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Extinction, stable pattern and their transition in a diffusive single species population with distributed maturity

PEIXUAN WENG

School of Mathematics, South China Normal University, Guangzhou 510631, P.R. China
email: wengpx@scnu.edu.cn

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We consider a single-species structured population with distributed maturity and spatial diffusion in a cylindrical domain subject to Neumann and Robin boundary conditions. We first establish the threshold property of the reaction–diffusion system with distributed delay and non-local interaction in a corresponding lower-dimensional domain, so that the system approaches either an extinction state or a stable spatially varying pattern. We then investigate the transition from the extinction state to the stable pattern of the system in the cylindrical domain.

1 Introduction

Al-Omari and Gourley (2005) considered the following population model for a diffusive single species with age structure and distributed maturity:

$$\begin{aligned} \frac{\partial u_i(t,x)}{\partial t} &= D_i \triangle_x u_i(t,x) + b(u_m(t,x)) - \gamma u_i(t,x) \\ &\quad - \int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} b(u_m(t-s,\xi))\, d\xi\, ds, \\ \frac{\partial u_m(t,x)}{\partial t} &= D_m \triangle_x u_m(t,x) - d(u_m(t,x)) \\ &\quad + \int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} b(u_m(t-s,\xi))\, d\xi\, ds, \end{aligned} \tag{1.1}$$

subject to the homogeneous Neumann boundary condition

$$\frac{\partial u_i}{\partial n} = 0 = \frac{\partial u_m}{\partial n} \quad \text{on } \partial\Omega,$$

where $x \in \Omega \subset \mathbb{R}^N$ with Ω being a smooth domain, $\triangle_x = \sum_{k=1}^N \frac{\partial^2}{\partial x_k^2}$, n is the outward normal to $\partial\Omega$, $u_i(t,x)$ and $u_m(t,x)$ are the number densities of juvenile and mature individuals at time t and spatial location $x \in \Omega$, $D_i > 0$ and $D_m > 0$ are the diffusion coefficients for the juvenile and mature individuals, respectively. $G(t,x,\xi)$ is the solution

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of initial value problem

$$\frac{\partial G}{\partial t} = \triangle_x G, \quad G(0, x, \xi) = \delta(x - \xi), \tag{1.2}$$

subject to the above Neumann boundary condition, and δ is the Dirac delta function. Furthermore, $f(s)$ is the function that measures the probability that a new-born at time s ago becomes mature, $b(u)$ is the birth function and γ is the juvenile death rate while $d(u)$ is the death function for the mature population; it can be non-linear. Under some technical yet biologically realistic conditions, they showed the convergence of all biologically interesting solutions to a positive equilibrium.

Such an equilibrium is a constant vector due to the nature of the homogeneous Neumann boundary condition, and the work of Al-Omari and Gourley depends heavily on this specific boundary condition and its implication that the positive equilibrium can be explicitly calculated. It is thus very natural to ask if their conclusions remain valid under the following general boundary condition

$$\begin{aligned} Bu_i(t,x) &:= p(x)u_i(t,x) + q(x)\frac{\partial u_i(t,x)}{\partial n} = 0, \\ Bu_m(t,x) &:= p(x)u_m(t,x) + q(x)\frac{\partial u_m(t,x)}{\partial n} = 0, \quad x \in \partial\Omega, \end{aligned} \tag{1.3}$$

with $[p(x)]^2 + [q(x)]^2 = 1, x \in \partial\Omega$. More specially, we shall concentrate on the following boundary conditions of biological interest:

(1) Neumann (NC): $p(x) \equiv 0,\ q(x) \equiv 1,\ x \in \partial\Omega$;

(2) Robin (RC): $p, q \in C^1(\partial\Omega)$, $p(x) \in [0,1]$ and $q(x) \in (0,1]$ for $x \in \partial\Omega$, and $p \not\equiv 0$ on $\partial\Omega$.

A challenging issue for the global dynamics of model (1.1) related to the Robin boundary conditions is the fact that a non-trivial equilibrium (if it exists) is given implicitly by a non-local elliptic equation, and the spatio-temporal weighted non-local interaction in the full parabolic equation adds further difficulty in the description of the dynamical behaviour of the system (1.1). Nevertheless, as shown in Section 2, applications of the theory of monotone dynamical systems, and some general results on threshold dynamics of abstract semiflows, allow us to obtain a threshold dynamics based on the sign of the leading zero of the transcendental equation

$$\lambda = -[\alpha_1 D_m + d'(0)] + b'(0)\int_0^\tau f(s)e^{-\gamma s}e^{-\lambda s}e^{-D_i s \alpha_1}\,ds,$$

where α_1 is the first eigenvalue of the operator $-\triangle_x$ on Ω subject to the above boundary condition. This threshold dynamics concludes that, under very general technical conditions, either all solutions tend to zero (extinction) or all solutions tend to a positive (possibly spatially varying) equilibrium.

With the result of the threshold dynamics for the model equation on the spatial domain Ω in section 2, we can then discuss the transition from the extinction state to the stable pattern of the single species population distributed in a one-dimensional higher

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cylindrical domain $\Omega \times R$. This kind of problem is motivated by the consideration of some kind of population growing and moving in a cylindrical domain, for example, the organism growing in a pipe or perhaps a blood vessel. If there is some leakage at the boundary, then it satisfies the Robin boundary value condition, and while there is no leakage, it corresponds to the Neumann boundary value condition. The problem arises also from combustion, chemical reaction and propagation in nerve impulses (see Field and Burger 1985; Cross and Hohenberg 1993; Merzhanov and Rumanov 1999). A ubiquitous feature of the systems of this kind is that they are capable of supporting travelling waves propagating with constant speed. The previous discussion for the propagation of disturbances for a reaction–diffusion system in a cylindrical domain can be found in Muratov (2004). Our model formulation and the discussion of semiflow of solutions will be given in section 3, and the transition in the form of travelling waves and their wave speeds as well as the rate of propagation will be discussed in section 4 based on an application of an abstract result of Liang and Zhao (2007, 2008) for monotone semiflows.

We conclude this section with a short remark that model (1.1) is a reaction–diffusion equation with non-local and delayed term arising from the interaction of spatial diffusion and distributed maturation delay. This idea of weighted spatial average for a population involving spatial diffusion and time delay was first introduced by Britton (1990), and further developed by Gourley and Britton (1996) and Gourley (2000). We refer to a recent article by Gourley and Wu (2006) for relevant references on the substantial progress. Our work on the transition from extinction to stable patterns in the form of travelling waves is directly related to the recent work on semiflows by Liang and Zhao (2007, 2008) that gives an abstract and very general formulation of some profound results for parabolic equations, integro-differential equations and lattice differential systems, with or without time-lags, such as those in Aronson and Weinberger (1975), Diekmann (1979), Schaaf (1987), Smith and Zhao (2000), So, Wu and Zou (2001), Thieme (1979), Lui (1989), Wu and Zou (2001), Weinberger (1982, 2002), Weinberger *et al.* (2002), Weng *et al.* (2003), Weng and Zhao (2006), Thieme and Zhao (2003).

2 Threshold dynamics

We now formulate the standing assumptions to be adopted in the remaining part of this paper:

(P1) $f : [0, \tau] \to [0, \infty)$ is continuous, $\int_0^\tau f(s) ds = 1$ for some $\tau > 0$;

(P2) $b \in C^1(\mathbb{R}_+, \mathbb{R}_+)$ with $b(0) = 0$, and b is strictly sublinear, i.e., $b(\rho u_m) > \rho b(u_m)$ for all $\rho \in (0, 1)$ and $u_m > 0$;

(P3) $d \in C^1(\mathbb{R}_+, \mathbb{R}_+)$ with $d(0) = 0$, d is strictly increasing and $-d$ is sublinear;

(P4) the maximum of b can be achieved at $u_m^* > 0$, b is non-decreasing on $[0, u_m^*]$ and there exists $\hat{u}_m \in (0, u_m^*]$ such that

$$b(u_m) \int_0^\tau f(s) e^{-\gamma s} \, ds < d(u_m) \quad \text{when } u_m > \hat{u}_m.$$

We emphasise that the kernel G in (1.1) takes different forms determined by the appropriate boundary condition and (1.2). More precisely, if we let $(\alpha_k, \psi_k), k = 1, 2, \ldots,$ be

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the eigenvalues and (normalised) eigenfunctions of $-\triangle_x$ on Ω subject to the corresponding boundary condition (either NC or RC) with $\alpha_1 < \alpha_2 < \cdots$, then

$$G(D_i t, x, \xi) = \sum_{k=1}^{\infty} e^{-D_i \alpha_k t} \psi_k(x)\psi_k(\xi). \tag{2.1}$$

We also note that the second equation in (1.1) is in fact decoupled from the first equation, and the behaviour of $u_i(t,x)$ is determined by a single linear reaction diffusion equation with a non-homogeneous term once $u_m(t,x)$ is known. Therefore, our focus will be on the second equation of (1.1).

Let $X = C(\bar{\Omega}, \mathbb{R})$ be the Banach space of all bounded and continuous functions with the usual supremum norm $\|\cdot\|$. If $X^+ = \{\phi \in X : \phi(x) \geqslant 0, \ \forall x \in \bar{\Omega}\}$ expresses the positive cone in X, then $\mathrm{int}X^+$ is non-empty under the boundary value condition (either NC or RC; see Smith, 1995). For any $L \geqslant 0$, let $[0,L]_X = \{\phi \in X : 0 \leqslant \phi(x) \leqslant L, \forall x \in \bar{\Omega}\}$. We know that X is a Banach lattice under the partial ordering induced by the closed set X^+.

Denote the analytic semi-group associated with the heat problem

$$\begin{aligned} &\frac{\partial w(t,x)}{\partial t} = \triangle_x w(t,x), && t > 0, x \in \Omega, \\ &Bw(t,x) = 0, && t \geqslant 0, x \in \partial\Omega \end{aligned} \tag{2.2}$$

by $T(t)$, then the solution of the initial value problem with an initial function $\varphi \in X$ is $[T(t)\varphi]$, and the standard parabolic maximum principle (see Smith, 1995 or Protter and Weinberger, 1967) implies that $T(t)X^+ \subset X^+$ for all $t \geqslant 0$.

Let $C = C([-\tau, 0], X)$ be the Banach space of continuous functions from $[-\tau, 0]$ to X, $C^+ = \{\phi \in C : \phi(s) \in X^+, \forall s \in [-\tau, 0]\}$. For any $L \geqslant 0$, let $[0,L]_C = \{\phi \in C : \phi(s) \in [0,L]_X, \ \forall s \in [-\tau, 0]\}$. Then C^+ is a closed cone of C. As usual, we identify an element $\phi \in C$ with a function from $[-\tau, 0] \times \bar{\Omega}$ into $\mathbb{R}$ defined by $\phi(s,x) = \phi(s)(x)$. For any function $w : [-\tau, \omega) \to X$, where $\omega > 0$, we define $w_t \in C$ with $t \in [0, \omega)$ by $w_t(\theta) = w(t+\theta)$ for $\theta \in [-\tau, 0]$.

