CANADIAN APPLIED
MATHEMATICS QUARTERLY
Volume 11, Number 3, Fall 2003

A NONLOCAL REACTION-DIFFUSION POPULATION MODEL WITH STAGE STRUCTURE

Dedicated to Professor Paul Waltman on the occasion of his retirement

DASHUN XU AND XIAO-QIANG ZHAO

ABSTRACT. A threshold dynamics and global attractivity of positive steady state are established in terms of principal eigenvalues for a nonlocal reaction-diffusion population model with stage structure, and the effects of spatial dispersal and maturation period on the evolutionary behavior are also discussed in two specific cases.

1 Introduction Recently, an increasing attention has been paid to nonlocal and time-delayed population models in order to study the effects of spatial diffusion and time delay on the evolutionary behavior of biological systems (see, e.g., [**16, 13, 3, 1, 19, 17**]). In the reality, species may drift from one spatial point at a time to another spatial point at another time, and may disperse from a domain to a larger domain. Moreover, the environment is often spatially heterogeneous. To describe the growth of a single species in a multi-patchy environment, certain delay differential equation models were proposed and analyzed in [**12, 14, 20**]. [**13, 1, 3**] also formulated the nonlocal and delayed reaction-diffusion models for a single species with stage structure, and established the existence of a family of traveling wave fronts for these models.

In order to obtain a general nonlocal and time delayed model for a single species in a bounded domain, we let $u(t, a, x)$ be the density of individuals with age a at a point x at time t, τ be the length of the juvenile period. Denote by $u_m(t, x)$ the density of mature adults. Then

Supported in part by the NSERC of Canada.
Keywords: Nonlocal and delayed model, persistence and extinction, positive steady states, global attractivity.
Copyright ©Applied Mathematics Institute, University of Alberta.

we have (see, e.g., [**10**])

$$
(1.1)\qquad \begin{cases} \partial_t u + \partial_a u = d_j(a)\triangle u - \mu_j(a)u, & 0 < a < \tau,\ x \in \Omega \subset \mathbb{R}^N, \\ Bu = 0, & a \in (0,\tau),\ x \in \partial\Omega, \end{cases}
$$

and u_m satisfies

$$
(1.2)\qquad \begin{cases} \partial_t u_m = d_m \triangle u_m - g(u_m) + u(t,\tau,x) & t > 0,\ x \in \Omega, \\ Bu = 0, & t > 0,\ x \in \partial\Omega, \end{cases}
$$

with $u(t,0,x) = f(u_m(t,x)), t \geq -\tau, x \in \Omega$, where $f(u_m)$ and $g(u_m)$ are the birth rate and the mortality rate of mature individuals, respectively, $\mu_j(a)$ denotes the per capita mortality rate of juveniles at age a, $\triangle$ is the Laplacian operator on $\mathbb{R}^N$, Ω is a bounded and open subset of $\mathbb{R}^N$ with a smooth boundary $\partial\Omega$, either $Bu = u$ or $Bu = \partial u/\partial n + \alpha u$ for some nonnegative function $\alpha \in C^{1+\theta}(\partial\Omega, \mathbb{R})$, $\theta > 0$, $\partial/\partial n$ denotes the differentiation in the direction of the outward normal n to $\partial\Omega$. In (1.2), the term $u(t,\tau,x)$ is the adults recruitment term, being those of maturation age τ. As in [**17,** Section 4.1], integrating (1.1) along characteristics yields

$$
u(t,a,x) = \int_\Omega \Gamma(\eta(a),x,y)\mathcal{F}(a) f(u_m(t-a,y))dy,
$$

where Γ is the Green function associated with the partial differential operator $\triangle$ and boundary condition $Bu = 0$, and

$$
\eta(a) = \int_0^a d_j(s)ds, \quad \mathcal{F}(a) = e^{-\int_0^a \mu_j(s)ds}.
$$

Thus, $u_m(t,x)$ satisfies

$$
(1.3)\qquad \begin{cases} \partial_t u_m = d_m \triangle u_m - g(u_m) \\ + \displaystyle\int_\Omega \Gamma(\eta(\tau),x,y)\mathcal{F}(\tau) f(u_m(t-\tau,y)\, dy, & t > 0,\ x \in \Omega, \\ Bu_m = 0, & t > 0,\ x \in \partial\Omega, \\ u_m(t,x) = \phi(t,x), & t \in [-\tau,0],\ x \in \Omega, \end{cases}
$$

where $\phi(t,x)$ is a positive initial function to be specified later.

In the case of $\Omega = \mathbb{R}^N$, [**17**] studied the traveling wave solutions, minimal wave speed and asymptotic speed of spread for (1.3). In the case where $\Omega = \mathbb{R}, g(u) = \beta u$, (1.3) reduces to the model derived in [**13**], where traveling wave fronts are investigated. In the case where $\Omega = \mathbb{R}, f(u) = \alpha u$ and $g(u) = \beta u^2$, (1.3) reduces to the model discussed in [**3**], where the linear stabilities of two spatially homogeneous equilibrium solutions, and traveling wave fronts are considered. A global convergence theorem in the case of bounded intervals was also obtained in [**3**]. The threshold dynamics and global convergence were established in [**19**] for a special case of (1.3).

The purpose of this paper is to study the global dynamics of model (1.3). In Section 2, we establish the global existence and positivity of solutions, and the existence of a global attractor for the associated solution semiflow. In Section 3, we first obtain a threshold type result on the global extinction and uniform persistence in terms of the principal eigenvalue of a nonlocal elliptic problem, and then obtain sufficient conditions for the global attractivity of the positive steady state. Section 4 is devoted to the discussion of the effects of spatial diffusion and time delay on the asymptotic behavior of system (1.3) in two specific cases.

