follows.

$$(\lambda+1)\left(\lambda-b_1e^{-(\gamma_1+\lambda)\tau(1)}\right)\left(\lambda-b_2e^{-(\gamma_2+\lambda)\tau(1)}\right)=0.$$

Obviously, $\lambda = -1 < 0$ is one of these eigenvalues. All the other eigenvalues λ satisfy the equations $\lambda e^{\tau(1)(\gamma_1+\lambda)} = b_1 > 0$ and $\lambda e^{\tau(1)(\gamma_2+\lambda)} = b_2 > 0$, which always have real, positive solutions. Hence, the conclusion about the linearized stability of E_1 is as follows.

Theorem 4.2. The trivial equilibrium $E_1 = (1, 0, 0)$ is a saddle point and unstable.

In order to obtain the linearized stability of E_2 and E_3 , we first give the results on the real positive roots of a quartic equation. Suppose that

$$v^{4} + K_{1}v^{3} + K_{2}v^{2} + K_{3}v + K_{4} = 0.$$
(4.2)

Let

$$M = \frac{1}{2}K_2 - \frac{3}{16}K_1^2, \quad N = \frac{1}{32}K_1^3 - \frac{1}{8}K_1K_2 + K_3,$$

$$\Delta = \left(\frac{N}{2}\right)^3 + \left(\frac{M}{2}\right)^3, \quad \sigma = \frac{-1 + \sqrt{3}i}{2},$$

$$y_1 = \sqrt[3]{-\frac{N}{2} + \sqrt{\Delta}} + \sqrt[3]{-\frac{N}{2} - \sqrt{\Delta}}, \quad y_2 = \sigma\sqrt[3]{-\frac{N}{2} + \sqrt{\Delta}} + \sigma^2\sqrt[3]{-\frac{N}{2} - \sqrt{\Delta}},$$

$$y_3 = \sigma^2\sqrt[3]{-\frac{N}{2} + \sqrt{\Delta}} + \sigma\sqrt[3]{-\frac{N}{2} - \sqrt{\Delta}}, \quad z_i = y_i - \frac{3K_1}{4}, \quad i = 1, 2, 3.$$

By virtue of [35], we have the following lemma.

Lemma 4.3. *The following statements hold true for Eq* (4.2)*:*

(i) If $K_4 < 0$, then Eq (4.2) has at least one positive root;

(ii) If $K_4 \ge 0$ and $\Delta \ge 0$, then Eq (4.2) has positive roots if and only if $z_1 > 0$ and $h(z_1) < 0$;

(iii) If $K_4 \ge 0$ and $\Delta < 0$, then Eq (4.2) has positive roots if and only if there exists at least one $z^* \in \{z_1, z_2, z_3\}$ such that $z^* > 0$ and $Q(z^*) \le 0$, where $Q(z) = z^4 + K_1 z^3 + K_2 z^2 + K_3 z + K_4$.

We are now in a position to prove the linearized stability of E_2 .

Theorem 4.4. If $\hat{z_1} < 3/(4a_1)$ and $b_1\mu_2 e^{-\gamma_1\tau(\hat{x})} > b_2\beta_1 e^{-\gamma_2\tau(\hat{x})}$, then the boundary equilibrium $E_2 = (\hat{x}, \hat{z_1}, 0)$ is locally asymptotically stable.

Proof. The characteristic equation for the boundary equilibrium E_2 is as follows:

$$\left(\lambda - C_2 - b_2 \hat{x} e^{-(\gamma_2 + \lambda)\tau(\hat{x})}\right) \left[(\lambda - A) \left(\lambda - B_1 - b_1 \hat{x} e^{-(\gamma_1 + \lambda)\tau(\hat{x})}\right) + a_1 \hat{x} \left(A_1 + b_1 \hat{z_1} e^{-(\gamma_1 + \lambda)\tau(\hat{x})}\right) \right] = 0.$$

$$(4.3)$$

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It is easy to see that some of the eigenvalues satisfy the following equation:

$$\lambda + \mu_2 \hat{z}_1 - b_2 \hat{x} e^{-(\gamma_2 + \lambda)\tau(\hat{x})} = 0.$$
(4.4)

Claim. If $b_1\mu_2 e^{-\gamma_1\tau(\hat{x})} > b_2\beta_1 e^{-\gamma_2\tau(\hat{x})}$, that is, $\hat{z}_1 > \mu_2^{-1}b_2\hat{x}e^{-\gamma_2\tau(\hat{x})}$, then all eigenvalues of Eq (4.4) have negative real parts.

Obviously, if $\tau(\hat{x}) = 0$, then Eq (4.4) has a unique negative real root $\lambda = b_2 \hat{x} - \mu_2 \hat{z}_1 < 0$. In order to study whether any roots cross the imaginary axis, let $\lambda = i\omega$ with $\omega > 0$ and substitute it into Eq (4.4), it follows from $\hat{z}_1 > \mu_2^{-1} b_2 \hat{x} e^{-\gamma_2 \tau(\hat{x})}$ that

$$\omega^{2} = \left(b_{2}\hat{x}e^{-\gamma_{2}\tau(\hat{x})}\right)^{2} - \left(\mu_{2}\hat{z_{1}}\right)^{2} < 0.$$

Therefore, Eq (4.4) has no purely imaginary roots and each root has a negative real part.

Other roots are given by equation:

$$G(\lambda) = (\lambda - A) \left(\lambda - B_1 - b_1 \hat{x} e^{-(\gamma_1 + \lambda)\tau(\hat{x})} \right) + a_1 \hat{x} \left(A_1 + b_1 \hat{z_1} e^{-(\gamma_1 + \lambda)\tau(\hat{x})} \right)$$

= $\lambda^2 + H_1 \lambda + H_2 + (N_1 \lambda + N_2) e^{-\lambda \tau(\hat{x})}$
= 0, (4.5)

where $H_1 = -A - B_1$, $H_2 = AB_1 + a_1A_1\hat{x}$, $N_1 = -\beta_1\hat{z_1}$, $N_2 = A\beta_1\hat{z_1} + a_1\beta_1\hat{z_1}^2$.

