



Research article

Asymptotic behaviors of jellyfish model with stage structure

Zin Thu Win¹, Boping Tian¹ and Shengqiang Liu^{2,*}

¹ School of Mathematics, Harbin Institute of Technology, Harbin 150001, China

² School of Mathematical Sciences, Tiangong University, Tianjin 300387, China

* **Correspondence:** Email: sqliu@tiangong.edu.cn.

Abstract: In this paper, a stage-structured jellyfish model with two time delays is formulated and analyzed, the first delay represents the time from the asexually reproduced young polyp to the mature polyp and the second denotes the time from the developed polyp to ephyra (incipient medusa). Global dynamics of the model are obtained via monotone dynamical theory: the jellyfish populations go extinct and the trivial equilibrium is globally asymptotically stable if the survival rate of polyp during cloning and the survival rate of the incipient medusa during strobilation are less than their death rates. And if the survival rate of polyp during cloning and the survival rate of the incipient medusa during strobilation are larger than their death rates, a unique positive equilibrium is globally asymptotically stable. Moreover, it is proved that the only stage of polyps will continue without growing into medusa and the boundary equilibrium is globally asymptotically stable if the survival rate of polyp is larger than its death rate during cloning and if there is no survival of the incipient medusa. Numerical simulations are performed to verify our analytical results and to explore the dynamics with/without delays.

Keywords: jellyfish; polyp-medusa; delay; global dynamics; stage structure

1. Introduction

Jellyfish plays an important role in the marine ecosystems as a keystone species and a potential resource for human consumption [1]. The amount of jellyfish has been significantly increasing in many waters since 1980s [2]. Jellyfish can be found in many regions worldwide such as Japan [3], the China Seas [4], the Mediterranean Sea [5], Taiwan [6], Southampton Water and Horsea Lake, England [7]. It can survive in a wide range of water temperatures (0–36 °C) and salinities (3–36‰) [8, 9].

Jellyfish has a complex life history with several different phases: planula, polyp, strobila, ephyra and medusa [10]. The polyp and medusa are two main stages of the life cycle of jellyfish. Medusae are dioecious, the sperm combines with egg to form a planula, which normally settles to the bottom and then occur metamorphosis of planula into tentacles-ring polyp (or scyphistoma) [11]. For *Aurelia*

aurita jellyfish, the scyphistoma produces external outgrowths asexually by budding, the vitally asexual reproduction of polyp (94%), stolon (5%) and podocysts (1%) [3]. The scyphistoma changes into strobila (strobilating polyp) through strobilation, which is asexual reproduction by division into segments developing into ephyra. After liberating from strobila, the ephyra becomes adult medusa. In addition, strobila reverts into the initial scyphistoma [11]. Since jellyfish has a distinct mobility patterns in different phases of its life history, it is interesting to take these facts into account for model formulation.

Temperature has a great effect on variations of jellyfish populations [12] as the asexual reproduction rate and strobilation rate depend on the functions of temperatures [11]. Global warming has affected the increase of jellyfish populations because it might cause the distribution, growth, and ephyrae production of medusae [13]. The rapid strobilation might be proceeded at the warmer temperature, but the continuous high temperature results in the fewer budding and increased mortality [6]. Hence the population explosions of polyps and medusae might be caused at the appropriate increase of temperature, but rising temperatures lead to the decreased populations.

Many approaches for jellyfish have been developed to discuss the nature of the correlations between environmental indices and population abundance [6, 14]. In particular, mathematical modeling is one of the important tools in analyzing the dynamical properties in aquatic systems. In [15], Oguz et al. presented food web model with an anchovy population and bioenergetics-based weight growth model governed by system of differential equations. In [16], Melica et al. conducted that the dynamics of polyps population by the logistic model. In [11], Xie et al. proposed the following two-dimensional dynamic model of scyphozoan jellyfish:

$$\begin{aligned}\frac{dP}{dt} &= \alpha(T)P + s_1\gamma M - d_1P - d_2P - b_1P^2, \\ \frac{dM}{dt} &= s_2\beta(T)nP - d_3M - d_4M - b_2M^2,\end{aligned}\tag{1.1}$$

where $P(t)$ and $M(t)$ are the population sizes of polyps and medusae at time t , respectively. For system (1.1), by using the Bendixson-Dulac's negative criterion and Poincare-Bendixson Theorem, the conditions for the global asymptotical stability of the equilibria E_0 , E_1 and E^* are given. The effects of temperature, substrate and predation on the population sizes of scyphozoan were investigated by numerical simulations.

Although multiple progresses have been seen in the above work of [11], for system (1.1), it is assumed that each population preserves an equal density dependent rate and each individual has the same opportunity to compete for their common resources during the whole life history. Unfortunately, this is not realistic due to the life history of jellyfish which has a diverse mobility body structures in different stages. The immature stages of jellyfish are much weaker than the mature stages and so they cannot compete for their common resources. Jellyfish reaches maturity after surviving the immature stages. Therefore, it is realistic and interesting for us to construct the stage-structured jellyfish model that exhibits a diversity between these different stages.

Recently, population dynamic models with stage structure and time delays have attracted more attention from authors [17–24]. For instance, Aiello and Freedman proposed a stage-structured model of single species containing of the immature and mature stages and using a discrete time delay taken from birth to maturity [18]. Liu et al. showed that the global stability for the two competitive Lotka-Volterra system with time delay that denotes the time taken from birth to maturity. They proposed

that the stage structure is one of the main reasons that cause permanence and extinction for the two competitive system [23]. There have been an increasing interest and progress in the study of the above stage-structured models which assume all individuals are in the same species that require the analogous amount of time to become mature at the same age. Unlike birds and mammals, jellyfish species have the different mobility shapes in the distinctive stages of its life cycle. Thus, the previous methods and techniques cannot be applied exactly to our system because we classify the single species jellyfish into two-stage structure. Mathematically, the proposed model has two delay terms and the equations are matched with each other, which is not similar with the previous models [18, 23, 24].

In this paper, we will propose a time-delayed jellyfish model with stage structure and will investigate how the stage structure parameters and temperature affect the dynamical behaviors of system (2.2). Our main purpose is to study the population dynamics of jellyfish for the largest surviving probability as well as for final population numbers. To find the largest surviving probability, we will take the global asymptotical behaviors of the model by applying the monotone dynamical properties (for reference, see [25] and [26, p. 90]).

This paper is organized as follows: in Section 2, we propose the model and show that the solutions are positiveness and ultimately bounded. The main results of this paper are presented in Section 3. In Section 4, we perform numerical simulations to explore the effects of two delays and temperature on the dynamics. Section 5 is the brief discussion of our results.

2. Model description and preliminaries

2.1. Model formulating

The life history of jellyfish is divided into two main stages; polyp and medusa. The larval stage of polyp is planula and the elementary phase of medusa is ephyra. Let $P(t)$ and $M(t)$ be the population size or number of polyps and medusae at time t , respectively. The model is based on the following assumptions and the diagram in Figure 1:

- (A1) τ_1 is the length of the stage from the young polyp to the mature polyp. The immature polyp reproduces asexually at time $t - \tau_1$ and surviving from time $t - \tau_1$ to t is $e^{-(d_1+d_2)\tau_1}$.
- (A2) τ_2 is the time lag taken from the developed polyp to ephyra (incipient medusa), i.e., the developed polyp reaches ephyra after surviving this stage. Denote $\tau = \max\{\tau_1, \tau_2\}$.
- (A3) Its maturity is denoted by $\tau = \max\{\tau_1, \tau_2\}$, $\tau > 0$.
- (A4) Each population competes for their common resources.
- (A5) Each population has its own natural death rate, the mortality of polyp is varied by the factors of silt coverage or nudibranch consumption while that of medusa is because of different types of predators.