2 Existence and boundedness of solutions For convenience, we drop the subscript m in (1.3), and write it as

$$(2.1)\quad \begin{cases} \partial_t u(t,x) = d\triangle u(t,x) - g(u(t,x)) \\ \quad + \displaystyle\int_\Omega \Gamma(\eta(\tau),x,y)\mathcal{F}(\tau)f(u(t-\tau,y))\,dy, & t>0,\ x\in\Omega, \\ Bu(t,x) = 0, & t>0,\ x\in\partial\Omega, \\ u(t,x) = \phi(t,x) \geq 0, & t\in[-\tau,0],\ x\in\Omega. \end{cases}$$

We assume that

(A1) $f \in C^1(\mathbb{R}^+,\mathbb{R}^+)$, $f(0) = 0, f'(0) > 0$, and f is sublinear, i.e., $f(\gamma u) \geq \gamma f(u)$ for all $\gamma \in (0,1)$ and $u \geq 0$.
(A2) $g \in C^1(\mathbb{R}^+,\mathbb{R}^+)$, $g(0) = 0, g'(0) \geq 0$, and $-g$ is sublinear.
(A3) There exists a number $M \geq 0$ such that for all $L > M$, $\bar{f}(L) - g(L) < 0$, where $\bar{f}(u) = \mathcal{F}(\tau)\max_{v\in[0,u]} f(v)$.

Let $p \in (N,\infty)$ be fixed. For each $\beta \in (\frac{1}{2} + \frac{N}{2p}, 1)$, let $\mathbb{X}_\beta$ be the fractional power space of $L^p(\Omega)$ with respect to (-A,B) (see, e.g., [**6**]), where $A := \triangle$. Then $\mathbb{X}_\beta$ is an ordered Banach space with respect to the positive cone $\mathbb{X}_\beta^+$ consisting of all nonnegative functions in $\mathbb{X}_\beta$, and $\mathbb{X}_\beta^+$ has nonempty interior $int(\mathbb{X}_\beta)$. Moreover, $\mathbb{X}_\beta \subset C^{1+\nu}(\overline{\Omega})$ with continuous inclusion for $\nu \in [0, 2\beta - 1 - N/p)$. Denote the norm on $\mathbb{X}_\beta$ by $\|\cdot\|_\beta$. Then there exists a constant $k_\beta > 0$ such that $\|\phi\|_\infty := \max_{x\in\overline{\Omega}} |\phi(x)| \le k_\beta \|\phi\|_\beta$, $\forall \phi \in \mathbb{X}_\beta$. It is well known that the differential operator A generates an analytic semigroup $T(t)$ on $L^p(\Omega)$. Moreover, the standard parabolic maximum principle (see, e.g., [**11,** Corollary 7.2.3]) implies that the semigroup $T(t) : \mathbb{X}_\beta \to \mathbb{X}_\beta$ is strongly positive in the sense that $T(t)(\mathbb{X}_\beta^+ \backslash \{0\}) \subset int(\mathbb{X}_\beta^+), \forall t > 0$.

Let $\mathbb{Y} := C([-\tau, 0], \mathbb{X}_\beta)$ and $\mathbb{Y}^+ := C([-\tau, 0], \mathbb{X}_\beta^+)$. For convenience, we will identify an element $\phi \in \mathbb{Y}$ as a function from $[-\tau, 0] \times \overline{\Omega}$ to $\mathbb{R}$ defined by $\phi(s, x) = \phi(s)(x)$, and for each $s \in [-\tau, 0]$, we regard $g(\phi(s))$ as a function on $\overline{\Omega}$ defined by $g(\phi(s)) = g(\phi(s, \cdot))$. For any function $y(\cdot) : [-\tau, b) \to \mathbb{X}_\beta$, where $b > 0$, define $y_t \in \mathbb{Y}, t \in [0, b)$ by $y_t(s) = y(t + s), \forall s \in [-\tau, 0]$. Define $F : \mathbb{Y}^+ \to \mathbb{X}_\beta$ by $F(\phi) = -g(\phi(0)) + \mathcal{F}(\tau) T(\eta(\tau)) f(\phi(-\tau, \cdot)), \forall \phi \in \mathbb{Y}^+$. Then we can rewrite (2.1) as an abstract functional differential equation

$$\begin{cases} \dfrac{du(t)}{dt} = d\,Au(t) + F(u_t), \quad t > 0, \\ u_0 = \phi \in \mathbb{Y}^+. \end{cases}$$

Therefore, we can write the above equation as an integral equation

$$u(t) = T(d\,t)\phi(0) + \int_0^t T(d\,(t-s))F(u_s)ds, \quad t \ge 0,$$

whose solutions are called mild solutions for (2.1).

Since $T(t) : \mathbb{X}_\beta \to \mathbb{X}_\beta$ is strongly positive, we have

$$\lim_{h\to 0^+} dist(\phi(0) + hF(\phi), \mathbb{X}_\beta^+) = 0, \quad \forall \phi \in \mathbb{Y}^+.$$

By [**8,** Proposition 3 and Remark 2.4] (see also [**18,** Corollary 8.1.3]), for each $\phi \in \mathbb{Y}^+$, (2.1) has a unique non-continuable mild solution $u(t, \phi)$ with $u_0 = \phi$, and $u(t, \phi) \in \mathbb{X}_\beta^+$ for all $t \in (0, \sigma_\phi)$. Moreover $u(t, \phi)$ is a classical solution of (2.1) for $t > \tau$ (see [**18,** Corollary 2.2.5]). We further have the following result.

Theorem 2.1. *Let* (A1)–(A3) *hold. Then for each* $\phi \in \mathbb{Y}^+$*, a unique solution* $u(t, \phi)$ *globally exists on* $[-\tau, \infty)$*, and the solution semiflow* $\Phi(t) = u_t(\cdot) : \mathbb{Y}^+ \to \mathbb{Y}^+, t \ge 0,$ *admits a connected global attractor.*

Proof. For any $L \geq M$, let $\Sigma_L = \{\phi \in \mathbb{X}_\beta^+ : \phi(x) \leq L, \forall x \in \overline{\Omega}\}$, $\mathbb{Z}_L = C([-\tau, 0], \Sigma_L)$. It then follows that

$$\lim_{h \to 0^+} dist(\phi(0) + hF(\phi), \Sigma_L) = 0, \quad \forall \phi \in \mathbb{Z}_L.$$

By [**11,** Corollary 7.2.4] and [**18,** Corollary 8.1.3], $\mathbb{Z}_L$ is a positively invariant set for (2.1). Thus for any $\phi \in \mathbb{Y}^+$, $u(t, \phi)$ globally exists on $[-\tau, \infty)$, and hence (2.1) defines a semiflow $\Phi(t) : \mathbb{Y}^+ \to \mathbb{Y}^+$ by $(\Phi(t)\phi)(s, x) = u(t + s, x, \phi), \forall s \in [-\tau, 0], x \in \bar{\Omega}$. Moreover, $\Phi(t)$ is compact for all $t > \tau$ ([**18,** Theorem 2.2.6]).

