Mathematical Biosciences and Engineering

http://www.aimspress.com/journal/MBE

Mathematical Biosciences and Engineering, 16(4): 2293–2304
DOI: 10.3934/mbe.2019114
Received: 31 August 2018
Accepted: 13 February 2019
Published: 15 March 2019

Research article

Global dynamics of a diffusive single species model with periodic delay

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Abstract: The growth of the species population is greatly influenced by seasonally varying environments. By regarding the maturation age of the species as a periodic developmental process, we propose a time periodic and diffusive model in bounded domain. To analyze this model with periodic delay, we first define the basic reproduction ratio $\mathcal{R}_0$ of the spatially homogeneous model and then show that the species population will be extinct when $\mathcal{R}_0 \leq 1$ while remains persistent and tends to periodic oscillation if $\mathcal{R}_0 > 1$. Finally, combining the comparison principle with the fact that solutions of the spatially homogeneous model are also solutions of our model subject to Neumann boundary condition, we establish the global dynamics of a threshold type for PDE model in terms of $\mathcal{R}_0$.

Keywords: reaction-diffusion model; periodic delay; basic reproduction ratio; threshold dynamics

1. Introduction

Structured population models can be used to describe the interaction of different population communities in such diverse fields as demography, epidemiology, ecology, etc [1]. One of the most important structuring variables in population dynamics is the chronological age. It reflects the reproduction and survival capabilities among individuals [2]. The earliest age-structured models dated back to the pioneering works of Sharpe and Lotka [3] and M'Kendrick [4]. Since then, various types of age-dependent models have been developed and studied, along with many generalizations (see, e.g., [2, 5, 6, 7, 8, 9, 10, 11, 12] and references therein).

In the real world, the dynamics of many populations is greatly affected by seasonally varying environmental factors, in particular, the weather conditions [8]. For example, during one year period, the birth rate may be high in spring and summer when the humidity and temperature are appropriate for the breeding of species and low in winter due to low temperature and dry weather [6]. Therefore, formulating seasonally forced mathematical models is a more effective way for describing population dynamics. In this paper, we will construct a time periodic and diffusive model by taking into account periodic birth, death and maturation rate by age.

In modeling the dynamics of the species with age-structure, the general approach is to divide the population into two stages by age: immature and mature, with the time delay being the maturation period [11]. Since the maturation age is determined by seasonally varying weather conditions, we will use a time dependent positive number $\tau(t)$ to describe the duration from newborn to being adult. That is, an individual at time t becomes mature only if its age exceeds $\tau(t)$. Within each age group, all individuals have the same behavior. Mathematically, we make the following assumptions for $\tau(t)$:

(B1) $\tau(t)$ is a C^1 periodic function in $[0, +\infty)$ with the period T, being one year.
(B2) $t - \tau(t)$ is strictly increasing in t, that is, $\tau'(t) < 1$.

The assumption (B1) is described as above. The assumption (B2) is well-understood in [10], namely, "*juveniles cannot reach maturation before those born ahead of them since the developmental rate depends only on time*". For more explanations on periodic delay $\tau(t)$, the reader further refer to [8, 10, 12] and their references.

Our model to be formulated is a time periodic and reaction-diffusion equation (see the model equation (2.5) in the next section). The emergence of periodic delay $\tau(t)$ in (2.5) makes dynamics analysis become a challenge. Currently, there is an increasing attention for such kind of models. Wu et al. [12] constructed a stage-structured population model by considering the interstadial development durations as time-dependent maturation delays. Although they defined the basic reproduction ratio $\mathcal{R}_0$ for the model, they didn't provide the mathematical analysis of threshold dynamics with respect to $\mathcal{R}_0$. The difficulty lies in how to deal with the periodic delays since the general theory of functional differential equation is not directly used. Fortunately, Lou and Zhao [8] developed an effective theoretical approach in studying the global dynamics of a host-parasite interaction model subject to seasonal effects. The basic idea is to first choose a suitable phase space on which a periodic semiflow can be defined, and then apply the theory of monotone dynamical systems. Further developments and applications for this approach can be found in recent works [2, 13, 14, 15, 16]. Our approach in the present study is also highly motivated by [8].

This work is organized as follows. Section 2 devotes to deriving the model in the form of a nonlocal reaction-diffusion equation with periodic delay. In Section 3, the basic reproduction ratio $\mathcal{R}_0$ for the spatially homogeneous model (3.1) is defined, and it is shown that the global asymptotic stability of zero or the positive periodic state is completely determined by the sign of $\mathcal{R}_0 - 1$. In order to lift the threshold type result for (3.1) to (2.5), Section 4 firstly gives some preliminary results concerning the well-posedness of (2.5), and then presents the main results on global dynamics. The final is a brief discussion.