By the preceding assumptions, we get the following polyp-medusa population with stage structure:

$$\begin{aligned}\frac{dP}{dt} &= \alpha(T)e^{-(d_1+d_2)\tau_1}P(t-\tau_1) + s_1\gamma M - d_1P - d_2P - b_1P^2, \\ \frac{dM}{dt} &= s_2\beta(T)ne^{-(d_3+d_4)\tau_2}P(t-\tau_2) - d_3M - d_4M - b_2M^2.\end{aligned}\tag{2.1}$$

As pointed out in [11], $\alpha(T)$ denotes the asexual reproduction rate affected by temperature, involving budding, stolon and podocyst et al., s_1 is the survival and metamorphosis rate of planula, γ represents

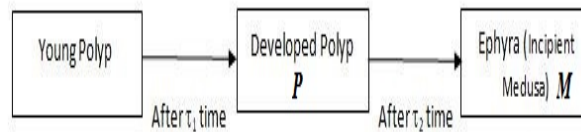


Figure 1. Diagram of the model (2.1).

the sexual reproduction rate, b_1 and b_2 denote the density-dependent rates of polyps and medusae respectively, s_2 is the survival and development rate of ephyra, $\beta(T)$ is the strobilation rate affected by temperature and n is strobilation times. Assuming that the death rate of the immature population is proportional to the existing immature population with proportionality constants $d_i > 0$, $i=1,2,3,4$. The loss of polyp is either due to natural death rate d_1 or due to the factors of silt coverage d_2 and τ_1 is the time taken from the immature polyp to the mature one; thus $e^{-(d_1+d_2)\tau_1}$ is the survival probability of each immature polyp to reach the mature one. The death of medusa is either from natural fatality rate d_3 or because of the predations d_4 and τ_2 is the time length between the developed polyp and ephyra (incipient medusa); thus $e^{-(d_3+d_4)\tau_2}$ is the survival rate of each developed polyp to reach the ephyra (incipient medusa) population. As it takes a few days in the larval stage of jellyfish life, the permanence and extinction criteria for the stage structured model are independent in this larval stage.

For the goal of simplicity, we denote $a = \alpha(T)$, $b = s_1\gamma$, $d = d_1 + d_2$, $c = s_2\beta(T)n$, $d_* = d_3 + d_4$. Thus the following system can be obtained from system (2.1).

$$\begin{aligned}\frac{dP}{dt} &= ae^{-\zeta_1}P(t - \tau_1) + bM - dP - b_1P^2, \\ \frac{dM}{dt} &= ce^{-\zeta_2}P(t - \tau_2) - d_*M - b_2M^2,\end{aligned}\tag{2.2}$$

where $\zeta_1 = d\tau_1$ and $\zeta_2 = d_*\tau_2$. Denote ζ_1 and ζ_2 the degrees of the stage structure.

Let $X = C([-\tau, 0], \mathbb{R}^2)$ be the Banach space of all continuous function from $[-\tau, 0]$ to \mathbb{R}^2 equipped with the supremum norm, where $\tau = \max\{\tau_1, \tau_2\}$. By the standard theory of functional differential equations (see, for example, Hale and Verduyn Lunel [27]), for any $\psi \in C([-\tau, 0], \mathbb{R}^2)$, there exists a unique solution $Y(t, \psi) = (P(t, \psi), M(t, \psi))$ of system (2.2); which satisfies $Y_0 = \psi$.

For system (2.2), we consider the initial conditions to either the positive cone $X^+ = \{\psi \in X | \psi_i(\theta) \geq 0 \text{ for all } \theta \in [-\tau, 0], i = 1, 2\}$ or the subset of X^+ of functions which are strictly positive at zero, $X_0^+ = \{\psi \in X^+ | \psi_i(0) > 0, i = 1, 2\}$.

2.2. Positivity and boundedness of solutions

Lemma 2.1. For equation

$$\frac{d\bar{W}}{dt} = ae^{-\zeta_1}\bar{W}(t - \tau_1) + \frac{bce^{-\zeta_2}}{d_*}\bar{W}(t - \tau_2) - \frac{B}{2}\bar{W}^2,\tag{2.3}$$

where $a, b, c, d_*, B > 0$, $\tau = \max\{\tau_1, \tau_2\}$, $\tau > 0$ and $\bar{W}(0) > 0$ and $\bar{W}(\theta) \geq 0$, $\theta \in [-\tau, 0]$, we have: $\lim_{t \rightarrow \infty} \bar{W}(t) = \frac{2d_*ae^{-\zeta_1} + 2bce^{-\zeta_2}}{d_*B}$ if $d_*ae^{-\zeta_1} + bce^{-\zeta_2} > 0$.

Proof. By using the similar argument of Lu et al. [28, Proposition 1], we will prove that $\bar{W}(t) > 0$, for all $t \geq 0$. Otherwise, there exists some constant $t_0 > 0$ such that $\min\{\bar{W}(t_0)\} = 0$. Let

$t_0 = \inf\{t_0 : \bar{W}(t_0) = 0\}$. Then we have that $\min\{\bar{W}(t_0) = 0\}$ and $\min\{\bar{W}(t)\} > 0, \forall t \in [0, t_0)$. From system (2.3), we have

$$\begin{aligned} \bar{W}(t) &= \bar{W}(0)e^{-\int_0^t \frac{B}{2}\bar{W}(\vartheta)d\vartheta} + ae^{-\zeta_1} \int_0^t \bar{W}(\omega - \tau_1)e^{-\int_\omega^t \frac{B}{2}\bar{W}(\vartheta)d\vartheta} d\omega \\ &+ \frac{bce^{-\zeta_2}}{d_*} \int_0^t \bar{W}(\omega - \tau_2)e^{-\int_\omega^t \frac{B}{2}\bar{W}(\vartheta)d\vartheta} d\omega. \end{aligned} \quad (2.4)$$

Incorporation initial conditions and Eq (2.4), we get $\bar{W}(t_0) > 0$, contradicting $\min\{\bar{W}(t_0)\} = 0$. Consequently, $\bar{W}(t) > 0$ for all $t \geq 0$.

Let $\bar{W}^* = \frac{2d_*ae^{-\zeta_1} + 2bce^{-\zeta_2}}{d_*B}$ denotes the unique positive equilibrium of system (2.3). Denote $u(t) = \bar{W}(t) - \bar{W}^*$, thus system (2.3) takes the form as

$$\frac{du}{dt} = ae^{-\zeta_1}u(t - \tau_1) + \frac{bce^{-\zeta_2}}{d_*}u(t - \tau_2) - \frac{B}{2}u^2(t) - B\bar{W}^*u(t). \quad (2.5)$$

Constructing the Lyapunov functional

$$V(u, u_\tau) = \frac{1}{2}u^2(t) + \frac{1}{2}ae^{-\zeta_1} \int_{t-\tau_1}^t u^2(s)ds + \frac{1}{2} \frac{bce^{-\zeta_2}}{d_*} \int_{t-\tau_2}^t u^2(s)ds,$$

we have

$$\begin{aligned} \left. \frac{dV}{dt} \right|_{(2.5)} &= ae^{-\zeta_1}u(t)u(t - \tau_1) + \frac{bce^{-\zeta_2}}{d_*}u(t)u(t - \tau_2) - \frac{B}{2}u^3(t) - B\bar{W}^*u^2(t) + \frac{1}{2}ae^{-\zeta_1}u^2(t) \\ &- \frac{1}{2}ae^{-\zeta_1}u^2(t - \tau_1) + \frac{1}{2} \frac{bce^{-\zeta_2}}{d_*}u^2(t) - \frac{1}{2} \frac{bce^{-\zeta_2}}{d_*}u^2(t - \tau_2) \\ &\leq \frac{1}{2}ae^{-\zeta_1}u^2(t) + \frac{1}{2}ae^{-\zeta_1}u^2(t - \tau_1) + \frac{1}{2} \frac{bce^{-\zeta_2}}{d_*}u^2(t) + \frac{1}{2} \frac{bce^{-\zeta_2}}{d_*}u^2(t - \tau_2) - \frac{B}{2}u^3(t) \\ &- B\bar{W}^*u^2(t) + \frac{1}{2}ae^{-\zeta_1}u^2(t) - \frac{1}{2}ae^{-\zeta_1}u^2(t - \tau_1) + \frac{1}{2} \frac{bce^{-\zeta_2}}{d_*}u^2(t) - \frac{1}{2} \frac{bce^{-\zeta_2}}{d_*}u^2(t - \tau_2) \\ &= ae^{-\zeta_1}u^2(t) + \frac{bce^{-\zeta_2}}{d_*}u^2(t) - B\bar{W}^*u^2(t) - \frac{B}{2}u^3(t) \\ &= (ae^{-\zeta_1} + \frac{bce^{-\zeta_2}}{d_*} - \frac{B}{2}\bar{W}^*)u^2(t) - (\bar{W}^* + u(t))\frac{B}{2}u^2(t) \\ &= -\frac{B}{2}\bar{W}(t)u^2(t) \leq 0, \end{aligned}$$

which is negative definite and $\left. \frac{dV}{dt} \right|_{(2.5)} = 0$ if and only if $u = 0$. By Lyapunov-LaSalle invariance principle ([29, Theorem 2.5.3]), we get $\lim_{t \rightarrow \infty} \bar{W}(t) = \bar{W}^* = \frac{2d_*ae^{-\zeta_1} + 2bce^{-\zeta_2}}{d_*B}$, this proves Lemma 2.1. \square

Lemma 2.2. *Given system (2.2), then:*

- (I) *Under the initial conditions, all the solutions of system (2.2) are positive for all $t \geq 0$.*
- (II) *Solutions of system (2.2) are ultimately bounded.*