Let us consider the delay differential equation

$$\text{(2.2)} \qquad \begin{cases} \dot{v}(t) = -g(v(t)) + \bar{f}(v(t - \tau)), \\ v(s) = \varphi(s) \in C([-\tau, 0], \mathbb{R}^+), \quad \forall s \in [-\tau, 0]. \end{cases}$$

Note that the function $\bar{f}$ is Lipschitz in any bounded subset of $\mathbb{R}^+$. For any $\varphi \in C([-\tau, 0], \mathbb{R}^+)$, (2.2) admits a unique solution $v(t, \varphi)$ with $v(s, \varphi) = \varphi(s)$, $\forall s \in [-\tau, 0]$. It is easy to see that $v(t, \varphi)$ is bounded. Hence $v(t, \varphi)$ exists globally on $[-\tau, \infty)$. Therefore, for any $\varphi \in C([-\tau, 0], \mathbb{R}^+)$, the omega limit set $\omega(\varphi)$ of the orbit $\gamma^+(\varphi)$ is nonempty, compact and invariant, where $\gamma^+(\varphi) = \{v_t(\varphi) : t \geq 0\}$. Let $G = \{\psi(s) : \psi \in \omega(\varphi), s \in [-\tau, 0]\}$. Then G is compact because of the compactness of $\omega(\varphi)$. Therefore, there exist $s_0 \in [-\tau, 0]$ and $\psi \in \omega(\varphi)$ such that $\psi(s_0) = \sup G := L_G$. By the invariance of $\omega(\varphi)$, there exists $\psi' \in \omega(\varphi)$ such that $v_\tau(\psi') = \psi$, i.e., $v(\tau + s, \psi') = \psi(s), \forall s \in [-\tau, 0]$. Without loss of generality, we can assume that $\psi(0) = L_G$. Thus,

$$\begin{aligned} \dot{v}(\tau, \psi') &= -g(v(\tau, \psi')) + \bar{f}(v(0, \psi')) \\ &\leq -g(L_G) + \bar{f}(L_G). \end{aligned}$$

If $L_G > M$, then $\dot{v}(\tau, \psi') < 0$, which implies that there exists some $s \in [-\tau, 0)$ such that $\psi(s) > \psi(0) = L_G$, a contradiction. Thus, $\limsup_{t \to \infty} v(t, \varphi) \leq M$, $\forall \varphi \in C([-\tau, 0], \mathbb{R}^+)$.

For any given $\phi \in \mathbb{Y}^+$, let $\widehat{L}(s) = \max\{\phi(\theta, x) : \theta \in [-\tau, 0], x \in \overline{\Omega}\}, \forall s \in [-\tau, 0]$. Then $\limsup_{t \to \infty} v(t, \widehat{L}) \leq M$. Note that for any

$\zeta \in \mathbb{Y}^+$ with $\zeta(s,\cdot) \leq v(t+s,\widehat{L})$, $\forall s \in [-\tau, 0]$, we have

$$\begin{aligned} v(t,\widehat{L}) &- \zeta(0,x) + h(-g(v(t,\widehat{L})) + \bar{f}(v(t-\tau,\widehat{L})) \\ &\qquad - h(-g(\zeta(0,x)) + \int_\Omega \Gamma(\eta(\tau),x,y)\mathcal{F}(\tau)f(\zeta(-\tau,y))dy \\ &\geq v(t,\widehat{L}) - \zeta(0,x) - h(g(v(t,\widehat{L})) - g(\zeta(0,x))) \\ &\geq 0 \quad \text{for} \quad 0 < h \ll 1,\ x \in \Omega. \end{aligned}$$

By [**8,** Proposition 3], $u(t,x,\phi) \leq v(t,\widehat{L})$, $\forall x \in \overline{\Omega}$, $t \geq -\tau$. Thus, $\limsup_{t\to\infty} u(t,x,\phi) \leq M, \forall x \in \bar{\Omega}$. That is, $\Phi(t) : \mathbb{Y}^+ \to \mathbb{Y}^+$ is point dissipative. By [**4,** Theorem 3.4.8], $\Phi(t)$ admits a connected global attractor on $\mathbb{Y}^+$, which attracts each bounded set in $\mathbb{Y}^+$. □

3 Uniform persistence and global attractivity Consider the nonlocal elliptic eigenvalue problem

$$\begin{cases} \lambda v(x) = d\triangle v(x) - g'(0)v(x) \\ \qquad\qquad +f'(0)\mathcal{F}(\tau)\displaystyle\int_\Omega \Gamma(\eta(\tau),x,y)v(y)dy, & x \in \Omega, \\ Bv(x) = 0, & x \in \partial\Omega. \end{cases} \tag{3.1}$$

By the same arguments as in [**11,** Theorem 7.6.1], it follows that problem (3.1) has a principal eigenvalue, denoted by λ_0. Then we have the following threshold dynamics for system (2.1), which shows that the linear stability of (2.1) at zero implies the extinction of the species while the instability implies the uniform persistence of the species.

Theorem 3.1. *Let $e^* \in int(\mathbb{X}^+_\beta)$ be fixed, and* (A1)–(A3) *hold. For any $\phi \in \mathbb{Y}^+$, denote by $u(t,x,\phi)$ or $u(t,\phi)$ the solution of* (2.1).

