THRESHOLD DYNAMICS OF A DELAYED NONLOCAL REACTION-DIFFUSION CHOLERA MODEL

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ABSTRACT. Taking account of spatial heterogeneity, latency in infected individuals, and time for shed bacteria to the aquatic environment, we build a delayed nonlocal reaction-diffusion cholera model. A feature of this model is that the incidences are of general nonlinear forms. By using the theories of monotone dynamical systems and uniform persistence, we obtain a threshold dynamics determined by the basic reproduction number $R_0$. Roughly speaking, the cholera will die out if $R_0 < 1$ while it persists if $R_0 > 1$. Moreover, we derive the explicit formulae of $R_0$ for two concrete situations.

1. Introduction. Cholera is an infectious disease that causes severe watery diarrhea, which can lead to dehydration and even death if untreated. It is caused by the bacterium Vibrio cholerae. According to the World Health Organization (WHO), cholera persists as a global threat and continues to challenge countries where access to safe drinking water and adequate sanitation is not assured. In fact, the WHO estimates 1.3 to 4.0 million cholera cases per year with 21,000 to 143,000 deaths worldwide [28]. Mathematical modeling has been playing a central role in understanding the transmission dynamics of cholera and the obtained theoretical results can help public agencies to draw appropriate control measures.

Like other waterborne diseases, cholera has multiple transmission pathways: it can be transmitted directly to humans by person-to-person contact or indirectly to humans via contaminated water. In [23], Tien and Earn proposed a model described by ordinary differential equations, which extends the classical SIR framework by adding a compartment (W) to track the pathogen concentration in water. The obtained SIRW model incorporates both direct and indirect transmissions. For this

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1
model, they not only derived fundamental quantities such as the basic reproduction number and the final outbreak size but also examined the dependence of them on transmission parameters for different pathways. In order to study differential infectivity in direct transmission, they also generalized the SIRW model to a staged age structure. However, differential infectivity is also crucial for indirect transmission. For example, laboratory studies suggest hyperinfectivity of freshly shed pathogen \cite{9}. Though one can add compartments for multiple stages of infectious individuals and multiple infection stages of pathogen to consider these features, it is more realistic to use continuous age structures. In \cite{3}, Brauer et al. formulated the following partial differential equation (PDE) cholera model that incorporates simultaneously the age-of-infection structure of individuals and the age structure of pathogen with infectivities given by kernel functions,

$$\begin{align}
\frac{dS(t)}{dt} &= A - \mu S(t) - \beta_d S(t) \int_0^\infty k(a)i(t,a)da - \beta_i S(t) \int_0^\infty q(b)p(t,b)db, \\
\frac{dS(t)}{dt} + \frac{dI(t)}{dt} + \frac{dR(t)}{dt} &= -\theta(a)i(t,a), \\
\frac{dW(t)}{dt} &= -\delta(b)p(t,b),
\end{align}$$

(1.1)

with boundary conditions

$$\begin{align}
i(t,0) &= \beta_d S(t) \int_0^\infty k(a)i(t,a)da + \beta_i S(t) \int_0^\infty q(b)p(t,b)db, \\
p(t,0) &= \int_0^\infty \xi(a)i(t,a)da,
\end{align}$$

and initial conditions

$$S(0) = S_0 > 0, \quad i(0,\cdot) = i_0(\cdot) \in L^1_+(0,\infty), \quad p(0,\cdot) = p_0(\cdot) \in L^1_+(0,\infty).$$

Here \(S(t)\) denotes the number of susceptible individuals at time \(t \geq 0\), \(i(t,a)\) denotes the number of infected individuals of infection age \(a \geq 0\) at time \(t \geq 0\), and \(p(t,b)\) denotes the quantity of pathogen of age \(b \geq 0\) at time \(t \geq 0\) in the contaminated water. We refer to \cite{3} for the meanings of the parameters. A threshold dynamics determined by the basic reproduction number is proved by constructing suitable Lyapunov functionals. Then Lin et al. \cite{11,12} established same results for cases with saturation incidences and with both saturation incidences and imperfect vaccination, respectively.

Besides temporal heterogeneity, another heterogeneity affecting cholera dynamics is spatial heterogeneity. Though lots have been done in recent years on cholera modeling and analysis (see, for example, the related references in \cite{25,27}), spatial heterogeneity has been rarely considered \cite{2,4,5,16,25,27,32,33}. Among them, patch models and PDE models are used in \cite{2,5,16} and \cite{4,25,27,32,33}, respectively. In particular, Wang and Wang \cite{25} proposed the following PDE cholera model,

$$\begin{align}
\frac{\partial S}{\partial t} &= D_1 \Delta S + \Lambda - S f_1(I) - S f_2(W) - dS + \sigma R, \quad x \in [0,1], \\
\frac{\partial I}{\partial t} &= D_2 \Delta I + S f_1(I) + S f_2(W) - (d + \gamma)I, \quad x \in [0,1], \\
\frac{\partial R}{\partial t} &= D_3 \Delta R + \gamma I - (d + \sigma)R, \quad x \in [0,1], \\
\frac{\partial W}{\partial x} &= D_4 \Delta W + \xi I + h(W) - \delta W, \quad x \in [0,1], \\
\frac{\partial S}{\partial x} + \frac{\partial I}{\partial x} + \frac{\partial R}{\partial x} &= \frac{\partial W}{\partial x} = 0, \quad x = 0,1.
\end{align}$$

(1.2)

One feature of model (1.2) is that intrinsic bacterial dynamics is incorporated and another is that general transmission rates \(f_1(I)\) and \(f_2(W)\) are employed. They investigated the effect of diffusive spatial spread on the disease spread and found that diffusive spatial spread does not produce a Turing instability to some extent.
It should be mentioned that, in applications, the domain is not necessarily to be one-dimensional. This motivates us to consider a PDE cholera model in a general bounded spatial domain. Another motivation comes from the fact that the parameters of PDE models for infectious diseases generally are space-dependent (see [1, 10, 24, 30, 31] as examples of some recent publications). However, in the above mentioned PDE cholera models, only Wang [27] considered the case where the transmission rates are dependent on both time and positions.

As discussed above, age structure and spatial heterogeneity are important characteristics in modeling cholera. To the best of our knowledge, so far there is no work on cholera to incorporate both. In this paper, we modify (1.1) to incorporate the latent period and diffusion to capture the movement of human hosts and bacteria in a heterogeneous environment. We first derive the model in Section 2. Due to the assumption that parameters are space-dependent, we build a delayed reaction-diffusion cholera model with nonlocal effects, which are caused by the mobility of the latent individuals and bacteria. As far as we know, this is the first time a delayed nonlocal reaction-diffusion cholera model has been built. Then we analyze the resulting model in Section 3. The main result is a threshold dynamics, which is determined by the principal eigenvalue of a linear scalar non-local reaction-diffusion equation. Roughly speaking, if the principal eigenvalue is less than 0 then the disease-free steady state is globally attractive while if the principal eigenvalue is larger than 0 then the model is uniformly persistent. It is shown in Section 4 that the principal eigenvalue has the same sign as that of $R_0 - 1$. Here $R_0$ is the basic reproduction number, which is defined as the spectral radius of the next infection operator. We further find the explicit expressions of $R_0$ for two special cases with the bilinear incidence and Beddington-DeAngelis incidence. The paper ends with a brief conclusion.

2. Model formulation. To build the model, we assume that the population lives in a bounded but still connected region $\Omega$. The population is divided into three disjoint compartments: susceptible, infected, and recovered. We assume that recovered individuals get permanent immunity and hence there is no need to consider the evolution of them. Let $S(t, x)$ denote the number of susceptible individuals in location $x$ at time $t \geq 0$ and $i(t, a, x)$ be the number of infected individuals of infection age $a \geq 0$ in location $x$ at time $t \geq 0$. Moreover, $p(t, b, x)$ denotes the concentration of Vibrio cholerae of biological age $b \geq 0$ in location $x$ at time $t \geq 0$. Suppose that $\tau_1$ is the average incubation period for infected individuals and $\tau_2$ is the average time for shed bacteria to the aquatic environment, that is, an individual infected by the disease becomes infectious $\tau_1$ time units after being infected while cholerae shed from infectious individuals can contact with susceptible individuals only $\tau_2$ time units after being shed and hence they cannot infect susceptible individuals for $b < \tau_2$. Then

$$i_E(t, x) = \int_0^{\tau_1} i(t, a, x) da \quad \text{and} \quad i_I(t, x) = \int_{\tau_1}^{\infty} i(t, a, x) da$$

are respectively the exposed individuals and infectious individuals in location $x$ at time $t$, and

$$p_E(t, x) = \int_0^{\tau_2} p(t, b, x) db \quad \text{and} \quad p_I(t, x) = \int_{\tau_2}^{\infty} p(t, b, x) db$$

are respectively the bacteria in location $x$ at time $t$ but not in the aquatic environment and in the aquatic environment.
We assume that there is a recruitment $\lambda(x)$ of the population and all recruitment are susceptible. The susceptible diffuses at the rate $D_S(x)$ and has a natural death rate $\mu(x)$. A susceptible can be infected directly with person-person contacts and indirectly with bacteria with the incidences $f_1(x, S(t, x), i_I(t, x))$ and $f_2(x, S(t, x), p_I(t, x))$ at location $x$, respectively. Then $S(t, x)$ is governed by the following reaction-diffusion equation,

$$\frac{\partial S(t, x)}{\partial t} = \nabla \cdot [D_S(x) \nabla S(t, x)] + \lambda(x) - f_1(x, S(t, x), i_I(t, x)) - f_2(x, S(t, x), p_I(t, x)) - \mu(x)S(t, x),$$