Let $w(t)(x) = u_m(t,x)$. For any $\phi \in C^+$, define $F : C^+ \to X$ by

$$F(\phi) = -d(\phi(0)) + \int_0^{\tau} T(D_i s) f(s) e^{-\gamma s} b(\phi(-s))\, ds. \tag{2.3}$$

Then F is Lipschitz continuous in any bounded subset of C^+. Further, let $A = \triangle_x$. The initial value problem for the second equation of (1.1), namely

$$\begin{aligned} &\frac{\partial u_m(t,x)}{\partial t} = D_m \triangle_x u_m(t,x) - d(u_m(t,x)) \\ &\qquad + \int_0^{\tau} \int_{\Omega} G(D_i s, x, \xi) f(s) e^{-\gamma s} b(u_m(t-s,\xi))\, d\xi\, ds, \quad t > 0, x \in \Omega, \\ &Bu_m(t,x) = 0, \quad t \geqslant 0, x \in \partial\Omega \end{aligned} \tag{2.4}$$

can be rewritten as

$$\begin{aligned} &\frac{dw}{dt} = D_m A w + F(w_t), \quad t > 0, \\ &w_0 = \phi \in C^+, \end{aligned} \tag{2.5}$$

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or equivalently

$$w(t) = T(D_m t)[\phi(0)] + \int_0^t T(D_m(t-\alpha))F(w_\alpha)\,d\alpha, \quad t \geqslant 0. \tag{2.6}$$

Definition 2.1 A supersolution (subsolution) of (2.4) is a function $v : [-\tau, \omega) \to X, \omega > 0$ satisfying

$$v(t) \geqslant (\leqslant) T(D_m t)[v(0)] + \int_0^t T(D_m(t-\alpha))F(v_\alpha)\,d\alpha, \quad t \in [0, \omega). \tag{2.7}$$

If v is both supersolution and subsolution on $[0, \omega)$, then it is called a mild solution of (2.4).

Remark 2.1 Assume that there is a bounded and continuous $v : [-\tau, \omega) \times \bar{\Omega} \to \mathbb{R}$, with $\omega > 0$ and such that v is in C^2 for $x \in \Omega$, C^1 for $t \in [-\tau, \omega)$ satisfying

$$\frac{\partial v(t,x)}{\partial t} \geqslant (\leqslant) D_m \triangle_x v(t,x) - d(v(t,x)) + \int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} b(v(t-s,\xi))\,d\xi\,ds,$$
$$t \in [-\tau, \omega),\ x \in \Omega,$$
$$Bv(t,x) \geqslant (\leqslant) 0, \quad t \in [-\tau, \omega),\ x \in \partial\Omega. \tag{2.8}$$

Then, by the fact $T(t)X^+ \subset X^+$ for all $t \geqslant 0$, it follows that (2.7) holds, and hence $v(t,x)$ is a supersolution (subsolution) of (2.4) on $[0, \omega)$.

The proving methods of the following theorems (Theorems 2.1 and 2.2) are motivated from Xu and Zhao (2003), and we shall omit some details if it is necessary.

Theorem 2.1 *Assume that (P1)–(P4) hold. For a given initial condition* $(u_{i0}, u_{m0}) \in C^+$, *there exists a unique nonnegative solution* $(u_i(t,x), u_m(t,x))$ *of (2.4) defined on* $[-\tau, \infty)$. *Furthermore, if* $u_{m0} \in [0, \hat{u}_m]_C$, *then* $u_{mt} \in [0, \hat{u}_m]_C$, *where* $u_{mt}(\theta, x) = u_m(t+\theta, x), (\theta, x) \in [-\tau, 0] \times \bar{\Omega}$. *Finally, the semiflow* $\Phi(t) = u_{mt}(\cdot) : C^+ \to C^+, t \geqslant 0$, *admits a connected global attractor which is in* $[0, \hat{u}_m]_C$.

Proof For any $L > u_m^*$ and any $\phi \in [0, L]_C$, we have

$$\phi(0) + hF(\phi) = \phi(0) + h\left[-d(\phi(0)) + \int_0^\tau T(D_i s) f(s) e^{-\gamma s} b(\phi(-s))\,ds\right]$$
$$\geqslant \phi(0)\left[1 - h \max_{u_m \in [0,L]} d'(u_m)\right] \geqslant 0,$$

when $h > 0$ is so small that $1 - h \max_{u_m \in [0,L]} d'(u_m) > 0$. On the other hand, for a given

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$x \in \bar{\Omega}$ such that $\phi(0)(x) = \phi(0,x) \geqslant u_m^*$, we have

$$\begin{aligned}\phi(0)(x) + hF(\phi)(x) &= \phi(0)(x) + h\left[-d(\phi(0)) + \int_0^\tau T(D_i s) f(s) e^{-\gamma s} b(\phi(-s))\, ds\right](x) \\ &\leqslant \phi(0)(x) + h\left[-d(u_m^*) + b(u_m^*)\int_0^\tau T(D_i s) f(s) e^{-\gamma s}\, ds\right] \\ &\leqslant \phi(0)(x) \leqslant L,\end{aligned}$$

and for $x \in \bar{\Omega}$ with $\phi(0)(x) < u_m^*$, we have

$$\begin{aligned}\phi(0)(x) + hF(\phi)(x) &= \phi(0)(x) + h\left[-d(\phi(0)) + \int_0^\tau T(D_i s) f(s) e^{-\gamma s} b(\phi(-s))\, ds\right](x) \\ &\leqslant \phi(0)(x) + hb(u_m^*)\int_0^\tau \left[T(D_i s) f(s) e^{-\gamma s}\, ds\right] \\ &\leqslant \phi(0)(x) + L - u_m^* \leqslant L,\end{aligned}$$

provided that $h > 0$ is so small that $hb(u_m^*)\int_0^\tau T(D_i s) f(s) e^{-\gamma s}\, ds \leqslant L - u_m^*$. Therefore, we always have $\phi(0) + hF(\phi) \in [0, L]_X$. Consequently, for $L > u_m^*$, we obtain

$$\lim_{h\to 0+} \frac{1}{h} \text{dist}\,(\phi(0) + hF(\phi); [0, L]_X) = 0, \ \forall \phi \in [0, L]_C.$$

By Corollary 4 in Martin and Smith (1990) with $K = [0, L]_C, S(t,s) = T(D_m(t-s)), B(t,\phi) = F(\phi)$, we conclude that (2.4) admits a unique mild solution $w(t;\phi)$ with $w_t(\phi) \in [0, L]_C$ for $t \in [0, \infty)$. Moreover, we have from Corollary 2.2.5 in Wu (1996) that $w(t;\phi)$ is a classical solution of (2.4) for $t > \tau$, and $[0, L]_C$ is an invariant subset in C^+ for (2.4).

For any $L \in [\hat{u}_m, u_m^*]$, F is globally Lipschitz continuous in $[0, L]_C$ and F is quasi-monotone on $[0, L]_C$ in the sense that

$$\lim_{h\to 0+} \frac{1}{h} \text{dist}\left([\phi_1(0) - \phi_2(0)] + h[F(\phi_1) - F(\phi_2)]; X^+\right) = 0 \tag{2.9}$$

for all $\phi_1, \phi_2 \in [0, L]_C$ with $\phi_1 \geqslant \phi_2$. In fact, it follows from (P4) that

$$\begin{aligned}F(\phi_1) - F(\phi_2) &= -[d(\phi_1(0)) - d(\phi_2(0))] + \int_0^\tau T(D_i s) e^{-\gamma s} f(s)[b(\phi_1(-s)) - b(\phi_2(-s))]\, ds \\ &\geqslant -[d(\phi_1(0)) - d(\phi_2(0))],\end{aligned}$$

hence, for any $h > 0$ with $1 > h \max_{\xi\in[0,L]}\{|d'(\xi)|\}$,

$$\phi_1(0) - \phi_2(0) + h[F(\phi_1) - F(\phi_2)] \geqslant \left[1 - h\max_{\xi\in[0,L]}\{|d'(\xi)|\}\right][\phi_1(0) - \phi_2(0)] \geqslant 0,$$

from which (2.9) follows. We note that L and 0 are a supersolution and subsolution of (2.4) in view of Definition 2.1. Therefore, the existence and uniqueness of $w \in [0, L]_C$ on $[0, \infty)$ follows from Corollary 5 in Martin and Smith (1990) with $S(t,s) = T(D_m(t-s))$ for $t \geqslant s \geqslant 0$, $v^+(t) = L, v^-(t) = 0$ and $B(t,\phi) = F(\phi)$. This also implies that $[0, L]_C$ is an

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invariant subset in C^+ for (2.4). Summarising the above discussion, we conclude that for any $\phi \in C^+$, (2.4) admits a unique solution $w(t;\phi)$ which exists on $[-\tau, \infty)$.

Let

$$g(t,x) = b(u_m(t,x)) - \int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} b(u_m(t-s,\xi))\, d\xi\, ds, \tag{2.10}$$

then the equation for $u_i(t,x)$ is

$$\frac{\partial u_i(t,x)}{\partial t} = D_i \triangle_x u_i(t,x) - \gamma u_i(t,x) + g(t,x),\ t > 0, x \in \Omega. \tag{2.11}$$

Now the existence and uniqueness of u_i with a corresponding boundary condition and a given initial data follow from the standard existence theorem for linear parabolic partial differential equations.

The rest of the proof is similar to that in Theorem 3.1 of Xu and Zhao (2003), and we omit it. □

We have from (P2) and (P3) that $(0,0)$ is an equilibrium of (1.1). The linearised equation of the second equation for (1.1) at zero solution is

$$\frac{\partial u(t,x)}{\partial t} = D_m \triangle_x u(t,x) - d'(0)u(t,x) + b'(0) \int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} u(t-s,\xi)\, d\xi\, ds. \tag{2.12}$$

Substituting $u(t,x) = e^{\lambda t} v(x)$ into (2.12), we obtain the following eigenvalue problem:

$$\lambda v(x) = D_m \triangle_x v(x) - d'(0)v(x) + b'(0) \int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} e^{-\lambda s} v(\xi)\, d\xi\, ds, \quad x \in \Omega,$$
$$Bv(x) = 0,\ x \in \partial\Omega. \tag{2.13}$$

Recall that $(\alpha_k, \psi_k), k = 1, 2, \ldots,$ are the eigenvalues and normalised eigenfunctions of $-\triangle_x$ on Ω subject to the given boundary condition with $\alpha_1 < \alpha_2 < \cdots$. Noting that

$$\int_\Omega G(D_i s, x, \xi) \psi_k(\xi)\, d\xi = e^{-D_i s \alpha_k} \psi_k(x), \quad k = 1, 2, \ldots,$$

we obtain from (2.13) that

$$\lambda = -(\alpha_k D_m + d'(0)) + b'(0) \int_0^\tau f(s) e^{-(\gamma+\lambda+D_i\alpha_k)s}\, ds, \quad k = 1, 2, \ldots. \tag{2.14}$$

It is well known that, as $b'(0) > 0$, each equation (2.14) with a fixed $k = 1, 2, \ldots$ has a real zero $\lambda_{k,1}$ and a complex conjugate pair of zeros $\lambda_{k,2}, \overline{\lambda_{k,2}}, \lambda_{k,3}, \overline{\lambda_{k,3}}, \ldots$ with

$$\lambda_{k,1} > \mathrm{Re}\lambda_{k,2} > \mathrm{Re}\lambda_{k,3} \ldots. \tag{2.15}$$

Furthermore, we can easily show that

$$\lambda_{1,1} > \lambda_{2,1} > \lambda_{3,1} \ldots. \tag{2.16}$$

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In fact, let $f(\lambda,\alpha) := \lambda + (\alpha D_m + d'(0)) - b'(0)\int_0^\tau f(s)e^{-(\gamma+\lambda+D_i\alpha)s}ds$ and $\lambda = \lambda(\alpha)$ be the function defined by $f(\lambda,\alpha) = 0$. We obtain

$$\frac{d\lambda}{d\alpha} = -\frac{\partial f/\partial\alpha}{\partial f/\partial\lambda} = -\frac{D_m + b'(0)D_i\int_0^\tau f(s)se^{-(\gamma+\lambda+D_i\alpha)s}\,ds}{1 + b'(0)\int_0^\tau f(s)se^{-(\gamma+\lambda+D_i\alpha)s}\,ds} < 0.$$