Since $\tau'(x) \le 0$, we have $G(0) = \beta_1 \hat{x} \hat{z_1} - a_1 \beta_1 \gamma_1 \hat{x} (\hat{z_1})^2 \tau'(\hat{x}) + a_1 \beta_1 (\hat{z_1})^2 > 0$, and thus Eq (4.5) has no zero roots.

Next, we prove that Eq (4.5) has no purely imaginary roots.

Assume, by contradiction, that Eq (4.5) has a purely imaginary root $\lambda = iv$, where v > 0. Substituting it into Eq (4.5) and separating the real and imaginary parts, we have

$$\begin{cases} v^2 - H_2 = N_1 v \sin(\tau(\hat{x})v) + N_2 \cos(\tau(\hat{x})v), \\ -H_1 v = N_1 v \cos(\tau(\hat{x})v) - N_2 \sin(\tau(\hat{x})v). \end{cases}$$

Considering $\sin(\tau(\hat{x})v)^2 + \cos(\tau(\hat{x})v)^2 = 1$, it follows that

$$v^4 + D_1 v^2 + D_2 = 0, (4.6)$$

where $D_1 = H_1^2 - 2H_2 - N_1^2$, $D_2 = H_2^2 - N_2^2$.

In view of $\tau'(\hat{x}) \leq 0$, there are the following two cases.

Case (1). If $\tau'(\hat{x}) = 0$, then $\tau(\hat{x}) \ge 0$, since $\hat{x} > 0$, it follows from the hypothesis (\mathcal{A}_2) that $\tau(\hat{x}) \ne 0$ and $\tau(\hat{x}) > 0$. Therefore, $D_1 = A^2 + 3\beta_1^2 \hat{z_1}^2 > 0$, $D_2 = \beta_1^2 \hat{z_1}^2 (4\hat{x} - 1) = \beta_1^2 \hat{z_1}^2 (3 - 4a_1 \hat{z_1}) > 0$, which implies that Eq (4.5) has no purely imaginary roots and each root of characteristic equation has a negative real part.

Case (2). If $\tau'(\hat{x}) < 0$, according to Lemma 4.3, we have $K_1 = 0, K_2 = D_1, K_3 = 0, K_4 = D_2 = \beta_1^2 \hat{z}_1^2 (3 - 4a_1 \hat{z}_1) - 4a_1 \beta_1^2 \gamma_1 \hat{x}^2 \hat{z}_1^3 \tau'(\hat{x}) + (a_1 \beta_1 \gamma_1 \hat{x} \hat{z}_1^2 \tau'(\hat{x}))^2 > 0$ providing $\hat{z}_1 < 3/(4a_1)$. Hence, Eq (4.6) has positive roots if the equation satisfies the case (i) or (ii) in Lemma 4.3. However, $Z_i = Y_i - 3K_1/4 = Y_i = 0, i = 1, 2, 3$. Then neither case (i) nor case (ii) in Lemma 4.3 holds true, Eq (4.6) has no positive roots, that is, Eq (4.5) has no purely imaginary roots. Therefore, all eigenvalues of Eq (4.3) have negative real parts, and E_2 is locally asymptotically stable. This completes the proof.

Similarly, we have the following observation about the boundary equilibrium E_3 .

Theorem 4.5. If $\tilde{z}_2 < 3/(4a_2)$ and $b_2\mu_1 e^{-\gamma_2\tau(\tilde{x})} > b_1\beta_2 e^{-\gamma_1\tau(\tilde{x})}$, then the boundary equilibrium $E_3 = (\tilde{x}, 0, \tilde{z}_2)$ is locally asymptotically stable.

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5. The global attractivity of E^* .

In this section, we investigate the global attractivity of the coexistence equilibrium E^* by a method of asymptotic estimates.

Theorem 5.1. Let condition (3.3) hold, and assume that:

$$1 > a_1 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(1)} + a_2 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(1)};$$
(5.1)

$$b_1 \left(1 - a_1 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(1)} - a_2 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(1)} \right) e^{-\gamma_1 \tau(0)} > \mu_1 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(1)};$$
(5.2)

$$b_2 \left(1 - a_1 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(1)} - a_2 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(1)} \right) e^{-\gamma_2 \tau(0)} > \mu_2 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(1)};$$
(5.3)

$$(a_1b_1\beta_2 + a_2b_1\mu_2)e^{-\gamma_1\tau(0)} + (a_1b_2\mu_1 + a_2b_2\beta_1)e^{-\gamma_2\tau(0)} > \beta_1\beta_2 - \mu_1\mu_2.$$
(5.4)

Then the coexistence equilibrium E^* is globally attractive.

Proof. Since $e^{-\gamma\tau(x)}$ is increase with respect to *x*, then $e^{-\gamma\tau(1)} > e^{-\gamma\tau(0)}$. It follows from inequality (5.2) that

$$b_1 e^{-\gamma_1 \tau(1)} > b_1 e^{-\gamma_1 \tau(0)} > b_1 \left(1 - a_1 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(1)} - a_2 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(1)} \right) e^{-\gamma_1 \tau(0)} > \mu_1 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(1)}.$$

Similarly, we have

$$b_2 e^{-\gamma_2 \tau(1)} > b_2 e^{-\gamma_2 \tau(0)} > b_2 \left(1 - a_1 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(1)} - a_2 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(1)} \right) e^{-\gamma_2 \tau(0)} > \mu_2 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(1)}.$$

Namely,

$$\frac{\mu_1}{\beta_2} < \frac{b_1 e^{-\gamma_1 \tau_M}}{b_2 e^{-\gamma_2 \tau_m}} < \frac{b_1 e^{-\gamma_1 \tau(1)}}{b_2 e^{-\gamma_2 \tau(1)}} < \frac{b_1 e^{-\gamma_1 \tau_m}}{b_2 e^{-\gamma_2 \tau_M}} < \frac{\beta_1}{\mu_2},$$

which implies that both the boundary equilibria E_2 and E_3 are unstable.