(2.1)

where $\nabla$ is the gradient with respect to the spatial variable $x$. Employing the standard argument on age-structured population and spatial diffusion (see, for example, [15, 6]), we get

$$\frac{\partial i(t, a, x)}{\partial t} + \frac{\partial i(t, a, x)}{\partial a} = \nabla \cdot [D(a, x) \nabla i(t, a, x)] - (\mu_i(x) + \theta(a, x))i(t, a, x)$$

(2.2)

and

$$\frac{\partial p(t, b, x)}{\partial t} + \frac{\partial p(t, b, x)}{\partial b} = \nabla \cdot [H(b, x) \nabla p(t, b, x)] - (\mu_p(x) + \delta(b, x))p(t, b, x)$$

(2.3)

with

$$\begin{align*}
&i(t, 0, x) = f_1(x, S(t, x), i_I(t, x)) + f_2(x, S(t, x), p_I(t, x)), \\
&p(t, 0, x) = \xi(x)i_I(t, x).
\end{align*}$$

Here $D(a, x)$ and $H(b, x)$ are the diffusion rates of the infected individuals and bacteria, respectively; $\mu_i(x)$ and $\mu_p(x)$ are their natural death rates, respectively; $\theta(a, x)$ and $\delta(b, x)$ represent respectively the recovery rate of infected individuals and the clearance rate of bacteria; and $\xi(x)$ represents the shedding rate of an infectious individual at $x$.

From the biological point of view, we consider a closed environment in the sense that the fluxes for the population and bacteria on the boundary of $\Omega$, $\partial\Omega$, are all zero, that is, we impose the following Neumann boundary conditions for $S(t, x)$, $i(t, a, x)$, $p(t, b, x)$,

$$\begin{align*}
&D_S(x) \nabla S(t, x) \cdot n = 0, \quad x \in \partial\Omega, t > 0, \\
&D(a, x) \nabla i(t, a, x) \cdot n = 0, \quad x \in \partial\Omega, t > 0, a \geq 0, \\
&H(b, x) \nabla p(t, b, x) \cdot n = 0, \quad x \in \partial\Omega, t > 0, b \geq 0,
\end{align*}$$

associated with (2.1), (2.2), and (2.3). Here $n$ is the outward normal to $\partial\Omega$.

For the ease of presentation, in the sequel, we assume

- $D(a, x) = \begin{cases} D_E(x) & \text{ for } a \in [0, \tau_1], \ x \in \Omega, \\ D_I(x) & \text{ for } a \in (\tau_1, \infty), \ x \in \Omega; \end{cases}$
- $\theta(a, x) = \begin{cases} \theta_E(x) & \text{ for } a \in [0, \tau_1], \ x \in \Omega, \\ \theta_I(x) & \text{ for } a \in (\tau_1, \infty), \ x \in \Omega; \end{cases}$
- $H(b, x) = \begin{cases} H_E(x) & \text{ for } b \in [0, \tau_2], \ x \in \Omega, \\ H_I(x) & \text{ for } b \in (\tau_2, \infty), \ x \in \Omega; \end{cases}$
- $\delta(b, x) = \begin{cases} \delta_E(x) & \text{ for } b \in [0, \tau_2], \ x \in \Omega, \\ \delta_I(x) & \text{ for } b \in (\tau_2, \infty), \ x \in \Omega. \end{cases}$

Under these assumptions, we obtain a system of reaction-diffusion equations with nonlocal effects as follows.
Integrating both sides of (2.2) from 0 to $\tau_1$ and from $\tau_1$ to $\infty$ yields

$$
\frac{\partial i(t, x)}{\partial t} = \nabla \cdot [D_E(x)\nabla i(t, x)] - (\mu_i(x) + \theta_i(x))i(t, x) + i(t, 0, x) - i(t, \tau_1, x)
$$

and

$$
\frac{\partial p(t, x)}{\partial t} = \nabla \cdot [D_I(x)\nabla p(t, x)] - (\mu_p(x) + \delta_p(x))p(t, x) + p(t, 0, x) - p(t, \tau_2, x)
$$

Biologically, we assume that $i(t, \tau_1, x) = 0$ and $p(t, \tau_2, x) = 0$. It then remains to determine $i(t, \tau_1, x)$ and $p(t, \tau_2, x)$, which are achieved below by applying the method of characteristics.

For any $r \geq 0$, consider solutions of (2.2) along the characteristic line $t = a + r$ by letting $v(r, a, x) = i(a + r, a, x)$. Then, for $a \in [0, \tau_1]$,

$$
\frac{\partial v(r, a, x)}{\partial a} = \left[ \frac{\partial i(t, a, x)}{\partial t} + \frac{\partial i(t, a, x)}{\partial a} \right]_{t=a+r}
$$

$$
= \nabla \cdot [D(a, x)\nabla i(a + r, a, x)] - (\mu_i(x) + \theta_i(a, x))i(a + r, a, x)
$$

$$
= \nabla \cdot [D_E(x)\nabla v(r, a, x)] - (\mu_i(x) + \theta_i(x))v(r, a, x)
$$

(2.4)

and

$$
v(r, 0, x) = i(r, 0, x) = f_1(x, S(t, x), i_1(t, x)) + f_2(x, S(t, x), p_1(t, x)).
$$

(2.5)

Regarding $r$ as a parameter and solving (2.4) with (2.5) produce

$$
v(r, a, x) = \int_\Omega G_2(a, x, y)[f_1(y, S(r, y), i_1(r, y)) + f_2(y, S(r, y), p_1(r, y))]dy,
$$

(2.6)

where $G_2$ is the Green function of the operator $\nabla \cdot [D_E(\cdot)\nabla] - (\mu_i(\cdot) + \theta_E(\cdot))$ associated with zero flux boundary condition. Evaluating (2.6) at $a = \tau_1$ (hence $r = t - \tau_1$) gives us

$$
i(t, \tau_1, x) = v(t - \tau_1, \tau_1, x)
$$

$$
= \int_\Omega G_2(\tau_1, x, y)[f_1(y, S(t - \tau_1, y), i_1(t - \tau_1, y))
$$

$$
+ f_2(y, S(t - \tau_1, y), p_1(t - \tau_1, y))]dy.
$$

(2.7)

Similarly we can get

$$
p(t, \tau_2, x) = \int_\Omega G_3(\tau_2, x, y)[\xi(y)i_1(t - \tau_2, y)]dy,
$$

(2.8)

where $G_3$ is the Green function of the operator $\nabla \cdot [D_I(\cdot)\nabla] - (\mu_p(\cdot) + \delta_p(\cdot))$ associated with zero flux boundary condition.

Plugging (2.7) into $\frac{\partial i(t, x)}{\partial t}$ and $\frac{\partial i(t, x)}{\partial t}$ and plugging (2.8) into $\frac{\partial p(t, x)}{\partial t}$ and $\frac{\partial p(t, x)}{\partial t}$, and also taking into consideration of (2.1), we obtain the following delayed
Note that for \( p \) and the initial conditions

\[
\begin{align*}
\frac{\partial i(t,x)}{\partial t} &= \nabla \cdot [D_S(x)\nabla S(t,x)] + \lambda(x) - \mu(x)S(t,x) \\
&\quad - f_1(x, S(t,x), i_1(t,x)) - f_2(x, S(t,x), p_1(t,x)), \\
\frac{\partial i_E(t,x)}{\partial t} &= \nabla \cdot [D_{E}(x)\nabla i_{E}(t,x)] - (\mu_{i}(x) + \theta_{E}(x))i_{E}(t,x) \\
&\quad + f_1(x, S(t,x), i_1(t,x)) + f_2(x, S(t,x), p_1(t,x)) \\
&\quad - \int_{\Omega} G_2(\tau, x, y)[f_1(y, S(t-\tau, y), i_1(t-\tau, y)) \\
&\quad + f_2(y, S(t-\tau, y), p_1(t-\tau, y))]dy, \\
\frac{\partial p(t,x)}{\partial t} &= \nabla \cdot [H_{E}(x)\nabla p_{E}(t,x)] - (\mu_{i}(x) + \delta_{E}(x))p_{E}(t,x) + \xi(x)i_1(t,x) \\
&\quad - \int_{\Omega} G_3(\tau, x, y)[f_1(y, S(t-\tau, y), i_1(t-\tau, y)) \\
&\quad + f_2(y, S(t-\tau, y), p_1(t-\tau, y))]dy,
\end{align*}
\]

for \((t, x) \in (0, \infty) \times \Omega\) with the boundary conditions

\[
[D_S(x)\nabla S(t,x)] \cdot v = [D_{I}(x)\nabla i_{I}(t,x)] \cdot v = [H_{I}(x)\nabla p_{I}(t,x)] \cdot v = 0.
\]

For convenience, we denote

\[
(u_1, u_2, u_3) = (S, i_1, p_1), \\
(D_1(\cdot), D_2(\cdot), D_3(\cdot)) = (D_S(\cdot), D_I(\cdot), H_I(\cdot)),
\]

\[
(\theta(\cdot), \delta(\cdot)) = (\mu_{i}(\cdot) + \theta_{I}(\cdot), \mu_{i}(\cdot) + \delta_{I}(\cdot)).
\]