Proof. (I) We start with proving the positivity of solutions by using the similar argument of Lu et al. [28, Proposition 1]. We will prove that $P(t) > 0$, $M(t) > 0$ for $t \geq 0$. Otherwise, there exists some constant $\tilde{t}_0 > 0$ such that $\min\{P(\tilde{t}_0), M(\tilde{t}_0)\} = 0$. Let $t_0 = \inf\{\tilde{t}_0 : P(\tilde{t}_0) = 0, M(\tilde{t}_0) = 0\}$. Then we have that $\min\{P(t_0), M(t_0)\} = 0$ and $\min\{P(t), M(t)\} > 0$, $\forall t \in [0, t_0)$. From system (2.2), we have

$$\begin{cases} P(t) = P(0)e^{-\int_0^t (d+b_1P(\eta))d\eta} + ae^{-\zeta_1} \int_0^t P(\kappa - \tau_1)e^{-\int_\kappa^t (d+b_1P(\eta))d\eta}d\kappa \\ \quad + b \int_0^t M(\kappa)e^{-\int_\kappa^t (d+b_1P(\eta))d\eta}d\kappa, \\ M(t) = M(0)e^{-\int_0^t (d_*+b_2M(\eta))d\eta} + ce^{-\zeta_2} \int_0^t P(\kappa - \tau_2)e^{-\int_\kappa^t (d_*+b_2M(\eta))d\eta}d\kappa. \end{cases} \quad (2.6)$$

Incorporation initial conditions and Eq (2.6), we obtain $P(t_0) > 0$ and $M(t_0) > 0$, contradicting $\min\{P(t_0), M(t_0)\} = 0$. Consequently, $P(t) > 0$, $M(t) > 0$ for all $t \geq 0$.

(II) We show that the boundedness of solutions as follows.

Let $W = \frac{d_*}{b}P + M$. By system (2.2), we have

$$\begin{aligned} \left. \frac{dW}{dt} \right|_{(2.2)} &= ae^{-\zeta_1} \frac{d_*}{b}P(t - \tau_1) + ce^{-\zeta_2}P(t - \tau_2) - \frac{dd_*}{b}P - \frac{d_*b_1}{b}P^2 - b_2M^2 \\ &= ae^{-\zeta_1} \left[\frac{d_*}{b}P(t - \tau_1) + M(t - \tau_1) \right] - ae^{-\zeta_1}M(t - \tau_1) + \frac{bce^{-\zeta_2}}{d_*} \left[\frac{d_*}{b}P(t - \tau_2) + M(t - \tau_2) \right] \\ &\quad - \frac{bce^{-\zeta_2}}{d_*}M(t - \tau_2) - \frac{dd_*}{b}P - \frac{bb_1}{d_*} \left(\frac{d_*}{b}P \right)^2 - b_2M^2 \\ &\leq ae^{-\zeta_1}W(t - \tau_1) + \frac{bce^{-\zeta_2}}{d_*}W(t - \tau_2) - B \left[\left(\frac{d_*}{b}P \right)^2 + M^2 \right], \end{aligned}$$

where $B := \min \left\{ \frac{bb_1}{d_*}, b_2 \right\}$.

$$\frac{dW}{dt} \leq ae^{-\zeta_1}W(t - \tau_1) + \frac{bce^{-\zeta_2}}{d_*}W(t - \tau_2) - \frac{B}{2}W^2,$$

where $-2\left(\left(\frac{d_*}{b}P\right)^2 + M^2\right) \leq -\left(\frac{d_*}{b}P + M\right)^2$.

Consider the equation

$$\frac{d\bar{W}}{dt} = ae^{-\zeta_1}\bar{W}(t - \tau_1) + \frac{bce^{-\zeta_2}}{d_*}\bar{W}(t - \tau_2) - \frac{B}{2}\bar{W}^2. \quad (2.7)$$

By using Lemma 2.1 and Comparison Theorem, we get

$\limsup_{t \rightarrow \infty} W(t) \leq \frac{2d_*ae^{-\zeta_1} + 2bce^{-\zeta_2}}{d_*B}$, which implies $P(t)$ and $M(t)$ are ultimately bounded. This completes the proof of Lemma 2.2. \square

2.3. Existence of equilibria

The equilibria (P, M) of system (2.2) satisfies the following system

$$\begin{aligned} ae^{-\zeta_1}P + bM - dP - b_1P^2 &= 0, \\ ce^{-\zeta_2}P - d_*M - b_2M^2 &= 0. \end{aligned} \quad (2.8)$$

System (2.2) has the equilibria $E_0 = (0, 0)$ for all parameter values and $E_1 = (\frac{ae^{-\zeta_1} - d}{b_1}, 0)$ if $ae^{-\zeta_1} - d > 0$ and $c = 0$.

Since Eq (2.8) can be rewritten as

$$(ae^{-\zeta_1} - d - b_1P)P = -bM, \quad ce^{-\zeta_2}P = (d_* + b_2M)M. \quad (2.9)$$

When $PM \neq 0$, from Eq (2.9) it follows that

$$\frac{ae^{-\zeta_1} - d - b_1P}{ce^{-\zeta_2}} + \frac{b}{d_* + b_2M} = 0. \quad (2.10)$$

Further, substituting $P = \frac{(d_* + b_2M)M}{ce^{-\zeta_2}}$ into Eq (2.10) and we get

$$\frac{ae^{-\zeta_1} - d - b_1 \frac{(d_* + b_2M)M}{ce^{-\zeta_2}}}{ce^{-\zeta_2}} + \frac{b}{d_* + b_2M} = 0.$$

Set

$$F(M) := \frac{ae^{-\zeta_1} - d - b_1 \frac{(d_* + b_2M)M}{ce^{-\zeta_2}}}{ce^{-\zeta_2}} + \frac{b}{d_* + b_2M},$$

thus $F(M)$ is a decreasing function of M for any $M > 0$.

Noting that the continuity and monotonicity of $F(M)$ and that $F(+\infty) < 0$, furthermore since one can get $F(0) > 0$ provided that

$$(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} > 0, \quad c \neq 0 \quad (2.11)$$

hold true, therefore we conclude that system (2.2) admits a unique positive equilibrium given Eq (2.11) is satisfied.

3. Stability and global attractiveness

The purpose of this section is to study the global stability of system (2.2).

3.1. Stability

Now we consider the local stability of the equilibria. The characteristic equation of system (2.2) takes the form as follows;

$$\det(\lambda I - G - H_1 e^{-\lambda\tau_1} - H_2 e^{-\lambda\tau_2}) = 0,$$

where

$$G = \begin{pmatrix} -d - 2b_1P & b \\ 0 & -d_* - 2b_2M \end{pmatrix}, H_1 = \begin{pmatrix} ae^{-\zeta_1} & 0 \\ 0 & 0 \end{pmatrix}, H_2 = \begin{pmatrix} 0 & 0 \\ ce^{-\zeta_2} & 0 \end{pmatrix}.$$

Lemma 3.1. *Suppose that $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} < 0$, then the equilibrium $E_0 = (0, 0)$ of system (2.2) is locally asymptotically stable.*

Proof. The characteristic equation of system (2.2) at the equilibrium E_0 is as follows:

$$C(\lambda) := (\lambda + d_*)(\lambda + d - ae^{-\zeta_1 - \lambda\tau_1}) - bce^{-\zeta_2 - \lambda\tau_2} = 0. \quad (3.1)$$

To show that it is asymptotically stable under assumption $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} < 0$, we just need to prove that the solutions of the characteristic equation $C(\lambda) = 0$ must have negative real parts. Let $\lambda = u + iv$, where u and v are real numbers. Denote

$$\begin{aligned} A_1 &= u + d_*, & B_1 &= v, \\ A_2 &= u + d - ae^{-\zeta_1 - u\tau_1} \cos(v\tau_1), & B_2 &= v + ae^{-\zeta_1 - u\tau_1} \sin(v\tau_1), \\ C_1 &= bce^{-\zeta_2 - u\tau_2} \cos(v\tau_2), & C_2 &= -bce^{-\zeta_2 - u\tau_2} \sin(v\tau_2). \end{aligned}$$

Substituting λ by $u + iv$ into Eq (3.1)

$$A_1A_2 - B_1B_2 = C_1, \quad A_1B_2 + A_2B_1 = C_2.$$

Then

$$(A_1A_2)^2 + (B_1B_2)^2 + (A_1B_2)^2 + (A_2B_1)^2 = (C_1)^2 + (C_2)^2. \quad (3.2)$$