Thus $\lambda(\alpha)$ is non-increasing on α, and (2.16) holds because $\alpha_k < \alpha_{k+1}$ for $\forall k$. By a similar argument in Theorem 2.2 of Thieme and Zhao (2003) that (2.13) has a principal eigenvalue λ_0 with a strictly positive eigenfunction. Therefore, the sign of

$$\lambda_0 := \lambda_{1,1} \in \mathbb{R} \tag{2.17}$$

determines the stability of the zero solution of (2.12). Let

$$g_k(\lambda) = \lambda + \alpha_k D_m + d'(0) - b'(0)\int_0^\tau f(s)e^{-\gamma s}e^{-\lambda s}e^{-D_i s\alpha_k}\,ds.$$

Then

$$\begin{aligned}
&g_k(-\infty) = -\infty < g_k(0) < g_k(\infty) = \infty,\\
&g_k'(\lambda) = 1 + b'(0)\int_0^\tau sf(s)e^{-\gamma s}e^{-\lambda s}e^{-D_i s\alpha_k}\,ds > 0,\\
&g_k(0) = \alpha_k D_m + d'(0) - b'(0)\int_0^\tau f(s)e^{-\gamma s}e^{-D_i s\alpha_k}\,ds.
\end{aligned}$$

Therefore,

$$\lambda_{k,1} > 0 \text{ if and only if } \alpha_k D_m + d'(0) - b'(0)\int_0^\tau f(s)e^{-\gamma s}e^{-D_i s\alpha_k}\,ds < 0.$$

Consequently,

$$\lambda_0 > 0 \text{ if and only if } \alpha_1 D_m + d'(0) - b'(0)\int_0^\tau f(s)e^{-\gamma s}e^{-D_i s\alpha_1}\,ds < 0. \tag{2.18}$$

The following theorem gives a threshold dynamics for the mature population of system (1.1): if the zero solution is linearly asymptotically stable, the mature population goes to extinction; if the zero solution is linearly unstable, the mature population is uniformly persistent and there exists a globally attractive positive steady state w^+.

Theorem 2.2 *Assume (P1)–(P4) and $\lambda_0 \neq 0$. We have the following threshold dynamics*:

(i) if $\lambda_0 < 0$, then $\lim_{t\to\infty}\|w(t;\phi)\| = 0\ \forall\phi \in C^+$;

(ii) if $\lambda_0 > 0$, then (2.4) admits a unique steady state w^+ with $w^+ \in int(X^+) \cap [0,\hat{u}_m]_X$, and $\lim_{t\to\infty}\|w(t;\phi) - w^+\| = 0\ \forall\phi \in C^+$.

Proof As discussed above, if $\lambda_0 < 0$, then $\lim_{t\to\infty}\|u(t,\cdot;\phi)\| = 0$, $\forall\phi \in C^+$, where $u(t,x;\phi)$ is the unique solution of (2.12). Note that (P2) and (P3) lead to $b(u) \leqslant b'(0)u$ and

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$d(u) \geqslant d'(0)u\ \forall u \geqslant 0$. Thus the solution of the second equation in (1.1) satisfies, for $t > 0$, that

$$\frac{\partial u_m(t,x)}{\partial t} \leqslant D_m \triangle_x u_m(t,x) - d'(0)u_m(t,x) + b'(0)\int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} u_m(t-s,\xi)\, d\xi\, ds.$$

The comparison theorem for abstract functional differential equations (see, for example, Proposition 3 in Martin and Smith, 1990) implies that $0 \leqslant u_m(t,\cdot;\phi) \leqslant u(t,\cdot;\phi), \forall t \geqslant -\tau$. It then follows that $\lim_{t\to\infty} \|u_m(t,\cdot;\phi)\| \leqslant \lim_{t\to\infty} \|u(t,\cdot;\phi)\| = 0\ \forall \phi \in C^+$.

The proof for the case $\lambda_0 > 0$ is similar to the proof of Theorem 3.2 in Xu and Zhao (2003), and thus the readers are referred to Xu and Zhao (2003). □

Let $\mathbb{C} := C([-\tau,0] \times \bar{\Omega}, \mathbb{R})$ with a norm of supremum, and $\mathbb{C}^+ := \{\phi \in \mathbb{C} : \phi(s,x) \geqslant 0, (s,x) \in [-\tau,0] \times \bar{\Omega}\}$. The following corollary gives the global attractivity of a unique non-trivial equilibrium.

Corollary 2.1 *Assume (P1)–(P4) and*

$$\alpha_1 D_m + d'(0) < b'(0)\int_0^\tau f(s) e^{-\gamma s} e^{-D_i s \alpha_1}\, ds. \tag{2.19}$$

Then (1.1) has a unique non-trivial nonnegative equilibrium (u_m^+, u_i^+) which is globally attractive, where the initial function is $(\phi,\psi) \in \mathbb{C}^+ \times \mathbb{C}^+$. Moreover, $u_m^+(x) \in [0, \hat{u}_m]_X$, and u_i^+ is given by the following boundary value problem:

$$\begin{aligned} &D_i \triangle_x u_i(x) - \gamma u_i(x) + \bar{g}(x) = 0,\ \ x \in \Omega, \quad Bu_i(x) = 0,\ \ x \in \partial\Omega, \\ &\bar{g}(x) := b(u_m^+(x)) - \int_0^\tau \int_\Omega G(D_i s, x, \xi) f(s) e^{-\gamma s} b(u_m^+(\xi))\, d\xi\, ds. \end{aligned} \tag{2.20}$$

Proof (2.19) implies $\lambda_0 > 0$. For any initial function $(\phi,\psi) \in \mathbb{C}^+ \times \mathbb{C}^+$, assume that the solution of (1.1)–(1.3) with the initial condition (ϕ,ψ) is $(u_+(t,x), u_i(t,x))$. In view of conclusion (ii) in Theorem 2.2, we only need to discuss the global attractivity of $u_i^+(x)$. Let $g(t,x), \bar{g}(x)$ be defined in (2.10) and (2.20), respectively. Since $u_m(t,x) \to u_m^+(x)$ as $t \to \infty$, we have

$$g(t,x) \to \bar{g}(x) = \frac{\partial u_m^+(x)}{\partial t} - \triangle_x u_m^+(x) \quad \text{as } t \to \infty,$$

$\forall \epsilon > 0$, there is a $t_1 > 0$ such that for $t \geqslant t_1$,

$$\frac{\partial u_i^+(x)}{\partial t} - \triangle_x u_i^+(x) - \epsilon \leqslant g(t,x) \leqslant \frac{\partial u_i^+(x)}{\partial t} - \triangle_x u_i^+(x) + \epsilon.$$

Let $v(t,x) = u_i(t,x) - u_i^+(x)$, then we have from (2.11) and the above inequality that

$$D_i \triangle_x v(t,x) - \gamma v(t,x) - \epsilon \leqslant \frac{\partial v(t,x)}{\partial t} \leqslant D_i \triangle_x v(t,x) - \gamma v(t,x) + \epsilon,\ \ t \geqslant t_1. \tag{2.21}$$

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Note that the solution of the initial boundary value problem

$$\begin{aligned} &\frac{\partial \bar{v}(t,x)}{\partial t} = D_i \triangle_x \bar{v}(t,x) - \gamma \bar{v}(t,x), \quad t > t_1, x \in \Omega, \\ &B\bar{v}(t,x) = 0, \quad t \geqslant t_1, x \in \partial\Omega, \\ &\bar{v}(t_1,x) = \varphi(x), \quad x \in \bar{\Omega}, \end{aligned}$$

is $\bar{v}(t,x) = \exp\{-\gamma(t-t_1)\}\int_\Omega G(s,x,\xi)\varphi(\xi)d\xi, t \geqslant t_1, x \in \bar{\Omega}$, which is convergent to zero uniformly for x as $t \to \infty$. On the other hand, the solution of

$$\frac{\partial \tilde{v}(t,x)}{\partial t} = D_i \triangle \tilde{v}(t,x) - \gamma \tilde{v}(t,x) + \epsilon, \quad t > t_1, x \in \Omega,$$

is $\tilde{v}(t,x) = \bar{v}(t,x) + \frac{\epsilon}{\gamma}$ with $B\tilde{v}(t,x) = \frac{\epsilon p(x)}{\gamma} \geqslant 0,\ t \geqslant t_1,\ x \in \partial\Omega$ and $\tilde{v}(t_1,x) = \varphi(x) + \frac{\epsilon}{\gamma}$. If $v(t_1,x) = \tilde{v}(t_1,x)$, then we have from the comparison theorem of parabolic PDEs that

$$v(t,x) \leqslant \bar{v}(t,x) + \frac{\epsilon}{\gamma} \quad \text{for } t \geqslant t_1, x \in \Omega.$$

Similarly, we have

$$v(t,x) \geqslant \bar{v}(t,x) - \frac{\epsilon}{\gamma} \quad \text{for } t \geqslant t_1, x \in \Omega.$$

Since $\epsilon > 0$ is arbitrary, the convergence of $\bar{v}(t,x)$ implies that $v(t,x) \to 0$ uniformly for x as $t \to \infty$. □

3 Model on a cylindrical domain and solution semi-flow

We now consider the situation when the species is distributed in a cylindrical domain $\Omega \times \mathbb{R}$. Let $u(t,a,x,y)$ be the density of individuals of age a at location $(x,y) \in \Omega \times \mathbb{R}$ and at time t. Then for any $s \in (0,\tau]$, the juvenile population evolves according to the von Foerster equation

$$\begin{aligned} &\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = D_i \triangle u - \gamma u, \quad a \in (0,s), t > 0, (x,y) \in \Omega \times \mathbb{R}, \\ &u(t,0,x,y) = b(u_m(t,x,y)), \quad t \geqslant -\tau, (x,y) \in \Omega \times \mathbb{R}, \\ &Bu(t,a,x,y) = 0, \quad x \in \partial\Omega,\ a \in (0,s), t \geqslant 0, y \in \mathbb{R}. \end{aligned} \tag{3.1}$$

Here and in what follows, we denote $\triangle = \triangle_x + \frac{\partial^2}{\partial y^2}$, and obviously the above boundary operator applies only to the $x \in \partial\Omega$ component. Furthermore, the mature population $u_m(t,x,y)$ satisfies

$$\begin{aligned} &\frac{\partial u_m}{\partial t} = D_m \triangle u_m - d(u_m) + U(t,x,y), \quad t > 0, (x,y) \in \Omega \times \mathbb{R}, \\ &Bu_m(t,x,y) = 0, \quad t \geqslant 0,\ (x,y) \in \partial\Omega \times \mathbb{R}, \end{aligned} \tag{3.2}$$

where $U(t,x,y)$ expresses the recruitment term to be derived in the following.

We want to calculate the rate of adult recruitment at (t,x,y), i.e., the rate at which individuals just reach maturity at the location (x,y). Of all the individuals just reaching maturity, some will take time s to mature (an amount of time between s and $s+ds$ with ds

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infinitesimal) with the given probability $f(s)$. These individuals will have born at various location in $\Omega \times \mathbb{R}$ and will have drifted around, being at point (x, y) upon becoming mature. We shall find an expression for $u(t, s, x, y)$ at this stage.