Then in the sequel, we focus on the following system

\[
\begin{align*}
\frac{\partial u_1(t,x)}{\partial t} &= \nabla \cdot [D_1(x)\nabla u_1(t,x)] + \lambda(x) - \mu(x)u_1(t,x) \\
&\quad - f_1(x, u_1(t,x), u_2(t,x)) - f_2(x, u_1(t,x), u_3(t,x)), \\
\frac{\partial u_2(t,x)}{\partial t} &= \nabla \cdot [D_2(x)\nabla u_2(t,x)] - \theta(x)u_2(t,x) \\
&\quad + \int_{\Omega} G_2(\tau, x, y)[f_1(y, u_1(t-\tau, y), u_2(t-\tau, y)) \\
&\quad + f_2(y, u_1(t-\tau, y), u_3(t-\tau, y))]dy, \\
\frac{\partial u_3(t,x)}{\partial t} &= \nabla \cdot [D_3(x)\nabla u_3(t,x)] - \delta(x)u_3(t,x) \\
&\quad + \int_{\Omega} G_3(\tau, x, y)[f_1(y, u_1(t-\tau, y), u_2(t-\tau, y)) \\
&\quad + f_2(y, u_1(t-\tau, y), u_3(t-\tau, y))]dy,
\end{align*}
\]

for \((t, x) \in (0, \infty) \times \Omega\) with the boundary conditions

\[
[D_i(x)\nabla u_i(t,x)] \cdot v = 0, \quad i = 1, 2, 3, x \in \partial \Omega, t > 0
\]

and the initial conditions

\[
(u_1(\theta, x), u_2(\theta, x), u_3(\theta, x)) = (\phi_1(\theta, x), \phi_2(\theta, x), \phi_3(\theta, x)) \in \mathbb{R}^3
\]
for \((\theta, x) \in [-\tau, 0] \times \Omega\), where \(\tau = \max\{\tau_1, \tau_2\}\).

To study the dynamics of (2.9), we impose the following assumptions on the parameter functions and incidences.

(H1): All \(D_i\) \((i = 1, 2, 3)\), \(\lambda, \mu, \theta, \) and \(\delta\) are positive and continuous functions on \(\bar{\Omega}\).

(H2): For \(i = 1, 2, f_i\) is nonnegative and continuous satisfying

(i) for \(x \in \bar{\Omega}\), \(f_i(x, u, v) = 0\) if and only if \(u = 0\) or \(v = 0\);

(ii) \(f_i\) is monotone non-decreasing and continuously differentiable with respect to the last two variables;

(iii) there exists \(\beta_i^+ > 0\) such that \(f_i(x, u, v) \leq \beta_i^+ uv\) for \(x \in \bar{\Omega}\) and \(u, v \in \mathbb{R}_+\);

(iv) \(f_i\) is concave down with respect to the last variable.

For a continuous function \(\phi\) on \(\bar{\Omega}\), we denote

\[
\phi_+ = \max_{x \in \bar{\Omega}} \phi(x) \quad \text{and} \quad \phi_- = \min_{x \in \bar{\Omega}} \phi(x).
\]

3. A threshold dynamics. The purpose of this section is to establish the main result of this paper, a threshold dynamics. We start with the well-posedness of (2.9).

Let \(X = C(\bar{\Omega}, \mathbb{R}^3)\) be the Banach space of all continuous functions from \(\bar{\Omega}\) to \(\mathbb{R}^3\) equipped with the supremum norm \(\| \cdot \|_X\). Denote \(C_\gamma \triangleq C([-\tau, 0], X)\) to be the set of all continuous mappings from \([-\tau, 0]\) into \(X\). Equipped with the norm \(\| \phi \| = \max_{\theta \in [-\tau, 0]} \| \phi(\theta) \|_X\) for \(\phi \in C_\gamma, C_\gamma\) is a Banach space. Let \(X^+ = C(\bar{\Omega}, \mathbb{R}_+^3)\) and \(C_\gamma^+ = C([-\tau, 0], \mathbb{R}_+^3)\). Then both \((X, X^+)\) and \((C_\gamma, C_\gamma^+)\) are strongly ordered Banach spaces. Given a continuous function \(u : [-\tau, \sigma) \to X\) with \(\sigma > 0\), for \(t \in [0, \sigma)\), we define \(u_t(\theta) = u(t + \theta)\) for \(\theta \in [-\tau, 0]\).

Let \(Y = C(\bar{\Omega}, \mathbb{R})\) and \(Y^+ = C(\bar{\Omega}, \mathbb{R}_+)\). Suppose that \(T_1(t), T_2(t), T_3(t) : Y \to Y, t \geq 0\), are strongly continuous semigroups associated with \(\nabla \cdot [D_1(\cdot) \nabla] - \mu(\cdot), \nabla \cdot [D_2(\cdot) \nabla] - \theta(\cdot), \) and \(\nu \cdot [D_3(\cdot) \nabla] - \delta(\cdot)\) respectively, subject to the zero flux boundary conditions. It is well-known that for any \(\varphi \in Y, t \geq 0\),

\[
(T_i(t)\varphi)(x) = \int_\Omega G_i(x, y, t)\varphi(y)dy, \quad i = 1, 2, 3, \tag{3.1}
\]

where \(G_i, i = 1, 2, 3,\) are the Green functions associated with \(\nabla \cdot [D_1(\cdot) \nabla] - \mu(\cdot), \nabla \cdot [D_2(\cdot) \nabla] - \theta(\cdot), \) and \(\nabla \cdot [D_3(\cdot) \nabla] - \delta(\cdot)\) respectively, subject to the zero flux boundary conditions. Moreover, for each \(t > 0\), \(T_i(t) : Y \to Y, i = 1, 2, 3\) is compact and strongly positive (see, for example, [18, Section 7.1 and Corollary 7.2.3]). Let \(A_i := \text{Dom}(A_i) \to Y\) be the generator of \(T_i(t), i = 1, 2, 3\). Then \(T(t) := (T_1(t), T_2(t), T_3(t)) : X \to X, t > 0\) is a \(C_0\)-semigroup generated by the operator \(A := (A_1, A_2, A_3)\) defined on \(\text{Dom}(A) := \text{Dom}(A_1) \times \text{Dom}(A_2) \times \text{Dom}(A_3)\).

Define \(F = (F_1, F_2, F_3) : C^+_{\gamma} \to X\) by

\[
\begin{aligned}
F_1(\phi)(x) &= \lambda(x) - f_1(x, \phi_1(0, x), \phi_2(0, x)) - f_2(x, \phi_1(0, x), \phi_3(0, x)), \\
F_2(\phi)(x) &= \int_0^x G_2(\tau, x, y)[f_1(y, \phi_1(-\tau_1, y), \phi_2(-\tau_1, y)) \\
&\quad + f_2(y, \phi_1(-\tau_1, y), \phi_3(-\tau_1, y))]dy, \\
F_3(\phi)(x) &= \int_0^x G_3(\tau, x, y)[f_1(y, \phi_1(-\tau_2, y)) - f_2(y, \phi_1(-\tau_2, y))]dy,
\end{aligned}
\]

for \(x \in \bar{\Omega}, \phi = (\phi_1, \phi_2, \phi_3)^T \in C^+_{\gamma}.\) Then system (2.9) can be rewritten as the following integral equation,

\[
u(t) = T(t)\phi + \int_0^t T(t - s)F(u_s)ds, \quad t > 0,
\]


Theorem 3.1. For any \( x \in H \), where \( 8 \in \text{WEIWEI LIU, JINLIANG WANG AND YUMING CHEN} \), which has a global compact attractor in \( \Omega \), admits a unique positive steady state \( (2.9) \) takes the following form

\[
\begin{aligned}
\frac{\partial u}{\partial t} &= \nabla \cdot [D(x) \nabla u] + H(x) - G(x)u, \quad x \in \Omega, t > 0, \\
[D(x) \nabla u] \cdot \nu &= 0, \quad x \in \partial \Omega, t > 0,
\end{aligned}
\]

where \( D(x) \), \( H(x) \), and \( G(x) \) are continuous and positive functions on \( \overline{\Omega} \). Then (3.2) admits a unique positive steady state \( \omega^*(x) \), which is globally attractive in \( \mathcal{Y}^+ \). Furthermore, if \( H(x) \equiv H \) and \( G(x) \equiv G \) for all \( x \in \Omega \), then \( \omega^*(x) \equiv H/G \) for all \( x \in \Omega \).

With the help of Lemma 3.2, we can obtain a solution semiflow of (2.9).

Theorem 3.1. For any \( \phi \in C^+_\tau \), system (2.9) admits a unique solution \( u(t, \cdot, \phi) \) on \( \mathbb{R}_+ \) with \( u_0 = \phi \), and the solution semiflow \( \Phi(t) = u_k(\cdot) : C^+_\tau \rightarrow C^+_\tau \), \( t \geq 0 \), generated by (2.9) takes the following form

\[
\Phi(t)\phi(\theta, x) = u(t + \theta, x, \phi) \quad \text{for} \ x \in \overline{\Omega}, \ t \geq 0, \ \theta \in [-\tau, 0],
\]

which has a global compact attractor in \( C^+_\tau \).