Assume that $u \geq 0$, then we get

$$A_1 \geq d_* > 0, \quad A_2 \geq d - ae^{-\zeta_1} > 0.$$

Hence

$$\begin{aligned} (A_1A_2)^2 &> ((d - ae^{-\zeta_1})d_*)^2, \\ (A_1A_2)^2 + (B_1B_2)^2 + (A_1B_2)^2 + (A_2B_1)^2 &\geq (A_1A_2)^2 > ((d - ae^{-\zeta_1})d_*)^2. \end{aligned} \quad (3.3)$$

From Eq (3.2), we obtain

$$\begin{aligned} (C_1)^2 + (C_2)^2 &\geq (A_1A_2)^2 > ((d - ae^{-\zeta_1})d_*)^2 \\ (bce^{-\zeta_2})^2(\cos^2(v\tau_2) + \sin^2(v\tau_2)) &\geq (A_1A_2)^2 > ((d - ae^{-\zeta_1})d_*)^2 \\ (bce^{-\zeta_2})^2 &\geq (A_1A_2)^2 > ((d - ae^{-\zeta_1})d_*)^2. \end{aligned}$$

Hence Eq (3.3) contradicts to the assumption $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} < 0$, thus $u < 0$, which means λ must have negative real parts. This proves Lemma 3.1. \square

Lemma 3.2. Suppose that $ae^{-\zeta_1} - d > 0$ and $c = 0$, then the equilibrium $E_1 = (\frac{ae^{-\zeta_1} - d}{b_1}, 0)$ of system (2.2) is locally asymptotically stable.

Proof. The characteristic equation of system (2.2) at the equilibrium E_1 is

$$X(\lambda) := (\lambda + d_*)(\lambda - d + 2ae^{-\zeta_1} - ae^{-\zeta_1 - \lambda\tau_1}) = 0. \quad (3.4)$$

Then $\lambda = -d_*$ is a negative root of the equation $X(\lambda) = 0$. Let $\lambda - d + 2ae^{-\zeta_1} - ae^{-\zeta_1 - \lambda\tau_1} = 0$; then if the root is $\lambda = u + iv$, we have $u + 2ae^{-\zeta_1} - d - ae^{-\zeta_1 - u\tau_1} \cos(v\tau_1) = 0$. Assume that $u \geq 0$, then $u + 2ae^{-\zeta_1} - d - ae^{-\zeta_1 - u\tau_1} \cos(v\tau_1) \geq ae^{-\zeta_1} - d > 0$ is a contradiction, hence $u < 0$. This shows that all the roots of $X(\lambda) = 0$ must have negative real parts, and therefore E_1 is locally asymptotically stable. This proves Lemma 3.2. \square

Lemma 3.3. Suppose that $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} > 0$ and $c \neq 0$, then the equilibrium $E^* = (P^*, M^*)$ of system (2.2) is locally asymptotically stable.

Proof. The characteristic equation of system (2.2) at the equilibrium E^* is

$$(\lambda + d + 2b_1P^* - ae^{-\zeta_1 - \lambda\tau_1})(\lambda + d_* + 2b_2M^*) - bce^{-\zeta_2 - \lambda\tau_2} = 0.$$

To show that it is asymptotically stable under $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} > 0$, we just need to prove that the solutions of the characteristic equation must have negative real parts. Let $\lambda = u + iv$ where u and v are real numbers. Denote

$$\begin{aligned} D_1 &= u + d + 2b_1P^* - ae^{-\zeta_1 - u\tau_1} \cos(v\tau_1), & E_1 &= v + ae^{-\zeta_1 - u\tau_1} \sin(v\tau_1), \\ D_2 &= u + d_* + 2b_2M^*, & E_2 &= v, \\ F_1 &= bce^{-\zeta_2 - u\tau_2} \cos(v\tau_2), & F_2 &= -bce^{-\zeta_2 - u\tau_2} \sin(v\tau_2). \end{aligned}$$

Substituting λ by $u + iv$ into the above equation.

$$D_1D_2 - E_1E_2 = F_1, \quad D_1E_2 + D_2E_1 = F_2.$$

Then

$$(D_1D_2)^2 + (E_1E_2)^2 + (D_1E_2)^2 + (D_2E_1)^2 = (F_1)^2 + (F_2)^2. \quad (3.5)$$

Assume that $u \geq 0$, then we get

$$\begin{aligned} D_1 &\geq d + 2b_1P^* - ae^{-\zeta_1} > d + 2b_1 \frac{ae^{-\zeta_1} - d}{b_1} - ae^{-\zeta_1} = ae^{-\zeta_1} - d > 0, \\ D_2 &\geq d_* + 2b_2M^* = d_* + 2b_2 \frac{b_1(P^*)^2 - (ae^{-\zeta_1} - d)P^*}{b_1} \\ &> d_* + 2b_2 \frac{b_1 \left(\frac{ae^{-\zeta_1} - d}{b_1}\right)^2 - (ae^{-\zeta_1} - d) \left(\frac{ae^{-\zeta_1} - d}{b_1}\right)}{b_1} = d_* > 0. \end{aligned}$$

Hence

$$(D_1D_2)^2 > ((ae^{-\zeta_1} - d)d_*)^2.$$

$$(D_1D_2)^2 + (E_1E_2)^2 + (D_1E_2)^2 + (D_2E_1)^2 \geq (D_1D_2)^2 > ((ae^{-\zeta_1} - d)d_*)^2.$$

By Eq (3.5), we get

$$\begin{aligned} (F_1)^2 + (F_2)^2 &\geq (D_1D_2)^2 > ((ae^{-\zeta_1} - d)d_*)^2 \\ (bce^{-\zeta_2})^2(\cos^2(v\tau_2) + \sin^2(v\tau_2)) &\geq (D_1D_2)^2 > ((ae^{-\zeta_1} - d)d_*)^2 \\ (bce^{-\zeta_2})^2 &\geq (D_1D_2)^2 > ((ae^{-\zeta_1} - d)d_*)^2. \end{aligned}$$

By assumption $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} > 0$, which is a contradiction, thus u must be negative real parts. This completes the proof of Lemma 3.3. \square

3.2. Global attractiveness

Before the details, we will present the notion from the literature [25]. We define

$$x_t \in C([- \tau, 0], \mathbb{R}^2),$$

by $x_t(\theta) = x(t + \theta), \forall \theta \in [- \tau, 0]$. Consider a delay system

$$x'(t) = f(x_t), \quad (3.6)$$

for which uniqueness of solutions is assumed, $x(t, \psi)$ designates the solution of Eq (3.6) with initial condition $x_0 = \psi$ ($\psi \in C$).

A non-negative equilibrium $v = (v_p, v_m) \in \mathbb{R}^2$ of system (2.2) is said to be globally attractive if $Y(t) \rightarrow v$ as $t \rightarrow \infty$, for all admissible solutions $Y(t)$ of system (2.2). We say that v is globally asymptotically stable if it is stable and globally attractive.

System (2.2) is written as Eq (3.6),

$$\begin{aligned} f_1(\psi) &= \psi_1(0)[-d - b_1\psi_1(0)] + ae^{-\zeta_1}\psi_1(-\tau_1) + b\psi_2(0), \\ f_2(\psi) &= \psi_2(0)[-d_* - b_2\psi_2(0)] + ce^{-\zeta_2}\psi_1(-\tau_2). \end{aligned} \quad (3.7)$$

Observe that system (2.2) is cooperative, i.e., $Df_i(\psi)\varphi \geq 0$, for all $\psi, \varphi \in X^+$ with $\varphi_i(0) = 0, i = 1, 2$. This implies that f satisfies quasi-monotonicity condition [26, p. 78]. Typically, in population dynamics the stability of equilibria is closely related to the algebraic properties of some kinds of competition matrix of the community. Denote

$$A = \begin{pmatrix} ae^{-\zeta_1} - d & 0 \\ 0 & -d_* \end{pmatrix}, \quad D = \begin{pmatrix} 0 & b \\ ce^{-\zeta_2} & 0 \end{pmatrix}.$$

For convenience, we shall refer to $N = A + D$ as the (linear) community matrix:

$$N = \begin{pmatrix} ae^{-\zeta_1} - d & b \\ ce^{-\zeta_2} & -d_* \end{pmatrix}. \quad (3.8)$$

Since $D \geq 0$, the matrix N in Eq (3.8) is called cooperative. If D is irreducible, then the matrix N in Eq (3.8) is also irreducible; in this case, system (2.2) is called an irreducible system [26, p. 88], and the semiflow $\psi \mapsto Y_t(\psi)$ is eventually strongly monotone. $f = (f_1, f_2)^T : \mathbb{R}^2 \rightarrow \mathbb{R}^2$ is strictly sublinear, i.e., for any $P \gg 0, M \gg 0$ and any $\alpha \in (0, 1)$,

$$\begin{aligned} f_1(\alpha P, \alpha M) &= \alpha P[-d - b_1\alpha P] + ae^{-\zeta_1}\alpha P(t - \tau_1) + b\alpha M \\ &> \alpha[P(-d - b_1P) + ae^{-\zeta_1}P(t - \tau_1) + bM] = \alpha f_1(P, M), \\ f_2(\alpha P, \alpha M) &= \alpha M[-d_* - b_2\alpha M] + ce^{-\zeta_2}\alpha P(t - \tau_2) \\ &> \alpha[M(-d_* - b_2M) + ce^{-\zeta_2}P(t - \tau_2)] = \alpha f_2(P, M). \end{aligned}$$

Cooperative *DDEs* satisfying these sublinearity conditions have significant properties [30, Proposition 4.3].