Let $v(r, a, x, y) = u(a + r, a, x, y)$. It follows that

$$\begin{aligned} \frac{\partial v}{\partial a}(r, a, x, y) &= \left[\frac{\partial u}{\partial t}(t, a, x, y) + \frac{\partial u}{\partial a}(t, a, x, y)\right]_{t=r+a} \\ &= D_i \triangle u(a + r, a, x, y) - \gamma u(a + r, a, x, y) \\ &= D_i \triangle v(r, a, x, y) - \gamma v(r, a, x, y), \\ v(r, 0, x, y) &= b(u_m(r, x, y)). \end{aligned}$$

Regarding r as a parameter and integrating the last equation, we get

$$v(r, a, x, y) = e^{-\gamma a} \int_{\mathbb{R}} \int_{\Omega} \Gamma(D_i a, x, z_x, y, z_y) b(u_m(r, z_x, z_y))\, dz_x\, dz_y,$$

where

$$\begin{aligned} \Gamma(D_i t, x, z_x, y, z_y) &= G(D_i t, x, z_x) G_1(D_i t, y, z_y), \\ G_1(D_i t, y, z_y) &= \frac{1}{\sqrt{4\pi D_i t}} e^{-\frac{(y-z_y)^2}{4D_i t}}, \end{aligned} \tag{3.3}$$

and G is defined in (2.1). Since $u(t, s, x, y) = v(t - s, s, x, y)$, we conclude that

$$u(t, s, x, y) = \int_{\mathbb{R}} \int_{\Omega} \Gamma(D_i s, x, z_x, y, z_y) e^{-\gamma s} b(u_m(t - s, z_x, z_y))\, dz_x\, dz_y.$$

The above quantity gives us the rate at which individuals born time s ago become mature at (t, x, y). The total rate for individuals becoming mature at (t, x, y) is

$$\begin{aligned} U(t, x, y) &= \int_0^{\tau} f(s) u(t, s, x, y)\, ds \\ &= \int_0^{\tau} \int_{\mathbb{R}} \int_{\Omega} \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} b(u_m(r, z_x, z_y))\, dz_x\, dz_y\, ds. \end{aligned} \tag{3.4}$$

Substituting (3.4) into (3.2), we obtain the system for the mature population

$$\begin{aligned} \frac{\partial u_m}{\partial t} &= D_m \triangle u_m - d(u_m) \\ &\quad + \int_0^{\tau} \int_{\mathbb{R}} \int_{\Omega} \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} b(u_m(t - s, z_x, z_y))\, dz_x\, dz_y\, ds, \\ &\qquad\qquad t > 0, (x, y) \in \Omega \times \mathbb{R}, \\ Bu_m(t, x, y) &= 0, \quad t \geqslant 0,\ (x, y) \in \partial\Omega \times \mathbb{R}. \end{aligned} \tag{3.5}$$

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Consequently, the subsystem for the juvenile population is

$$\begin{aligned}
\frac{\partial u_i}{\partial t} &= D_i \triangle u_i - \gamma u_i + b(u_m(t,x,y)) \\
&\quad - \int_0^\tau \int_{\mathbb{R}} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} b(u_m(t-s, z_x, z_y))\, dz_x\, dz_y\, ds, \\
&\quad t > 0, (x,y) \in \Omega \times \mathbb{R}, \\
Bu_i(t,x,y) &= 0, t \geqslant 0, \ (x,y) \in \partial\Omega \times \mathbb{R}.
\end{aligned} \tag{3.6}$$

Note that

$$\int_{\mathbb{R}} G_1(D_i t, y, z_y)\, dz_y = 1, \quad \forall t > 0, y \in \mathbb{R},$$

$$\int_\Omega G(D_i t, x, z_x)\, dz_x \begin{cases} = 1, & t \geqslant 0, x \in \Omega \quad \text{in case of NC}, \\ \leqslant 1 & t \geqslant 0, x \in \Omega \quad \text{in case of RC}. \end{cases}$$

An equilibrium of (3.5) and (3.6) invariant with respect to the y-variable is given by the equilibrium of (1.1). Therefore, by Corollary 2.1, (3.5) and (3.6) have a y-invariant equilibrium $(0,0)$ and a nontrivial nonnegative equilibrium (u_m^+, u_i^+), if (P1)–(P4) and (2.19) are satisfied.

Let $Y = BC(\bar{\Omega} \times \mathbb{R}, \mathbb{R})$ be the set of all bounded and continuous functions from $\bar{\Omega} \times \mathbb{R}$ to $\mathbb{R}$. Let $Y^+ = \{\phi \in Y : \ \phi(x,y) \geqslant 0, \forall (x,y) \in \bar{\Omega} \times \mathbb{R}\}$, and $[0, u_m^+]_Y = \{\phi \in Y^+ : \ 0 \leqslant \phi(x,y) \leqslant u_m^+(x), \forall (x,y) \in \bar{\Omega} \times \mathbb{R}\}$. It is easy to see that Y^+ is a closed cone of Y under the partial ordering induced by Y^+. We equip Y with a compact open topology. That is, $v^n \to v$ in Y means that the sequence of functions $v^n(x,y)$ converges to $v(x,y)$ uniformly for (x,y) in every compact set. Moreover, we define a norm $\|u\|_Y$ by

$$\|u\|_Y = \sum_{k=0}^{\infty} \frac{\max_{x \in \bar{\Omega}, |y| \leqslant k} |u(x,y)|}{2^k}.$$

It follows that $(Y, \|u\|_Y)$ is a normed space. Let $\rho(u,v)$ be the metric on Y induced by the norm $\|u\|_Y$. It can be seen that Y is a Banach lattice.

Let the Green's function of

$$\begin{aligned}
\frac{\partial w}{\partial t} &= D_m \triangle w, \quad (x,y) \in \Omega \times \mathbb{R}, t > 0, \\
Bw(t,x,y) &= 0, \quad x \in \partial\Omega, \ y \in \mathbb{R}, t \geqslant 0.
\end{aligned}$$

be $\Gamma(D_m t, x, \xi, y, \zeta)$. The solution of the above equation with the initial function $\psi(x,y)$ is

$$\begin{aligned}
w(t,x,y,\psi) &= \int_{\mathbb{R}} \int_\Omega \Gamma(D_m t, x, \xi, y, \zeta) \psi(\xi, \zeta)\, d\xi\, d\zeta \\
&=: [\bar{T}(D_m t)\psi](x,y).
\end{aligned}$$

Then $\bar{T}(t) : Y \to Y$ is a linear C_0-semigroup with $\bar{T}(t) Y^+ \subset Y^+$ for all $t \geqslant 0$ (see Lunardi (1995)).

Let $C_Y = C([-\tau, 0], Y)$ be the set of continuous functions from $[-\tau, 0]$ to Y and let $C_Y^+ = \{\phi \in C_Y : \phi(s) \in Y^+, \forall s \in [-\tau, 0]\}$, and $[0, u_m^+]_{C_Y} = \{\phi \in C_Y^+ : \phi(s, \cdot) \in [0, u_m^+]_Y,$

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$s \in [-\tau, 0]\}$. Then C_Y^+ is a closed cone of C_Y. For any continuous function $w : [-\tau, \omega) \to Y$, where $\omega > 0$, we define $w_t \in C_Y$ with $t \in [0, \omega)$ by $w_t(\theta) = w(t + \theta)$ for $\theta \in [-\tau, 0]$.

For any $\phi \in C_Y^+$, define $\bar{F} : [0, u_m^+]_{C_Y} \to Y$ by

$$\bar{F}(\phi) = -d(\phi(0)) + \int_0^\tau \bar{T}(D_i s) f(s) e^{-\gamma s} b(\phi(-s))\, ds. \tag{3.7}$$

Then $\bar{F}$ is Lipschitz continuous in any bounded subset of C_Y^+. Further, the initial value problem for (3.5) can be rewritten as

$$w(t) = \bar{T}(D_m t)[\phi(0)] + \int_0^t \bar{T}(D_m(t-\alpha))\bar{F}(w_\alpha)\, d\alpha, \quad t \geqslant 0. \tag{3.8}$$

We can define the notion of supersolution, subsolution and mild solution of (3.5) similarly to Definition 2.1. Now if we use $Y, C_Y, [0, u_m^+]_Y, [0, u_m^+]_{C_Y}, A = \triangle$ and $\bar{T}, \bar{F}$ to replace $X, C_X, [0, \hat{u}_m]_X, [0, \hat{u}_m]_C, A = \triangle_x$ and T, F in (2.3)–(2.6) respectively, we can obtain the following lemma.

Lemma 3.1 *Assume (P1)–(P4) and (2.19) hold. Then we have the following conclusions.*

(1) *If $\phi \in [0, u_m^+]_{C_Y}$, then the solution $u_m(t, x, y; \phi)$ of (3.5) exists to be unique and satisfies $u_{mt}(\cdot; \phi) \in [0, u_m^+]_{C_Y}$ for $\forall t > 0$, where $u_{mt}(\cdot; \phi) = u_m(t + \theta, x, y; \phi)$, $\theta \in [-\tau, 0], (x, y) \in \Omega \times \mathbb{R}$.*

(2) *Let $\bar{u}_m, \underline{u}_m$ be a pair of supersolution and subsolution of (3.5) with $\bar{u}_m(t, x, y), \underline{u}_m(t, x, y) \in [0, \hat{u}_m]$ for $\forall t \in [-\tau, \infty), (x, y) \in \Omega \times \mathbb{R}$, respectively. If $\bar{u}_m(\theta, x, y) \geqslant \underline{u}_m(\theta, x, y)$ for $(\theta, x, y) \in [-\tau, 0] \times \Omega \times \mathbb{R}$, then $\bar{u}_m(t, \cdot, \cdot) \geqslant \underline{u}_m(t, \cdot, \cdot)$ for all $t \geqslant 0$. Moreover, if $\bar{u}_m(\theta, x, y) \geqslant \underline{u}_m(\theta, x, y), (\theta, x, y) \in [-\tau, 0] \times \Omega \times \mathbb{R}$ with $\bar{u}_m(0, \cdot, \cdot) \not\equiv \underline{u}_m(0, \cdot, \cdot)$ on $\Omega \times \mathbb{R}$, then $\bar{u}_m(t, x, y) > \underline{u}_m(t, x, y)$ for all $(t, x, y) \in (0, \infty) \times \bar{\Omega} \times \mathbb{R}$.*

Proof Under the abstract setting (see Martin and Smith, 1990) and by a similar argument as for the existence of solutions for (2.4) in Theorem 2.1, one can obtain the conclusion (1). We omit it here.

Now, we show conclusion (2). Let $\bar{u}_m, \underline{u}_m$ be a pair of supersolution and subsolution of (3.5) with $\bar{u}_m(t, x, y), \underline{u}_m(t, x, y) \in [0, \hat{u}_m]$ for $\forall t \in [-\tau, \infty), (x, y) \in \Omega \times \mathbb{R}$, respectively. We have from Corollary 5 in Martin and Smith (1990) and the fact $\bar{u}_m(\theta, x, y) \geqslant \underline{u}_m(\theta, x, y)$ for $(\theta, x, y) \in [-\tau, 0] \times \Omega \times \mathbb{R}$, that the solutions of (3.8) satisfy

$$0 \leqslant w(t, \cdot; \underline{u}_{m0}) \leqslant w(t, \cdot; \bar{u}_{m0}) \leqslant \hat{u}_m, \quad t \geqslant 0.$$

Again by applying Corollary 5 in Martin and Smith (1990) with $[v^+(t, \cdot) = \hat{u}_m, v^-(t, \cdot) = \underline{u}_m(t, \cdot)]$, $[v^+(t, \cdot) = \bar{u}_m(t, \cdot), v^-(t, \cdot) = 0]$ respectively, we obtain

$$\underline{u}_m(t, \cdot) \leqslant w(t, \cdot; \underline{u}_{m0}) \leqslant \hat{u}_m, \quad t \geqslant 0$$
$$0 \leqslant w(t, \cdot; \bar{u}_{m0}) \leqslant \bar{u}_m(t, \cdot), \quad t \geqslant 0.$$

Combining the above three inequalities, we have $\underline{u}_m(t, x, y) \leqslant \bar{u}_m(t, x, y)$ for all $(t, x, y) \in (0, \infty) \times \bar{\Omega} \times \mathbb{R}$.