Proof. By way of contradiction, we assume that \( t_\phi < \infty \). Then on \( [0, t_\phi) \), we have

\[
\begin{aligned}
\frac{\partial u(t, x)}{\partial t} &\leq \nabla \cdot [D_1(x) \nabla u(t, x)] + \lambda(x) - \mu(x)u(t, x), \quad x \in \Omega, \\
[D_1(x) \nabla u(t, x)] \cdot \nu &= 0, \quad x \in \partial \Omega, \\
u_1(\theta, x) &= \phi_1(\theta, x), \quad \theta \in [-\tau, 0], x \in \Omega.
\end{aligned}
\]

Let \( \omega(t, x) \) be the solution of

\[
\begin{aligned}
\frac{\partial \omega(t, x)}{\partial t} &= \nabla \cdot [D_1(x) \nabla \omega(t, x)] + \lambda(x) - \mu(x)\omega(t, x), \quad x \in \Omega, t > 0, \\
[D_1(x) \nabla \omega(t, x)] \cdot \nu &= 0, \quad x \in \partial \Omega, t > 0, \\
\omega(\theta, x) &= \phi_1(\theta, x), \quad \theta \in [-\tau, 0], x \in \Omega.
\end{aligned}
\]
By comparison principle, \( u_1(t, x) \leq \omega(t, x) \) for \( (t, x) \in [0, t_\phi) \times \Omega \). On the other hand, by Lemma 3.2, system (3.3) admits a unique positive steady state \( \omega^*(x) \), which is globally asymptotically stable in \( \mathbb{R}^+ \). Thus we can conclude that there is \( B_1 > 0 \) such that \( u_1(t, \cdot, \phi) \leq B_1 \) for all \( t \in [0, t_\phi) \).

Denote \( \bar{u}_i(t) = \int u_i(t, x) dx \) for \( i = 1, 2, 3 \). Then by the results above, there exists a constant \( C > 0 \) such that
\[
\frac{\partial u_2(t, x)}{\partial t} \leq \nabla \cdot [D_2(x) \nabla u_2(t, x)] - \theta(x) u_2(t, x) + C[\bar{u}_2(t - \tau) + \bar{u}_3(t - \tau)] \quad \text{for} \ t \in [0, t_\phi).
\] (3.4)

We claim that \( \bar{u}_2(t) \) is bounded on \([0, t_\phi)\). For \( t \in [0, t_\phi) \), integrating the first equation in (2.9) over the interval \([0, t]\) yields
\[
\frac{d\bar{u}_1(t)}{dt} \leq \int_\Omega \lambda(x) dx - \int_\Omega \mu(x) u_1(t, x) dx - \int_\Omega f_1(x, u_1(t, x), u_2(t, x)) dx
- \int_\Omega f_2(x, u_1(t, x), u_3(t, x)) dx
\leq \lambda_+|\Omega| - \mu_- \bar{u}_1(t) - \int_\Omega f_1(x, u_1(t, x), u_2(t, x)) dx
- \int_\Omega f_2(x, u_1(t, x), u_3(t, x)) dx,
\] or equivalently,
\[
\int_\Omega f_1(x, u_1(t, x), u_2(t, x)) dx + \int_\Omega f_2(x, u_1(t, x), u_3(t, x)) dx
\leq \lambda_+|\Omega| - \mu_- \bar{u}_1(t) - \frac{d\bar{u}_1(t)}{dt},
\] (3.5)

where \( |\Omega| \) is the volume of \( \Omega \). Similarly, with the assistance of (3.5), we can get
\[
\frac{d\bar{u}_2(t)}{dt} \leq -\theta_- \bar{u}_2(t) + \lambda_+|\Omega|^2 - \mu_-|\Omega| \bar{u}_1(t - \tau_1) - |\Omega| \frac{d\bar{u}_1(t - \tau_1)}{dt}
\]
or
\[
\frac{d}{dt} [\bar{u}_2(t) + |\Omega| \bar{u}_1(t - \tau_1)] \leq -\theta_- \bar{u}_2(t) + \lambda_+|\Omega|^2 - \mu_-|\Omega| \bar{u}_1(t - \tau_1)
\leq - \min \{\theta_-, \mu_-\} [\bar{u}_2(t) + |\Omega| \bar{u}_1(t - \tau_1)] + \lambda_+|\Omega|^2
\]
for \( t \in [0, t_\phi) \). It follows that \( \bar{u}_2(t) + |\Omega| \bar{u}_1(t - \tau_1) \) and hence \( \bar{u}_2(t) \) is bounded on \([0, t_\phi)\). This proves the claim. This claim implies that there exists a positive number \( Q \) such that
\[
\begin{align*}
0 &\leq \nabla \cdot [D_3(x) \nabla u_3(t, x)] - \delta(x) u_3(t, x) + Q, & x \in \Omega, t \in (0, t_\phi), \\
[D_3(x) \nabla u_3(t, x)] \cdot \nu &\leq 0, & x \in \partial \Omega, t > 0, \\
u_3(\theta, x) &\leq \phi_3(\theta, x), & (\theta, x) \in [-\tau, 0] \times \Omega.
\end{align*}
\]
Again, it follows from Lemma 3.2 and the comparison principle that \( u_3(t, \cdot, \phi) \) is bounded on \([0, t_\phi)\).

Since \( u_3(t, \cdot, \phi) \) is bounded on \([0, t_\phi)\), we see that \( \bar{u}_3(t) \) is also bounded on \([0, t_\phi)\). The boundedness of \( \bar{u}_2(t) \) and \( \bar{u}_3(t) \) on \([0, t_\phi)\), combined with (3.4) and the comparison theorem for delayed parabolic equation [29], implies that \( u_2(t, x) \) is bounded on \([0, t_\phi)\).
In summary, we have shown that \( u(t, \cdot, \phi) \) is bounded on \([0, t_\phi)\), a contradiction to \( \lim_{t \to t_\phi^-} \|u(t)\| = \infty \). Therefore, \( t_\phi = \infty \) and the solution \( u(t, \cdot, \phi) \) is defined on \( \mathbb{R}_+ \).

By the above discussion, we also know that there exists a positive constant \( B \) such that, for any \( \phi \in C^+_\tau \), there exists a \( t_\phi \in [0, \infty) \) making the solution \( (u_1(t, x, \phi), u_2(t, x, \phi), u_3(t, x, \phi)) \) satisfy \( u_i(t, x, \phi) \leq B \) \( (i = 1, 2, 3) \) for \( t \geq t_\phi \) and \( x \in \Omega \). In other words, the solution semiflow \( \Phi(t) = u_i(\cdot) : C^+_\tau \to C^+_\tau \) is point dissipative. Furthermore, by Theorem 2.1.8 of Wu [29], \( \Phi(t) \) is compact for each \( t > \tau \). It follows from Theorem 3.4.8 [8] that \( \Phi(t) \) has a global compact attractor in \( C^+_\tau \).

The following results will be used in proving the persistence of (2.9).

**Lemma 3.3.** Let \( u(t, x, \phi) \) be the solution of system (2.9) with \( u_0 = \phi \in C^+_\tau \). Then the following statements hold.

(i) \( u_1(t, x, \phi) > 0 \) for \( t > 0, \ x \in \overline{\Omega}, \) and

\[
\liminf_{t \to \infty} u_1(t, x, \phi) \geq \frac{\lambda_-}{\mu_+ + \beta_1^+ B + \beta_2^+ B} \text{ uniformly for } x \in \overline{\Omega},
\]

where \( B \) is the positive constant specified in the proof of Theorem 3.1.

(ii) Let \( i \in \{2, 3\} \). If there exists \( t_0 \geq 0 \) such that \( u_i(t_0, \cdot, \phi) \neq 0 \) then \( u_i(t, x, \phi) > 0 \) for \( t > t_0 \) and \( x \in \Omega \).

**Proof.** (i) We know that there exists \( \hat{t}_\phi \geq 0 \) such that \( u_2(t, \cdot, \phi) \leq B \) and \( u_3(t, \cdot, \phi) \leq B \) for \( t \geq \hat{t}_\phi \). Then

\[
\left\{ \begin{array}{rl}
\frac{\partial u_1(t, x)}{\partial t} & \geq \nabla \cdot [D_1(x) \nabla u_1(t, x)] + \lambda_- \\
& \quad - (\mu_+ + \beta_1^+ B + \beta_2^+ B) u_1(t, x), \quad x \in \Omega, t \geq \hat{t}_\phi,
\end{array} \right.
\]

\[
0 = [D_1(x) \nabla u_1(t, x)] \cdot \nu, \quad x \in \partial \Omega, t \geq \hat{t}_\phi.
\]

Let \( v(t, x, u_1(\hat{t}_\phi, \cdot, \phi)) \) be the solution of

\[
\left\{ \begin{array}{rl}
\frac{\partial u_1(x)}{\partial t} & = \nabla \cdot [D_1(x) \nabla v(t, x)] + \lambda_- - (\mu_+ + \beta_1^+ B + \beta_2^+ B) v(t, x), \quad x \in \Omega, t > 0,
\end{array} \right.
\]

\[
[D_1(x) \nabla v(t, x)] \cdot \nu = 0, \quad x \in \partial \Omega, t > 0.
\]

Then by the standard parabolic comparison theorem we have \( u_1(t + \hat{t}_\phi, x, \phi) \geq v(t, x, u_1(\hat{t}_\phi, \cdot, \phi)) \) \( > 0 \) for \( x \in \Omega \) and \( t \geq 0 \). By applying Lemma 3.2, we immediately get \( \liminf_{t \to \infty} u_1(t, x, \phi) \geq \frac{\lambda_-}{\mu_+ + \beta_1^+ B + \beta_2^+ B} \) uniformly for \( x \in \overline{\Omega} \).