Recall that the stability modulus of square matrix N in Eq (3.8), denoted by $s(N)$, is defined by $s(N) = \max\{\operatorname{Re} \lambda : \lambda \text{ is an eigenvalue of } N\}$. If the matrix N in Eq (3.8) has nonnegative off diagonal

elements and is irreducible, then $s(N)$ is a simple eigenvalue of the matrix N with a (componentwise) positive eigenvector (see, e.g., [31, Theorem A.5]).

The matrix N in Eq (3.8) is

$$N = \begin{pmatrix} ae^{-\zeta_1} - d & b \\ ce^{-\zeta_2} & -d_* \end{pmatrix},$$

then we can easily get the following:

$s(N) > 0$ if and only if $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} > 0$ and $s(N) < 0$ if and only if $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} < 0$.

Definition 3.4. [32] A square matrix $A = [a_{ij}]$ with non-positive off diagonal entries, i.e., $a_{ij} \leq 0$ for all $i \neq j$, is said to be an M-matrix if all the eigenvalues of A have a non-negative real part, or equivalently, if all its principal minors are non-negative, and A is said to be a non singular M-matrix if all the eigenvalues of A have positive real part, or, equivalently, if all its principal minors are positive.

Theorem 3.5. Suppose that $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} < 0$, then the equilibrium E_0 of system (2.2) is globally asymptotically stable.

Proof. Let $P(t, l)$, $M(t, k)$ be the solutions of system (2.2) with $P(0 + \theta, l) = l$, $M(0 + \theta, k) = k$ for $\theta \in [-\tau, 0]$. Note that $f_1(l) = l[-d + b + ae^{-\zeta_1} - b_1l] < 0$ for $l > 0$ sufficiently large and $f_2(k) = k[-d_* + ce^{-\zeta_2} - b_2k] < 0$ for $k > 0$ sufficiently large. Hence we can easily conclude that all admissible solutions of system (2.2) are bounded [26, Corollary 5.2.2]. We have $s(N) < 0$ if and only if $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} < 0$. By the assumption $(ae^{-\zeta_1} - d)d_* + bce^{-\zeta_2} < 0$, we observed that it is equivalent to having $-N$ a non singular M-matrix. Since matrix $-N$ is a non singular M-matrix, there exists the equilibrium $v = (v_p, v_m) \in \mathbb{R}^2$, $v > 0$, such that $Nv < 0$, hence we get

$$\begin{aligned} ae^{-\zeta_1}v_p - dv_p + bv_m &< 0, \\ ce^{-\zeta_2}v_p - d_*v_m &< 0. \end{aligned} \quad (3.9)$$

Let $P(t) \geq 0$, $M(t) \geq 0$ be solutions of system (2.2). Denote $y_p(t) = \frac{P(t)}{v_p}$ and $y_m(t) = \frac{M(t)}{v_m}$, thus system (2.2) takes the form as

$$\begin{aligned} y'_p(t) &= y_p(t)[-d - b_1y_p(t)v_p] + ae^{-\zeta_1}y_p(t - \tau_1) + \frac{bv_m}{v_p}y_m(t), \\ y'_m(t) &= y_m(t)[-d_* - b_2y_m(t)v_m] + ce^{-\zeta_2}\frac{v_p}{v_m}y_p(t - \tau_2). \end{aligned} \quad (3.10)$$

It suffices to prove that $(L_p, L_m) := \limsup_{t \rightarrow \infty} (y_p(t), y_m(t)) = (0, 0)$. Let $L_p := \limsup\{y_p(t)\}$, $L_m := \limsup\{y_m(t)\}$, $\tilde{L} := \max\{L_p, L_m\}$ and suppose that $\tilde{L} > 0$. From Eq (3.9), we can choose $\varepsilon > 0$ such that

$$\begin{aligned} \tilde{L}[-d - b_1\tilde{L}v_p + ae^{-\zeta_1} + \frac{bv_m}{v_p}] + \varepsilon[ae^{-\zeta_1} + \frac{bv_m}{v_p}] &=: \gamma_p < 0, \\ \tilde{L}[-d_* - b_2\tilde{L}v_m + ce^{-\zeta_2}\frac{v_p}{v_m}] + \varepsilon[ce^{-\zeta_2}\frac{v_p}{v_m}] &=: \gamma_m < 0. \end{aligned}$$

Let $T > 0$ be such that $y_p(t) \leq \tilde{L} + \varepsilon$, $y_m(t) \leq \tilde{L} + \varepsilon$ for all $t > T - \tau$ and the cases of $y_p(t)$ and $y_m(t)$ are separated as eventually monotone and not eventually monotone. By [26, Proposition 5.4.2], if $y_p(t)$

and $y_m(t)$ are eventually monotone, then $y_p(t) \rightarrow \tilde{L}$ and $y_m(t) \rightarrow \tilde{L}$ as $t \rightarrow \infty$ for $t \geq T$ and we obtain

$$\begin{aligned} y'_p(t) &\leq y_p(t)[-d - b_1 y_p(t) v_p] + a e^{-\zeta_1} (\tilde{L} + \varepsilon) + (\tilde{L} + \varepsilon) \frac{b v_m}{v_p} \rightarrow \gamma_p, \\ y'_m(t) &\leq y_m(t)[-d_* - b_2 y_m(t) v_m] + c e^{-\zeta_2} \frac{v_p}{v_m} (\tilde{L} + \varepsilon) \rightarrow \gamma_m \text{ as } t \rightarrow \infty. \end{aligned} \quad (3.11)$$

Since $\gamma_p < 0$ and $\gamma_m < 0$, these imply that $\lim_{t \rightarrow \infty} (y_p(t), y_m(t)) = -\infty$, which is impossible. By using the similar argument of Aiello and Freedman [18, Theorem 2], if $y_p(t)$ and $y_m(t)$ are not eventually monotone, there is a sequence $t_n \rightarrow \infty$ such that $y_p(t_n) \rightarrow \tilde{L}$, $y'_p(t_n) = 0$ and $y_m(t_n) \rightarrow \tilde{L}$, $y'_m(t_n) = 0$. We obtain (3.11) with t replaced by t_n , again a contradiction. This proves $\lim_{t \rightarrow \infty} (y_p(t), y_m(t)) = (0, 0)$. Using Lemma 3.1, we complete the proof of Theorem 3.5. \square

Theorem 3.6. *Suppose that $ae^{-\zeta_1} - d > 0$ and $c = 0$, then the equilibrium E_1 of system (2.2) is globally asymptotically stable.*

Proof. If $c = 0$, the second equation of system (2.2) becomes

$$M'(t) = -d_* M - b_2 M^2, \quad (3.12)$$

For the independent subsystem (3.12), it is obvious that $\lim_{t \rightarrow \infty} M(t) = 0$.

Then the first equation of system (2.2) becomes

$$P'(t) = a e^{-\zeta_1} P(t - \tau_1) - d P(t) - b_1 P^2(t). \quad (3.13)$$

Let $\varepsilon > 0$ be sufficiently small and $L > 0$ be sufficiently large such that $\varepsilon \leq P(t) \leq L$, $t \in [-\tau, 0]$, and

$$a e^{-\zeta_1} \varepsilon - d \varepsilon - b_1 \varepsilon^2 > 0, \quad a e^{-\zeta_1} L - d L - b_1 L^2 < 0.$$

Let $P_\varepsilon(t)$ and $P_L(t)$ be the solutions of Eq (3.13) with $P_\varepsilon(t) = \varepsilon$ and $P_L(t) = L$ for $t \in [-\tau, 0]$. From the monotone properties of the equation [26], the function $P_\varepsilon(t)$ is increasing and $P_L(t)$ is decreasing for $t \geq 0$ and

$$P_\varepsilon(t) \leq P(t) \leq P_L(t), t \geq 0.$$

It therefore follows that

$$\frac{a e^{-\zeta_1} - d}{b_1} = \lim_{t \rightarrow \infty} P(t) \leq \lim_{t \rightarrow \infty} P_L(t) = \frac{a e^{-\zeta_1} - d}{b_1}$$

because the only equilibrium of the equation between ε and L is $\frac{a e^{-\zeta_1} - d}{b_1}$. Using Lemma 3.2, we complete the proof of Theorem 3.6. \square

