A DELAYED SUCCESSION MODEL WITH DIFFUSION FOR THE IMPACT OF DIAPAUSE ON POPULATION GROWTH[*]

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Abstract. Diapause, a period of arrested development driven by adverse environmental conditions, plays an important role in the establishment and invasion of insects and other invertebrate organisms in temperate and subtropical areas. In order to describe the spatial dynamics of diapausing species, we propose a novel model involving (a) seasonal succession to distinguish the normal growth period, diapause period, and postdiapause period; (b) a diffusion term to represent the random movement of species; and (c) a maturation delay term to describe the developmental duration of species. We first study the model in a bounded domain for the survival and establishment of a species. The extinction and persistence of the species can be predicted by the basic reproduction ratio $\mathcal{R}_0$. Then we investigate the model in an unbounded domain for the spreading of the species. Our results show that the minimal wave speed for a periodic traveling wave is equal to the spreading speed. Numerical simulations are performed to validate theoretical results and in particular to compare the effects of two diapausing strategies: diapausing in the adult stage and in the immature stage.

Key words. diapause, basic reproduction ratio, spreading speed, traveling waves

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1. Introduction. In a thermally stressful environment, insects, which have limited ability to regulate their body temperature, require a range of strategies to overcome unfavorable seasons, to exploit favorable seasons, and to mitigate the stresses of unfavorable seasons [23, 40]. For example, during the long dry season, mosquitoes are expected to perish since no larval sites are available. However, days after the first rains, mosquitoes reappear in large numbers. Diapause is hypothesized to contribute to the persistence of some mosquito species during the dry season [1]. This process of physiological rest can be commonly found among other invertebrate organisms, which include temperate zone insects or some tropical species occasionally and their arthropod relatives [7, 22], such as ticks [14], ladybirds [19], dragonflies [39], and silkworms [17]. Diapause is a widespread adaptation to seasonality across invertebrate taxa [40], which is a genetically programmed preemptive developmental response to changing seasons and environmental conditions [3] and can be triggered by climactic signals, especially the photoperiod and relative humidity [10]. It is a genetically mediated process of increased resistance to environmental extremes associated with low metabolic activity, a reduced morphogenesis, and altered or reduced physical activities [44].

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Diapause plays a key role in the life cycle of species therefore poses a fascinating question in developmental biology. Knowledge of diapause is essential for understanding the seasonal distribution of a species, and such information is essential to generate effective management strategies for economically important insect pests [8], manipulate domesticated species used in pollination and silk production, increase the shelf-life of parasitoids and predatory mites used in the biological control industry [8], and accurately predict insect populations' responses to climate change [23]. Studies on different aspects of diapause are believed to contribute to understanding how inherent mechanisms regulate organisms surviving through diapause [7] and the critical roles of the diapause stage on linking the favorable and adverse seasons and synchronizing the life cycle of organisms with seasonal environmental variations [1, 9]. Despite some promising progress that has been made in recent studies, such as [4, 11, 13, 20, 32, 45, 53], few modeling efforts have been made to qualitatively and quantitatively evaluate the impact of diapause on species persistence and spreading in a spatial habitat.

There are several possible ways to incorporate the diapause effects into the population modeling process, for example, using piecewise parameter functions to differ either the survival or the development rates between the normal growth and diapause periods [11, 13, 45] or regarding the diapause period as an independent dynamic process during which the population dynamics are completely different from that in the normal growth period [4, 20]. In this paper, we are going to formulate a theoretical model by extending that in [32] with the consideration of the spatial movement of individuals in section 2. Then the model in a bounded domain and an unbounded domain will be analyzed in sections 3 and 4, respectively. Finally, numerical simulations and discussions will be performed to validate the theoretical results and investigate the effect of diapause on species establishment and spreading in section 5.