(ii) Note that \( u_2(t, x, \phi) \) and \( u_3(t, x, \phi) \) satisfy

\[
\left\{ \begin{array}{rl}
\frac{\partial u_2(t, x)}{\partial t} & \geq \nabla \cdot [D_2(x) \nabla u_2(t, x)] - \theta(x) u_2(t, x), \quad x \in \Omega, t > 0,
\end{array} \right.
\]

\[
\left\{ \begin{array}{rl}
\frac{\partial u_3(t, x)}{\partial t} & \geq \nabla \cdot [D_3(x) \nabla u_3(t, x)] - \delta(x) u_3(t, x), \quad x \in \Omega, t > 0,
\end{array} \right.
\]

with boundary conditions

\[
[D_i(x) \nabla u_i(t, x)] \cdot \nu = 0, \quad i = 2, 3, x \in \partial \Omega, t > 0.
\]

Suppose that there exists some \( t_0 \geq 0 \) and \( i \in \{2, 3\} \) such that \( u_i(t_0, \cdot, \phi) \neq 0 \). Then \( u_i(t, x, \phi) > 0 \) for \( t > t_0 \) and \( x \in \overline{\Omega} \) by the strong maximum principle and the Hopf boundary lemma (see, for instance, [17, Theorem 3.4]). This completes the proof. \( \square \)
Set \( u_2 = u_3 = 0 \) in (2.9). Then \( u_1 \) satisfies
\[
\frac{\partial u_1(t,x)}{\partial t} = \nabla \cdot [D_1(x)\nabla u_1(t,x)] + \lambda(x) - \mu(x)u_1(t,x).
\] (3.6)

It follows from Lemma 3.2 that (3.6) admits a unique positive steady state \( U_{\text{steady state}} \), which is globally asymptotically stable in \( \mathbb{V}^+ \). Therefore, (2.9) has a disease-free steady state \((U(x),0,0)\).

Linearizing system (2.9) at the disease-free steady state \((U(x),0,0)\), we get the following nonlocal and cooperative system for \( u_2 \) and \( u_3 \):
\[
\begin{align*}
\frac{\partial u_2(t,x)}{\partial t} &= \nabla \cdot [D_2(x)\nabla u_2(t,x)] - \theta(x)u_2(t,x) \\
&\quad + \int_{\Omega} G_2(\tau_1, x, y) \left[ \frac{\partial f}{\partial u_2}(y, U(y), 0)u_2(t-\tau_1, y) \right] dy, \quad x \in \Omega, t > 0, \\
\frac{\partial u_3(t,x)}{\partial t} &= \nabla \cdot [D_3(x)\nabla u_3(t,x)] - \delta(x)u_3(t,x) \\
&\quad + \int_{\Omega} G_3(\tau_2, x, y)\xi(y)u_2(t-\tau_2, y)dy, \quad x \in \Omega, t > 0, \\
0 &= \left[ D_i(x)\nabla u_i(t,x) \right] \cdot \nu, \quad i = 2, 3, x \in \partial \Omega, t > 0.
\end{align*}
\] (3.7)

In order to characterize the principal eigenvalue together with the associated eigenfunctions of (3.7), we first consider these for
\[
\begin{align*}
\frac{\partial u_2(t,x)}{\partial t} &= \nabla \cdot [D_2(x)\nabla u_2(t,x)] - \theta(x)u_2(t,x) \\
&\quad + \int_{\Omega} G_2(\tau_1, x, y) \left[ \frac{\partial f}{\partial u_2}(y, U(y), 0)u_2(t,y) \right] dy, \quad x \in \Omega, t > 0, \\
\frac{\partial u_3(t,x)}{\partial t} &= \nabla \cdot [D_3(x)\nabla u_3(t,x)] - \delta(x)u_3(t,x) \\
&\quad + \int_{\Omega} G_3(\tau_2, x, y)\xi(y)u_2(t,y)dy, \quad x \in \Omega, t > 0, \\
0 &= \left[ D_i(x)\nabla u_i(t,x) \right] \cdot \nu, \quad i = 2, 3, x \in \partial \Omega, t > 0.
\end{align*}
\] (3.8)

Substituting \( u_2(t,x) = e^{\lambda t}\psi_2(x) \) and \( u_3(t,x) = e^{\lambda t}\psi_3(x) \) into (3.8), we obtain the following nonlocal eigenvalue problem,
\[
\begin{align*}
\lambda\psi_2(x) &= \nabla \cdot [D_2(x)\nabla \psi_2(x)] - \theta(x)\psi_2(x) \\
&\quad + \int_{\Omega} G_2(\tau_1, x, y) \left[ \frac{\partial f}{\partial u_2}(y, U(y), 0)\psi_2(y) \right] dy, \quad x \in \Omega, t > 0, \\
\lambda\psi_3(x) &= \nabla \cdot [D_3(x)\nabla \psi_3(x)] - \delta(x)\psi_3(x) \\
&\quad + \int_{\Omega} G_3(\tau_2, x, y)\xi(y)\psi_2(y)dy, \quad x \in \Omega, t > 0, \\
0 &= \left[ D_i(x)\nabla \psi_i(t,x) \right] \cdot \nu, \quad i = 2, 3, x \in \partial \Omega, t > 0.
\end{align*}
\] (3.9)

Arguing similarly as obtaining [18, Theorem 7.6.1], we see that (3.9) admits a principal eigenvalue \( \lambda(U, \tau) \), which has a positive eigenfunction. Return to (3.7), we substitute \( u_2(t,x) = e^{\lambda t}\psi_2(x) \) and \( u_3(t,x) = e^{\lambda t}\psi_3(x) \) to get the following nonlocal eigenvalue problem,
\[
\begin{align*}
\lambda\psi_2(x) &= \nabla \cdot [D_2(x)\nabla \psi_2(x)] - \theta(x)\psi_2(x) \\
&\quad + e^{-\lambda\tau_1} \int_{\Omega} G_2(\tau_1, x, y) \left[ \frac{\partial f}{\partial u_2}(y, U(y), 0)\psi_2(y) \right] dy, \quad x \in \Omega, t > 0, \\
\lambda\psi_3(x) &= \nabla \cdot [D_3(x)\nabla \psi_3(x)] - \delta(x)\psi_3(x) \\
&\quad + e^{-\lambda\tau_2} \int_{\Omega} G_3(\tau_2, x, y)\xi(y)\psi_2(y)dy, \quad x \in \Omega, t > 0, \\
0 &= \left[ D_i(x)\nabla \psi_i(t,x) \right] \cdot \nu, \quad i = 2, 3, x \in \partial \Omega, t > 0.
\end{align*}
\] (3.10)

With similar arguments as those in the proof of [22, Theorem 2.2], one can have the following result on the principal eigenvalue of (3.10).

**Lemma 3.4.** Problem (3.10) has a principal eigenvalue \( \lambda(U, \tau) \), which has a strongly positive eigenfunction. Moreover, \( \lambda(U, \tau) \) has the same sign as \( \lambda(U, \tau). \)
Proof. Denote
\[ \mathbb{E} = C([-\tau, 0], \mathbb{Y}) \times C([-\tau, 0], \mathbb{Y}) \]
and
\[ \mathbb{E}^+ = C([-\tau, 0], \mathbb{Y}^+) \times C([-\tau, 0], \mathbb{Y}^+) \].

For any \( \psi = (\psi_2, \psi_3) \in \mathbb{E}^+ \setminus \{0\} \), let \( v(t, \psi) = (v_2(t, \psi), v_3(t, \psi)) \), \( t \geq 0 \), be the solution of system (3.7). We claim that there exists a \( t_0 \in [0, \tau] \) such that \( v_2(t_0, \psi) \neq 0 \) or \( v_3(t_0, \psi) \neq 0 \). By assumption, there exists a \( \theta_0 \in [-\tau, 0] \) such that \( \psi_2(\theta_0, \cdot) \neq 0 \) or \( \psi_3(\theta_0, \cdot) \neq 0 \). If \( \theta_0 = 0 \), then the claim is obvious. Now assume that \( \theta_0 < 0 \).

First assume that \( \theta_0 \geq -\tau_1 \). Then \( v_2(\tau_1 + \theta_0) \neq 0 \). Otherwise, \( v_2(\tau_1 + \theta_0, \psi)(x) \equiv 0 \) and hence for \( x \in \Omega \),
\[
\frac{\partial v_2(\tau_1 + \theta_0, x)}{\partial t} = \int_{\Omega} \mathcal{G}_2(\tau_1, x, y) \left[ \frac{\partial f_1}{\partial u_2}(y, U(y), 0)\psi_2(\theta_0, y) + \frac{\partial f_2}{\partial \psi_3}(y, U(y), 0)\psi_3(\theta_0, y) \right] dy \]
\[
> 0,
\]
which contradicts the fact that \( \frac{\partial v_2(\tau_1 + \theta_0, x)}{\partial t} \leq 0 \) (as \( v_2(t, \psi)(x) \geq 0 \) for \( t < \tau_1 + \theta_0 \) and \( v_2(\tau_1 + \theta_0)(x) = 0 \) for \( x \in \Omega \)). Next, if \( \theta_0 \geq -\tau_2 \), then similarly we can get \( v_2(\tau_2 + \theta_0, \psi) \neq 0 \). This proves the claim. The claim, together with the strong maximum principle and the Hopf boundary lemma, implies that \( v_i(t, \psi)(x) > 0 \) for \( t > t_0 + \tau, x \in \Omega, i = 2, 3 \). Therefore, we have verified that the solution semiflow associated with (3.7) is strongly positive from \( \mathbb{E} \) to \( \mathbb{E} \). Then we can complete the proof with similar arguments as those for [7, Lemma 2.4] and [22, Theorem 2.2]. \( \Box \)

Now we are in the position to state and prove the main result of this paper, which indicates that \( \lambda(U, \tau) \) is a threshold parameter in determining disease persistence and extinction.