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Let $v = \bar{u}_m - \underline{u}_m$. Then we have already known that $v(t,x,y) \geqslant 0$ for all $(t,x,y) \in (0,\infty) \times \bar{\Omega} \times \mathbb{R}$. We have from the definition of supersolution and subsolution, the monotonicity of b on $[0,\hat{u}_m]$, and the fact $\bar{T}Y^+ \subset Y^+$ for $t \geqslant 0$ that

$$\begin{aligned} v(t) &\geqslant \bar{T}(D_m t)v(0) + \int_0^t \bar{T}(D_m(t-\alpha))[\bar{F}(\bar{u}_{m\alpha}) - \bar{F}(\underline{u}_{m\alpha})]\,d\alpha \\ &\geqslant \bar{T}(D_m t)v(0) + \int_0^t \bar{T}(D_m(t-\alpha))[d(\underline{u}_m(\alpha)) - d(\bar{u}_m(\alpha))]\,d\alpha \\ &= \bar{T}(D_m t)v(0) - \int_0^t \bar{T}(D_m(t-\alpha))d'(\xi(\alpha))v(\alpha)\,d\alpha, \qquad t \geqslant 0, \end{aligned}$$

where $\xi(\alpha) \in [\underline{u}_m(\alpha), \bar{u}_m(\alpha)] \subset [0,\hat{u}_m]$ for $\forall \alpha \in [0,\infty)$. Therefore, let $d_M = \max_{u \in [0,\hat{u}_m]} d'(u)$, we have

$$v(t) \geqslant \bar{T}(D_m t)v(0) - d_M \int_0^t \bar{T}(D_m(t-\alpha))v(\alpha)d\alpha.$$

Define

$$z(t) = e^{-d_M t}\bar{T}(D_m t)v(0), \qquad t \geqslant 0.$$

Then $z(t)$ satisfies

$$\bar{T}(D_m t)z(0) - d_M \int_0^t \bar{T}(D_m(t-\alpha))z(\alpha)\,d\alpha = z(t), \quad t \geqslant 0. \tag{3.9}$$

By Proposition 3 in Martin and Smith (1990) with $v^-(t) = z(t), v^+(t) = +\infty, S(t,s) = \bar{T}(D_m(t-s)), B(t,\phi) = B^-(t,\phi) = -d_M\phi(0)$, we get $v(t) \geqslant z(t)$ for $t \geqslant 0$, that is

$$v(t) \geqslant e^{-d_M t}\bar{T}(D_m t)v(0) = e^{-d_M t}\int_{\mathbb{R}}\int_{\Omega} \Gamma(D_m t, x, \xi, y, \zeta)v(0,\xi,\zeta)\,d\xi\,d\zeta \quad \text{for all } t \geqslant 0.$$

Thus it follows that $v(t) > 0$ for $t > 0$ if $v(0,x,y) \not\equiv 0$ on $\Omega \times \mathbb{R}$. □

Let $\mathscr{C}$ be the set of all bounded and continuous functions from $[-\tau,0] \times \Omega \times \mathbb{R}$ to $\mathbb{R}$. For $u,v \in \mathscr{C}$, we write $u \geqslant v (u \gg v)$ provided $u(\theta,x,y) \geqslant v(\theta,x,y)(u(\theta,x,y) > v(\theta,x,y)), \forall(\theta,x,y) \in [-r,0] \times \Omega \times \mathbb{R}$, and $u > v$ provided $u \geqslant v$ but $u \not\equiv v$. Define $\mathscr{C}_- = C([-\tau,0] \times \Omega, \mathbb{R})$. Clearly every element in $\mathscr{C}_-$ can be regarded as an element in $\mathscr{C}$. For any $r \in \mathbb{R}$ with $r > 0$, we define $\mathscr{C}_r := \{u \in \mathscr{C} : r \geqslant u \geqslant 0\}, \mathscr{C}_{r-} := \{u \in \mathscr{C}_- : r \geqslant u \geqslant 0\}$. Specially, we let $\mathscr{C}_{u_m^+} := \{u \in \mathscr{C} : u_m^+(x) \geqslant u \geqslant 0\}$. Since we identify an element $\phi \in C_Y$ as a function from $[-\tau,0] \times \bar{\Omega} \times \mathbb{R}$ into $\mathbb{R}$ defined by $\phi(s,x,y) = \phi(s)(x,y)$, $\phi \in \mathscr{C}$ implies $\phi \in C_Y$ and vice versa. We also have the same interpretation for $\phi \in \mathscr{C}_{u_m^+}$ and $\phi \in [0,u_m^+]_{C_Y}$.

In the following, we equip $\mathscr{C}$ with the compact open topology. Thus, $v^n \to v$ in $\mathscr{C}$ means that the sequence of functions $v^n(\theta,x,y)$ converges to $v(\theta,x,y)$ uniformly for (θ,x,y) in every compact set. Moreover, we define the norm $\|u\|$ by

$$\|u\| = \sum_{k=0}^{\infty} \frac{\max_{(\theta,x) \in [-r,0] \times \bar{\Omega}, |y| \leqslant k} |u(\theta,x,y)|}{2^k},$$

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and let $\rho(u,v)$ be the metric on $\mathscr{C}$ induced by the norm $\|u\|$. Note that $\mathscr{C}_{u_m^+}$ is a completed subset of $\mathscr{C}$ under this norm. We also equip $\mathscr{C}_-$ with the maximum norm $\|\cdot\|$ such that $\mathscr{C}_-$ is a Banach space.

Recall that a family of operators $\Sigma_t, t \geqslant 0$, is said to be a semiflow on a metric space $(\mathbb{X}, d)$ with metric d provided Σ_t has the following properties:

(i) $\Sigma_0(v) = v, \forall v \in \mathbb{X}$;

(ii) $\Sigma_{t_1}(\Sigma_{t_2}(v)) = \Sigma_{t_1+t_2}(v), \forall t_1, t_2 \geqslant 0, v \in \mathbb{X}$;

(iii) $\Sigma(t,v) := \Sigma_t(v)$ is continuous in (t,v) on $[0,\infty) \times \mathbb{X}$.

It is easy to see that the property (iii) holds if $\Sigma(\cdot, v)$ is continuous on $[0,+\infty)$ for each $v \in \mathbb{X}$, and $\Sigma(t,\cdot)$ is uniformly continuous for t in bounded intervals in the sense that for any $v_0 \in \mathbb{X}$, bounded interval I and $\epsilon > 0$, there exists $\delta = \delta(v_0, I, \epsilon) > 0$ such that if $d(v, v_0) < \delta$, then $d(\Sigma_t(v), \Sigma_t(v_0)) < \epsilon$ for all $t \in I$.

Define a group of maps $Q_t(\phi) : \mathscr{C}_{u_m^+} \to \mathscr{C}_{u_m^+}, t \geqslant 0$ as follows:

$$(Q_t(\phi))(\theta, x, y) = u_{mt}(\theta, x, y; \phi), \ \ \forall \theta \in [-\tau, 0], (x,y) \in \Omega \times \mathbb{R}.$$

Then we have the following.

Theorem 3.1 *Assume that (P1)–(P4) and (2.19) hold. Then $Q_t, t \geqslant 0$, is a monotone and subhomogeneous semiflow on $\mathscr{C}_{u_m^+}$.*

Proof Clearly, Q_t satisfies property (i) of semiflow. The semiflow property (ii) follows from (3.8) and the properties of linear semigroup $\bar{T}(t)$ (see Pazy, 1983; Garroni and Menaldi, 1992). Furthermore, for any given $\phi \in \mathscr{C}_{u_m^+}$, it then follows from (3.8) and the theory of semigroup that $Q_t(\phi) = u_m(t+\cdot, \cdot; \phi)$ is continuous in $t \in \mathbb{R}_+$ with respect to the compact open topology (see also Section 5.3 in Liang and Zhao, 2007).

Let $u_m(t,x,y)$ and $\bar{u}_m(t,x,y)$ be two solutions of system (3.5) with initial functions $\phi(\theta,\cdot)$, $\bar{\phi}(\theta,\cdot) \in \mathscr{C}_{u_m^+}$. Then we have the following.

Claim. For any $\epsilon > 0$ and $t_0 > 0$, there exist $\delta > 0$ and $M > 0$ such that $|u_m(t,x,z) - \bar{u}_m(t,x,z)| < \epsilon$, $\forall (t,x) \in [0,t_0] \times \bar{\Omega}$ whenever $|\phi(\theta,x,y) - \bar{\phi}(\theta,x,y)| < \delta, \forall \theta \in [-\tau,0], (x,y) \in \bar{\Omega} \times [z-M, z+M]$ with some $z \in \mathbb{R}$.

By the spatial translation invariance of equation (3.5), we only need to verify the claim for the case when $z = 0$. Indeed, letting $v = u_m - \bar{u}_m$, we have

$$\begin{aligned} \frac{\partial v}{\partial t} &= D_m \triangle v - [d(u_m) - d(\bar{u}_m)] + \int_0^\tau \int_{\mathbb{R}} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} \\ &\quad \times [b(u_m(t-s, z_x, z_y)) - b(\bar{u}_m(t-s, z_x, z_y))] \, dz_x \, dz_y \, ds, \ \ \forall t > 0, \ (x,y) \in \Omega \times \mathbb{R}; \\ Bv(t,x,y) &= 0, \forall t \geqslant 0, \ (x,y) \in \partial\Omega \times \mathbb{R}; \\ v(\theta,x,y) &= \phi(\theta,x,y) - \bar{\phi}(\theta,x,y), \forall \theta \in [-\tau,0], (x,y) \in \Omega \times \mathbb{R}. \end{aligned} \tag{3.10}$$

First we assume $\phi \geqslant \bar{\phi}$, and thus $v \geqslant 0$. Note that

$$\int_{\mathbb{R}} G_1(D_i s, y, z_y) \, dz_y = \int_{\mathbb{R}} \frac{1}{\sqrt{4\pi D_i s}} e^{-\frac{(y-z_y)^2}{4D_i s}} \, dz_y = \int_{\mathbb{R}} \frac{1}{\sqrt{4\pi D_i s}} e^{-\frac{u^2}{4D_i s}} \, du = 1.$$

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Let $\gamma_0 > 0$ is the Lipschitz constant of b on $[0, \hat{u}_m]$. Noting that $\tau > 0$, for any $\epsilon > 0$, $t_0 = \tau$ and each $\bar{s} \in [0, \tau]$, we can choose $\bar{M}(\bar{s}) > 0$ such that

$$\int_{-\infty}^{-\bar{M}(\bar{s})} \frac{1}{\sqrt{4\pi D_i s}} e^{-\frac{u^2}{4D_i s}}\, du + \int_{\bar{M}(\bar{s})}^{\infty} \frac{1}{\sqrt{4\pi D_i s}} e^{-\frac{u^2}{4D_i s}}\, du < \frac{\epsilon}{4\gamma_0 \hat{u}_m}.$$