(i) *If $\lambda_0 < 0$, $\lim_{t\to\infty} \|u(t,\phi)\|_\beta = 0$ for every $\phi \in \mathbb{Y}^+$.*
(ii) *If $\lambda_0 > 0$, then (2.1) admits at least one steady state solution φ^* with $\varphi^*(x) \in (0, M]$, $\forall x \in \Omega$, and there exists $\delta > 0$ such that for every $\phi \in \mathbb{Y}^+$ with $\phi(0,\cdot) \not\equiv 0$, there is $t_0 = t_0(\phi) > 0$ such that $u(t,x,\phi) \geq \delta e^*(x)$, $\forall x \in \overline{\Omega}, t \geq t_0$.*

Proof. Note that zero is an equilibrium of (2.1). The variational equation about zero is given by

$$\begin{cases} \partial_t v(t,x) = d\triangle v(t,x) - g'(0)v(t,x) \\ +f'(0)\mathcal{F}(\tau)\displaystyle\int_\Omega \Gamma(\eta(\tau),x,y)v(t-\tau,y)\,dy, & t>0,\ x\in\Omega, \\ Bv(t,x)=0, & t>0,\ x\in\partial\Omega, \\ v(s,x)=\phi(s,x)\geq 0, & s\in[-\tau,0],\ x\in\Omega. \end{cases} \tag{3.2}$$

By [**22,** Theorem 9.2.1] and a similar argument in the case of Dirichlet boundary condition, it follows that the eigenvalue problem

$$\begin{cases} \lambda v(x) = d\triangle v(x) - g'(0)v(x) \\ +f'(0)\mathcal{F}(\tau)e^{-\lambda\tau}\displaystyle\int_\Omega \Gamma(\eta(\tau),x,y)v(y)\,dy, & x\in\Omega, \\ Bv(x)=0, & x\in\partial\Omega, \end{cases} \tag{3.3}$$

has a principle eigenvalue $\bar{\lambda}_0$, and $\bar{\lambda}_0$ shares the same sign with λ_0.

(i) In the case of $\lambda_0<0$, the properties of the principal eigenvalue $\bar{\lambda}_0$ and linear semigroups imply that $\lim_{t\to\infty}\|v(t,\cdot,\phi)\|_\beta=0,\ \forall\phi\in\mathbb{Y}$, where $v(t,x,\phi)$ is the unique solution of (3.2). Note that a solution $u(t,x)$ of (2.1) satisfies

$$\partial_t u(t,x)\leq d\triangle u(t,x)-g'(0)u(t,x) \\ +f'(0)\mathcal{F}(\tau)\int_\Omega \Gamma(\eta(\tau),x,y)u(t-\tau,y)dy, \quad t>0.$$

The comparison theorem for abstract functional differential equations ([**8,** Proposition 3]) implies that $u(t,\cdot,\phi)\leq v(t,\cdot,\phi),\ \forall t\geq-\tau$. It then follows that $\lim_{t\to\infty}\|u(t,\phi)\|_\beta=0,\ \forall\phi\in\mathbb{Y}^+$.

(ii) In the case of $\lambda_0>0$, let $\mathbb{Y}_0=\{\phi\in\mathbb{Y}^+:\phi(0,\cdot)\not\equiv 0\}$, $\partial\mathbb{Y}_0:=\mathbb{Y}^+\setminus\mathbb{Y}_0$. For any $\phi\in\mathbb{Y}^+$, the solution $u(t,x,\phi)$ of (2.1) satisfies

$$\partial_t u(t,x)\geq d\triangle u(t,x)-g(u(t,x)),\quad t>0,\ x\in\Omega.$$

By the standard parabolic maximum principle, it then follows that $\Phi(t)(\mathbb{Y}_0)\subset int(\mathbb{Y}^+),\ \forall t>0$. Let $Z_1=\{\phi\in\partial\mathbb{Y}_0:\Phi(t)\phi\in\partial\mathbb{Y}_0,\forall t\geq 0\}$.

Then $\bigcup_{\phi\in Z_1}\omega(\phi)=\{0\}$, where $\omega(\phi)$ denotes the omega limit set of the orbit $\gamma^+(\phi):=\{\Phi(t)\phi:\forall t\geq 0\}$. We claim that

Claim. Zero is a uniform weak repeller for $\mathbb{Y}_0$ in the sense that there exists $\delta_0>0$ such that $\limsup_{t\to\infty}\|\Phi(t)\phi\|_\beta\geq\delta_0,\forall\phi\in\mathbb{Y}_0$.

Let us consider the following eigenvalue problem

$$
(3.4)\qquad \begin{cases} \lambda v(x)=d\triangle v(x)-(g'(0)+\varepsilon)v(x)+(f'(0)-\varepsilon) \\ \qquad \times\mathcal{F}(\tau)e^{-\lambda\tau}\int_\Omega\Gamma(\eta(\tau),x,y)v(y)dy, & x\in\Omega, \\ Bv(x)=0, & x\in\partial\Omega. \end{cases}
$$

Since (3.3) admits a positive principal eigenvalue $\bar{\lambda}_0$, there exists a sufficiently small positive number ε such that (3.4) admits a positive principal eigenvalue λ_ε. For this ε, there exists $\delta_\varepsilon>0$ such that $g(u)<(g'(0)+\varepsilon)u$ and $f(u)>(f'(0)-\varepsilon)u$ for all $u\in(0,\delta_\varepsilon)$. Let $\delta_0=\delta_\varepsilon/k_\beta$. Suppose, by contradiction, that there exists $\phi_0\in\mathbb{Y}_0$ such that $\limsup_{t\to\infty}\|\Phi(t)\phi_0\|_\beta<\delta_0$. Then there exists $t'>\tau$ such that $\|u(t,\cdot,\phi_0)\|_\infty\leq k_\beta\|u(t,\cdot,\phi_0)\|_\beta<\delta_\varepsilon$ for all $t\geq t'-\tau$. Therefore, $u(t,x,\phi_0)$ satisfies

$$
(3.5)\quad \partial_t u(t,x)>d\triangle u(t,x)-(g'(0)+\varepsilon)u(t,x) \\ +(f'(0)-\varepsilon)\mathcal{F}(\tau)\int_\Omega\Gamma(\eta(\tau),x,y)u(t-\tau,y)dy,\quad t\geq t',\quad x\in\Omega.
$$

Let $\varphi\in\mathbb{X}_\beta$ be the positive eigenfunction associated with the principal eigenvalue λ_ε. Then $u_\varepsilon(t,x)=\varphi(x)e^{\lambda_\varepsilon t}$ is a solution to

$$
\begin{cases} \partial_t u(t,x)=d\triangle u(t,x)-(g'(0)+\varepsilon)u(t,x) \\ \qquad +(f'(0)-\varepsilon)\mathcal{F}(\tau)\int_\Omega\Gamma(\eta(\tau),x,y)u(t-\tau,y)dy, & t>0,\ x\in\Omega, \\ Bu(t,x)=0, & t>0,\ x\in\partial\Omega. \end{cases}
$$

Since $u(t,x,\phi_0)>0$, $\forall t>0, x\in\Omega$, there exists $\varsigma>0$ such that $u(t'+s,x,\phi_0)\geq\varsigma u_\varepsilon(s,x)$ for $s\in[-\tau,0]$, $x\in\bar{\Omega}$. By inequality (3.5) and the comparison theorem ([**8,** Proposition 3]), we have $u(t,x,\phi_0)\geq\varsigma u_\varepsilon(t-t',x)=\varsigma\varphi(x)e^{\lambda_\varepsilon(t-t')}$, $\forall t\geq t'$, $x\in\bar{\Omega}$. Since $\lambda_\varepsilon>0$, $u(t,x,\phi_0)$ is unbounded, a contradiction.