**Theorem 3.2.**
(i) If \( \lambda(U, \tau) < 0 \), then the disease-free steady state \((U, 0, 0)\) is globally attractive in \( C^+_\tau \).
(ii) If \( \lambda(U, \tau) > 0 \), then system (2.9) admits at least one positive steady state \((u_1(x), u_2(x), u_3(x))\). Moreover, there exists \( \eta > 0 \) such that
\[
\liminf_{t \to \infty} u_i(t, x) \geq \eta \quad \text{uniformly in } x \in \Omega, i = 1, 2, 3
\]
for any \( \phi \in C^+_\tau \) with \( \phi_i(0, \cdot) \neq 0 \) for \( i = 2, 3 \).

**Proof.** (i) Since \( \lambda(U, \tau) < 0 \), by the continuity of \( \lambda(U, \tau) \), there is an \( \varepsilon_0 > 0 \) such that \( \lambda(U + \varepsilon_0, \tau) < 0 \). Note that
\[
\begin{cases}
\frac{\partial u_1(t, x)}{\partial t} \leq \nabla \cdot \left[ D_1(x) \nabla u_1(t, x) \right] + \lambda(x) - \mu(x) u_1(t, x), & x \in \Omega, t > 0, \\
\left[ D_1(x) \nabla u_1(t, x) \right] \cdot \nu = 0, & x \in \partial \Omega, t > 0.
\end{cases}
\]
It follows from Lemma 3.2 and the comparison principle that there exists \( t_0 \) such that \( u_1(t, x) \leq U(x) + \varepsilon_0 \) for \( t \geq t_0 \) and \( x \in \Omega \). Then by the monotonicity and concavity of \( f_1 \) and \( f_2 \), we have
\[
\begin{cases}
\frac{\partial u_2(t, x)}{\partial t} & \leq \nabla \cdot \left[ D_2(x) \nabla u_2(t, x) \right] - \theta(x) u_2(t, x) \\
& + \int_{\Omega} \mathcal{G}_2(\tau_1, x, y) \left[ \frac{\partial f_1}{\partial u_2}(y, U(y), \varepsilon_0, 0) u_2(t - \tau_1, y) \\
& + \frac{\partial f_3}{\partial \psi_3}(y, U(y), \varepsilon_0, 0) u_3(t - \tau_1, y) \right] dy, & x \in \Omega, t \geq t_0, \\
\frac{\partial u_3(t, x)}{\partial t} & \leq \nabla \cdot \left[ D_3(x) \nabla u_3(t, x) \right] - \delta(x) u_3(t, x) \\
& + \int_{\Omega} \mathcal{G}_3(\tau_2, x, y) \left[ \xi(y) u_2(t - \tau_2, y) \right] dy, & x \in \Omega, t \geq t_0, \\
0 & = \left[ D_i(x) \nabla u_i(t, x) \right] \cdot \nu, & i = 2, 3, x \in \partial \Omega.
\end{cases}
\]
Let $\psi^+(x)$ be the strongly positive eigenfunction corresponding to $\tilde{\lambda}(U + \varepsilon_0, \tau)$ for (3.7). Then the linear system

$$
\begin{align*}
\frac{\partial v_2(t,x)}{\partial t} &= \nabla \cdot \left[ D_2(x) \nabla v_2(t,x) \right] - \theta(x)v_2(t,x) \\
&+ \int_{\Omega} G_2(t_1, x, y) \frac{\partial f_1}{\partial u_2}(y, U(y) + \varepsilon_0, 0)v_2(t - t_1, y) \\
&+ \frac{\partial f_1}{\partial u_3}(0, U(y) + \varepsilon_0, 0)v_3(t - t_1, y) dy,
\end{align*}
$$

and

$$
\begin{align*}
\frac{\partial v_3(t,x)}{\partial t} &= \nabla \cdot \left[ D_3(x) \nabla v_3(t,x) \right] - \delta(x)v_3(t,x) \\
&+ \int_{\Omega} G_3(t_2, x, y) \xi(y)v_2(t - t_2, y) dy,
\end{align*}
$$

has a solution $v(t, x) = (v_2(t, x), v_3(t, x)) = e^{\tilde{\lambda}(U + \varepsilon_0, \tau)(t-t_0)}\psi^+(x)$. Since for any $\phi \in C^+_\tau$, there exists $\alpha > 0$ such that

$$(u_2(t, x, \phi), u_3(t, x, \phi)) \leq \alpha v(t, x)$$

for $t \in [t_0 - \tau, t_0]$ and $x \in \overline{\Omega}$. By the comparison principle, one gets

$$(u_2(t, x, \phi), u_3(t, x, \phi)) \leq e^{\tilde{\lambda}(U + \varepsilon_0, \tau)(t-t_0)}\psi^+(x)$$

for $t \geq t_0$.

which implies that $\lim_{t \to \infty} (u_2(t, x, \phi), u_3(t, x, \phi)) = 0$ uniformly for $x \in \overline{\Omega}$. Thus the equation for $u_1$ is asymptotic to (3.6). Then we conclude that $\lim_{t \to \infty} u_1(t, x, \phi) = U(x)$ from [20, Corollary 4.3]

(ii) We shall use the theory developed by Smith and Zhao [19] to prove the persistence. For this purpose, define

$${\mathcal{W}}_0 = \{ \phi \in C^+_{\tau} : \phi_2(0, \cdot) \neq 0 \text{ and } \phi_3(0, \cdot) \neq 0 \}.$$

Then

$${\partial}{\mathcal{W}}_0 := C^+_{\tau} \setminus {\mathcal{W}}_0 = \{ \phi \in C^+_{\tau} : \phi_2(0, \cdot) \equiv 0 \text{ or } \phi_3(0, \cdot) \equiv 0 \}.$$ 

We prove the following three claims.

**Claim 1.** $\Phi(t){\mathcal{W}}_0 \subset {\mathcal{W}}_0$ for $t \geq 0$. This is obvious by Lemma 3.3(ii).

Let

$${\mathcal{M}}_0 = \{ \phi \in {\partial}{\mathcal{W}}_0 : \Phi(t)\phi \in {\partial}{\mathcal{W}}_0, t \geq 0 \}$$

and $\omega(\phi)$ be the omega limit set of the orbit $\gamma^+(\phi) := \{ \Phi(t)\phi : t \geq 0 \}$.

**Claim 2.** $\omega(\phi) = (U(x), 0, 0)$ for $\psi \in {\mathcal{M}}_0$.

Let $\psi \in {\mathcal{M}}_0$. Then for $t \geq 0$, either $u_2(t, \cdot, \psi) \equiv 0$ or $u_3(t, \cdot, \psi) \equiv 0$. In fact, if $u_2(t_0, \cdot, \psi) \neq 0$ for some $t_0 \geq 0$, then Lemma 3.3(ii) ensures that $u_2(t, \cdot, \psi) > 0$ for $t > t_0$ and $x \in \overline{\Omega}$. It follows that $u_3(t, \cdot, \psi) \equiv 0$ for $t > t_0$. With the help of the equation for $u_3$ in (2.9), we have $u_2(t - t_2, \cdot, \psi) \equiv 0$ for $t > t_0$. Therefore, there exists a $\hat{t} \geq 0$ such that $u_2(t, \cdot, \psi) \equiv 0$ for $t \geq \hat{t}$. Using the equation for $u_3$ in (2.9) again, we see that $\lim_{t \to \infty} u_3(t, x, \psi) = 0$ uniformly for $x \in \overline{\Omega}$. It then follows from the equation for $u_1$ in (2.9) and Lemma 3.2 that $\lim_{t \to \infty} u_1(t, x, \psi) = U(x)$ uniformly for $x \in \overline{\Omega}$. In summary, we have shown that $\omega(\psi) = \{(U(x), 0, 0)\}$.

**Claim 3.** $(U(x), 0, 0)$ is a uniform weak repeller for ${\mathcal{W}}_0$ in the sense that there exists $\varepsilon > 0$ such that

$$\lim_{t \to 0} \sup_{\phi \in {\mathcal{W}}_0} ||\Phi(t)\phi - (U(x), 0, 0)|| \geq \varepsilon$$

for all $\phi \in {\mathcal{W}}_0$.