For the system

$$\begin{cases} \frac{dm_1}{dt} = m_1(t)(1 - m_1(t)), \\ \frac{dm_1^{(1)}}{dt} = b_1[1 - \tau'(m_1)m_1'(t)]m_1(t - \tau(m_1))m_1^{(1)}(t - \tau(m_1))e^{-\gamma_1\tau(m_1)} - \beta_1(m_1^{(1)}(t))^2, \\ \frac{dm_1^{(2)}}{dt} = b_2[1 - \tau'(m_1)m_1'(t)]m_1(t - \tau(m_1))m_1^{(2)}(t - \tau(m_1))e^{-\gamma_2\tau(m_1)} - \beta_2(m_1^{(2)}(t))^2, \end{cases}$$

we have the unique positive equilibrium $m^* = (1, b_1/\beta_1 e^{-\gamma_1 \tau(1)}, b_2/\beta_2 e^{-\gamma_2 \tau(1)}).$

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Clearly, for system (3.1), we obtain that

$$\frac{dx}{dt} < x(t)(1 - x(t)),
\frac{dz_1}{dt} < b_1[1 - \tau'(x)x'(t)]x(t - \tau(x(t)))z_1(t - \tau(x(t)))e^{-\gamma_1\tau(x(t))} - \beta_1 z_1^2(t),
\frac{dz_2}{dt} < b_2[1 - \tau'(x)x'(t)]x(t - \tau(x(t)))z_2(t - \tau(x(t)))e^{-\gamma_2\tau(x(t))} - \beta_2 z_2^2(t).$$
(5.5)

By Theorem 3.1, for any $\epsilon_1 > 0$, we can prove that there exists a $t_1 > 0$ such that the following inequalities hold true for all $t \ge t_1$.

$$\begin{cases} x(t) < M_1 = 1 + \epsilon_1, \\ z_1(t) < M_1^{(1)} = \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(M_1)} + \frac{\epsilon_1}{2}, \\ z_2(t) < M_1^{(2)} = \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(M_1)} + \frac{\epsilon_1}{2}. \end{cases}$$
(5.6)

We first select $\epsilon_1 > 0$ and the corresponding $t_1 > 0$ such that

$$\begin{cases} 1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} > 0, \\ b_1 \left(1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} \right) e^{-\gamma_1 \tau(M_1)} > \mu_1 M_1^{(2)}, \\ b_2 \left(1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} \right) e^{-\gamma_2 \tau(M_1)} > \mu_2 M_1^{(1)}. \end{cases}$$
(5.7)

Conditions (5.1)-(5.3) can guarantee the existence of ϵ_1 to satisfy conditions (5.6) and (5.7). Based on $\epsilon_1 > 0$, $t_1 > 0$, we choose sufficiently small $\epsilon_2 > 0$ to make that $\epsilon_2 < \min\{1/2, \epsilon_1\}$, and

$$\begin{cases} 1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} - \epsilon_2 > 0, \\ \left[b_1 \left(1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} \right) e^{-\gamma_1 \tau(M_1)} - \mu_1 M_1^{(2)} \right] \frac{1}{\beta_1} - \frac{\epsilon_2}{2} > 0, \\ \left[b_2 \left(1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} \right) e^{-\gamma_2 \tau(M_1)} - \mu_2 M_1^{(1)} \right] \frac{1}{\beta_1} - \frac{\epsilon_2}{2} > 0. \end{cases}$$
(5.8)

In view of inequality (5.7), it is possible to choose positive number ϵ_2 satisfying inequality (5.8). Combining with inequalities (5.6) and (5.8), we obtain that

$$\begin{cases} \frac{dx}{dt} > x(t) \Big[\Big(1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} \Big) - x(t) \Big], \\ \frac{dz_1}{dt} > b_1 [1 - \tau'(x) x'(t)] x(t - \tau(x(t))) z_1(t - \tau(x(t))) e^{-\gamma_1 \tau(x(t))} - \beta_1 z_1^2(t) - \mu_1 M_1^{(2)} z_1(t), \\ \frac{dz_2}{dt} > b_2 [1 - \tau'(x) x'(t)] x(t - \tau(x(t))) z_2(t - \tau(x(t))) e^{-\gamma_2 \tau(x(t))} - \beta_2 z_2^2(t) - \mu_2 M_1^{(1)} z_2(t). \end{cases}$$

It follows that there exists a $t_2 > t_1$ to make that

$$\begin{cases} x(t) > N_1 = 1 - a_1 M_1^{(1)} - a_2 M_1^{(2)} - \epsilon_2, \\ z_1(t) > N_1^{(1)} = \left(b_1 N_1 e^{-\gamma_1 \tau(N_1)} - \mu_1 M_1^{(2)} \right) \frac{1}{\beta_1} - \frac{\epsilon_2}{2}, \\ z_2(t) > N_1^{(2)} = \left(b_2 N_1 e^{-\gamma_2 \tau(N_1)} - \mu_2 M_1^{(1)} \right) \frac{1}{\beta_2} - \frac{\epsilon_2}{2}. \end{cases}$$
(5.9)

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By system (3.1) and inequality (5.9), we have for $t > t_2$,

$$\begin{cases} \frac{dx}{dt} < x(t) \Big[\Big(1 - a_1 N_1^{(1)} - a_2 N_1^{(2)} \Big) - x(t) \Big], \\ \frac{dz_1}{dt} < b_1 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_1(t - \tau(x)) e^{-\gamma_1 \tau(x)} - \beta_1 z_1^2(t) - \mu_1 N_1^{(2)} z_1(t), \\ \frac{dz_2}{dt} < b_2 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_2(t - \tau(x)) e^{-\gamma_2 \tau(x)} - \beta_2 z_2^2(t) - \mu_2 N_1^{(1)} z_2(t). \end{cases}$$
(5.10)