Lemma 3.7. *Suppose there is a positive equilibrium (P^*, M^*) of system (2.2), and that $(a e^{-\zeta_1} - d) d_* + b c e^{-\zeta_2} > 0$ and $c \neq 0$. Then all solutions $P(t, \psi_1)$, $M(t, \psi_2)$ of system (2.2) with $\psi_i \in X_0^+$, $i = 1, 2$ satisfy $\liminf_{t \rightarrow \infty} (P(t, \psi_1), M(t, \psi_2)) \geq (P^*, M^*)$.*

Proof. For (P^*, M^*) an equilibrium of system (2.2), we have

$$\begin{aligned} ae^{-\zeta_1} - d + b \frac{M^*}{P^*} &= b_1 P^* > 0, \\ -d_* + ce^{-\zeta_2} \frac{P^*}{M^*} &= b_2 M^* > 0. \end{aligned} \quad (3.14)$$

Denote $\bar{P}(t) = \frac{P(t)}{P^*}$ and $\bar{M}(t) = \frac{M(t)}{M^*}$ in system (2.2), and dropping the bar for simplicity, we get

$$\begin{aligned} P'(t) &= P(t)[-d - b_1 P(t)P^*] + ae^{-\zeta_1} P(t - \tau_1) + \frac{bM^*}{P^*} M(t), \\ M'(t) &= M(t)[-d_* - b_2 M(t)M^*] + ce^{-\zeta_2} \frac{P^*}{M^*} P(t - \tau_2). \end{aligned} \quad (3.15)$$

For the solutions $P(t) = P(t, \psi_1)$ and $M(t) = M(t, \psi_2)$ of Eq (3.15) with $\psi_i \in X_0^+$ for $i = 1, 2$, we first claim that $(l_p, l_m) := \liminf_{t \rightarrow \infty} (P(t), M(t)) > (0, 0)$. Otherwise, there exist $\delta \in (0, 1)$ and $t_0 > \tau$ such that $\tilde{l} = \min\{P(t), M(t) : t \in [0, t_0]\}$ and $\tilde{l} < \delta$. By using Eq (3.14),

$$\begin{aligned} P'(t_0) &= P(t_0)[-d - b_1 P(t_0)P^*] + ae^{-\zeta_1} P(t_0 - \tau_1) + \frac{bM^*}{P^*} M(t_0) \\ &\geq \tilde{l}[-d - b_1 \tilde{l}P^*] + ae^{-\zeta_1} \tilde{l} + \frac{bM^*}{P^*} \tilde{l} \\ &= \tilde{l}(b_1 P^* - b_1 \tilde{l}P^*) = \tilde{l}b_1 P^*(1 - \tilde{l}) > 0, \\ M'(t_0) &= M(t_0)[-d_* - b_2 M(t_0)M^*] + ce^{-\zeta_2} \frac{P^*}{M^*} P(t_0 - \tau_2) \\ &\geq \tilde{l}[-d_* - b_2 \tilde{l}M^*] + ce^{-\zeta_2} \frac{P^*}{M^*} \tilde{l} \\ &= \tilde{l}(b_2 M^* - b_2 \tilde{l}M^*) = \tilde{l}b_2 M^*(1 - \tilde{l}) > 0. \end{aligned}$$

But these are not possible. Since the definition of t_0 , $P'(t_0) \leq 0$ and $M'(t_0) \leq 0$.

Next we prove that $(l_p, l_m) \geq (1, 1)$. Choose $\tilde{l} = \min\{l_p, l_m\}$ and suppose that $\tilde{l} < 1$. Let $T > 0$ and $\varepsilon > 0$ be chosen so that $P(t) \geq \tilde{l} - \varepsilon$ and $M(t) \geq \tilde{l} - \varepsilon$ for all $t > T - \tau$.

$$\begin{aligned} \tilde{l}b_1 P^*(1 - \tilde{l}) - \varepsilon[ae^{-\zeta_1} \tilde{l} + \frac{bM^*}{P^*}] &=: n_p > 0, \\ \tilde{l}b_2 M^*(1 - \tilde{l}) - \varepsilon[ce^{-\zeta_2} \frac{P^*}{M^*}] &=: n_m > 0. \end{aligned}$$

By [26, Proposition 5.4.2], if $P(t)$ and $M(t)$ are eventually monotone, then $P(t) \rightarrow \tilde{l}$ and $M(t) \rightarrow \tilde{l}$ and for $t \geq T$, we have

$$\begin{aligned} P'(t) &\geq P(t)[-d - b_1 P(t)P^*] + ae^{-\zeta_1} (\tilde{l} - \varepsilon) + (\tilde{l} - \varepsilon) \frac{bM^*}{P^*} \rightarrow n_p, \\ M'(t) &\geq M(t)[-d_* - b_2 M(t)M^*] + (\tilde{l} - \varepsilon) ce^{-\zeta_2} \frac{P^*}{M^*} \rightarrow n_m \text{ as } t \rightarrow \infty, \end{aligned}$$

leading to $P(t) \rightarrow \infty$ and $M(t) \rightarrow \infty$ as $t \rightarrow \infty$, contradicting $\tilde{l} < 1$. By using the similar argument of Aiello and Freedman [18, Theorem 2], if $P(t)$ and $M(t)$ are not eventually monotone, there is a sequence $t_n \rightarrow \infty$ such that $P(t_n) \rightarrow \tilde{l}$, $P'(t_n) = 0$ and $M(t_n) \rightarrow \tilde{l}$, $M'(t_n) = 0$. For $t_n \geq T$, we obtain the above inequalities t_n instead of t , which yield that $0 = P'(t_n) \geq n_p$ and $0 = M'(t_n) \geq n_m$, again contradicting $\tilde{l} < 1$. This proves that $\tilde{l} \geq 1$. \square

Theorem 3.8. Suppose that $(ae^{-\zeta_1} - d)_* + bce^{-\zeta_2} > 0$ and $c \neq 0$, then the equilibrium E^* of system (2.2) is globally asymptotically stable.

Proof. For (P^*, M^*) of system (2.2), after the changes $P(t) \mapsto \frac{P(t)}{P^*}$ and $M(t) \mapsto \frac{M(t)}{M^*}$, consider system (3.15) with positive equilibrium $(1, 1) \in \mathbb{R}^2$. In view of Lemmas 3.3 and 3.7, we only need to prove that $(L_p, L_m) := \limsup_{t \rightarrow \infty} (P(t), M(t)) \leq (1, 1)$ and any positive solution $P(t), M(t)$ of Eq (3.15).

For the sake of contradiction, suppose that $\tilde{L} = \max\{L_p, L_m\} > 1$. Choose $\varepsilon > 0$ and $t > \tau$, such that $P(t) \leq \tilde{L} + \varepsilon$ and $M(t) \leq \tilde{L} + \varepsilon$ for all $t > T - \tau$ and

$$\begin{aligned} \tilde{L}b_1P^*(1 - \tilde{L}) + \varepsilon[ae^{-\zeta_1}\tilde{L} + \frac{bM^*}{P^*}] &=: N_p < 0, \\ \tilde{L}b_2M^*(1 - \tilde{L}) + \varepsilon[ce^{-\zeta_2}\frac{P^*}{M^*}] &=: N_m < 0. \end{aligned}$$

Separating the cases of $P(t)$ and $M(t)$ eventually monotone and not eventually monotone, and reasoning as in the proofs of Theorem 3.5 and Lemma 3.7, we obtain a contradiction, thus $\tilde{L} \leq 1$. Finally we get $\lim_{t \rightarrow \infty} (P(t), M(t)) = (P^*, M^*)$. Using Lemma 3.3, we complete the proof of Theorem 3.8. \square

Remark 1. Note that when $\tau_1 = \tau_2 = 0$, system (2.2) becomes system (1.1). Theorems 4–6 in [11] are the corresponding results of Theorems 3.5, 3.6 and 3.8 for system (2.2), respectively. Our main results not only extend the results in [11] but also generalize the related results into the stage-structured system with two delays. But the proof methods of our results are quite different to those in [11].

4. Numerical simulations

In this section, we numerically simulate the dynamics of system (2.2) for a range of parameters which are the same as those in [11]. In this paper, we add the values of two delays τ_1 and τ_2 from [10, 33]. The parameters are given in Table 1.

Table 1. Two sets of parameter values used in numerical simulations.