Since $\tilde{\lambda}(U, \tau) > 0$, by continuity, there exists a sufficiently small $\varepsilon > 0$ such that $\tilde{\lambda}(U - \varepsilon, \tau) > 0$ and

$$\frac{\partial f_1}{\partial u_2}(y, U(x) - \varepsilon, \varepsilon) > 0 \text{ and } \frac{\partial f_1}{\partial u_3}(y, U(x) - \varepsilon, \varepsilon) > 0.$$
We claim that this $\varepsilon$ is what we are looking for. Otherwise, there exists $\phi_0 \in \mathbb{W}_0$ such that $\limsup_{t \to 0} \|\Phi(t)(\phi) - (U(x), 0, 0)\| \leq \varepsilon$. It then follows that there exists $t_1 > 0$ such that $u_1(t, x, \phi_0) \geq U(x) - \varepsilon$, $u_2(t, x, \phi_0) < \varepsilon$, and $u_3(t, x, \phi_0) < \varepsilon$ for $t \geq t_1$ and $x \in \Omega$. Again, with the help of the monotonicity and concavity of $f_1$ and $f_2$, we can get

$$
\begin{cases}
\frac{\partial u_2(t, x)}{\partial t} \geq \nabla \cdot [D_2(x)\nabla u_2(t, x)] - \theta(x)u_2(t, x) \\
+ \int_{\Omega} G_2(t_1, x, y)[\frac{\partial f_1}{\partial y}(y, U(y) - \varepsilon, \varepsilon)u_2(t - t_1, y)]dy, \quad x \in \Omega, t > t_1, \\
\frac{\partial u_3(t, x)}{\partial t} \geq \nabla \cdot [D_3(x)\nabla u_3(t, x)] - \delta(x)u_3(t, x) \\
+ \int_{\Omega} G_3(t_2, x, y)[\xi(y)u_2(t - t_2, y)]dy, \quad x \in \Omega, t > t_1.
\end{cases}
$$

Recall that the following nonlocal eigenvalue problem,

$$
\begin{cases}
\lambda \psi_{2}(x) = \nabla \cdot [D_2(x)\nabla \psi_{2}(x)] - \theta(x)\psi_{2}(x) \\
+ e^{-\lambda \tau_1} \int_{\Omega} G_2(t_1, x, y)[\frac{\partial f_1}{\partial y}(y, U(y) - \varepsilon, \varepsilon)\psi_{2}(y)]dy, \quad x \in \Omega, t > 0, \\
\lambda \psi_{3}(x) = \nabla \cdot [D_3(x)\nabla \psi_{3}(x)] - \delta(x)\psi_{3}(x) \\
+ e^{-\lambda \tau_2} \int_{\Omega} G_3(t_2, x, y)[\xi(y)\psi_{3}(y)]dy, \quad x \in \Omega, t > 0, \\
0 = [D_i(x)\nabla u_i(t, x)] \cdot \nu, \quad i = 2, 3, x \in \partial \Omega, t > 0,
\end{cases}
$$

admits a principal eigenvalue $\lambda(U - \varepsilon, \tau)$, corresponding to which, there is a unique strongly positive eigenfunction $(\varphi_2, \varphi_3)$ of $\lambda(U - \varepsilon, \tau)$ and $u_3(t_1, x) \geq \zeta e^{\lambda(U - \varepsilon, \tau)t_1}\varphi_3(x)$ for all $x \in \Omega$. Let $(p_2(t, x), p_3(t, x)) \in \mathbb{Y}^+ \times \mathbb{Y}^+, t \geq 0$ with

$$(p_2(t_1, x), p_3(t_1, x)) = (\zeta e^{\lambda(U - \varepsilon, \tau)t_1}\varphi_3(x), \zeta e^{\lambda(U - \varepsilon, \tau)t_1}\psi_3(x)), \quad x \in \Omega,$$

be the solution of the following auxiliary system

$$
\begin{cases}
\frac{\partial p_2(t, x)}{\partial t} = \nabla \cdot [D_2(x)\nabla p_2(t, x)] - \theta(x)p_2(t, x) \\
+ \int_{\Omega} G_2(t_1, x, y)[\frac{\partial f_1}{\partial y}(y, U(y) - \varepsilon, \varepsilon)p_2(t - t_1, y)]dy, \quad x \in \Omega, t > t_1, \\
\frac{\partial p_3(t, x)}{\partial t} = \nabla \cdot [D_3(x)\nabla p_3(t, x)] - \delta(x)p_3(t, x) \\
+ \int_{\Omega} G_3(t_2, x, y)[\xi(y)p_2(t - t_2, y)]dy, \quad x \in \Omega, t > t_1.
\end{cases}
$$

Employing the comparison principle, we can obtain

$$(u_2(t, x, \phi_0), u_3(t, x, \phi_0)) \geq (p_2(t, x), p_3(t, x)) = (\zeta e^{\lambda(U - \varepsilon, \tau)t_1}\varphi_3(x), \zeta e^{\lambda(U - \varepsilon, \tau)t_1}\psi_3(x))$$

for $t \geq t_1$ and $x \in \Omega$. Since $\lambda(U - \varepsilon, \tau) > 0$, it follows that $(u_2(t, x, \phi_0), u_3(t, x, \phi_0))$ is unbounded, a contradiction. This proves the claim.

Define a continuous function $p : C^+_\tau \rightarrow \mathbb{R}_+$ by

$$p(\phi) = \min \left\{ \min_{x \in \Omega} \phi_2(0, x), \min_{x \in \Omega} \phi_3(0, x) \right\}$$

for $\phi \in C^+_\tau$.

Clearly, $p^{-1}(0, 0) \subset \mathbb{W}_0$. By Lemma 3.3, $p(\cdot)$ has the property that if $p(\phi) = 0$ and $\phi \in \mathbb{W}_0$ or $p(\phi) > 0$, then $p(\Phi(t)(\phi)) > 0$ for all $t > 0$. Thus $p(\cdot)$ is a generalized distance function for the semiflow $\Phi(t) : C^+_\tau \rightarrow C^+_\tau$ (see, Smith and Zhao [19]).

Note that any forward orbit of $\Phi(t)$ in $M_0$ converges to $(U(x), 0, 0)$. Moreover, the claim above implies that $(U(x), 0, 0)$ is isolated in $C^+_\tau$ and $W^S(M) \cap \mathbb{W}_0 = \emptyset$, where $W^S(M)$ is the stable set of $(U(x), 0, 0)$. Further, there is no cycle in $M_0$ from
(U(x), 0, 0) to (U(x), 0, 0). Therefore, by [19, Theorem 2.3], there exists \( \eta > 0 \) such that \( \min \{ p(\psi) : \psi \in \omega(\phi) \} > \eta \) for any \( \phi \in \mathbb{W}_0 \). In particular,

\[
\liminf_{t \to \infty} u_i(t, x) \geq \eta, \quad i = 2, 3,
\]

uniformly for \( x \in \overline{\Omega} \). It also follows from Lemma 3.3(i) that we can choose \( \eta \) small enough such that \( \liminf_{t \to \infty} u_i(t, x) \geq \eta \) uniformly for \( x \in \overline{\Omega} \). This completes the proof on persistence of (2.9).

Now, it follows from [13, Theorem 3.7 and Remark 3.10] that the induced semiflow \( \Phi(t) : \mathbb{W}_0 \to \mathbb{W}_0 \) admits a global attractor \( A_0 \). Further by [13, Theorem 4.7], \( \Phi(t) \) admits a positive steady state \( (u_1^*, x_2^*, u_3^*) \in \mathbb{W}_0 \). Clearly, Lemma 3.3 ensures that \( (u_1^*(x), u_2^*(x), u_3^*(x)) \) is a positive steady state of (2.9). This completes the proof.

4. The basic reproduction number. In this section, we shall adopt the method of Wang and Zhao [26] to derive the expression of the basic reproduction number.

Assume that both populations of infectious individuals and bacteria are near the disease-free steady state \( (U, 0, 0) \) with \( u_2(\theta) = u_3(\theta) = 0 \) for \( \theta \in [-\tau, 0) \), before some initial infectious individuals and bacteria with a spatial distribution \( \psi := (\psi_2(x), \psi_3(x)) \in C(\overline{\Omega}, \mathbb{R}^2) \) are brought into the populations at \( t = 0 \) (i.e., \( u_2(0, x) = \psi_2(x) \) and \( u_3(0, x) = \psi_3(x) \)). We further assume that the temporal distribution of \( \psi \) is homogeneous. Denote by

\[
\mathcal{S}(t) \psi = (T_2(t)\psi_2, T_3(t)\psi_3)
\]

the \( C_0 \)-semigroup on \( C(\overline{\Omega}, \mathbb{R}^2) \), where \( T_2(t) \) and \( T_3(t) \) are defined in (3.1). Here \( \mathcal{S}(t) \psi \) stands for the remaining distribution of infectious individuals and bacteria as time evolves.

Let \( \mathcal{V} \) be the positive linear operator on \( \mathbb{Y} \times \mathbb{Y} \) defined by

\[
\mathcal{V}(\psi)(x) = (\mathcal{V}_1(\psi)(x), \mathcal{V}_2(\psi)(x)) \quad \text{for } \psi \in \mathbb{Y} \times \mathbb{Y} \text{ and } x \in \overline{\Omega},
\]

where

\[
\mathcal{V}_1(\psi)(x) = \int_\Omega G_2(\tau_1, x, y) \left[ \frac{\partial f_1}{\partial y_2}(y, U(y), 0)\psi_2(y) + \frac{\partial f_2}{\partial y_3}(y, U(y), 0)\psi_3(y) \right] dy, \quad x \in \Omega
\]

and

\[
\mathcal{V}_2(\psi)(x) = \int_\Omega G_3(\tau_2, x, y) \xi(y)\psi_2(y) dy, \quad x \in \Omega.
\]

Then \( \mathcal{V}(\mathcal{S}(t)\psi) \) is the distribution of newly infectious individuals and shed bacteria at time \( t \). It follows that

\[
\mathcal{L}(\psi) := \int_0^\infty \mathcal{V}(\mathcal{S}(t)\psi) dt = \mathcal{V} \left( \int_0^\infty \mathcal{S}(t)\psi dt \right)
\]

represents the distribution of the total infectious individuals and shed bacteria during the infection period and hence \( \mathcal{L} \) is the next infection operator. The spectral radius of \( \mathcal{L} \) is defined as the basic reproduction number \( R_0 \) of (2.9), that is,

\[
R_0 := r(\mathcal{L}).
\]

Lemma 4.1. \( R_0 - 1 \) has the same sign as \( \lambda(U, \tau) \).

Proof. The result follows from the general results in [21] and the same arguments in [26, Lemma 2.2].