2. Model formation. Recently, there are expanding studies on the population models to incorporate the seasonal development duration, for example, [2, 31, 34, 50]. However, the periodic development duration induced by diapause is a discontinuous delay, which makes the previous modeling framework invalid. In this section, we extend the model in [32] by considering the diffusion of individuals during the favorable season. Suppose in each year there are generally two seasons in terms of population growth: favorable (with good environment) and unfavorable ones (with adverse environmental conditions, such as winter seasons in temperate zones and dry seasons in tropical zones, and its duration is τ_d year). Then the duration for the favorable season in each year is $1 - \tau_d$ year. Species development is paused during the unfavorable season due to diapause while the development duration during the favorable season is τ. It is easy to see that immature individuals surviving through the unfavorable season need a longer developmental duration $\tau + \tau_d$; therefore, a careful account of this extended development duration should be incorporated. For that purpose, instead of partitioning 1 year into two seasons based on the environmental conditions, we divide 1 year into three intervals and formulate equations of population density in each interval. These intervals are set in such a way one by one: (a) the unfavorable season is denoted as T_2 with length τ_d; (b) following interval T_2, there is an interval T_3 with favorable environmental conditions, and its length is set exactly being τ; and (c) the remaining favorable season in 1 year is denoted as T_1 with length $1 - \tau - \tau_d$. Due to the succession of years, we set the starting time as the beginning of the interval T_1, and then the population growth process can be described as in Figure 2.1. We also assume that both the immature and the adult individuals can diffuse during
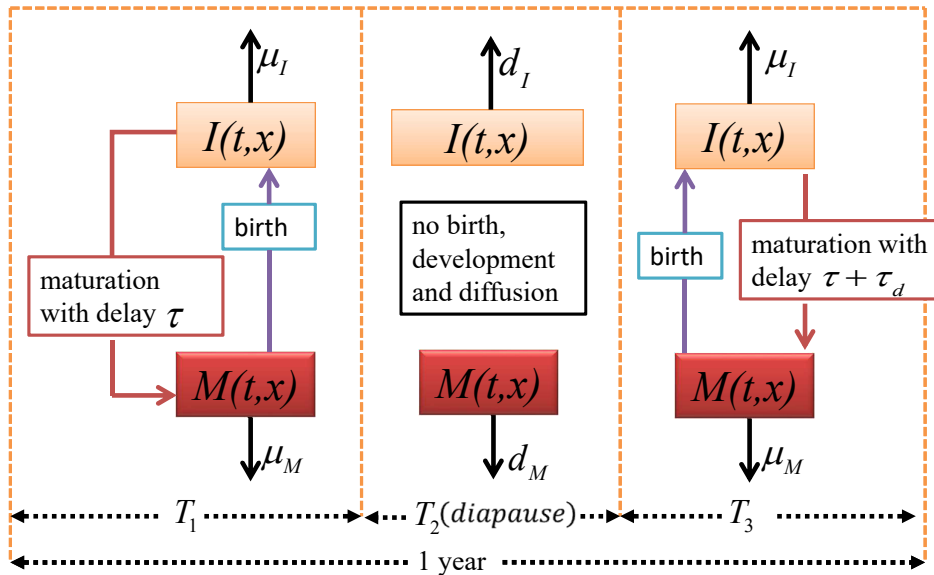
FIG. 2.1. *Diagram for the population growth in 1 year. The 1-year period is divided into three seasons T_1, T_2, T_3 with lengths $1 - \tau_d - \tau$, τ_d, and τ, respectively.*

the favorable season while remaining immobile during the diapausing season. Since diapause may occur in various stages of growth, a two-stage structured model is the simplest choice to characterize this important feature, and we use $I(t, x)$ and $M(t, x)$ to represent the population densities of juveniles and adults at time t and spatial location $x \in \Omega \subseteq \mathbb{R}^N$ ($N \geq 1$) Then we can write down a seasonal succession system based on the diagram in Figure 2.1.