Parameter	Ranges	Ref.	Unit	data 1	data 2
$\alpha(T)$	$0.03 \sim 0.15^a$	[14]	$\text{ind} \cdot \text{d}^{-1} P^{-1}$	0.12	0.15
$\beta(T)$	$0.065 \sim 0.139^a$	[14]	$\text{ind} \cdot \text{d}^{-1} \text{time}^{-1} P^{-1}$	0.108	0.122
γ	$19 \sim 178^a$	[33, 34]	$\text{ind} \cdot \text{d}^{-1} M^{-1}$	100	170
s_1	$0.001 \sim 0.3^b$	[34, 35]	no unit	0.008	0.01
s_2	$0.01 \sim 0.8^b$	[34]	no unit	0.2	0.8
n	$1 \sim 2$	[14]	times	1	1
d_1	$0 \sim 0.028^{a,b}$	[6, 14]	d^{-1}	0.0001	0.0001
d_2	$0.0001 \sim 0.3^b$	[34]	d^{-1}	0.0001	0.0001
d_3	$0.004 \sim 0.02^a$	[34, 36]	d^{-1}	0.006	0.004
d_4	$0.0001 \sim 0.8^b$	[1]	d^{-1}	0.0001	0.0001
b_1	$0.00001 \sim 0.1^b$	[3, 37]	$\text{d}^{-1} \text{ind}^{-1}$	0.0012	0.0001
b_2	$0 \sim 0.1^b$		$\text{d}^{-1} \text{ind}^{-1}$	0.0001	0.0001
τ_1	$30 \sim 120^b$	[10, 33]	d	120	120
τ_2	$60 \sim 300^b$	[10, 33]	d	90	150

Values signatred by a are from experimental data with unit innovation and those signatred by b are estimated from references.

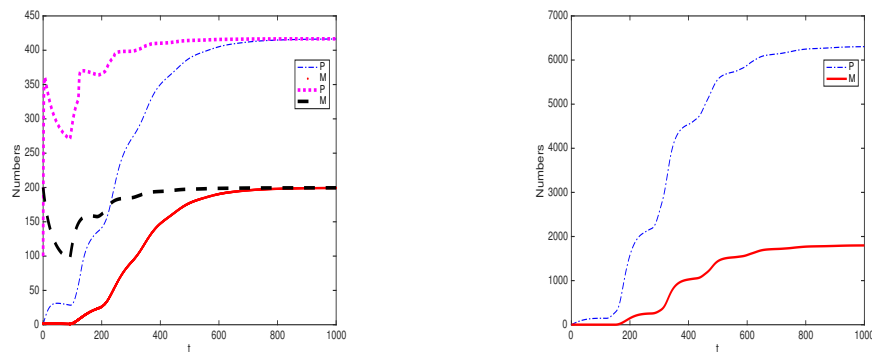


Figure 2. Global stability of E^* under different initial values and the population sizes for data 1 and data 2, respectively.

The left figure of Figure 2 shows that the positive equilibrium E^* of system (2.2) is globally asymptotically stable under different initial values. The left figure and right figure of Figure 2 take the parameters data 1 and data 2, respectively. Figure 2 shows that the population sizes change with respect to environmental indices but do not depend on the initial values. The population explosion occurs even though the initial values ($P = 0, M = 2$) are small (see the right figure of Figure 2). The numbers of two stages in the right figure of Figure 2 are larger than those in the left figure of Figure 2 because the reproduction is high while the destructions and competitions are low in the right figure of Figure 2. The trajectories of the right figure of Figure 2 finally tend towards a higher population level up to 10–15 times than the trajectories in the left figure of Figure 2 (in the corresponding Figure 3 of [11], the populations of Figure 3(b) is higher 30–50 times than Figure 3(a)) although the initial values (0, 2) are of equal values.

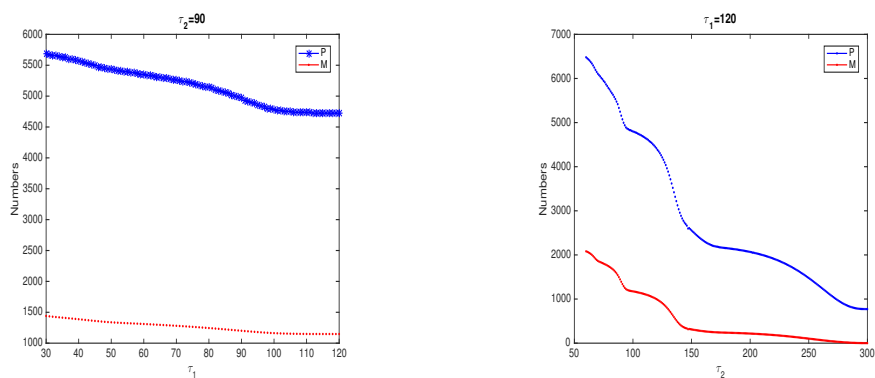


Figure 3. The effects of delays on the population sizes for data 2.

Based on data 2, Figure 3 illustrates how time delays affect the population dynamics. In the left figure of Figure 3, we fix the delay τ_2 as the best fit value and increase the delay $\tau_1 \in [30, 120]$. We find that the populations are slightly fallen over the longer period τ_1 (see the left figure of Figure 3). This is because of the lack of needed temperature and resources and so the asexual reproduction period is long, and the results of the population are low. When we fix the delay τ_1 and change the delay τ_2

from 60 to 300, the populations are significantly decreased over the longer period τ_2 (see the right figure of Figure 3). Overall, Figure 3 can be seen that the peaks of population abundance occur at the small τ_1 and τ_2 while the longer maturation periods may be responsible for the lower populations.

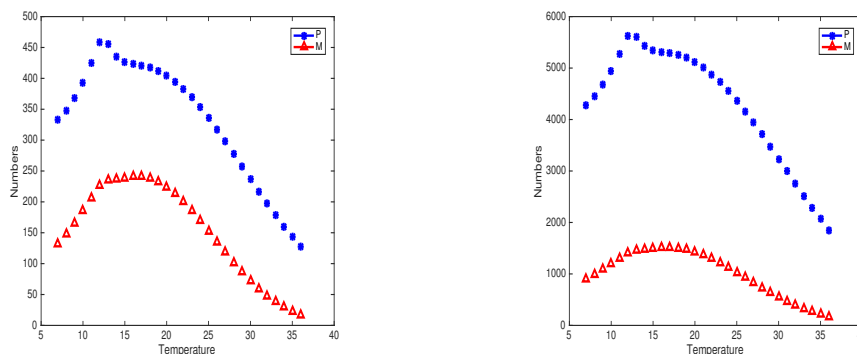


Figure 4. The effects of temperature on the population sizes for data 1 and data 2, respectively.

Figure 4 depicts the effect of temperature $T \in [7, 36]$ on the populations. Temperature is the impact factor that affects the asexual reproduction and strobilation of the jellyfish. In [11], Xie et al. presented that

$$\alpha(T) = \frac{1.9272}{T^3 - 30.3904T^2 + 294.7234T - 871.29} + 0.0378,$$

$$\beta(T) = 0.1430 \exp \left\{ -\left(\frac{T - 16.8108}{10.5302} \right)^2 \right\}.$$

In Figure 4, the numbers of polyp reach a peak at 12.5 °C, which correlates with the maximum budding rate of experimental data [14] and then gradually declined over the high temperature. From 12.5 °C to 16.8 °C is the maximum level of the number of medusae which is different from the experimental result 15 °C [14]. Figure 4 reveals that an appropriate increase of temperature might cause a large increase in the number of populations but the rise of temperatures would result in the fewer populations. Comparing the corresponding Figure (4d) in [11] with the right figure of Figure 4 in this paper, we find out that we can exactly see the peak populations due to the stage structure and can exactly know the effects of temperature on the population dynamics because the temperature is considered up to 36 °C in this paper.

5. Discussion

In this paper, we propose and analyze a delayed jellyfish model with stage structure, which is an extension of ODE model studied by Xie et al. in [11]. We have investigated how the phenomena of budding and strobilation influence the population dynamics of the jellyfish population. τ_1 stands the time needed from the stage of the young polyp to the developed polyp and τ_2 stands the time taken from the mature polyp to ephyra (incipient medusa). We have developed the systematic analysis of the model in both theoretical and numerical ways.

We have proved the global stability of the equilibria under suitable conditions. Our results not only extend but also improve some related results of literature [11]. Our Theorems 3.5, 3.6 and 3.8

straightly extend the corresponding Theorems 4–6 in [11], respectively. Comparing the corresponding Theorems 4–6 in [11] for the ODE system (1.1) with Theorem 3.5, 3.6 and 3.8 for system (2.2), we find out that there are two extra terms $e^{-d\tau_1}$ and $e^{-d_*\tau_2}$ in our permanence and extinction criteria, i.e., the surviving probability of each immature population to develop into mature, which obtains due to the stage structure. From our results, we find that the jellyfish population will be extinct in the large immature mortality rate d, d_* or the long maturation τ_1, τ_2 . Thus we may suggest that the proper increases of $d\tau_1$ and $d_*\tau_2$ have a negative effect of jellyfish population.