By [**15,** Theorem 4.6], $\Phi(t)$ is uniformly persistent with respect to $\mathbb{Y}_0$ in the sense that there exists $\delta_1 > 0$ such that

$$\liminf_{t\to\infty} dist(\Phi(t)\phi, \partial\mathbb{Y}_0) \geq \delta_1, \quad \forall\phi \in \mathbb{Y}_0.$$

Since $\Phi(t) : \mathbb{Y}^+ \to \mathbb{Y}^+$ is compact for each $t > \tau$, [**22,** Theorem 1.3.9] with $e = e^* \in int(\mathbb{Y}^+)$ implies that there exists $\delta > 0$ such that for any $\phi \in \mathbb{Y}_0$, $u(t,x,\phi) \geq \delta e^*(x)$ for all $t \geq t(\phi)$, $x \in \overline{\Omega}$.

It remains to prove the existence of a positive steady state. We consider

$$\begin{cases} \partial_t u(t,x) = d\triangle u(t,x) - g(u(t,x)) \\ \qquad\qquad + \displaystyle\int_\Omega \Gamma(\eta(\tau),x,y)\mathcal{F}(\tau)f(u(t,y))dy, & t > 0, \quad x \in \Omega, \\ Bu(t,x) = 0, & t > 0, \quad x \in \partial\Omega, \\ u(0,x) = \varphi(x) \geq 0, & x \in \Omega. \end{cases}$$

Let $\Phi_0(t) : \mathbb{X}_\beta^+ \to \mathbb{X}_\beta^+$, $t \geq 0$, be the solution semiflow. As proven for $\Phi(t) : \mathbb{Y}^+ \to \mathbb{Y}^+$, it follows that $\Phi_0(t)$ is point dissipative on $\mathbb{X}_\beta^+$, compact for each $t > 0$, and uniformly persistent with respect to $\mathbb{X}_\beta^+ \setminus \{0\}$. Then, by [**22,** Theorem 1.3.7], $\Phi_0(t)$ has an equilibrium $\varphi^* \in \mathbb{X}_\beta^+ \setminus \{0\}$, i.e., $\Phi_0(t)\varphi^* = \varphi^*$ for all $t \geq 0$. Clearly, $\varphi^* \in int(\mathbb{X}_\beta^+)$. □

Theorem 3.2. *Let* (A1)–(A3) *hold and* $\lambda_0 > 0$. *Suppose that either* f *or* $-g$ *is strictly sublinear on* $[0, M]$, *and that* f *is monotone increasing on* $[0, M]$. *Then* (2.1) *admits a unique positive steady state* φ^*, *and* $\lim_{t\to\infty} \|u(t,\phi) - \varphi^*\|_\beta = 0$ *for every* $\phi \in \mathbb{Y}^+$ *with* $\phi(0,\cdot) \not\equiv 0$, *where* $u(t,\phi)$ *is the solution of* (2.1).

Proof. We use notations in the proofs of Theorems 2.1 and 3.1. Note that f is monotone increasing on $[0, M]$. It then follows that

$$\lim_{h\to 0^+} \frac{1}{h} dist\,(\psi(0) - \varphi(0) + h(F(\psi) - F(\varphi)), \mathbb{X}_\beta^+) = 0,$$

for all $\varphi, \psi \in \mathbb{Z}_M$ with $\varphi(s,x) \leq \psi(s,x)$, $\forall s \in [-\tau, 0]$, $x \in \bar{\Omega}$. By [**8,** Proposition 3 and Corollary 5], $\Phi(t) : \mathbb{Z}_M \to \mathbb{Z}_M$ is a monotone semiflow with respect to the order on $\mathbb{Y}$ induced by $\mathbb{Y}^+$. By the proof of Theorem 2.1, every omega limits set $\omega(\phi)$ of $\Phi(t)$ is contained in $\mathbb{Z}_M$.

In particular, every nonnegative steady state φ of (2.1) is contained in Σ_M. We further claim that (2.1) admits at most one positive steady state. Indeed, it suffices to show that $\Phi_0(t)$ has at most one positive equilibrium in Σ_M. By [**8,** Corollary 5] with $\tau = 0$, it then follows that $\Phi_0(t) : \Sigma_M \to \Sigma_M$ is a monotone semiflow with respect to the order on $\mathbb{X}_\beta$ induced by $\mathbb{X}_\beta^+$. Moreover, for any $\varphi_1, \varphi_2 \in \Sigma_M$ with $\varphi_1 - \varphi_2 \in \mathbb{X}_\beta^+ \setminus \{0\}$, $u(t,x) := (\Phi_0(t)\varphi_1)(x) - (\Phi_0(t)\varphi_2)(x)$ satisfies

$$\begin{aligned}\partial_t u(t,x) &\geq d\triangle u(t,x) \\ &\qquad - u(t,x)\int_0^1 g'(s\Phi_0(t)\varphi_1(x) + (1-s)\Phi_0(t)\varphi_2(x))ds \\ &\geq d\triangle u(t,x) - ku(t,x), \quad t > 0, x \in \Omega,\end{aligned}$$