During the normal growth period of the nth year, $t \in T_1^n := (n, n + 1 - \tau - \tau_d]$, $n = 0, 1, 2, \ldots$, population densities for juveniles and adults can be described by the system

(2.1)
$$
\begin{cases}
\dfrac{\partial I(t, x)}{\partial t} = \underbrace{D_I \Delta I(t, x)}_{\text{diffusion}} + \underbrace{b(M(t, x))}_{\text{birth}} - \underbrace{B_1(t, x; M)}_{\text{maturation}} - \underbrace{\mu_I I(t, x)}_{\text{death}}, \\[2ex]
\dfrac{\partial M(t, x)}{\partial t} = \underbrace{D_M \Delta M(t, x)}_{\text{diffusion}} + \underbrace{B_1(t, x; M)}_{\text{maturation}} - \underbrace{\mu_M M(t, x)}_{\text{death}}
\end{cases}
$$

with the maturation rate

$$
B_1(t, x; M) = e^{-\mu_I \tau} \int_\Omega \Gamma(D_I \tau, x, y) b(M(t - \tau, y)) dy
$$

by incorporating the immature diffusion and the survival probability of the immature population $e^{-\mu_I \tau}$ during the development process. Here $\Gamma(t, x, y)$ is the fundamental solution corresponding to the partial differential operator $[\partial_t - \Delta]$. The term $B_1(t, x; M)$ can be derived from the evolution viewpoint, and the details are given in Appendix A. All parameters are summarized in Table 1.

During the diapause period of the nth year, $t \in T_2^n := (n + 1 - \tau - \tau_d, n + 1 - \tau]$, there is no birth, development, and diffusion by taking the extreme case of low metabolic

TABLE 1
Biological interpretations for parameters in model.

Parameter	Description
τ	Developmental duration under favorable environmental conditions
τ_d	Diapause period (same as the length of the unfavorable season)
μ_I	Mortality rate for juveniles during the favorable season
μ_M	Mortality rate for adults during the favorable season
d_I	Mortality rate for juveniles during the diapause period
d_M	Mortality rate for adults during the diapause period
D_M	Diffusion coefficient for adults
D_I	Diffusion coefficient for juveniles

activity and reduced physical activity. The system becomes

$$(2.2) \qquad \begin{cases} \frac{\partial I(t,x)}{\partial t} = -\underbrace{d_I I(t,x)}_{\text{death}}, \\ \frac{\partial M(t,x)}{\partial t} = -\underbrace{d_M M(t,x)}_{\text{death}}. \end{cases}$$

Normally, the death rates d_I and d_M during the diapause period are greater than those during the favorable season μ_I and μ_M.

After the diapause period, there is a short postdiapause period: $t \in T_3^n := (n+1-\tau, n+1]$. During this period, we have the system

$$(2.3) \qquad \begin{cases} \frac{\partial I(t,x)}{\partial t} = \underbrace{D_I \Delta I(t,x)}_{\text{diffusion}} + \underbrace{b(M(t,x))}_{\text{birth}} - \underbrace{B_2(t,x;M)}_{\text{maturation}} - \underbrace{\mu_I I(t,x)}_{\text{death}}, \\ \frac{\partial M(t,x)}{\partial t} = \underbrace{D_M \Delta M(t,x)}_{\text{diffusion}} + \underbrace{B_2(t,x;M)}_{\text{maturation}} - \underbrace{\mu_M M(t,x)}_{\text{death}} \end{cases}$$

with the maturation rate

$$B_2(t,x;M) = e^{-\mu_I \tau - d_I \tau_d} \int_\Omega \Gamma(D_I \tau, x, y) b(M(t-\tau-\tau_d, y)) dy.$$

We would like to highlight that the survival probability contains two terms by taking into account the probabilities of surviving through the diapause period $e^{-d_I \tau_d}$ and normal development duration $e^{-\mu_I \tau}$. The individuals matured in this period take a longer time duration $\tau + \tau_d$ to mature. However, the nonlocal kernel is the same as that in (2.1), as juveniles are not able to move during the diapause period. More details on model derivation can be found in Appendix A.

Here and in what follows, unless stated otherwise, n is taken as $n = 0, 1, 2, \ldots$. We make the following assumptions for the birthrate $b(\cdot)$ and the delays:

(H1) $b(\cdot)$ is Lipschitz continuous and strictly increasing on $\mathbb{R}_+$ with $b(0) = 0$ and $b'(0) > 0$;

(H2) there exists $L > 0$ such that $b(M)e^{-\mu_I \tau} > \mu_M M$ when $0 < M < L$, $b(M)e^{-\mu_I \tau} < \mu_M M$ whenever $M > L$;

(H3) $b(\cdot)$ is strictly subhomogeneous on $\mathbb{R}_+$ in the sense that $b(su) > sb(u) \ \forall u > 0$, $s \in (0, 1)$;

(H4) $2\tau + \tau_d < 1$.