2. Derivation of the model

Let $u(t, a, x)$ denote the population density of the species under consideration at time $t \geq 0$, age $a \geq 0$ and location $x \in \Omega$. Here our focus is on the case of a open bounded $\Omega \subset \mathbb{R}^n$ with smooth boundary $\partial\Omega$. By a standard argument on population with age structure and diffusion, Metz and Diekmann [9] give

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = D(t, a)\Delta u - d(t, a)u,$$

where $\Delta = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2} + \cdots + \frac{\partial^2}{\partial x_n^2}$ is the Laplacian operator, and $D(t, a)$ and $d(t, a)$ are the diffusion rate and the death rate of species of age a at time t, respectively. Then the total matured population M at time t and location x is given by

$$M(t,x) = \int_{\tau(t)}^{+\infty} u(t,a,x)da. \tag{2.1}$$

The density of age $+\infty$ is assumed to be zero, that is, $u(t,+\infty,x) = 0$. Differentiating the both sides of (2.1) in time leads to

$$\begin{aligned}
\frac{\partial}{\partial t}M(t,x) &= \int_{\tau(t)}^{+\infty} \frac{\partial}{\partial t}u(t,a,x)da - \tau'(t)u(t,\tau(t),x) \\
&= \int_{\tau(t)}^{+\infty} \left[-\frac{\partial}{\partial a} + D(t,a)\Delta - d(t,a)\right] u(t,a,x)da - \tau'(t)u(t,\tau(t),x) \\
&= \int_{\tau(t)}^{+\infty} [D(t,a)\Delta - d(t,a)]\, u(t,a,x)da + (1-\tau'(t))u(t,\tau(t),x).
\end{aligned} \tag{2.2}$$

To proceed further, we assume that only the mature can reproduce, namely,

$$u(t,0,x) = f(t,M(t,x)),$$

where $f(t,\cdot)$ is the birth rate at time t. We also suppose that the diffusion and death rates are age-independent for mature individuals, that is, $D(t,a) = D_M(t)$ and $d(t,a) = d_M(t)$ for $a \in [\tau(t),+\infty)$. Then one deduces from (2.2) that

$$\frac{\partial M}{\partial t} = D_M(t)\Delta M - d_M(t)M + (1-\tau'(t))u(t,\tau(t),x). \tag{2.3}$$

To close the system, one needs to calculate $u(t,\tau(t),x)$. For this purpose, fix $s \geq 0$ and let $V^s(t,x) = u(t,t-s,x)$ for $s \leq t \leq s+\tau(t)$. Then

$$\begin{aligned}
\frac{\partial}{\partial t}V^s(t,x) &= \frac{\partial}{\partial t}u(t,a,x)\Big|_{a=t-s} + \frac{\partial}{\partial a}u(t,a,x)\Big|_{a=t-s} \\
&= D(t,t-s)\Delta V^s(t,x) - d(t,t-s)V^s(t,x),
\end{aligned}$$

with $V^s(s,x) = u(s,0,x) = f(s,M(s,x))$. It follows that

$$V^s(t,x) = e^{-\int_s^t d(\xi,\xi-s)d\xi} \int_\Omega \Gamma\left(\int_s^t D(\xi,\xi-s)d\xi, x, y\right) V^s(s,y)dy,$$

where Γ is the Green function associated with Δ and the Neumann boundary condition. Biologically, this implies that all populations remain confined to the domain Ω for all time.

Setting $s = t-\tau(t)$, we have, for $t \geq \tau(t)$,

$$u(t,\tau(t),x) = V^{t-\tau(t)}(t,x) = b(t)\int_\Omega \Gamma(a(t),x,y)f(t-\tau(t),M(t-\tau(t),y))dy, \tag{2.4}$$

where

$$a(t) = \int_{t-\tau(t)}^t D(\xi,\xi-t+\tau(t))d\xi, \quad b(t) = e^{-\int_{t-\tau(t)}^t d(\xi,\xi-t+\tau(t))d\xi}.$$

Substituting (2.4) into (2.3), we obtain the following reaction-diffusion equation:

$$\begin{cases} \dfrac{\partial M}{\partial t} = D_M(t)\Delta M - d_M(t)M \\ \quad + (1-\tau'(t))b(t)\displaystyle\int_\Omega \Gamma(a(t),x,y)f(t-\tau(t),M(t-\tau(t),y))dy, \quad t>0, x\in\Omega, \\ \dfrac{\partial M}{\partial \nu} = 0, \quad t>0, x\in\partial\Omega, \end{cases} \tag{2.5}$$

where $\frac{\partial}{\partial \nu}$ denotes the differentiation along the unit outward normal ν to $\partial\Omega$. In model (2.5), $D(t,\cdot) \geq 0, d(t,\cdot) \geq 0, D_M(t) > 0, d_M(t) > 0$ and $f(t,\cdot) \geq 0$ are all C^1 functions and T-periodic in time t. Moreover, we assume