With the first inequality of (5.7), we see that

$$1 - a_1 N_1^{(1)} - a_2 N_1^{(2)} = 1 - a_1 \left[\left(b_1 N_1 e^{-\gamma_1 \tau(N_1)} - \mu_1 M_1^{(2)} \right) \frac{1}{\beta_1} - \frac{\epsilon_2}{2} \right] - a_2 \left[\left(b_2 N_1 e^{-\gamma_2 \tau(N_1)} - \mu_2 M_1^{(1)} \right) \frac{1}{\beta_2} - \frac{\epsilon_2}{2} \right] > 1 - a_1 \frac{b_1}{\beta_1} N_1 e^{-\gamma_1 \tau(N_1)} - a_2 \frac{b_2}{\beta_2} N_1 e^{-\gamma_2 \tau(N_1)} > 1 - a_1 \frac{b_1}{\beta_1} M_1 e^{-\gamma_1 \tau(M_1)} - a_2 \frac{b_2}{\beta_2} M_1 e^{-\gamma_2 \tau(M_1)} > 0.$$
(5.11)

Then from inequalities (5.10) and (5.11), there exists a $t_3 > t_2$ and $0 < \epsilon_3 < \min\{1/3, \epsilon_2\}$ such that, for $t > t_3$,

$$\begin{cases} x(t) < M_2 = 1 - a_1 N_1^{(1)} - a_2 N_1^{(2)} + \epsilon_3, \\ z_1(t) < M_2^{(1)} = \left(b_1 M_2 e^{-\gamma_1 \tau(M_2)} - \mu_1 N_1^{(2)} \right) \frac{1}{\beta_1} + \frac{\epsilon_3}{2}, \\ z_2(t) < M_2^{(2)} = \left(b_2 M_2 e^{-\gamma_2 \tau(M_2)} - \mu_2 N_1^{(1)} \right) \frac{1}{\beta_2} + \frac{\epsilon_3}{2}. \end{cases}$$
(5.12)

We next prove that the estimates $M_2^{(1)}$ and $M_2^{(2)}$ are positive.

$$b_{1}M_{2}e^{-\gamma_{1}\tau(M_{2})} - \mu_{1}N_{1}^{(2)} = b_{1}\left(1 - a_{1}N_{1}^{(1)} - a_{2}N_{1}^{(2)} + \epsilon_{3}\right)e^{-\gamma_{1}\tau(M_{2})} - \mu_{1}\left[\left(b_{2}N_{1}e^{-\gamma_{2}\tau(N_{1})} - \mu_{2}M_{1}^{(1)}\right)\frac{1}{\beta_{2}} - \frac{\epsilon_{2}}{2}\right] > b_{1}\left(1 - a_{1}N_{1}^{(1)} - a_{2}N_{1}^{(2)}\right)e^{-\gamma_{1}\tau(M_{2})} - \mu_{1}\frac{b_{2}}{\beta_{2}}N_{1}e^{-\gamma_{2}\tau(N_{1})} > b_{1}\left(1 - a_{1}M_{1}^{(1)} - a_{2}M_{1}^{(2)}\right)e^{-\gamma_{1}\tau(0)} - \mu_{1}\frac{b_{2}}{\beta_{2}}M_{1}e^{-\gamma_{2}\tau(M_{1})} > 0,$$
(5.13)

and

$$b_2 M_2 e^{-\gamma_2 \tau(M_2)} - \mu_2 N_1^{(1)} = b_2 \left(1 - a_1 N_1^{(1)} - a_2 N_1^{(2)} + \epsilon_3 \right) e^{-\gamma_2 \tau(M_2)} - \mu_2 \left[\left(b_1 N_1 e^{-\gamma_1 \tau(N_1)} - \mu_1 M_1^{(2)} \right) \frac{1}{\beta_1} - \frac{\epsilon_2}{2} \right]$$

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$$>b_{2}\left(1-a_{1}N_{1}^{(1)}-a_{2}N_{1}^{(2)}\right)e^{-\gamma_{2}\tau(M_{2})}-\mu_{2}\frac{b_{1}}{\beta_{1}}N_{1}e^{-\gamma_{1}\tau(N_{1})}$$

$$>b_{2}\left(1-a_{1}M_{1}^{(1)}-a_{2}M_{1}^{(2)}\right)e^{-\gamma_{2}\tau(0)}-\mu_{2}\frac{b_{1}}{\beta_{1}}M_{1}e^{-\gamma_{1}\tau(M_{1})}$$

$$>0.$$
(5.14)

In view of the upper estimates in equality (5.12), we will get a lower set of estimates. Since $\epsilon_3 < \epsilon_1$, inequalities (5.13) and (5.14), the following result is valid.

$$1 - a_{1}M_{2}^{(1)} - a_{2}M_{2}^{(2)} = 1 - a_{1}\left[\left(b_{1}M_{2}e^{-\gamma_{1}\tau(M_{2})} - \mu_{1}N_{1}^{(2)}\right)\frac{1}{\beta_{1}} + \frac{\epsilon_{3}}{2}\right] \\ - a_{2}\left[\left(b_{2}M_{2}e^{-\gamma_{2}\tau(M_{2})} - \mu_{2}N_{1}^{(1)}\right)\frac{1}{\beta_{2}} + \frac{\epsilon_{3}}{2}\right] \\ > 1 - a_{1}\left(\frac{b_{1}}{\beta_{1}}M_{2}e^{-\gamma_{1}\tau(M_{2})} + \frac{\epsilon_{3}}{2}\right) - a_{2}\left(\frac{b_{2}}{\beta_{2}}M_{2}e^{-\gamma_{2}\tau(M_{2})} + \frac{\epsilon_{3}}{2}\right) \\ > 1 - a_{1}\left(\frac{b_{1}}{\beta_{1}}M_{1}e^{-\gamma_{1}\tau(M_{1})} + \frac{\epsilon_{3}}{2}\right) - a_{2}\left(\frac{b_{2}}{\beta_{2}}M_{1}e^{-\gamma_{2}\tau(M_{1})} + \frac{\epsilon_{3}}{2}\right) \\ > 0.$$

$$(5.15)$$

Denote $n_2, n_2^{(1)}, n_2^{(2)}$ as follows:

$$\begin{cases} n_2 = 1 - a_1 M_2^{(1)} - a_2 M_2^{(2)}, \\ n_2^{(1)} = b_1 n_2 e^{-\gamma_1 \tau(n_2)} - \mu_1 M_2^{(2)}, \\ n_2^{(2)} = b_2 n_2 e^{-\gamma_2 \tau(n_2)} - \mu_2 M_2^{(1)}. \end{cases}$$
(5.16)