In fact, many birth functions satisfy these assumptions; see, e.g., those in [33]. It is biologically reasonable to assume that $2\tau + \tau_d$ is smaller than 1 year. For example,

the unfavorable season may range from 3 to 5 months among different species and geographies for mosquitoes, while the lifespan of mosquitoes is averaged at around 2–4 weeks [41]. However, we should mention that (H4) can be released with a more complicated model.

The purpose of the following two sections is to study the global dynamics of (2.1)–(2.3) in a bounded domain and the spreading speed and periodic traveling waves of (2.1)–(2.3) in an unbounded spatial domain, respectively.

3. Global dynamics in a bounded domain. In this section, we study the global dynamics of (2.1)–(2.3) in a bounded domain $\Omega \subset \mathbb{R}^N$ with smooth boundary $\partial\Omega$. The main goal is to establish the well-posedness in subsection 3.1, and to derive the basic reproduction ratio $\mathcal{R}_0$ in subsection 3.2. The threshold dynamics in terms of $\mathcal{R}_0$ is obtained first for the adult mosquito system (3.1). Then we lift the dynamics to the full model system (2.1)–(2.3) in subsection 3.3.

Assume that all individuals stay in the domain Ω for all time, and hence we impose the Neumann boundary condition

$$\frac{\partial I(t,x)}{\partial \nu} = \frac{\partial M(t,x)}{\partial \nu} = 0, \quad t \in T_1^n \cup T_3^n, \ x \in \partial\Omega,$$

where ν is the outward unit normal vector on $\partial\Omega$.

Note that equations for $M(t,x)$ can be decoupled from system (2.1)–(2.3). Thus, we first analyze the global dynamics of the following model:
(3.1)
$$\begin{cases} \dfrac{\partial M(t,x)}{\partial t} = D_M \Delta M(t,x) + B_1(t,x;M) - \mu_M M(t,x), & t \in T_1^n, \ x \in \Omega, \\[2mm] \dfrac{\partial M(t,x)}{\partial t} = -d_M M(t,x), & t \in T_2^n, \ x \in \Omega, \\[2mm] \dfrac{\partial M(t,x)}{\partial t} = D_M \Delta M(t,x) + B_2(t,x;M) - \mu_M M(t,x), & t \in T_3^n, \ x \in \Omega, \\[2mm] \dfrac{\partial M(t,x)}{\partial \nu} = 0, & t \in T_1^n \cup T_3^n, \ x \in \partial\Omega. \end{cases}$$

Before proceeding, we introduce several notations. Let $\mathbb{X} := C(\bar{\Omega}, \mathbb{R})$ be the Banach space with the supremum norm $\|\cdot\|_{\mathbb{X}}$. For $\tau > 0$, define $\mathbb{Y} := C([-\tau, 0], \mathbb{X})$ with the norm $\|\phi\| = \max_{\theta \in [-\tau, 0]} \|\phi(\theta)\|_{\mathbb{X}}, \forall \phi \in \mathbb{Y}$. Then $\mathbb{Y}$ is a Banach space. Define $\mathbb{X}^+ := C(\bar{\Omega}, \mathbb{R}_+)$ and $\mathbb{Y}^+ := C([-\tau, 0], \mathbb{X}^+)$. Then both $(\mathbb{X}, \mathbb{X}^+)$ and $(\mathbb{Y}, \mathbb{Y}^+)$ are strongly ordered Banach spaces. For a continuous function $z : [-\tau, \sigma) \to \mathbb{X}$ for $\sigma > 0$ and $t \in [0, \sigma)$, we denote $z_t \in \mathbb{Y}$ by

$$z_t(\theta) = z(t+\theta) \quad \forall \theta \in [-\tau, 0].$$

For convenience, we identify an element $\phi \in \mathbb{Y}$ as a function from $[-\tau, 0] \times \bar{\Omega}$ to $\mathbb{R}$ defined as $\phi(s, x) = \phi(s)(x)$. Set

$$\mathbb{Y}_L := \{\phi \in \mathbb{Y} : 0 \le \phi(\theta, x) \le L \quad \forall \theta \in [-\tau, 0], x \in \bar{\Omega}\}.$$

3.1. Well-posedness. We first prove the existence, uniqueness, and positivity and then establish the comparison principle for upper and lower solutions of (3.1). For this purpose, we introduce the following definition.