(H1) $f(t,0) = 0, \partial_2 f(t,u) > 0$ for all $t \geq -\hat{\tau}$ and $u \geq 0$, where $\hat{\tau} = \max_{t\in[0,T]} \tau(t)$;
(H2) $f(t,v)$ is strictly subhomogeneous in v in the sense that for any $\lambda \in (0,1)$ $f(t,\lambda v) > \lambda f(t,v)$ for all $t \geq -\hat{\tau}$ and $v > 0$;
(H3) there exists positive number $L > 0$ such that

$$-d_M(t)M + (1-\tau'(t))b(t)f(t-\tau(t),M) \leq 0$$

for all $t \geq 0$ and $M \geq L$.

Assumption (H1) represents the case that when the population size is small, the birth rate increases with respect to the size, and the birth rate is zero if there is no adult population. (H2) implies that $f(t,u) \leq \partial_2 f(t,0)u$ for all $t \geq -\hat{\tau}$ and $u \geq 0$, that is, the birth rate is bounded above by its linearization at zero. As mentioned in [17], (H3) means that the population growth is density dependent and is negative when the density is over L, and hence, the population will not explode. In the biological literature, one of typical examples is the linear birth rate $f(t,u) = p(t)u$ with $p > 0$ being T-periodic in time. It describes the circumstance in which the resources are plentiful.

Here we should mention that the paper [10] has studied the propagation dynamics of (2.5) in unbounded domain, but not considered the bounded case. The motivation of the current study stems from this.

3. Dynamics of the spatially homogeneous model

In this section, we consider the spatially homogeneous model corresponding to (2.5):

$$\frac{dM}{dt} = -d_M(t)M + (1-\tau'(t))b(t)f(t-\tau(t),M(t-\tau(t))). \tag{3.1}$$

We first establish the well-posedness of (3.1), then define the basic reproduction ratio $\mathcal{R}_0$ of (3.1), and finally investigate the global dynamics of (3.1) in terms of $\mathcal{R}_0$.

3.1. Well-posedness and the basic reproduction ratio

To address the well-posedness of (3.1), we introduce some notations. Recalling that $\hat{\tau} = \max_{t\in[0,T]} \tau(t)$, then let $X := C([-\hat{\tau},0],\mathbb{R})$ and $X^+ := C([-\hat{\tau},0],\mathbb{R}_+)$. For $\phi \in X$, denote $\|\phi\| =$

$\max_{-\hat{\tau}\le\theta\le 0}|\phi(\theta)|$. Then, (X, X^+) is an ordered Banach space with X^+ being normal and $\mathrm{Int}(X^+) \neq \emptyset$. For any continuous function $u(\cdot) \in C([-\hat{\tau}, \sigma), \mathbb{R})$, where $\sigma > 0$, we define $u_t \in X, t \in [0, \sigma)$, by

$$u_t(\theta) = u(t+\theta), \quad \theta \in [-\hat{\tau}, 0].$$

Then we have the following preliminary result for (3.1).

Lemma 3.1. *For any $\varphi \in X^+$,* (3.1) *has a unique nonnegative and bounded solution $u(t, \varphi)$ with $u_0 = \varphi$ on* $[0, +\infty)$.

Proof. For any $\varphi \in X^+$, we define

$$\tilde{f}(t, \varphi) = -d_M(t)\varphi(0) + (1 - \tau'(t))b(t)f(t - \tau(t), \varphi(-\tau(t))).$$

One easily sees that $\tilde{f}(t, \varphi)$ is continuous and Lipschitz in φ on each compact subset of X^+. It follows from [18, Theorem 2.2.3] that (3.1) has a unique solution $u(t, \varphi)$ on its maximal interval $[0, \sigma_\varphi)$ of existence with $u_0 = \varphi$.