From the continuity, we can find an interval $(\bar{s} - \delta_{\bar{s}}, \bar{s} + \delta_{\bar{s}})$ such that

$$\int_{-\infty}^{-\bar{M}(s)} \frac{1}{\sqrt{4\pi D_i s}} e^{-\frac{u^2}{4D_i s}}\, du + \int_{\bar{M}(s)}^{\infty} \frac{1}{\sqrt{4\pi D_i s}} e^{-\frac{u^2}{4D_i s}}\, du < \frac{\epsilon}{2\gamma_0 \hat{u}_m} \quad \text{for } s \in (\bar{s} - \delta_{\bar{s}}, \bar{s} + \delta_{\bar{s}}).$$

By using Borel's finite covering theorem, there is a $\bar{M} > 0$ which is independent of $s \in [0, \tau]$ such that

$$\int_{-\infty}^{-\bar{M}} \sqrt{4\pi D_i s} e^{-\frac{u^2}{4D_i s}}\, du + \int_{\bar{M}}^{\infty} \sqrt{4\pi D_i s} e^{-\frac{u^2}{4D_i s}}\, du < \frac{\epsilon}{2\gamma_0 \hat{u}_m}.$$

Let $M := 2\bar{M}$, then we have

$$\int_{-\infty}^{-M} G_1(D_i s, y, z_y)\, dz_y + \int_{M}^{\infty} G_1(D_i s, y, z_y)\, dz_y < \frac{\epsilon}{2\gamma_0 \hat{u}_m},$$

which holds uniformly for $y \in [-\bar{M}, \bar{M}]$. Let $\delta > 0$ be chosen such that

$$v(t, x, y) = u_m(t, x, y) - \bar{u}_m(t, x, y) < \frac{\epsilon}{2\gamma_0}, \ \forall t \in [0, \tau], (x, y) \in \bar{\Omega} \times [-M, M],$$

as $|\phi(\theta, x, y) - \bar{\phi}(\theta, x, y)| < \delta, \forall \theta \in [-\tau, 0], (x, y) \in \bar{\Omega} \times [-M, M]$. Therefore, we have from the above conclusions and the Lipschitz condition of b that

$$\begin{aligned}
&\int_0^\tau \int_{\mathbb{R}} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} [b(w(t-s, z_x, z_y)) - b(\bar{w}(t-s, z_x, z_y))]\, dz_x\, dz_y\, ds \\
&\leqslant \gamma_0 \int_0^\tau \int_{-\infty}^{-M} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} v(t-s, z_x, z_y)\, dz_x\, dz_y\, ds \\
&\quad + \gamma_0 \int_0^\tau \int_M^\infty \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} v(t-s, z_x, z_y)\, dz_x\, dz_y\, ds \\
&\quad + \gamma_0 \int_0^\tau \int_{-M}^{M} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} v(t-s, z_x, z_y)\, dz_x\, dz_y\, ds \\
&\leqslant 2\gamma_0 \hat{u}_m \Big[\int_0^\tau \int_{-\infty}^{-M} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s}\, dz_x\, dz_y\, ds \\
&\quad + \int_0^\tau \int_M^\infty \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s}\, dz_x\, dz_y\, ds\Big] \\
&\quad + \frac{\epsilon}{2} \int_0^\tau \int_{-M}^{M} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s}\, dz_x\, dz_y\, ds \\
&\leqslant \frac{\epsilon}{2} + \frac{\epsilon}{2} = \epsilon \qquad \text{for } t \in [0, \tau], (x, y) \in \Omega \times [-\bar{M}, \bar{M}].
\end{aligned}$$

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This, together with (3.10), leads to

$$\begin{aligned}&\frac{\partial v}{\partial t} \leqslant D_m \triangle v - \min_{u\in[0,\hat{u}_m]}\{d'(u)\}v + \epsilon, \quad t \in [0,\tau], (x,y) \in \Omega \times (-\bar{M},\bar{M});\\ &Bv(t,x,y) = 0, \quad t \in [0,\tau],\ x \in \partial\Omega,\ y \in \mathbb{R};\\ &v(\theta,x,y) = \phi(\theta,x,y) - \bar{\phi}(\theta,x,y) \geqslant 0, \quad \theta \in [-\tau,0], (x,y) \in \bar{\Omega} \times \mathbb{R}.\end{aligned} \tag{3.11}$$

Let $d_0 := \min_{u\in[0,\hat{u}_m]}\{d'(u)\}$, then by (P3), we know that $d_0 > 0$. Since the following function

$$u(t,x,y) = \exp\{-d_0 t\}\int_{\mathbb{R}}\int_{\Omega}\Gamma(D_m t,x,\xi,y,\zeta)v(0,\xi,\zeta)\,d\xi\,d\zeta + \frac{\epsilon}{d_0},$$

satisfies

$$\begin{aligned}&\frac{\partial u}{\partial t} = D_m \triangle u - d_0 u + \epsilon, \quad t \in [0,\tau], (x,y) \in \Omega \times (-\bar{M},\bar{M}),\\ &\frac{\partial u}{\partial n}(t,x,y) = 0, \quad t \in [0,\tau], (x,y) \in \partial\Omega \times \mathbb{R} \quad \text{in case of NC},\\ &\text{or } p(x)u(t,x,y) + q(x)\frac{\partial u}{\partial n}(t,x,y) = p(x)\frac{\epsilon}{d_m}, \quad t \in [0,\tau], (x,y) \in \partial\Omega \times \mathbb{R} \quad \text{in case of RC},\\ &u(0,x,y) = v(0,x,y) + \frac{\epsilon}{d_0}, \quad (x,y) \in \bar{\Omega} \times \mathbb{R},\end{aligned}$$

we have from (3.10) and the standard comparison theorem of linear parabolic partial differential equations that v satisfies

$$\begin{aligned}v(t,x,y) \leqslant \exp\{-d_0 t\}\int_{\mathbb{R}}\int_{\Omega}\Gamma(D_m t,x,\xi,y,\zeta)v(0,\xi,\zeta)\,d\xi\,d\zeta + \frac{\epsilon}{d_0},\\ t \in [0,\tau], (x,y) \in \Omega \times (-\bar{M},\bar{M}),\end{aligned}$$

and thus

$$v(t,x,0) \leqslant \exp\{-d_0 t\}\int_{\mathbb{R}}\int_{\Omega}G(D_m t,x,\xi)G_1(D_m t,0,\zeta)v(0,\xi,\zeta)\,d\xi\,d\zeta + \frac{\epsilon}{d_0}.$$

Note that $\int_{\mathbb{R}} G_1(D_m t,0,\zeta)d\zeta = 1$. Similar to the above discussion, we can choose $M > 0$ and $\delta > 0$ (say, the same M and δ as above, otherwise, take a larger M and a smaller δ) such that $v(t,x,0) < \frac{2\epsilon}{d_0}, \forall t \in [0,\tau], x \in \Omega$, when $|\phi(\theta,x,y) - \bar{\phi}(\theta,x,y)| < \delta$ for $\theta \in [-\tau,0], (x,y) \in \Omega \times [-M,M]$.

If $\phi \ngeqslant \bar{\phi}$ on $[-\tau,0]$, define

$$\check{\phi} = \max\{\phi,\bar{\phi}\}, \quad \tilde{\phi} = \min\{\phi,\bar{\phi}\},$$

and assume that $\check{u}_m$ and $\tilde{u}_m$ are solutions of (3.5), with initial functions $\check{\phi}$ and $\tilde{\phi}$, then Lemma 3.1 yields $\tilde{u}_m \leqslant u_m, \bar{u}_m \leqslant \check{u}_m$. As

$$|u_m(t,x,y) - \bar{u}_m(t,x,y)| \leqslant \check{u}_m(t,x,y) - \tilde{u}_m(t,x,y),\ \forall (t,x,y) \in \mathbb{R}_+ \times \Omega \times \mathbb{R},$$

the claim is true for $t_0 = \tau$.

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For any $t \in [m\tau, (m+1)\tau]$, $Q_t = Q_{t-m\tau}Q_{m\tau}$. Thus $Q_t(\cdot)$ is uniformly continuous for $t \in [m\tau, (m+1)\tau]$, which implies that $Q_t(\cdot)$ is uniformly continuous for t on any bounded interval. It follows that $Q_t(\phi)$ is continuous in $(t, \phi) \in \mathbb{R}_+ \times \mathscr{C}_{u_m^+}$ with respect to the compact open topology, i.e., Q_t satisfies (iii) of a semiflow. Consequently, Q_t is a continuous semiflow on $\mathscr{C}_{u_m^+}$.

Clearly, Lemma 3.1 implies that Q_t is monotone on $\mathscr{C}_{u_m^+}$. It remains to prove that Q_t is subhomogeneous in $\mathscr{C}_{u_m^+}$ in the sense that $Q_t(\rho\phi) \geqslant \rho Q_t(\phi)$ for all $\rho \in [0,1]$ and $\phi \in \mathscr{C}_{u_m^+}$. In fact, let $\bar{u}_m = u_m(t,x,y;\rho\phi)$, $u_m = u_m(t,x,y;\phi)$ and $\underline{u}_m = \rho u_m(t,x,y;\phi)$. We have $\bar{u}_{mt}, \underline{u}_{mt} \in \mathscr{C}_{u_m^+}$ and

$$\begin{aligned}
\frac{\partial \bar{u}_m}{\partial t} &= D_m \triangle \bar{u}_m - d(\bar{u}_m) + \int_0^\tau \int_{\mathbb{R}} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) \\
&\quad \times f(s) e^{-\gamma s} b(\bar{u}_m(t-s, z_x, z_y))\, dz_x\, dz_y\, ds, \quad t > 0, (x,y) \in \Omega \times \mathbb{R}, \\
B\bar{u}_m(t,x,y) &= 0, \quad t \geqslant 0, (x,y) \in \partial\Omega \times \mathbb{R}, \\
\bar{u}_m(\theta, x, y) &= \rho\phi(\theta, x, y), t \in [-\tau, 0], (x,y) \in \Omega \times \mathbb{R},
\end{aligned}$$

and

$$\begin{aligned}
\frac{\partial \underline{u}_m}{\partial t} &= D_m \triangle \underline{u}_m - \rho d(u_m) + \int_0^\tau \int_{\mathbb{R}} \int_\Omega \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} \rho b(u_m(t-s, z_x, z_y))\, dz_x\, dz_y\, ds \\
&\leqslant D_m \triangle \underline{u}_m - d(\underline{u}_m) \\
&\quad + \int_0^\tau \int_{\mathbb{R}} \int_0^L \Gamma(\alpha, x, z_x, y, z_y) f(s) e^{-\gamma s} b(\underline{u}_m(t-s, z_x, z_y))\, dz_x\, dz_y\, ds \quad t > 0, (x,y) \in \Omega \times \mathbb{R}, \\
B\underline{u}_m(t,x,y) &= 0, \quad t \geqslant 0, (x,y) \in \partial\Omega \times \mathbb{R}, \\
\underline{u}_m(\theta, x, y) &= \rho\phi(\theta, x, y), t \in [-\tau, 0], (x,y) \in \Omega \times \mathbb{R}.
\end{aligned}$$

Therefore, $\bar{u}_m$ and $\underline{u}_m$ are supersolution and subsolution of (3.5), respectively, with $\bar{u}_m(\theta, x, y) = \underline{u}_m(\theta, x, y)$ for $\theta \in [-\tau, 0], (x,y) \in \Omega$. Again, Lemma 3.1 yields the subhomogeneous property of Q_t in $\mathscr{C}_{u_m^+}$. □

4 Asymptotic speed of spread and travelling waves

Define the reflection operator $\mathscr{R}$ by $\mathscr{R}(\phi)(\theta, x, y) = \phi(\theta, x, -y)$. Given $z \in \mathbb{R}$, define the translation operator T_z by $T_z(\phi)(\theta, x, y) = \phi(\theta, x, y - z)$. $W \subset \mathscr{C}$ is said T-invariant if $T_z W = W$ for all $z \in \mathbb{R}$.