Recall that \( \mathcal{V}(x) \) is a matrix-valued function defined by

\[
\mathcal{V}(x) := \mathcal{V}(\psi)(x) = (\mathcal{V}_1(\psi)(x), \mathcal{V}_2(\psi)(x)), \quad x \in \overline{\Omega},
\]
and \( \{S(t)\}_{t \geq 0} : \mathbb{Y} \to \mathbb{Y} \) is the solution semigroup associated with the following linear system:

\[
\begin{align*}
\frac{\partial u_1(t,x)}{\partial t} &= \nabla \cdot [D_1(x)\nabla u_1(t,x)] + \lambda - \mu u_1(t,x) \\
\frac{\partial u_2(t,x)}{\partial t} &= \nabla \cdot [D_2(x)\nabla u_2(t,x)] - \delta u_2(t,x) + f_1(u_1(t,x), u_2(t,x)) - f_2(u_1(t,x), u_3(t,x)), \\
\frac{\partial u_3(t,x)}{\partial t} &= \nabla \cdot [D_3(x)\nabla u_3(t,x)] - \delta u_3(t,x) + f_3(u_1(t,x), u_3(t,x)), \\
0 &= [D_i(x)\nabla u_i(t,x)] \cdot \nu, \quad i = 1, 2, 3, x \in \partial \Omega, t > 0.
\end{align*}
\]

Let us define the following matrix-valued function

\[
\mathcal{B}(x) = \begin{pmatrix}
\nabla \cdot [D_2(x)\nabla] - \theta(x) & 0 \\
0 & \nabla \cdot [D_3(x)\nabla] - \delta(x)
\end{pmatrix}, \quad x \in \overline{\Omega}.
\]

We then see that \( \mathcal{B} \) is resolvent-positive and \( s(\mathcal{B}) < 0 \), where \( s(\cdot) \) denotes the spectral bound of an operator. Moreover, by the arguments in [22, Theorem 2.2], we see that \( \mathcal{L} = \mathbb{V} + \mathcal{B} \) is resolvent-positive, and thus, it follows from [21, Theorem 3.5] that \( s(\mathcal{L}) = s(\mathbb{V} + \mathcal{B}) \) has the same sign as \( r(\mathbb{V}(-\mathcal{B})^{-1}) - 1 \). Since \( \mathcal{L} = \mathbb{V}(-\mathcal{B})^{-1} \) and \( \mathcal{R}_0 = r(\mathcal{L}) \), we complete the proof. \( \square \)

Theorem 3.2, combined with Lemma 4.1, tells us that the basic reproduction number \( \mathcal{R}_0 \) can also be regarded as a threshold parameter for (2.9).

**Corollary 4.1.**

(i) If \( \mathcal{R}_0 < 1 \), then the disease-free steady state \( (U, 0, 0) \) is globally attractive in \( C_+^\circ \).

(ii) If \( \mathcal{R}_0 > 1 \), then system (2.9) admits at least one positive steady state. Moreover, there exists \( \eta > 0 \) such that

\[
\liminf_{t \to \infty} u_i(t,x) \geq \eta \quad \text{uniformly in} \quad x \in \overline{\Omega}, \quad i = 1, 2, 3
\]

for any \( \phi \in C_+^\circ \) with \( \phi_i(0, \cdot) \neq 0 \) for \( i = 2, 3 \).

Note that the basic reproduction number \( \mathcal{R}_0 \) is defined in terms of the spectral radius of the operator \( \mathcal{L} \), which is inconvenient in application. As a result, we compute it in the case where all parameters except the diffusion rates are position independent, that is, we assume that

\[
\lambda(x) \equiv \mu, \quad \mu(x) \equiv \mu, \quad \theta(x) = \theta, \quad \delta(x) \equiv \delta, \quad \xi(x) \equiv \xi,
\]

and

\[
\mu_i(x) + \theta_E(x) \equiv \theta_1, \quad \mu_i(x) + \delta_E(x) \equiv \delta_1.
\]

Then (2.9) reduces to

\[
\begin{align*}
\frac{\partial u_1(t,x)}{\partial t} &= \nabla \cdot [D_1(x)\nabla u_1(t,x)] + \lambda - \mu u_1(t,x) \\
\frac{\partial u_2(t,x)}{\partial t} &= \nabla \cdot [D_2(x)\nabla u_2(t,x)] - \theta u_2(t,x) + f_1(u_1(t,x), u_2(t,x)) - f_2(u_1(t,x), u_3(t,x)), \\
\frac{\partial u_3(t,x)}{\partial t} &= \nabla \cdot [D_3(x)\nabla u_3(t,x)] - \delta u_3(t,x) + f_3(u_1(t,x), u_3(t,x)), \\
0 &= [D_i(x)\nabla u_i(t,x)] \cdot \nu, \quad i = 1, 2, 3, x \in \partial \Omega, t > 0.
\end{align*}
\]

Clearly, system (4.1) has the disease-free equilibrium \( E^0 = (U, 0, 0) \), where \( U = \lambda/\mu \).

Following the above discussions, the next generation operator \( \mathcal{L} \) of system (4.1) is given by

\[
\mathcal{L}\psi = \int_0^\infty \mathbb{V}(S(t)\psi)dt, \quad \psi \in \mathbb{Y} \times \mathbb{Y},
\]
It follows that
\[ f \text{ and } f \] if
\[ f \] and
\[ f \] for the convenience of application, we also calculated the explicit formulae of the basic reproduction number in two particular cases of the incidences, bilinear and Beddington-DeAngelis ones.

Recall that \( G_i(t, s, y) \) \((i = 2, 3)\) are Green functions associated with \( \nabla \cdot [D_2(x)\nabla] - \theta \) and \( \nabla \cdot [D_2(x)\nabla] - \delta \) subject to the homogeneous Neumann boundary condition, respectively. It follows that \( \int_\Omega G_2(t, s, y)dy = e^{-\delta t} \) and \( \int_\Omega G_3(t, s, y)dy = e^{-\delta t} \). Also note that
\[ \int_\Omega G_2(s, x, y)dy = e^{-\delta s} \text{ and } \int_\Omega G_3(s, x, y)dy = e^{-\delta s}. \]

Then the next infection operator defined by (4.2) becomes
\[
\mathcal{L} \left( \begin{array}{c} \psi_2 \\ \psi_3 \end{array} \right) = \left( \begin{array}{cc}
-\theta_1 \tau_1 \frac{\partial f_1(U, 0)}{\partial u_2} & e^{\theta_1 \tau_1} \frac{\partial f_2(U, 0)}{\partial u_3} \\
e^{\delta_1 \tau_2} \xi & 0
\end{array} \right) \left( \begin{array}{c} \frac{1}{\theta} \\ 0 \end{array} \right) \left( \begin{array}{c} \psi_2 \\ \psi_3 \end{array} \right).
\]

It follows that
\[
R_0 = \frac{1}{2} \left[ e^{-\theta_1 \tau_1} \frac{\beta_1 \lambda}{\mu \theta} \frac{1}{\theta} + \sqrt{\left( e^{-\theta_1 \tau_1} \frac{\beta_1 \lambda}{\mu \theta} \frac{1}{\theta} \right)^2 + 4 e^{-\theta_1 \tau_1} e^{-\delta_1 \tau_2} \frac{\beta_2 \lambda \xi}{\mu \delta \theta}} \right].
\]

In particular, if \( f_1 \) and \( f_2 \) are bilinear, namely, \( f_1(u_1, u_2) = \beta_1 u_1 u_2 \) and \( f_2(u_1, u_3) = \beta_2 u_1 u_3 \), then it follows from (4.3) that
\[
R_0 = \frac{1}{2} \left[ \frac{e^{-\theta_1 \tau_1} \beta_1 \lambda}{\mu \theta} + \sqrt{\left( \frac{e^{-\theta_1 \tau_1} \beta_1 \lambda}{\mu \theta} \right)^2 + \frac{4 e^{-\theta_1 \tau_1} e^{-\delta_1 \tau_2} \beta_2 \lambda \xi}{\mu \delta \theta}} \right];
\]

if \( f_1 \) and \( f_2 \) take the Beddington-DeAngelis form, that is, \( f_1(u_1, u_2) = \frac{\beta_1 u_1 u_2}{1 + \alpha_1 u_1 + \beta_1 u_2} \) and \( f_2(u_1, u_3) = \frac{\beta_2 u_1 u_3}{1 + \alpha_2 u_1 + \beta_2 u_3} \), then in this case, the basic reproduction number calculated by (4.3) is
\[
R_0 = \frac{1}{2} \left[ \frac{e^{-\theta_1 \tau_1} \beta_1 \lambda}{(\mu + a_1 \lambda) \theta} + \sqrt{\left( \frac{e^{-\theta_1 \tau_1} \beta_1 \lambda}{(\mu + a_1 \lambda) \theta} \right)^2 + \frac{4 e^{-\theta_1 \tau_1} e^{-\delta_1 \tau_2} \beta_2 \lambda \xi}{(\mu + a_2 \lambda) \delta \theta}} \right].
\]

5. Conclusion. In this paper, for the first time, we incorporated the spatial heterogeneity and temporal heterogeneity (for age structures in populations of individuals and bacteria) in the modeling of cholera spread. This results in a delayed reaction-diffusion model with nonlocal effects. Note that the incidences are in general nonlinear form. By employing the theories of monotone dynamical systems and persistence, we established a threshold dynamics completely determined by the principal eigenvalue of a linear nonlocal reaction-diffusion equation. In fact, the threshold dynamics is also characterized by the basic reproduction number, which is the spectral radius of the next infection operator. For the convenience of application, we also calculated the explicit formulae of the basic reproduction number in two particular cases of the incidences, bilinear and Beddington-DeAngelis ones.
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