In view of (H3), for any given $\rho \ge 1$, denote $[0, \rho L]_X$ be the order interval in X by

$$[0, \rho L]_X := \{\phi \in X : 0 \le \phi(\theta) \le \rho L, \forall \theta \in [-\hat{\tau}, 0]\}.$$

If $\varphi \in [0, \rho L]_X$ and $\varphi(0) = 0(\varphi(0) = \rho L)$, then $\tilde{f}(t, \varphi) \ge 0(\tilde{f}(t, \varphi) \le 0)$. By [19, Theorem 5.2.1 and Remark 5.2.1], one deduces that $[0, \rho L]_X$ is positively invariant for (3.1). Since ρ can be chosen as large as we wish, one obtains the positivity and boundedness of solutions in X^+. Hence, $\sigma_\varphi = +\infty$, as desired. □

Now we apply the recent theory developed in [20] to introduce the basic reproduction ratio for (3.1). It should be pointed out that the general definition of $\mathcal{R}_0$ proposed in [21] can also be used for (3.1). However, its derivation is technical. For convenience, we directly use the method in [20]. Linearizing (3.1) at its zero solution yields a T-periodic linear delay equation

$$\frac{dv}{dt} = -d_M(t)v + (1 - \tau'(t))b(t)\partial_2 f(t - \tau(t), 0)v(t - \tau(t)). \tag{3.2}$$

Define $\beta(t) = (1 - \tau'(t))b(t)\partial_2 f(t - \tau(t), 0)$ and let

$$F(t)\phi = \beta(t)\phi(-\tau(t)), \quad V(t) = d_M(t).$$

One easily sees that $F(t)$ and $V(t)$ satisfy assumptions (H1) and (H2) given in [20]. Let C_T be the Banach space of all T-periodic functions from $\mathbb{R}$ to $\mathbb{R}$, equipped with the maximum norm and the positive cone $C_T^+ := \{u \in C_T : u(t) \ge 0, \forall t \in \mathbb{R}\}$. The next generation operator $\mathcal{L}$ on C_T is defined as

$$[\mathcal{L}w](t) = \int_0^{+\infty} e^{-\int_{t-s}^{t} d_M(\eta)d\eta}\beta(t-s)w(t-s-\tau(t-s))ds, \quad t \in \mathbb{R}, w \in C_T.$$

Then we denote the basic reproduction ratio as the spectral radius of $\mathcal{L}$, i.e. $\mathcal{R}_0 = r(\mathcal{L})$.

For any given $t \ge 0$, let $\hat{P}(t)$ be the time-t map of (3.2) on X, that is, $\hat{P}(t)\phi = \bar{v}_t(\phi)$, where $\bar{v}(t, \phi)$ is the unique solution of (3.2) with $\bar{v}_0 = \phi \in X$. Then $\hat{P} := \hat{P}(T)$ is the Poincaré map associated with (3.2). Let $r(\hat{P})$ be the spectral radius of $\hat{P}$. By [20, Theorem 2.1], we have the following observation.

Lemma 3.2. $\mathcal{R}_0 - 1$ *has the same sign as* $r(\hat{P}) - 1$.

3.2. The global dynamics

The basic approach to studying the threshold dynamics of (3.1) is to use the theory of monotone and subhomogeneous (see [22, Sect. 2.3]). To this end, we define a new phase space on which (3.1) can generate an eventually strongly monotone periodic semiflow. Let

$$Y := C([-\tau(0), 0], \mathbb{R}), \quad Y^+ := C([-\tau(0), 0], \mathbb{R}_+).$$

Then we have the following result.

Lemma 3.3. *For any $\phi \in Y^+$,* (3.1) *admits a unique nonnegative solution $M(t, \phi)$ on* $[0, +\infty)$ *with $M_0 = \phi$, where for $t \geq 0$, M_t is defined by*

$$M_t(\theta) = M(t + \theta), \quad \theta \in [-\tau(0), 0].$$

Proof. Let $\bar{\tau} = \min_{t\in[0,T]} \tau(t)$. For any $t \in (0, \bar{\tau}]$, since $t - \tau(t)$ is strictly increasing, we have

$$-\tau(0) \leq t - \tau(t) \leq \bar{\tau} - \tau(\bar{\tau}) \leq \bar{\tau} - \bar{\tau} = 0,$$

and hence, $M(t - \tau(t)) = \phi(t - \tau(t))$. As a result, we get the following equation for $t \in (0, \bar{\tau}]$:

$$\frac{dM}{dt} = -d_M(t)M + (1 - \tau'(t))b(t)f(t - \tau(t), \phi(t - \tau(t))).$$

For given $\phi \in Y^+$, the solution $M(t)$ of the above equation exists on $(0, \bar{\tau}]$. In other words, we obtain the value of $\psi(\theta) = M(\theta)$ for $\theta \in [-\tau(0), \bar{\tau}]$.