By inequalities (5.2) and (5.15) and the second inequality of (5.7), we get that

$$n_{2}^{(1)} = b_{1} \left(1 - a_{1} M_{2}^{(1)} - a_{2} M_{2}^{(2)} \right) e^{-\gamma_{1} \tau(n_{2})} - \mu_{1} M_{2}^{(2)}$$

> $b_{1} \left(1 - a_{1} M_{2}^{(1)} - a_{2} M_{2}^{(2)} \right) e^{-\gamma_{1} \tau(0)} - \mu_{1} M_{1}^{(2)}$
> $0.$ (5.17)

It follows from inequalities (5.3) and (5.15) and the third inequality of (5.7) that

$$n_{2}^{(2)} = b_{2} \left(1 - a_{1} M_{2}^{(1)} - a_{2} M_{2}^{(2)} \right) e^{-\gamma_{2} \tau(n_{2})} - \mu_{2} M_{2}^{(1)}$$

> $b_{2} \left(1 - a_{1} M_{2}^{(1)} - a_{2} M_{2}^{(2)} \right) e^{-\gamma_{2} \tau(0)} - \mu_{2} M_{1}^{(1)}$
> $0.$ (5.18)

Combining with inequalities (5.15)–(5.18), there exists a $0 < \epsilon_4 < \min\{1/4, \epsilon_3\}$ satisfying

$$\begin{cases} n_2 - \epsilon_4 > 0, \\ \left(b_1 n_2 e^{-\gamma_1 \tau(n_2)} - \mu_1 M_2^{(2)}\right) \frac{1}{\beta_1} - \frac{\epsilon_4}{2} > 0, \\ \left(b_2 n_2 e^{-\gamma_2 \tau(n_2)} - \mu_2 M_2^{(1)}\right) \frac{1}{\beta_2} - \frac{\epsilon_4}{2} > 0. \end{cases}$$
(5.19)

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With the upper estimates in inequality (5.12), we obtain the following comparative system for all $t > t_3$.

$$\begin{cases} \frac{dx}{dt} > x(t) \Big[\Big(1 - a_1 M_2^{(1)} - a_2 M_2^{(2)} \Big) - x(t) \Big], \\ \frac{dz_1}{dt} > b_1 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_1(t - \tau(x)) e^{-\gamma_1 \tau(x)} - \beta_1 z_1^2(t) - \mu_1 M_2^{(2)} z_1(t), \\ \frac{dz_2}{dt} > b_2 [1 - \tau'(x) x'(t)] x(t - \tau(x)) z_2(t - \tau(x)) e^{-\gamma_2 \tau(x)} - \beta_2 z_2^2(t) - \mu_2 M_2^{(1)} z_2(t). \end{cases}$$

Using inequality (5.19), there exists a $t_4 > t_3$ such that

$$\begin{cases} x(t) > N_2 = 1 - a_1 M_2^{(1)} - a_2 M_2^{(2)} - \epsilon_4, \\ z_1(t) > N_2^{(1)} = \left(b_1 N_2 e^{-\gamma_1 \tau(N_2)} - \mu_1 M_2^{(2)} \right) \frac{1}{\beta_1} - \frac{\epsilon_4}{2}, \\ z_2(t) > N_2^{(2)} = \left(b_2 N_2 e^{-\gamma_2 \tau(N_2)} - \mu_2 M_2^{(1)} \right) \frac{1}{\beta_2} - \frac{\epsilon_4}{2}. \end{cases}$$

The estimates N_2 , $N_2^{(1)}$ and $N_2^{(2)}$ are all positive by inequality (5.19). Therefore, we obtain that, for $t > t_2$,

$$N_1 < x(t) < M_1, \ N_1^{(1)} < z_1(t) < M_1^{(1)}, \ N_1^{(2)} < z_2(t) < M_1^{(2)},$$

and for $t > t_4$,

$$N_2 < x(t) < M_2, \ N_2^{(1)} < z_1(t) < M_2^{(1)}, \ N_2^{(2)} < z_2(t) < M_2^{(2)}.$$

Now we compare the obtained estimates, respectively:

$$\begin{split} M_2 - M_1 &= 1 - a_1 N_1^{(1)} - a_2 N_1^{(2)} + \epsilon_3 - (1 - \epsilon_1) \\ &< \epsilon_3 - \epsilon_1 < 0, \\ M_2^{(1)} - M_1^{(1)} &= \left(b_1 M_2 e^{-\gamma_1 \tau(M_2)} - \mu_1 N_1^{(2)} \right) \frac{1}{\beta_1} + \frac{\epsilon_3}{2} - \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(M_1)} - \frac{\epsilon_1}{2} \\ &< \frac{b_1}{\beta_1} M_2 e^{-\gamma_1 \tau(M_2)} - \frac{b_1}{\beta_1} M_1 e^{-\gamma_1 \tau(M_1)} + \frac{1}{2} (\epsilon_3 - \epsilon_1) \\ &< \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(M_1)} (M_2 - M_1) + \frac{1}{2} (\epsilon_3 - \epsilon_1) \\ &< 0. \end{split}$$