Let $\beta \in \mathscr{C}_-$ with $\beta \gg 0$ and fix a mapping $Q : \mathscr{C}_\beta \to \mathscr{C}_\beta$. The following hypotheses on Q, formulated in Liang and Zhao (2007, 2008), are essential to describe our results on asymptotic speed of spread.

(A1) $Q(\mathscr{R}(\phi)) = \mathscr{R}(Q(\phi))$, $T_z(Q(\phi)) = Q(T_z(\phi))$, $\forall y \in \mathbb{R}$.

(A2) $Q : \mathscr{C}_\beta \to \mathscr{C}_\beta$ is continuous with respect to the compact open topology.

(A3) One of the following two properties holds:

(a) $\{Q(\phi)(\cdot, y) : \phi \in \mathscr{C}_\beta, y \in \mathbb{R}\}$ is a pre-compact subset of $\mathscr{C}_-$;

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(b′) The set $Q[\mathscr{C}_\beta](0,\cdot)$ is precompact in Y, and there is a positive number $\zeta \leqslant \tau$ such that $Q(\phi)(\theta,x,y) = \phi(\theta+\zeta,x,y)$ for $-\tau \leqslant \theta \leqslant -\zeta$, and the operator

$$S(\phi)(\theta,x,y) = \begin{cases} \phi(0,x,y), & -\tau \leqslant \theta < -\zeta, \\ Q(\phi)(\theta,x,y), & -\zeta \leqslant \theta \leqslant 0, \end{cases} \tag{4.1}$$

has the property that $\{S(\phi)(\cdot,0) : \phi \in D\}$ is a precompact subset of $\mathscr{C}_-$ for any T-invariant set $D \subset \mathscr{C}_\beta$ with $D(0,\cdot)$ precompact in Y.

(A4) $Q : \mathscr{C}_\beta \to \mathscr{C}_\beta$ is monotone (order-preserving) in the sense that $Q(\phi) \geqslant Q(\psi)$ whenever $\phi \geqslant \psi$ in $\mathscr{C}_\beta$.

(A5) $Q : \mathscr{C}_{\beta-} \to \mathscr{C}_{\beta-}$ admits exactly two fixed points 0 and β, and for any positive number ϵ, there is $\alpha \in \mathscr{C}_{\beta-}$ with $\|\alpha\| < \epsilon$ such that $Q(\alpha) \gg \alpha$.

(A6) One of the following two properties holds:

(a) $Q(\mathscr{C}_\beta)$ is precompact in $\mathscr{C}_\beta$;

(b′) The set $Q(\mathscr{C}_\beta)(0,\cdot)$ is precompact in Y, and there is a positive number $\zeta \leqslant \tau$ such that $Q(\phi)(\theta,x,y) = \phi(\theta+\zeta,x,y)$ for $-\tau \leqslant \theta \leqslant -\zeta$, and the operator defined by (4.1) has the property that $S(D)$ is a precompact subset of $\mathscr{C}_\beta$ for any T-invariant set $D \subset \mathscr{C}_\beta$ with $D(0,\cdot)$ precompact in Y.

Lemma 4.1 *Assume (P1)–(P4) and (2.19) hold. Then for each* $t > 0$, *the map* Q_t *satisfies* $(A1)$–$(A6)$ *with* $\beta = u_m^+(x)$.

Proof By (3.5), we know that Q_t satisfies $(A1)$. By Theorem 3.1, we obtain that Q_t satisfies $(A2)$ and $(A4)$. We now verify that Q_t satisfies $(A6)$. For $\forall t \geqslant 0$, define

$$L(t)(\phi)(\theta,x,y) = \begin{cases} \phi(t+\theta,x,y) - \phi(0,x,y), & t+\theta < 0, (x,y) \in \bar{\Omega} \times \mathbb{R}, \\ 0, & t+\theta \geqslant 0, -\tau \leqslant \theta \leqslant 0, (x,y) \in \bar{\Omega} \times \mathbb{R}. \end{cases}$$

Then $L(t) = 0$ as $t \geqslant \tau$. Let $S(t) = Q_t - L(t),\ t \geqslant 0$. We have from the smoothness of the semigroup generated from the heat equation that Q_t satisfies $(A6)(a)$ as $t \geqslant \tau$. If $t \in (0,\tau)$, let $\zeta = t$, then we have $Q_t(\phi)(\theta,x,y) = \phi(\theta+t,x,y), \forall \theta \in [-\tau,-t]$, and

$$S(t)(\phi)(\theta,x,y) = \begin{cases} \phi(0,x,y), & -\tau \leqslant \theta < -t, \\ Q_t(\phi)(\theta,x,y), & -t \leqslant \theta \leqslant 0. \end{cases}$$

We obtain from the above expression that $S(t)(\phi)$ is continuous on $\mathscr{C}_{u_m^+}$, and we can show that $S(t)(D)$ is pre-compact in $\mathscr{C}_{u_m^+}$ for any T-invariant set $D \subset \mathscr{C}_{u_m^+}$ with $D(0,\cdot)$ precompact in Y by a method similar to Theorem 6.1 in Hale and Lunel (1993). Therefore, Q_t satisfies $(A6)$, and this implies $(A3)$.

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Let $\hat{Q}_t$ be the restriction of Q_t on $\mathscr{C}_-$. Then $\hat{Q}_t$ is the semiflow generated from the initial boundary value problem:

$$\begin{aligned}
&\frac{\partial u_m}{\partial t} = D_m \triangle_x u_m - d(u_m) + \int_0^\tau \int_\Omega G(D_i s, x, z_x) f(s) e^{-\gamma s} b(w(t-s, z_x))\, dz_x\, ds, \quad t > 0, x \in \Omega,\\
&Bu_m(t,x) = 0, \quad t \geqslant 0,\ x \in \partial\Omega,\\
&u_m(\theta, x) = \phi(\theta, x), \quad \theta \in [-\tau, 0], x \in \bar{\Omega}.
\end{aligned} \tag{4.2}$$

As discussed in section 2, the boundary value problem (4.2) has two equilibria $u_m = 0$ and $u_m = u_m^+(x)$. Furthermore, similar to Lemma 3.1, we have the conclusion that $\hat{Q}_t$ is strongly monotone in $[0, \hat{u}_m]_C$. By Corollary 2.1, $u_m^+(x)$ is asymptotically stable, and $u_m = 0$ is unstable. By the Dancer–Hess connecting orbit Lemma (see, e.g., page 39 in Zhao, 2003), the semiflow $\hat{Q}_t$ admits a strongly monotone entire orbit connecting 0 and $u_m^+(x)$. Thus assumption (A5) holds for each map $Q_t, \forall t > 0$. □

By Lemma 4.1 and Theorems 2.11 and 2.15 in Liang and Zhao (2007), the map Q_1 has the asymptotic speed of spread $c^* > 0$ with the meaning:

$$\begin{aligned}
&\forall c > c^*, \lim_{n\to\infty, |y|\geqslant nc} Q_1^n(\phi)(\theta, x, y) = 0 \quad \text{uniformly for } \theta \in [-\tau, 0],\ x \in \Omega,\\
&\forall 0 < c < c^*, \lim_{n\to\infty, |y|\leqslant nc} Q_1^n(\phi)(\theta, x, y) = u_m^+(x) \quad \text{uniformly for } \theta \in [-\tau, 0],\ x \in \Omega.
\end{aligned}$$

The following result shows that c^* is also the spreading speed for the solutions of (3.5).

Theorem 4.1 *Assume (P1)–(P4) and (2.19) hold. Let c^* be the asymptotic speed of spread of Q_1. Then the following statements hold:*

(i) *If $\phi \in \mathscr{C}_{u_m^+}$ with $0 \leqslant \phi \ll u_m^+$, and $\phi(\cdot, x, y) = 0$ for $x \in \bar{\Omega}$ and y outside a bounded interval, then for each $c > c^*$, every solution of (3.5) satisfies $\lim_{t\to\infty, |y|\geqslant tc} u_m(t, x, y; \phi) = 0$ uniformly for $x \in \bar{\Omega}$.*

(ii) *If $\phi \in \mathscr{C}_{u_m^+}$ with $\phi(0, \cdot) \not\equiv 0$, then for any $0 < c < c^*$, every solution of (3.5) satisfies $\lim_{t\to\infty, |y|\leqslant tc} u_m(t, x, y; \phi) = u_m^+(x)$ uniformly for $x \in \bar{\Omega}$.*

Proof Conclusion (i) can be derived from the first part of Theorem 2.17 of Liang and Zhao (2007). To obtain the conclusion (ii), we use our Lemma 3.1 combined with Theorem 2.17 of Liang and Zhao (2007). We know from Lemma 3.1 that for any $\phi \in \mathscr{C}_{u_m^+}$ with $\phi(0, \cdot) \not\equiv 0$, we have $u_m(t, x, y; \phi) \gg 0, \forall t > 0, (x, y) \in \bar{\Omega} \times \mathbb{R}$. Since Q_t is subhomogeneous, r_σ in Theorem 2.17 in Liang and Zhao (2007) can be chosen to be independent of $\sigma > 0$. Let $r_\sigma = r$.

Fix $t_0 > 0$, we see that $u_m(t_0, x, y; \phi) \gg 0, \forall (x, y) \in \bar{\Omega} \times \mathbb{R}$. So there exists a $\sigma \in \mathbb{R}, \sigma > 0$ such that $u_m(t_0, x, y; \phi) \gg \sigma, \forall (x, y) \in \bar{\Omega} \times [-r, r]$. Thus we can take $u_m(t_0, x, y; \phi)$ as a new initial data, and use the second part of Theorem 2.17 from Liang and Zhao (2007) to obtain our second conclusion. This completes the proof. □

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A travelling wave solution of (3.5) is a solution with the form $u_m(t,x,y) = \varphi(x, y - ct)$, where $c > 0$ is the wave speed. The asymptotic spreading speed is closely related to the minimal wave speed of travelling waves. According to our Lemma 4.1 and Theorems 4.3 and 4.4 in Liang and Zhao (2007), we have the following result for the existence of travelling waves of (3.5).

Theorem 4.2 *Assume (P1)–(P4) and (2.19) holds. Let c^* be the asymptotic speed of spread of Q_1. Then the following statements hold:*

(i) *For each $c \geqslant c^*$, system (3.5) has a travelling wave $\varphi(x,s)$ connecting $u_m^+(x)$ to 0 such that $\varphi(x,s)$ is continuous and non-increasing in $s \in \mathbb{R}$.*

(ii) *For each $c \in (0, c^*)$, system (3.5) has no travelling wave $\varphi(x,s)$ connecting $u_m^+(x)$ to 0.*

We conclude this paper with the calculation of c^*. In what follows, we need the condition $b(u_m) \leqslant b'(0)u_m$ for $u_m \in [0, \hat{u}_m]$ that are implied by assumptions (P2).