For any $t \in (\bar{\tau}, 2\bar{\tau}]$, we have

$$-\tau(0) \leq \bar{\tau} - \tau(\bar{\tau}) \leq t - \tau(t) \leq 2\bar{\tau} - \tau(2\bar{\tau}) \leq 2\bar{\tau} - \bar{\tau} = \bar{\tau},$$

which implies $M(t-\tau(t)) = \psi(t-\tau(t))$. Solving the following ordinary differential equation on $t \in (\bar{\tau}, 2\bar{\tau}]$ with $M(\bar{\tau}) = \psi(\bar{\tau})$:

$$\frac{dM}{dt} = -d_M(t)M + (1 - \tau'(t))b(t)f(t - \tau(t), \psi(t - \tau(t))),$$

we then get the solution $M(t)$ on $(\bar{\tau}, 2\bar{\tau}]$. Extending this procedure to $(n\bar{\tau}, (n + 1)\bar{\tau}]$ for $n = 2, 3, \cdots$. Then one can derive that for any $\phi \in Y^+$, the solution $M(t, \phi)$ of (3.1) exists uniquely for all $t \geq 0$. □

Remark 3.1. By the uniqueness of solutions in Lemmas 3.1 and 3.3, it follows that for any $\varphi \in X^+$ and $\phi \in Y^+$ with $\varphi(\theta) = \phi(\theta), \forall\theta \in [-\tau(0), 0]$, then $u(t, \varphi) = M(t, \phi), \forall t \geq 0$, where $u(t, \varphi)$ and $M(t, \phi)$ are solutions of (3.1) satisfying $u_0 = \varphi$ and $M_0 = \phi$, respectively.

Define $Q(t)$ as the solution map of (3.1) on the space Y, that is,

$$Q(t)\phi = M_t(\phi), \qquad t \geq 0, \phi \in Y,$$

where $M(t, \phi)$ is the unique solution of (3.1) with $M_0 = \phi \in Y$. By arguments similar to those in [8, Lemma 3.5], we can show that $Q(t)$ is a T-periodic semiflow on Y^+ in the sense that (i) $Q(0) = I$; (ii) $Q(t + T) = Q(t) \circ Q(T), \forall t \geq 0$; (iii) $Q(t)\varphi$ is continuous in $(t, \varphi) \in [0, +\infty) \times Y^+$.

Lemma 3.4. *The periodic semiflow $Q(t)$ is eventually strongly monotone and strictly subhomogeneous.*

Proof. Noting that $\partial_2 f(t,v) > 0$, a simple comparison argument on each interval $(n\bar{\tau},(n+1)\bar{\tau}], n \in \mathbb{N}$, implies that for each $t > 0$, $Q(t) : Y^+ \to Y^+$ is monotone. Next we show that $Q(t)$ is eventually strongly monotone. In view of Lemma 3.1 and Remark 3.1, $M(t)$ is bounded on $[0,+\infty)$, and hence, there is a real number $q > 0$ such that $M_t \in [0,q]_Y$ for all $t \geq 0$. Due to this fact, we can choose a large number $K > \max_{t\in[0,T]} d_M(t)$ such that for each $t \in \mathbb{R}_+$, $g(t,v) := -d_M(t)v + Kv$ is increasing in $v \in [0,q]$. It then follows that $M(t)$ satisfies the following integral equation:

$$\begin{aligned} M(t) =& e^{-Kt}M(0) + \int_0^t e^{-K(t-s)}g(s,M(s))ds \\ &+ \int_0^t e^{-K(t-s)}(1-\tau'(s))b(s)f(s-\tau(s),M(s-\tau(s)))ds, \quad t \geq 0. \end{aligned} \tag{3.3}$$

Since $m(t) := t - \tau(t)$ is increasing in $t \in \mathbb{R}_+$, one sees that $[-\tau(0),0] \subset m([0,\hat{\tau}])$. Let $\phi > \psi$, that is, $\phi \geq \psi$ but $\phi \neq \psi$. Then there exists an $\eta \in [-\tau(0),0]$ such that $\phi(\eta) > \psi(\eta)$. Therefore, we can deduce from (3.3) that $z(t,\phi) > z(t,\psi)$ for all $t > \hat{\tau}$, and hence, $z_t(\phi) > z_t(\psi), t > \hat{\tau} + \tau(0)$. This shows that $Q(t)$ is strongly monotone whenever $t > \hat{\tau} + \tau(0)$.

For any given $\phi \gg 0$ in Y and $\lambda \in (0,1)$, denote $x(t) = \lambda M(t,\phi)$ and $y(t) = M(t,\lambda\phi)$. From the proof in Lemma 3.3, we see that $x(t), y(t) > 0$ for $t \geq 0$. Moreover, for all $\theta \in [-\tau(0),0]$, we have $x(\theta) = \lambda\phi(\theta) = y(\theta)$. For $t \in [0,\bar{\tau}]$, one immediately finds

$$-\tau(0) \leq t - \tau(t) \leq \bar{\tau} - \bar{\tau} = 0,$$

and hence, $y(t-\tau(t)) = x(t-\tau(t)) = \lambda\phi(t-\tau(t))$. Then

$$\begin{aligned} \frac{dx}{dt} &= -d_m(t)x + \lambda(1-\tau'(t))b(t)f(t-\tau(t),M(t-\tau(t))) \\ &< -d_m(t)x + (1-\tau'(t))b(t)f(t-\tau(t),x(t-\tau(t))) =: h(t,x), \quad t \in [0,\bar{\tau}], \end{aligned}$$

which implies

$$\frac{dx}{dt} - h(t,x) < 0 = \frac{dy}{dt} - h(t,y), \quad t \in [0,\bar{\tau}].$$