Similarly, $M_2^{(2)} - M_1^{(2)} < 0$. Moreover,

$$\begin{split} N_2 - N_1 &= 1 - a_1 M_2^{(1)} - a_2 M_2^{(2)} - \epsilon_4 - \left(1 - a_1 M_1^{(1)} - a_2 M_1^{(2)}\right) + \epsilon_2 \\ &= -a_1 \left(M_2^{(1)} - M_1^{(1)}\right) - a_2 \left(M_2^{(2)} - M_1^{(2)}\right) + (\epsilon_2 - \epsilon_4) \\ &> 0, \end{split}$$

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and

$$\begin{split} N_{2}^{(1)} - N_{1}^{(1)} &= \left(b_{1} N_{2} e^{-\gamma_{1} \tau(N_{2})} - \mu_{1} M_{2}^{(2)}\right) \frac{1}{\beta_{1}} - \frac{\epsilon_{4}}{2} - \left(b_{1} N_{1} e^{-\gamma_{1} \tau(N_{1})} - \mu_{1} M_{1}^{(2)}\right) \frac{1}{\beta_{1}} + \frac{\epsilon_{2}}{2} \\ &> \frac{b_{1}}{\beta_{1}} e^{-\gamma_{1} \tau(N_{1})} (N_{2} - N_{1}) - \frac{\mu_{1}}{\beta_{1}} \left(M_{2}^{(2)} - M_{1}^{(2)}\right) + \frac{1}{2} (\epsilon_{2} - \epsilon_{4}) \\ &> 0. \end{split}$$

Similarly, $N_2^{(2)} - N_1^{(2)} > 0$. Hence, from the above arguments, we have for $t > t_4$

$$\begin{split} N_1 &< N_2 < x(t) < M_2 < M_1, \\ N_1^{(1)} &< N_2^{(1)} < z_1(t) < M_2^{(1)} < M_1^{(1)}, \\ N_1^{(2)} &< N_2^{(2)} < z_2(t) < M_2^{(2)} < M_1^{(2)}. \end{split}$$

By extending the above step, it then follows that

$$N_{1} < N_{2} < N_{3} < \dots < N_{n} < x(t) < M_{n} < \dots < M_{3} < M_{2} < M_{1},$$

$$N_{1}^{(1)} < N_{2}^{(1)} < N_{3}^{(1)} < \dots < N_{n}^{(1)} < z_{1}(t) < M_{n}^{(1)} < \dots < M_{3}^{(1)} < M_{2}^{(1)} < M_{1}^{(1)},$$

$$N_{1}^{(2)} < N_{2}^{(2)} < N_{3}^{(2)} < \dots < N_{n}^{(2)} < z_{2}(t) < M_{n}^{(2)} < \dots < M_{3}^{(2)} < M_{2}^{(2)} < M_{1}^{(2)},$$

where

$$M_{n} = 1 - a_{1}N_{n-1}^{(1)} - a_{2}N_{n-1}^{(2)} + \epsilon_{2n-1},$$

$$M_{n}^{(1)} = \left(b_{1}M_{n}e^{-\gamma_{1}\tau(M_{n})} - \mu_{1}N_{n-1}^{(2)}\right)\frac{1}{\beta_{1}} + \frac{\epsilon_{2n-1}}{2},$$

$$M_{n}^{(2)} = \left(b_{2}M_{n}e^{-\gamma_{2}\tau(M_{n})} - \mu_{2}N_{n-1}^{(2)}\right)\frac{1}{\beta_{2}} + \frac{\epsilon_{2n-1}}{2},$$
(5.20)

with $n = 2, 3, 4, \dots$, and

$$N_{n} = 1 - a_{1}M_{n}^{(1)} - a_{2}M_{n}^{(2)} - \epsilon_{2n},$$

$$N_{n}^{(1)} = \left(b_{1}N_{n}e^{-\gamma_{1}\tau(N_{n})} - \mu_{1}M_{n}^{(2)}\right)\frac{1}{\beta_{1}} - \frac{\epsilon_{2n}}{2},$$

$$N_{n}^{(2)} = \left(b_{2}N_{n}e^{-\gamma_{2}\tau(N_{n})} - \mu_{2}M_{n}^{(2)}\right)\frac{1}{\beta_{2}} - \frac{\epsilon_{2n-1}}{2},$$
(5.21)

with $n = 1, 2, 3, \cdots$.

Since $\epsilon_n < 1/n$, we have $\epsilon_n \to 0$ as $n \to \infty$. And the monotone sequences N_n , $N_n^{(1)}$, $N_n^{(2)}$, M_n , $M_n^{(1)}$, and $M_n^{(2)}$ converge to positive limits as $n \to \infty$. Let

$$M_{*} = \lim_{n \to \infty} M_{n} \text{ and } N_{*} = \lim_{n \to \infty} N_{n},$$

$$M_{*}^{(1)} = \lim_{n \to \infty} M_{n}^{(1)} \text{ and } N_{*}^{(1)} = \lim_{n \to \infty} N_{n}^{(1)},$$

$$M_{*}^{(2)} = \lim_{n \to \infty} M_{n}^{(2)} \text{ and } N_{*}^{(2)} = \lim_{n \to \infty} N_{n}^{(2)}.$$

(5.22)

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By virtue of Eqs (5.20)–(5.22) and $\lim_{n\to\infty} \epsilon_n = 0$, it follows that

$$M_* = 1 - a_1 N_*^{(1)} - a_2 N_*^{(2)},$$

$$N_* = 1 - a_1 M_*^{(1)} - a_2 M_*^{(2)},$$
(5.23)

and

$$\beta_1 M_*^{(1)} = b_1 M_* e^{-\gamma_1 \tau(M_*)} - \mu_1 N_*^{(2)}, \ \beta_1 N_*^{(1)} = b_1 N_* e^{-\gamma_1 \tau(N_*)} - \mu_1 M_*^{(2)}, \beta_2 M_*^{(2)} = b_2 M_* e^{-\gamma_2 \tau(M_*)} - \mu_2 N_*^{(1)}, \ \beta_2 N_*^{(2)} = b_2 N_* e^{-\gamma_2 \tau(N_*)} - \mu_2 M_*^{(1)}.$$
(5.24)