Biologically, our results suggest that (i) jellyfish species go extinct if the survival rate of polyp during cloning and the survival rate of the incipient medusa during strobilation are less than their death rates; (ii) polyps will continue and there is no complement from polyp to medusa if the survival rate of polyp during cloning is larger than its death rate and the temperature is not enough to strobilate; (iii) both polyp and medusa will survive in a certain ideal environment and our result converges to the positive constant when the survival rate of polyp during cloning and the survival rate of the incipient medusa during strobilation are larger than their death rates.

Besides the above systematic theoretical results, we have performed the numerical simulations to support the theoretical results. Our numerical results suggest that the positive equilibrium is globally asymptotically stable under distinctive initial values and the population sizes don't deal with the initial values but they change with respect to environmental factors. In Figures 3 and 4, our results suggest that the abundance in population occurs at the smaller periods τ_1 and τ_2 whereas the longer periods τ_1 and τ_2 will lower the peak population of polyp and medusa. In addition to the problem due to increasing τ_1 and τ_2 , the increase of temperatures might cause the outburst of the population dynamics. If there is much higher temperature, the population rate leads to decline. Since temperature has a great impact on jellyfish population, it is interesting for one to consider the populations under the relevance to temperature. We leave this interesting problem as our future work.

Acknowledgments

We would like to take this chance to thank the editor and the anonymous referees for their very valuable comments, which led to a significant improvement of our previous versions. The authors would like to thank Dr. Zhanwen Yang for his warm help on the numeric simulations. Z. Win, B. Tian and S. Liu are supported by the Natural Science Foundation of China (NSFC) (No. 11871179, 11771374, 91646106).

Conflict of interest

All authors declare no conflicts of interest in this paper.

References

1. D. Pauly, W. Graham, S. Libralato, L. Morissette, M. D. Palomares, Jellyfish in ecosystems, online databases, and ecosystem models, *Hydrobiologia*, **616** (2009), 67–85.
2. M. Grove, D. L. Breitburg, Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen, *Mar. Ecol. Prog. Ser.*, **301** (2005), 185–198.

3. C. H. Han, S. I. Uye, Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* sl., *Plankton Benthos Res.*, **5** (2010), 98–105.
4. Z. Dong, D. Liu, J. K. Keesing, Jellyfish blooms in China: Dominant species, causes and consequences, *Mar. Pollut. Bull.*, **60** (2010), 954–963.
5. E. Papathanassiou, P. Panayotidis, K. Anagnostaki, Notes on the biology and ecology of the jellyfish *Aurelia aurita* Lam. in Elefsis Bay (Saronikos Gulf, Greece), *Mar. Ecol.*, **8** (1987), 49–58.
6. W. C. Liu, W. T. Lo, J. E. Purcell, H. H. Chang, Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan, *Hydrobiologia*, **616** (2009), 247–258.
7. C. H. Lucas, S. Lawes, Sexual reproduction of the scyphomedusa *Aurelia aurita* in relation to temperature and variable food supply, *Mar. Biol.*, **131** (1998), 629–638.
8. M. N. Arai, *A Functional Biology of Scyphozoa*, Chapman and Hall, London, 1997.
9. L. E. Martin, *The Population Biology and Ecology of Aurelia sp. (Scyphozoa: Semaestomeae) in a Tropical Meromictic Marine Lake in Palau*, Ph.D thesis, University of California, Los Angeles, 1999.
10. H. Ishii, T. Ohba, T. Kobayashi, Effects of low dissolved oxygen on planula settlement, polyp growth and asexual reproduction of *Aurelia aurita*, *Plankton Benthos Res.*, **3** (2008), 107–113.
11. C. Xie, M. Fan, X. Wang, M. Chen, Dynamic model for life history of scyphozoa, *PLoS ONE*, **10** (2015), e0130669.
12. J. E. Purcell, Climate effects on jellyfish populations, *J. Mar. Biol. Assoc. UK*, **85** (2005), 461–476.
13. A. J. Richardson, A. Bakun, G. C. Hays, M. J. Gibbons, The jellyfish joyride: causes, consequences and management responses to a more gelatinous future, *Trends Ecol. Evolution*, **24** (2009), 312–322.
14. J. E. Purcell, Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata*, *Mar. Ecol. Prog. Ser.*, **348** (2007), 183–196.
15. T. Oguz, B. Salihoglu, B. Fach, A coupled plankton-anchovy population dynamics model assessing nonlinear controls of anchovy and gelatinous biomass in the Black Sea, *Mar. Ecol. Prog. Ser.*, **369** (2008), 229–256.
16. V. Melica, S. Invernizzi, G. Caristi, Logistic density-dependent growth of an *Aurelia aurita* polyps population, *Ecol. Model.*, **291** (2014), 1–5.
17. W. G. Aiello, H. I. Freedman, J. Wu, Analysis of a model representing stage-structured populations growth with state-dependent time delay, *SIAM J. Appl. Math.*, **3** (1992), 855–869.
18. W. G. Aiello, H. I. Freedman, A time-delay model of single species growth with stage structure, *Math. Biosci.*, **101** (1990), 139–153.
19. I. Al-Darabsah, Y. Yuan, A stage-structured mathematical model for fish stock with harvesting, *SIAM J. Appl. Math.*, **78** (2018), 145–170.
20. S. A. Gourley, Y. Kuang, A stage structured predator-prey model and its dependence on through-stage delay and death rate, *J. Math. Biol.*, **49** (2004), 188–200.
21. S. Liu, E. Beretta, A stage-structured predator-prey model of Beddington-DeAngelis type, *SIAM J. Appl. Math.*, **66** (2006), 1101–1129.

22. S. Liu, M. Kouche, N. E. Tatar, Permanence, extinction and global asymptotic stability in a stage structured system with distributed delays, *J. Math. Anal. Appl.*, **301** (2005), 187–207.
23. S. Liu, L. Chen, G. Luo, Y. Jiang, Asymptotic behaviors of competitive Lotka-Volterra system with stage structure, *J. Math. Anal. Appl.*, **271** (2002), 124–138.
24. S. Liu, L. Chen, G. Luo, Extinction and permanence in competitive stage structured system with time-delays, *Nonlinear Anal.*, **51** (2002), 1347–1361.
25. T. Faria, Asymptotic Behaviour for a class of delayed cooperative models with patch structure, *Discrete Continuous Dyn. Syst. Ser. B*, **18** (2013), 1567–1579.
26. H. L. Smith, Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems, in *Mathematical Surveys and Monographs*, American Mathematical Society, **41** (1995).
27. J. K. Hale, S. V. Lunel, *Introduction to Functional Differential Equations*, Springer-Verlag, New York, 1993.
28. Y. Lu, D. Li, S. Liu, Modeling of hunting strategies of the predators in susceptible and infected prey, *Appl. Math. Comput.*, **284** (2016), 268–285.
29. Y. Kuang, *Delay Differential Equations with Applications in Population Dynamics*, Academic Press, New York, 1993.
30. X. Q. Zhao, Z. J. Jing, Global asymptotic behavior in some cooperative systems of functional differential equations, *Cann. Appl. Math. Quart.*, **4** (1996), 421–444.
31. H. L. Smith, P. Waltman, *The Theory of the Chemostat (Dynamics of Microbial Competition)*, Cambridge University Press, Cambridge, 1995.
32. T. Faria, J. J. Oliveira, Local and global stability for Lotka-Volterra systems with distributed delays and instantaneous negative feedbacks, *J. Differ. Equations*, **244** (2008), 1049–1079.
33. C. H. Lucas, Population dynamics of *Aurelia aurita* (Scyphozoa) from an isolated brackish lake, with particular reference to sexual reproduction, *J. Plankton Res.*, **18** (1996), 987–1007.
34. C. H. Lucas, Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment, *Hydrobiologia*, **451** (2001), 229–246.
35. K. Conley, S. I. Uye, Effects of hyposalinity on survival and settlement of moon jellyfish (*Aurelia aurita*) planulae, *J. Exp. Mar. Biol. Ecol.*, **462** (2015), 14–19.
36. M. Palomares, D. Pauly, The growth of jellyfishes, in *Jellyfish Blooms: Causes, Consequences, and Recent Advances*, Springer, (2009), 11–21.
37. F. Gröndahl, Evidence of gregarious settlement of planula larvae of the scyphozoan *Aurelia aurita*: An experimental study, *Mar. Ecol. Prog. Ser.*, **56** (1989), 119–125.



AIMS Press

©2021 the Author(s), licensee AIMS Press. This is an open access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>)