Note that $x(0) = y(0)$. By [23, Theorem 4], we then obtain $x(t) < y(t)$ for $t \in (0,\bar{\tau}]$. By similar arguments for any interval $(n\bar{\tau},(n+1)\bar{\tau}], n \in \mathbb{N}^+$, we can get $x(t) < y(t)$ for all $t > 0$, that is, $M(t,\lambda\phi) > \lambda M(t,\phi)$ for all $t > 0$. Therefore, $M_t(\lambda\phi) \gg \lambda M_t(\phi)$ for all $t > \tau(0)$, which indicates that for each $t > \tau(0)$, $Q(t)$ is strictly subhomogeneous. □

Theorem 3.5. *The following statements are valid:*

(i) If $\mathcal{R}_0 \leq 1$, then zero solution is globally asymptotically stable for (3.1) *in Y^+.*
(ii) If $\mathcal{R}_0 > 1$, then (3.1) *admits a unique positive T-periodic solution $M^*(t)$ which is globally asymptotically stable in $Y^+ \setminus \{0\}$.*

Proof. Choose an integer n_0 such that $n_0T > \hat{\tau} + \tau(0)$. Then $Q^{n_0} := Q(n_0T)$ is a strongly monotone and strictly subhomogeneous map on Y^+. By [22, Theorem 2.3.4 and Lemma 2.2.1] as applied to Q^{n_0}, we have the following threshold type result:

(a) If $r(DQ^{n_0}(0)) \leq 1$, then zero solution is globally asymptotically stable for (3.1) in Y^+.

(b) If $r(DQ^{n_0}(0)) > 1$, then (3.1) admits a unique positive n_0T-periodic solution $M^*(t)$ which is globally asymptotically stable in $Y^+ \setminus \{0\}$.

For any given $t \geq 0$, let $P(t)$ be the solution map of (3.2) on Y, that is, $P(t)\phi = v_t(\phi)$, where $v(t, \phi)$ is the unique solution of (3.2) with $v_0 = \phi \in Y$. Then $P := P(T)$ is the Poincaré map associated with (3.2). By the same arguments as in [8, Lemma 3.8], we get $r(\hat{P}) = r(P)$. This together with Lemma 3.2 yields $\text{sign}(\mathcal{R}_0 - 1) = \text{sign}(r(P) - 1)$. Noting that $r(DQ^{n_0}(0)) = r(P(n_0T)) = [r(P)]^{n_0}$, we see that

$$\text{sign}(r(DQ^{n_0}(0)) - 1) = \text{sign}(r(P) - 1) = \text{sign}(\mathcal{R}_0 - 1).$$

It remains to prove that $M^*(t)$ is also a T-periodic solution of (3.1). Let $\psi^* = M_0^* \in Y$ and $Q := Q(T)$. Then we have

$$Q^{n_0}(Q\psi^*) = Q(Q^{n_0}\psi^*) = Q(\psi^*).$$

The uniqueness of the positive fixed point of Q^{n_0} implies that $Q\psi^* = \psi^*$, and hence, $M^*(t) = M(t, \psi^*)$ is a T-periodic solution of (3.1). □

4. Dynamics of model (2.5) in terms of $\mathcal{R}_0$

In this part, we first establish the well-posedness of (2.5), and then with the help of Theorem 3.5, we show that for model (2.5), $\mathcal{R}_0$ is also a threshold parameter which determines the uniform persistence or extinction of the species.

Let $\mathbb{X} := C(\bar{\Omega}, \mathbb{R})$ be the Banach space of continuous functions from $\bar{\Omega}$ to $\mathbb{R}$ with the supremum norm $\|\cdot\|_{\mathbb{X}}$, and let $\mathbb{X}^+ := \{\varphi \in \mathbb{X} : \varphi(x) \geq 0, \forall x \in \bar{\Omega}\}$. It is easily seen that $\mathbb{X}^+$ is a closed cone of $\mathbb{X}$ and $\mathbb{X}$ is a Banach lattice under the partial ordering induced by $\mathbb{X}^+$. Let $C := C([-\tau(0), 0], \mathbb{X})$ be the Banach space of continuous functions from $[-\tau(0), 0]$ into $\mathbb{X}$ with the supremum norm $\|\cdot\|$ and let $C^+ := C([-\tau(0), 0], \mathbb{X}^+)$. Then C^+ is a closed cone of C. As usual, we identify an element $\phi \in C$ as a function from $[-\tau(0), 0] \times \bar{\Omega}$ into $\mathbb{R}$ defined by $\phi(\theta, x) = \phi(\theta)(x)$.