From Eq (5.24), we have

$$M_*^{(1)} - N_*^{(1)} = \frac{b_1 \beta_2 B_1 + b_2 \mu_1 B_2}{\beta_1 \beta_2 - \mu_1 \mu_2}, \ M_*^{(2)} - N_*^{(2)} = \frac{b_1 \mu_2 B_1 + b_2 \beta_1 B_2}{\beta_1 \beta_2 - \mu_1 \mu_2},$$
(5.25)

where $B_1 = (M_* e^{-\gamma_1 \tau(M_*)} - N_* e^{-\gamma_1 \tau(N_*)}), B_2 = (M_* e^{-\gamma_2 \tau(M_*)} - N_* e^{-\gamma_2 \tau(N_*)}).$ Combining Eqs (5.23) and (5.25), we see that

$$M_* - N_* = a_1 \Big(M_*^{(1)} - N_*^{(1)} \Big) - a_2 \Big(M_*^{(2)} - N_*^{(2)} \Big) \\ = \frac{(a_1 b_1 \beta_2 + a_2 b_1 \mu_2) B_1 + (a_1 b_2 \mu_1 + a_2 b_2 \beta_1) B_2}{\beta_1 \beta_2 - \mu_1 \mu_2}.$$

Let $Q_1 = (a_1b_1\beta_2 + a_2b_1\mu_2)/(\beta_1\beta_2 - \mu_1\mu_2), Q_2 = (a_1b_2\mu_1 + a_2b_2\beta_1)/(\beta_1\beta_2 - \mu_1\mu_2)$, then

$$M_* \left(1 - Q_1 e^{-\gamma_1 \tau(M_*)} - Q_2 e^{-\gamma_2 \tau(M_*)} \right) = N_* \left(1 - Q_1 e^{-\gamma_1 \tau(N_*)} - Q_2 e^{-\gamma_2 \tau(N_*)} \right).$$
(5.26)

Denote $h(x) = x(1 - Q_1 e^{-\gamma_1 \tau(x)} - Q_2 e^{-\gamma_2 \tau(x)})$, for all $x \ge 0$. From (5.4) and $\tau'(x) \le 0$, we have

$$\begin{split} h'(x) &= 1 - Q_1 e^{-\gamma_1 \tau(x)} - Q_2 e^{-\gamma_2 \tau(x)} + x \Big[Q_1 \gamma_1 \tau'(x) e^{-\gamma_1 \tau(x)} + Q_2 \gamma_2 \tau'(x) e^{-\gamma_2 \tau(x)} \\ &< 1 - Q_1 e^{-\gamma_1 \tau(x)} - Q_2 e^{-\gamma_2 \tau(x)} \\ &< 1 - Q_1 e^{-\gamma_1 \tau(0)} - Q_2 e^{-\gamma_2 \tau(0)} < 0, \end{split}$$

and thus, h(x) is a monotone decrease function with respect to x. It then follows from Eq (5.26) that $M_* = N_*$. Therefore, $M_*^{(1)} = N_*^{(1)}$ and $M_*^{(2)} = N_*^{(2)}$. Further, the relations in Eqs (5.23) and (5.24) are also true for $E^* = (x^*, z_1^*, z_2^*)$. Then by the uniqueness of the coexistence equilibrium of system (3.1), we know that $(M_*, M_*^{(1)}, M_*^{(2)})$ and $(N_*, N_*^{(1)}, N_*^{(2)})$ are the coexistence equilibrium of system (3.1), and hence $M_* = N_* = x^*$, $M_*^{(1)} = M_*^{(1)} = z_1^*$, $M_*^{(2)} = M_*^{(2)} = z_2^*$. Accordingly, $x^* = \lim_{t\to\infty} x(t)$, $z_1^* = \lim_{t\to\infty} z_1(t)$ and $z_2^* = \lim_{t\to\infty} z_2(t)$. The proof is complete.

Next we deduce the global attractivity for the other variables y_1 and y_2 in system (2.3). By using the integral form for y_1 and y_2 , we obtain that

$$y_i^* = \lim_{t \to \infty} y_i(t) = \int_{t-\tau(x^*)}^t b_i x^* z_i^* e^{-\gamma_i(t-s)} ds, \qquad i = 1, 2$$

Therefore, we have the following result.

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Theorem 5.2. Let condition (3.3) hold. Assume that conditions (5.1)-(5.4) hold true, then the coexistence equilibrium $E^* = (x^*, y_1^*, z_1^*, y_2^*, z_2^*)$ is globally attractive for system (2.3).

At the end of this section, we give the dynamical results of two boundary equilibria and coexistence equilibrium for the original system (2.2). The reduced system of model (2.2) is as follows.

$$\begin{cases}
\frac{dx}{dt} = rx(t)\left(1 - \frac{x(t)}{K}\right) - a_1x(t)z_1(t) - a_2x(t)z_2(t), \\
\frac{dz_1}{dt} = b_1[1 - \tau'(x)x'(t)]x(t - \tau(x))z_1(t - \tau(x))e^{-\gamma_1\tau(x)} - \beta_1z_1^2(t) - \mu_1z_1(t)z_2(t), \\
\frac{dz_2}{dt} = b_2[1 - \tau'(x)x'(t)]x(t - \tau(x))z_2(t - \tau(x))e^{-\gamma_2\tau(x)} - \beta_2z_2^2(t) - \mu_2z_1(t)z_2(t).
\end{cases}$$
(5.27)

Obviously, system (5.27) has exactly one trivial equilibrium $E_0 = (0, 0, 0)$, one semitrivial equilibrium $E_1 = (K, 0, 0)$, two boundary equilibria $E_2 = (\hat{x}, \hat{z_1}, 0)$ and $E_3 = (\tilde{x}, 0, \tilde{z_2})$. And condition (3.3) holds true, then there exists a unique coexistence equilibrium $E^* = (x^*, z_1^*, z_2^*)$.