where $k = \sup_{u\in[0,M]} g'(u)$. Then the standard parabolic maximum principle implies that $u(t) \in int(\mathbb{X}_\beta^+), \forall t > 0$. That is, $\Phi_0(t) : \Sigma_M \to \Sigma_M$ is strongly monotone. By the strict sublinearity of f or $-g$, it easily follows that for each $t > 0$, $\Phi_0(t) : \Sigma_M \to \Sigma_M$ is strictly sublinear (see, e.g., [**2,** Theorem 2.2]). Now fix a real number $t_0 > 0$. Then [**21,** Lemma 1] implies that the map $\Phi_0(t_0)$ has at most one positive fixed point in Σ_M, and hence the semiflow $\Phi_0(t)$ has at most one positive equilibrium in Σ_M. Note that $\Phi(t) : \mathbb{Y}^+ \to \mathbb{Y}^+$ is compact for $t > \tau$, admits a global attractor in $\mathbb{Y}^+$, and is uniformly persistent with respect to $\mathbb{Y}_0$. By [**5,** Theorem 3.2], $\Phi(t) : \mathbb{Z}_M \cap \mathbb{Y}_0 \to \mathbb{Z}_M \cap \mathbb{Y}_0$ has a global attractor A_0. Theorem 3.1, together with the uniqueness of the positive steady state, implies that A_0 contains only on equilibrium φ^*. By the Hirsch attractivity theorem ([**7,** Theorem 3.3]), it then follows that φ^* attracts every point in $\mathbb{Z}_M \cap \mathbb{Y}_0$. Consequently, every orbit in $\mathbb{Z}_M$ converges to either the trivial equilibrium or the positive equilibrium φ^*. Note that the equilibria 0 and φ^* are also isolated invariant sets in $\mathbb{Z}_M$, and there is no cyclic chain of equilibria. By the continuous time version of [**22,** Theorem 1.2.2], every compact internally chain transitive set for $\Phi(t) : \mathbb{Z}_M \to \mathbb{Z}_M$ is an equilibrium. For any given $\phi \in \mathbb{Y}^+$, by the proof of Theorem 2.1, $\omega(\phi) \subset \mathbb{Z}_M$, and hence $\omega(\phi)$ is an equilibrium. If $\phi \in \mathbb{Y}^+$ with $\phi(0,\cdot) \not\equiv 0$, we then have $\omega(\phi) = \varphi^*$. □

4 Discussion In this section, we discuss the effects of spatial diffusion and time delay on the global behavior of model (1.3) in two specific cases.

First let us compute the principal eigenvalue λ_0 for problem (3.1). In the case of the Neumann boundary condition, it easily follows that the eigenvalue problem (3.1) admits the principle eigenvalue $\lambda_0 = -g'(0) + f'(0)\mathcal{F}(\tau)$ (with the eigenfunction $v(\cdot) \equiv 1$). In the case of the Dirichlet boundary condition, we consider (3.1) with $\Omega = (0, \pi)$. Let

$$T_0(t)\varphi = \int_\Omega \Gamma(t, x, y)\varphi(y)dy,$$

which is the linear semigroup generated by

$$\begin{cases} \partial_t u = \triangle u, \\ u(t, 0) = u(t, \pi) = 0, \\ u(0, x) = \varphi(x) \in \mathbb{X}_\beta^+. \end{cases} \tag{4.1}$$

It then follows that $e^{-t} \sin x$ is a solution of (4.1) with $\varphi(x) = \sin x$. Thus, we have

$$\int_\Omega \Gamma(t, x, y) \sin y \, dy = e^{-t} \sin x, \quad \forall t \geq 0, \ x \in (0, \pi).$$

In particular,

$$\int_\Omega \Gamma(\eta(\tau), x, y) \sin y \, dy = e^{-\eta(\tau)} \sin x.$$

It is easy to verify that $\sin x$ is a positive solution of (3.1) with $\lambda = -d - g'(0) + f'(0)\mathcal{F}(\tau)e^{-\eta(\tau)}$. Therefore,

$$\lambda_0 = -d - g'(0) + f'(0)\mathcal{F}(\tau)e^{-\eta(\tau)}.$$

Example 1. Consider the model (1.3) with $g(u) = \beta u^2$, $f(u) = \alpha u$ and $\mathcal{F}(\tau) = e^{-\mu_j \tau}$, where α, β, μ_j and the immature diffusion coefficient d_j in (1.1) are all positive constants.

In the case of the Neumann boundary condition, we have $\lambda_0 = \alpha e^{-\mu_j \tau} > 0$. By Theorem 3.2 with $M = (\alpha/\beta)e^{-\mu_j \tau}$, it follows that for each $\phi \in \mathbb{Y}^+$ with $\phi(0, \cdot) \not\equiv 0$, $\lim_{t\to\infty} u_m(t, x, \phi) = \varphi^*(x) \equiv (\alpha/\beta)e^{-\mu_j \tau}$ uniformly for $x \in \Omega$, where $u_m(t, x, \phi)$ is the solution of (1.3) with the initial function ϕ. This convergence result is consistent with that in [**3**]. In this case, we can see that the maturation period τ and the diffusion of the species do not affect the persistence of the species.

In the case of the Dirichlet boundary condition, let $\Omega = (0, \pi)$. Then, $\lambda_0 = -d_m + \alpha e^{-(\mu_j + d_j)\tau}$ (d_m in (1.3) is equivalent to d in (3.1)). Note that $\lambda_0 < 0$ if $\alpha < d_m$, and in the case of $\alpha > d_m$, we have $\lambda_0 > 0$ if $\tau \in [0, \tau_0)$, and $\lambda_0 < 0$ if $\tau > \tau_0$, where $\tau_0 = 1/(\mu_j + d_j)\ln(\alpha/d_m) > 0$. By Theorems 3.1 and 3.2 with $M = (\alpha/\beta)e^{-\mu_j\tau}$, we have the following result for this case.

Proposition 4.1. *Let $u_m(t, x, \phi)$ denote the solution of* (1.3) *subject to the Dirichlet boundary condition and with the initial function $\phi \in \mathbb{Y}^+$.*

(1) *If $\alpha < d_m$, then for any $\phi \in \mathbb{Y}^+$, $\lim_{t\to\infty} u_m(t, x, \phi) = 0$ uniformly for $x \in [0, \pi]$.*
(2) *In the case of $\alpha > d_m$, let $\tau_0 = 1/(\mu_j + d_j)\ln(\alpha/d_m) > 0$.*
    (a) *If $\tau \in [0, \tau_0)$, then for any $\phi \in \mathbb{Y}^+$ with $\phi(0, \cdot) \not\equiv 0$, $\lim_{t\to\infty} u_m(t, x, \phi) = \varphi^*(x)$ uniformly for $x \in [0, \pi]$, where φ^* is the unique positive steady state of* (1.3).
    (b) *If $\tau > \tau_0$, then for any $\phi \in \mathbb{Y}^+$, $\lim_{t\to\infty} u_m(t, x, \phi) = 0$ uniformly for $x \in [0, \pi]$.*

By Proposition 4.1, we have the following observations on the model (1.3) subject to the Dirichlet boundary condition.