Recall that $\bar{\tau} = \min_{t\in[0,T]} \tau(t)$. For any $\varphi \in C^+$, we can solve (2.5) on $(0, \bar{\tau}] \times \bar{\Omega}$ and then $(\bar{\tau}, 2\bar{\tau}] \times \bar{\Omega}$, etc. However, this will lead to an question: the smoothness of $M(t, x)$ on $(0, +\infty) \times \bar{\Omega}$. So instead we will use the following abstract approach.

Choose the phase space $W := C([-\hat{\tau}, 0], \mathbb{X})$. The nonnegative cone of W is denoted by $W^+ := \{\phi \in W : \phi(\theta) \in \mathbb{X}^+, \forall\theta \in [-\hat{\tau}, 0]\}$. For any continuous function $z(\cdot) : [-\hat{\tau}, d) \to \mathbb{X}$, where $d > 0$, we define $z_t \in W, t \in [0, d)$, by $z_t(\theta) = z(t + \theta), \theta \in [-\hat{\tau}, 0]$. Let $U(t, s) : \mathbb{X} \to \mathbb{X}, t \geq s$, be the evolution operator determined by the following reaction-diffusion equation

$$\begin{cases} \frac{\partial w}{\partial t} = D_M(t)\Delta w - d_M(t)w, & t > 0, x \in \Omega \\ \frac{\partial w}{\partial \nu} = 0, & t > 0, x \in \partial\Omega. \end{cases}$$

Since $D_M(t)$ and $d_M(t)$ are T-periodic in t, [24, Lemma 6.1] implies that $U(t + T, s + T) = U(t, s)$ for $(t, s) \in \mathbb{R}^2$ with $t \geq s$. Moreover, for $(t, s) \in \mathbb{R}^2$ with $t > s$, $U(t, s)$ is compact and strongly positive. Define $F : [0, +\infty) \times W^+ \to \mathbb{X}$ by

$$F(t, \phi) := (1 - \tau'(t))b(t) \int_\Omega \Gamma(a(t), \cdot, y) f(t - \tau(t), \phi(-\tau(t), y)) dy.$$

Then (2.5) with the following initial condition

$$z(\theta, x) = \phi(\theta, x), \quad (\theta, x) \in [-\hat{\tau}, 0] \times \bar{\Omega},$$

can be rewritten as an integral equation

$$z(t, \cdot, \phi) = U(t, 0)\phi(0, \cdot) + \int_0^t U(t, s)F(s, z_s)ds, \quad t \geq 0, \phi \in W^+.$$

Such a solution is called a mild solution of (2.5).

Lemma 4.1. *For any $\phi \in W^+$, (2.5) has a unique mild solution $z(t, \cdot, \phi)$ with $z_0 = \phi$ and $z_t(\cdot, \cdot, \phi) \in W^+$ for all $t > 0$, and $z(t, \cdot, \phi)$ is a classic solution when $t > \hat{\tau}$.*

Proof. Firstly, we show the local existence of the unique mild solution. It is obvious that $F(t, \phi)$ is locally Lipschitz in ϕ. It suffices to show

$$\lim_{h \to 0^+} \text{dist}(\phi(0, \cdot) + hF(t, \phi), \mathbb{X}^+) = 0, \quad (t, \phi) \in [0, +\infty) \times W^+. \tag{4.1}$$

For any $(t, \phi) \in [0, +\infty) \times W^+$ and $h > 0$, we have

$$\begin{aligned}
&\phi(0, x) + hF(t, \phi)(x) \\
&= \phi(0, x) + h(1 - \tau'(t))b(t) \int_\Omega \Gamma(a(t), \cdot, y) f(t - \tau(t), \phi(-\tau(t), y))dy \\
&\geq \phi(0, x), \quad t \geq 0, x \in \bar{\Omega}.
\end{aligned}$$

The above inequality implies that (4.1) holds. Consequently, by [25, Corollary 4] with $K = \mathbb{X}^+$ and $S(t, s) = U(t, s)$, (2.5) has a unique non-continuable mild solution $z(t, \cdot, \phi)$ with $z_0 = \phi$ and $z_t(\cdot, \cdot, \phi) \in W^+$ on $[0, t_\phi)$, where $t_\phi \leq +\infty$. Moreover, by the analyticity of $U(t, s), s, t \in \mathbb{R}, t > s$, $z(t, \cdot, \phi)$ is a classical solution when $t > \hat{\tau}$.