In order to compute c^*, we consider the linearised boundary value problem

$$\begin{aligned}\frac{\partial w}{\partial t} &= D_m \triangle w - d'(0)w + b'(0)\int_0^\tau \int_{\mathbb{R}} \int_{\Omega} \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} w(t-s, z_x, z_y)\, dz_x\, dz_y\, ds, \\ &\qquad\qquad t > 0, (x,y) \in \Omega \times \mathbb{R}, \\ Bw(t,x,y) &= 0, \quad t \geqslant 0,\ (x,y) \in \partial\Omega \times \mathbb{R}. \end{aligned} \tag{4.3}$$

Assume that $\{M_t\}_0^\infty$ is the linear solution map defined by (4.3). Let $w(t,x,y) = \eta(t,x)e^{-\nu y}$. Note

$$\begin{aligned} & b'(0)\int_0^\tau \int_{\mathbb{R}} \int_{\Omega} \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} w(t-s, z_x, z_y)\, dz_x\, dz_y\, ds \\ &= b'(0)\int_0^\tau \int_{\mathbb{R}} \int_{\Omega} \Gamma(D_i s, x, z_x, y, z_y) f(s) e^{-\gamma s} e^{-\nu z_y} \eta(t-r, z_x)\, dz_x\, dz_y\, ds \\ &= b'(0)e^{-\nu y}\int_0^\tau \int_{\mathbb{R}} \int_{\Omega} \frac{1}{\sqrt{4D_i s\pi}} G(D_i s, x, z_x) e^{-\frac{(y-z_y)^2}{4D_i s} + \nu(y-z_y)} f(s) e^{-\gamma s} \eta(t-s, z_x)\, dz_x\, dz_y\, ds \\ &= b'(0)e^{-\nu y}\int_0^\tau \left\{ \int_{\mathbb{R}} \frac{1}{\sqrt{4D_i s\pi}} e^{-\frac{(z-2D_i s\nu)^2}{4D_i s}}\, dz \right\} \int_{\Omega} G(D_i s, x, z_x) f(s) e^{-\gamma s + D_i s \nu^2} \eta(t-s, z_x)\, dz_x\, ds \\ &= b'(0)e^{-\nu y}\int_0^\tau \int_{\Omega} G(D_i s, x, z_x) f(s) e^{-\gamma s + D_i s\nu^2} \eta(t-s, z_x)\, dz_x\, ds. \end{aligned} \tag{4.4}$$

We have from (4.3) and (4.4) that $\eta(t,x)$ satisfies

$$\begin{aligned} \frac{\partial \eta(t,x)}{\partial t} &= D_m \triangle_x \eta(t,x) + D_m \nu^2 \eta(t,x) - d'(0)\eta(t,x) \\ &\quad + b'(0)\int_0^\tau \int_{\Omega} G(D_i s, x, z_x) f(s) e^{-\gamma s + D_i s\nu^2} \eta(t-s, z_x)\, dz_x\, ds, \quad t > 0, x \in \Omega, \\ B\eta(t,x) &= 0, \quad t \geqslant 0,\ x \in \partial\Omega. \end{aligned} \tag{4.5}$$

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Substituting $\eta(t,x) = e^{\lambda t}H(x), \lambda > 0, H(x) \geqslant 0$ into (4.5) yields

$$\begin{aligned}\lambda H(x) &= D_m \triangle_x H(x) + (D_m v^2 - d'(0))H(x) \\ &\quad + \int_0^\tau \int_\Omega G(D_i s, x, z_x) e^{-\lambda s} g(v,s) H(z_x)\, dz_x\, ds, \quad x \in \Omega, \\ BH(x) &= 0, \ x \in \partial\Omega,\end{aligned} \tag{4.6}$$

where $g(v,s) := b'(0)f(s)e^{-\gamma s + D_i s v^2}$.

Similarly to the statement before Theorem 2.2, one can show that (4.6) has a principal eigenvalue $\lambda(v)$ with a positive eigenfunction. Furthermore, we shall show that $\lambda(v) > 0$ for $\forall v \geqslant 0$. In fact, define $F_1(\lambda, v) := \lambda + D_m\alpha_1 - D_m v^2 + d'(0) - \int_0^\tau g(v,s)e^{-\lambda s}e^{-D_i\alpha_1 s}ds$. We have from (2.19) that

$$F_1(0,v) = D_m\alpha_1 - D_m v^2 + d'(0) - \int_0^\tau g(v,s)e^{-D_i\alpha_1 s}\, ds < 0,$$
$$\frac{\partial F_1(\lambda,v)}{\partial \lambda} = 1 + \int_0^\tau g(v,s)se^{-\lambda s}e^{-D_i\alpha_1 s}\, ds > 1,$$

which leads to that $F_1(\lambda, v) = 0$ has exact one positive root $\bar\lambda(v) \in (0,\infty)$ with positive eigenfunction $H(x) = \psi_1(x) > 0$. In view of the definition of a principal eigenvalue, we know that $\lambda(v) \geqslant \bar\lambda(v) > 0$. Thus $e^{\lambda(v)t}$ is the principal eigenvalue of B_v^t, where B_v^t is the solution map associated with (4.5). Note that for $\phi = e^{\lambda\theta}\psi_1(x) \in \mathscr{C}_{u_m^+}$, we have

$$B_v^t[\phi](\theta,x) = M_t[\phi e^{-vy}](\theta,x,0) = e^{\lambda(v)t}\phi(\theta,x), \quad t > 0.$$

Let $t = 1$. Then $\Gamma(v) := \exp\{\lambda(v)\}$ is the principal eigenvalue of $B_v^1 =: B_v$ with a positive eigenfunction ϕ. Note $\lambda(v) > 0$ for $v \geqslant 0$. This implies $\Gamma(0) = e^{\lambda(0)t} > 1$ and (C7) in Liang and Zhao (2007) is satisfied.

Define the function

$$\Phi(v) := \frac{1}{v}\ln\Gamma(v) = \frac{\lambda(v)}{v}.$$

By Lemma 3.8 in Liang and Zhao (2007), we then have the following result.

Lemma 4.2 *The following statements are valid:*

(1) $\Phi(v) \to \infty$ *as* $v \downarrow 0$.

(2) $\Phi(v)$ *is decreasing near* 0.

(3) $\Phi'(v)$ *changes sign at most once on* $(0,\infty)$.

(4) $\lim_{v\to\infty}\Phi(v)$ *exists, where the limits may be infinite.*

Theorem 4.3 *Assume (P1)–(P4) and (2.19) hold. Then* $c^* = \inf_{v>0}\Phi(v) = \inf_{v>0}\frac{\lambda(v)}{v}$.

Proof We want to prove that $\Phi(+\infty) = +\infty$. Note that $F_1(\bar\lambda(v), v) \equiv 0$, and

$$\frac{d\bar\lambda}{dv} = -\frac{\partial F_1(\lambda,v)/\partial v}{\partial F_1(\lambda,v)/\partial\lambda}\Big|_{\lambda=\bar\lambda(v)} = \frac{2D_m v + 2\int_0^\tau D_i s v g(\mu,s)e^{-\bar\lambda s}e^{-D_i\alpha_1 s}\, ds}{1 + \int_0^\tau s g(v,s)e^{-\bar\lambda s}e^{-D_i\alpha_1 s}\, ds} \to \infty \text{ as } v \to \infty.$$

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Thus, we obtain

$$\lim_{v\to\infty}\Phi(v)=\lim_{v\to\infty}\frac{\lambda(v)}{v}\geqslant\lim_{v\to\infty}\frac{\bar{\lambda}(v)}{v}=\lim_{v\to\infty}\frac{d\bar{\lambda}}{dv}=+\infty.$$

Note that M_1 and B_v satisfy (C1)–(C7) in Liang and Zhao (2007) and the infimum of $\Phi(v)$ is attained at some finite value v^*. Since $Q_1(\phi)\leqslant M_1(\phi)$ for $\phi\in\mathscr{C}_{u_m^+}$, Theorem 3.10 in Liang and Zhao (2007) implies that $c^*\leqslant\inf_{v>0}\Phi(v)$.

For any $\epsilon\in(0,1)$, there is a $\delta>0$ such that for any $\phi\in\mathscr{C}_\delta$, we have

$$\begin{aligned}&b(u_m(t-r,x,y))\geqslant(1-\epsilon)b'(0)u_m(t-r,x,y),\\&d(u_m(t,x,y))\leqslant(1+\epsilon)d'(0)u_m(t,x,y),\qquad\forall(x,y)\in\Omega\times\mathbb{R},\ t\in[0,1].\end{aligned}$$

Thus, $u_m(t,x,y)=u_m(t,x,y;\phi)$ satisfies

$$\begin{aligned}\frac{\partial u_m}{\partial t}\geqslant{}&D_m\triangle u_m-(1+\epsilon)d'(0)u_m\\&+(1-\epsilon)b'(0)\int_0^\tau\int_{\mathbb{R}}\int_\Omega\Gamma(D_is,x,z_x,y,z_y)f(s)e^{-\gamma s}u_m(t-r,z_x,z_y)\,dz_x\,dz_y\,ds\end{aligned}$$

for $t\in[0,1],(x,y)\in\Omega\times\mathbb{R}$. Consider the linear system

$$\begin{aligned}\frac{\partial w}{\partial t}&=D_m\triangle w-(1+\epsilon)d'(0)w+(1-\epsilon)b'(0)\int_0^\tau\int_{\mathbb{R}}\int_\Omega\Gamma(D_is,x,z_x,y,z_y)\\&\qquad f(s)e^{-\gamma s}w(t-r,z_x,z_y)\,dz_x\,dz_y\,ds\qquad t>0,(x,y)\in\Omega\times\mathbb{R},\\Bw(t,x,y)&=0,\quad t\geqslant0,\ x\in\partial\Omega,\ y\in\mathbb{R}.\end{aligned}\tag{4.7}$$

Let M_t^ϵ, $t\geqslant0$, be the solution map associated with the linear system (4.7). Then the comparison principle implies that $M_t^\epsilon(\phi)\leqslant Q_t(\phi)$, $\forall\phi\in\mathscr{C}_\delta$, $t\in[0,1]$. In particular, $M_1^\epsilon(\phi)\leqslant Q_1(\phi)$, $\forall\phi\in\mathscr{C}_\delta$. As we did for M_t, a similar analysis can be made for M_t^ϵ. It then follows from Theorem 3.10 in Liang and Zhao (2007) that $\inf_{v>0}\Phi_\epsilon(v)\leqslant c^*$. Thus, we have

$$\inf_{v>0}\Phi_\epsilon(v)\leqslant c^*\leqslant\inf_{v>0}\Phi(v),\ \forall\epsilon\in(0,1).$$

Letting $\epsilon\to0$, we obtain $c^*=\inf_{v>0}\Phi(v)$. □

5 Concluding remarks

The main aim of this article is to discuss the travelling waves, the minimal wave speed and the rate of propagation for the population model (3.5) in a cylindrical domain by using the theory for monotone semiflows developed by Liang and Zhao (2007, 2008). The conclusion of the existence of travelling waves implies the transition from the extinction state $u_m(x)\equiv0$ to the stable positive state $u_m^+(x)$. The existence of this stable positive state $u_m^+(x)$ is guaranteed by assumptions (P1)–(P4), (2.19) and the threshold dynamics of (2.4), which is expressed in Theorem 2.2.

We note the assumptions (P1)–(P4) are almost the same as (A2) in Al-Omari and Gourley (2005) except for the sublinear property of b and $-d$. The role of the sublinear

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property of b and $-d$ in the proof of Theorem 2.2 comes from an application of Lemma 1 in Zhao (1996). See Xu and Zhao (2003) for the details.

We also note that the Dirichlet boundary value problem is not discussed in this article, since the non-empty property of intX^+ is not satisfied under this situation (see Smith, 1995). We leave this as an open problem.

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