Conclusion 1. If all parameters except for d_m are fixed, then the fast mature dispersal in space brings negative effect on persistence of the species.

Conclusion 2. If all parameters except for the delay τ are fixed, then the large maturation time τ brings negative effect on persistence of the species.

Example 2. Consider the model (1.3) with $g(u) = \beta u, f(u) = pue^{-qu}$ and $\mathcal{F}(\tau) = e^{-\mu_j\tau}$, where β, p, q, μ_j and d_j are all positive constants. A direct computation shows that

$$f'(u) = pe^{-qu}(1 - qu), \qquad f''(u) = -pqe^{-qu}(2 - qu),$$

and $f(u)$ reaches its maximum value $f(1/q) = (p/q)e^{-1}$.

In the case of the Neumann boundary condition, $\lambda_0 = -\beta + pe^{-\mu_j\tau}$. Therefore, if $\beta > pe^{-\mu_j\tau}$, then Theorem 3.1 (i) with $M = 0$ implies that the species goes extinct; if $\beta < pe^{-\mu_j\tau}$, then Theorem 3.1 (ii) with $M = (p/\beta q)e^{-1-\mu_j\tau}$ implies that the species persists. If, in addition,

$pe^{-1-\mu_j\tau} \leq \beta < pe^{-\mu_j\tau}$, Theorem 3.2 with the last M implies that (1.3) admits the unique positive steady state

$$\varphi^*(x) \equiv \frac{1}{q}\left(\ln\frac{p}{\beta} - \mu_j\tau \right) > 0,$$

which is globally attractive.

The above analysis supports our second conclusion. For suitable values of the maturation time τ, the species goes extinct, persists, or stabilizes at a positive steady state. However, the diffusion coefficient d_m has no effects on the persistence of the species.

In the case of the Dirichlet boundary condition, $\lambda_0 = -(d_m + \beta) + pe^{-(\mu_j+d_j)\tau}$. By Theorems 3.1 and 3.2 with $M = 0$, or $(p/\beta q)e^{-1-\mu_j\tau}$ and $(1/q)(\ln(p/\beta) - \mu_j\tau)$, we have the following result, which implies the same conclusions about the effects of the maturation period τ and the diffusion coefficient d_m as in Example 1.

Proposition 4.2. *Let $u_m(t,x,\phi)$ denote the solution of* (1.3) *subject to the Dirichlet boundary condition and with the initial function $\phi \in \mathbb{Y}^+$.*

(1) *If $p < d_m + \beta$, then for any $\phi \in \mathbb{Y}^+$, $\lim_{t\to\infty} u_m(t,x,\phi) = 0$ uniformly for $x \in [0,\pi]$.*

(2) *In the case of $p > d_m + \beta$, let*

$$\tau_0 = \frac{1}{\mu_j + d_j}\ln\frac{p}{d_m+\beta}, \qquad \tau_1 = \frac{1}{\mu_j}(\ln\frac{p}{\beta} - 1).$$

   (a) *If $\tau_1 \leq \tau < \tau_0$, then for any $\phi \in \mathbb{Y}$, $\phi(0,\cdot) \not\equiv 0$, $\lim_{t\to\infty} u_m(t,x,\phi) = \varphi^*(x)$ uniformly for $x \in [0,\pi]$, where φ^* is the unique positive steady state of* (1.3).

   (b) *If $\tau > \tau_0$, then for any $\phi \in \mathbb{Y}^+$, $\lim_{t\to\infty} u_m(t,x,\phi) = 0$ uniformly for $x \in [0,\pi]$.*

Numerical simulation. We numerically simulate Example 2 with the domain $\Omega = (0,\pi)$. Model (1.3) is discretised by using the finite difference method, where the nonlocal term is approximated by composite integration formulas. Note that in the case of the Neumann boundary condition,

$$\Gamma(\eta(\tau),x,y) = \frac{1}{\pi} + \frac{2}{\pi}\sum_{n=1}^{\infty} e^{-n^2 d_j\tau}\cos nx\cos ny,$$

and in the case of the Dirichlet boundary condition,

$$\Gamma(\eta(\tau), x, y) = \frac{2}{\pi} \sum_{n=1}^{\infty} e^{-n^2 d_j \tau} \sin nx \sin ny.$$

In what follows we only present the numerical simulations for the case of the Dirichlet boundary condition since we have the similar results for the case of the Neumann boundary condition.

Let $p = 5, q = \beta = 1, \mu_j = 1.2, d_j = 0.25, d_m = 0.5$. When $\tau > 0.8303$, zero solution attracts every solution of (1.3) (Theorem 3.1); when $\tau \in (0.5078, 0.8303)$, model (1.3) admits a globally attractive and positive steady state (Theorem 3.2). In Figure 1, the solution of (1.3) with initial function $\phi(t, x) = \sin x$ and $\tau = 1$ converges to zero, while in Figure 2, the solution with the same initial function and $\tau = 0.65$ converges to the unique steady state $\varphi^*(x)$. Our theoretical results are consistent with the numerical simulations. We also simulate the solutions of (1.3) in the case of $\tau < 0.5078$ (see, e.g., Figure 3). Our further numerical simulations suggest that $\varphi^*(x)$ would be globally attractive even if the monotonicity condition in Theorem 3.2 is not satisfied. We leave this open problem for future investigation.