Due to (H3), it is easy to see that for any $q > 1$, qL is an upper solution of (2.5). This implies that solutions of (2.5) are uniformly bounded, and hence, $t_\phi = +\infty$. □

Remark 4.1. Let $M(t, \cdot, \varphi)$ be the solution of (2.5) with $M_0 = \varphi \in C^+$, where M_t is defined by $M_t(\theta, x, \varphi) = M(t + \theta, x, \varphi), (\theta, x) \in [-\tau(0), 0] \times \bar{\Omega}$. By the uniqueness of solutions, one deduces

$$z(t, \cdot, \phi) = M(t, \cdot, \varphi), \quad t \geq 0,$$

provided that $\phi \in W^+$ and $\varphi \in C^+$ satisfy $\phi(\theta, \cdot) = \varphi(\theta, \cdot), \forall \theta \in [-\tau(0), 0]$. Hence, according to Lemma 4.1, the regularity of $z(t, \cdot, \phi)$ implies that of $M(t, \cdot, \varphi)$.

Following the procedure in [20], we can also define the basic reproduction ratio $\tilde{\mathcal{R}}_0$ for (2.5). Observe that the coefficients in (2.5) are independent of spatial variable x, and hence $\tilde{\mathcal{R}}_0 = \mathcal{R}_0$. Now we are in a position to prove the global dynamics of (2.5) in terms of $\mathcal{R}_0$.

Theorem 4.2. *The following results hold:*

(i) If $\mathcal{R}_0 \leq 1$, then zero solution is globally asymptotically stable for (2.5) in C^+.

(ii) If $\mathcal{R}_0 > 1$, then (2.5) *admits a unique positive T-periodic solution $M^*(t)$ which is globally asymptotically stable in $C^+ \setminus \{0\}$.*

Proof. Note that solutions of (3.1) are also solutions of (2.5) subject to Neumann boundary condition. Thus, Theorem 3.5, together with the standard comparison argument, implies that the threshold result holds true for (2.5). □

To finish this section, we remark that after this paper has been accepted for publication, we got knowledge of Liu's doctoral thesis [26] which studied the similar model by using different methods from ours.

5. Discussion

Seasonal variations in temperature, rainfall and resource availability are the pervasive external environmental factors affecting the development, abundance and behaviour of single-species population. In order to explore the effects of seasonality on the evolution of an age-structured species, we have formulated a reaction-diffusion model with periodic delay by considering the maturation age as a seasonal developmental rate. For the spatially homogeneous model (3.1), we have showed that the basic reproduction ratio $\mathcal{R}_0$ acts as a threshold parameter in determining the global dynamics, that is, the zero solution of (3.1) is globally asymptotically stable if $\mathcal{R}_0 \leq 1$, and (3.1) has a globally asymptotically stable positive periodic solution when $\mathcal{R}_0 > 1$. Here we remark that the introduction of periodic delay brings challenges for our analysis. This is because (3.1) cannot generate a periodic semiflow on the space $X := C([-\hat{\tau}, 0], \mathbb{R})$, and hence the theory of monotone and subhomogeneous semiflows is not applied. For this reason, we have defined a new space $Y := C([-\tau(0), 0], \mathbb{R})$ and showed that the solution semiflow is eventually strongly monotone and strictly subhomogeneous on this space. Furthermore, we have extended the threshold type result for (3.1) to (2.5).

This paper is devoted to the mathematical analysis of the model and simulations have not been carried out. However, the following simulations are interesting: (1) the long-term behavior of solutions with respect to $\mathcal{R}_0$; (2) the influences of some key parameters in model (2.5) on $\mathcal{R}_0$; and (3) compare the difference of $\mathcal{R}_0$ values between the use of $\tau(t)$ and its average $[\tau] := \int_0^T \tau(t)dt/T$. One easily finds that one key point in simulations is the numerical computation of $\mathcal{R}_0$, which can be realized by the method developed in [27, Remark 3.2].

There are several questions for further study. For instance, the monotonicity condition in model (2.5) is too restrictive. A natural question is what if this condition is not satisfied for (2.5)? Another possible project, as mentioned in [10], how to formulate the model when time and spatial heterogeneities are taken into account and further how to analyze the dynamics in bounded or unbounded domain. We leave these interesting yet challenging problems for future investigation.

Acknowledgments

We are very grateful to the anonymous referee for careful reading and helpful comments which led to improvements of our original manuscript. This research was supported by the NSF of Shaanxi Province of China (No. 2017JM1001) and the NSF of China (No. 11671315).

Conflict of interest

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

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