Theorem 5.3. If $\hat{z_1} < 3r/(4a_1)$ and $b_1\mu_2 e^{-\gamma_1\tau(\hat{x})} > b_2\beta_1 e^{-\gamma_2\tau(\hat{x})}$, then the boundary equilibrium $E_2 = (\hat{x}, \hat{z_1}, 0)$ of system (5.27) is locally asymptotically stable.

Theorem 5.4. If $\tilde{z}_2 < 3r/(4a_2)$ and $b_2\mu_1 e^{-\gamma_2\tau(\tilde{x})} > b_1\beta_2 e^{-\gamma_1\tau(\tilde{x})}$, then the boundary equilibrium $E_3 = (\tilde{x}, 0, \tilde{z}_2)$ of system (5.27) is locally asymptotically stable.

Theorem 5.5. Let condition (3.3) hold, and assume that:

$$r > a_1 \frac{b_1}{\beta_1} K e^{-\gamma_1 \tau(K)} + a_2 \frac{b_2}{\beta_2} K e^{-\gamma_2 \tau(K)};$$
(5.28)

$$b_1\left(r - a_1 K \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(K)} - a_2 K \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(K)}\right) e^{-\gamma_1 \tau(0)} \frac{1}{r} > \mu_1 \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(K)};$$
(5.29)

$$b_2\left(r - a_1 K \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(K)} - a_2 K \frac{b_2}{\beta_2} e^{-\gamma_2 \tau(K)}\right) e^{-\gamma_2 \tau(0)} \frac{1}{r} > \mu_2 \frac{b_1}{\beta_1} e^{-\gamma_1 \tau(K)};$$
(5.30)

$$\frac{K}{r} \left[(a_1 b_1 \beta_2 + a_2 b_1 \mu_2) e^{-\gamma_1 \tau(0)} + (a_1 b_2 \mu_1 + a_2 b_2 \beta_1) e^{-\gamma_2 \tau(0)} \right] > \beta_1 \beta_2 - \mu_1 \mu_2.$$
(5.31)

Then the coexistence equilibrium E^* of system (5.27) is globally attractive.

6. Conclusions and discussions

In this paper, given that the maturity time of Antarctic whales and seals varies with the number of krill available around the Second World War, we formulated a consumer-resource competition model that, for the first time, incorporates a state-dependent maturity time delay associated with resource changes and structured consumer species. The main difference from the state-dependent delay

equations previously studied is that model (2.3) directly manifests the relationship between resources and maturity time of consumers through the correction term, $1 - \tau'(x(t))x'(t)$.

Besides, the state-dependent delay $\tau(x(t))$ reflects exploitation and interference competition effects of two consumer species. On one hand, the exploitative ability of the mature individual is stronger, the juvenile will get more resources, which leads to a shorter maturation time. On the other hand, because of the limited resource, the consumer species spend more time and energy to obtain resource for keeping themselves alive. Unfortunately, what often happens is that there is not enough food for their children and so they take longer time to mature. Further, it is clear that the greater the ability of an adult to intervene is, the shorter the maturity time is.

From mathematical point of view, firstly, we study the well-posedness of the solution for model (2.3) and the existence and uniqueness of all equilibria. We then show the linear stability of equilibria. The trivial equilibria $E_0 = (0, 0, 0)$ and $E_1 = (1, 0, 0)$ are always unstable, which can be explained by the fact that since the resource is self-renewing with a logistic growth and two competitive species depend entirely on it, the resource are not used up or maximized. For the linear stability of boundary equilibrium $E_2 = (\hat{x}, \hat{z_1}, 0)$, according to Theorem 4.4, the first sufficient condition $\hat{z_1} < 3/(4a_1)$ is equivalent to $\hat{x} > 1/4$, which means the resource must be the specific level to make sure that one of the consumer species survives. For the original system (2.2), in Theorem 5.3, the condition is changed to $\hat{z_1} < 3r/(4a_1)$, which is equivalent to $\hat{x} > K - 3K/(4r)$ and implies that the resource must be above a certain value of the interaction between the growth rate of resource and its carrying capacity. And another sufficient condition $b_1\mu_2 e^{-\gamma_1\tau(\hat{x})} > b_2\beta_1 e^{-\gamma_2\tau(\hat{x})}$ implies $(b_1\hat{x}e^{-\gamma_1\hat{x}})/\beta_1 > (b_2\hat{x}e^{-\gamma_2\hat{x}})/\mu_2$, on the basis of the threshold resource \hat{x} , when the maximum growth of the first species is large than the interspecific competitive effect on the second species, the second species has a negative growth effect, which illustrates the first species will win the competition. There is a similar biological explanation for the linear stability of $E_3 = (\tilde{x}, 0, \tilde{z_2})$. Finally, we discuss the global properties of E^* . Theorem 5.1 shows the sufficient conditions for E^* to be globally attractive. The condition (5.1) implies that the number of the two consumers are at their potential maximum, and the maximum self-updating value of the resource is large than the exploitation effects; conditions (5.2) and (5.3) imply that when the resource is at its minimum, the number of the consumers who were born at time $t - \tau(x(t))$ and still alive now are enough to make up for the possible interspecific competition effects; condition (5.4) is a technical assumption and has no practical biological significance. For the global properties of E^* in original system (2.2), the condition (5.28) implies that when the maximum carrying capacity K of the resource is reached, the two consumers are at their potential maximum, and the growth rate r of the resource is larger than the exploitation effect. Conditions (5.29) and (5.30) have biological explanations similar to conditions (5.2) and (5.3).

This paper only considers the case of one resource. And since the fitting of state-dependent delay $\tau(x(t))$ is very challenging, we are unable to validate theoretical results by numerical simulations. We would like to leave this problem and propose a competition model with state-dependent delay between two species for two resources in the further research.

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Conflict of interest

The authors declared that they have no conflicts of interest to this work.

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