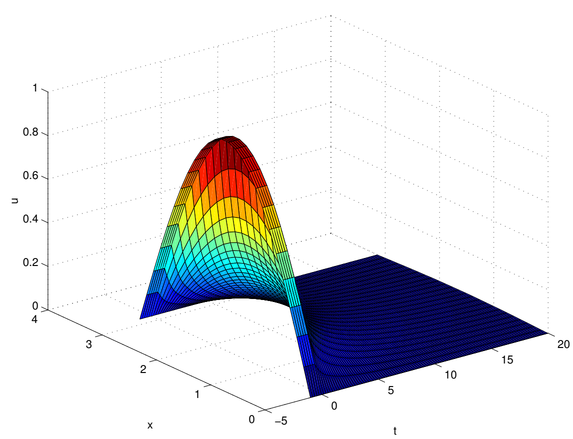

FIGURE 1: $\tau = 1, \phi(t, x) = \sin x$.

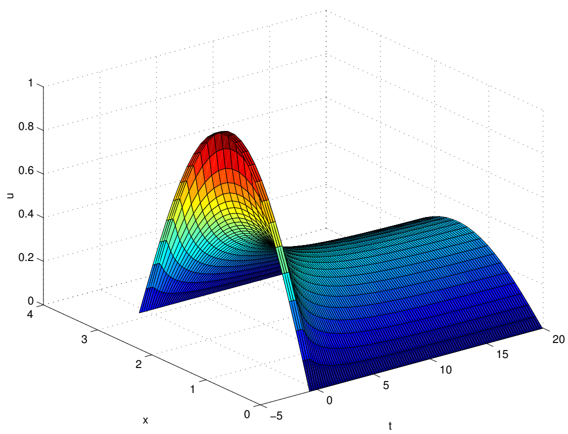

FIGURE 2: $\tau = 0.65, \phi(t,x) = \sin x$.

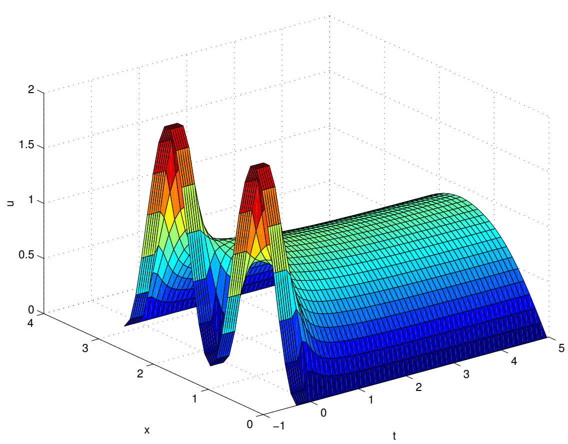

FIGURE 3: $\tau = 0.3, \phi(t,x) = 1 - \cos 4x$.

REFERENCES

1. J. Al-Omari and S. A. Gourley, *Monotone travelling fronts in an age-structured reaction-diffusion model of a single species,* J. Math. Biol. **45** (2002), 294–312.
2. H. I. Freedman and X.-Q. Zhao, *Global asymptotics in some quasimonotone reaction-diffusion systems with delay*, J. Differential Equations **137** (1997), 340–362.
3. S. A. Gourley and Y. Kuang, *Wavefronts and global stability in a time-delayed population model with stage structure*, R. Soc. Lond. Proc., Ser. A: Math. Phys. Eng. Sci. **459** (2003), 1563–1579.
4. J. K. Hale, *Asymptotic Behavior of Dissipative Systems,* Math. Surveys and Monographs 25, Amer. Math. Soc., Providence, RI, 1988.
5. J. K. Hale and P. Waltman, *Persistence in infinite-dimensional systems*, SIAM J. Math. Anal. **20** (1989), 388–395.
6. D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Math., Vol. 840, Springer-Verlag, Berlin and New York, 1981.
7. M. W. Hirsch, *The dynamical systems approach to differential equations*, Bull. Amer. Math. Soc. **11** (1984), 1–64.
8. R. H. Martin and H. L. Smith, *Abstract functional differential equations and reaction-diffusion systems*, Trans. Amer. Math. Soc. **321** (1990), 144.
9. R. Mcowen, *Partial Differential Equations, Methods and Applications,* Prentice-Hall, New Jersey, 1996.
10. A. A. J. Metz and O. Diekmann, *The Dynamics of Physiologically Structured Populations,* (J. A. J. Metz and O. Diekmann, eds.), Springer-Verlag, New York, 1986.
11. H. L. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Mathematical surveys and Monographs 41, Amer. Math. Soc., Providence, 1995.
12. H. L. Smith, H. R. Thieme, *Strongly order preserving semiflows generated by functional differential equations*, J. Differential Equations **93** (1991), 332–363.
13. J. W.-H. So, J. Wu and X. Zou, *A reaction-diffusion model for a single species with age structure, I. Travelling wave fronts on unbounded domains*, Proc. Roy. Soc. London Ser-A. **457** (2001), 1841–1853.
14. J. W.-H. So, J. Wu and X. Zou, *Structured population in two patches: modeling dispersal and delay*, J. Math. Biol. **43** (2001), 37–51.
15. H. R. Thieme, *Persistence under relaxed point-dissipativity (with application to an epidemic model)*, SIAM J. Math. Anal. **24** (1993), 407–435.
16. H. R. Thieme and X.-Q. Zhao, *A non-local delayed and diffusive predator-prey model*, Nonlinear Analysis: Real World Appl. **2** (2001), 145–160.
17. H. R. Thieme and X.-Q. Zhao, *Asymptotic speeds of spread and traveling waves for integral equations and delayed reaction-diffusion models*, J. Differential Equations **195** (2003), 430–470.
18. J. Wu, *Theory and Applications of Partial Functional Differential Equations*, Applied Math. Sci. **119**, Springer-Verlag, New York, 1996.
19. J. Wu and X.-Q. Zhao, *Diffusive monotonicity and threshold dynamics of delayed reaction diffusion equations*, J. Differential Equations **186** (2002), 470–484.

20. D. Xu, *Global dynamics and Hopf bifurcation of a structured population model*, Nonlinear Anal. Real World Appl., in press, 2004.
21. X.-Q. Zhao, *Global attractivity and stability in some monotone discrete dynamical systems*, Bull. Austral. Math. Soc. **53** (1996), 305–324.
22. X.-Q. Zhao, *Dynamical Systems in Population Biology*, Springer-Verlag, New York, 2003.

Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada

E-mail address: dxu@math.mun.ca

E-mail address: xzhao@math.mun.ca