DEFINITION 3.1. *A function* $\overline{M} : [-\tau, \infty) \times \Omega \to \mathbb{R}$ *is said to be an upper solution of* (3.1) *if for* $t \geq 0$, $\overline{M}_t \in \mathbb{Y}_L$, *and*

(3.2)

$$\overline{M}(t,x) \geq T(t-n)\overline{M}(n,\cdot)(x) + \int_n^t T(t-s)B_1(s,\cdot;\overline{M})(x)ds, \ t \in T_1^n, \ x \in \Omega,$$

$$\overline{M}(t,x) \geq e^{-d_M(t-(n+1-\tau-\tau_d))}\overline{M}(n+1-\tau-\tau_d, x), \qquad t \in T_2^n, \ x \in \Omega,$$

$$\overline{M}(t,x) \geq T(t-(n+1-\tau))\overline{M}(n+1-\tau,\cdot)(x)$$
$$+ \int_{n+1-\tau}^t T(t-s)B_2(s,\cdot;\overline{M})(x)ds, \qquad t \in T_3^n, \ x \in \Omega,$$

$$\frac{\partial \overline{M}(t,x)}{\partial \nu} \geq 0, \qquad t \in T_1^n \cup T_3^n, \ x \in \partial\Omega,$$

where $T(t)$ *is the solution semigroup of the linear equation* $\frac{\partial M}{\partial t} = D_M \triangle M - \mu_M M$ *subject to the Neumann boundary condition and* $B_1(t, x; M)$ *and* $B_2(t, x; M)$ *are defined above in section* 2. *A lower solution can be defined similarly by reversing the inequalities in* (3.2).

LEMMA 3.2. *For any* $\phi \in \mathbb{Y}_L$, *system* (3.1) *has a unique solution* $M(t, x; \phi)$ *which exists globally for* $t \geq -\tau$ *such that* $M_0 = \phi$ *and* $M_t \in \mathbb{Y}_L$ *for all* $t \geq 0$, *where* M_t *is defined by*

$$M_t(\theta, x; \phi) = M(t+\theta, x; \phi) \quad \forall \theta \in [-\tau, 0], \ x \in \bar{\Omega}.$$

Moreover, if $\overline{M}(t,x)$ *and* $\underline{M}(t,x)$ *are a pair of upper and lower solutions of* (3.1) *with* $\overline{M}_0 \geq \underline{M}_0$, *then* $\overline{M}_t \geq \underline{M}_t$ *for all* $t > 0$.

The proof of Lemma 3.2 is given in Appendix B. Moreover, by a similar method, we can establish the existence and uniqueness of a solution to (2.1)–(2.3) with Neumann boundary condition. Note that the spatially homogeneous system of (3.1) is of the form

(3.3)
$$\begin{cases} \frac{dM(t)}{dt} = b(M(t-\tau))e^{-\mu_I \tau} - \mu_M M(t), & t \in T_1^n, \\ \frac{dM(t)}{dt} = -d_M M(t), & t \in T_2^n, \\ \frac{dM(t)}{dt} = b(M(t-\tau-\tau_d))e^{-\mu_I \tau - d_I \tau_d} - \mu_M M(t), & t \in T_3^n. \end{cases}$$

By employing arguments similar to those in Lemma 3.2, it follows that for any $\varphi \in C([-\tau, 0], [0, L])$, (3.3) admits a unique solution $M(t, \varphi)$ which exists globally for $t \geq -\tau$ such that $M_0 = \varphi$ and $M_t \in C([-\tau, 0], [0, L])$ for all $t \geq 0$.

3.2. Basic reproduction ratio. In what follows, we employ the theory developed in [51] to introduce the basic reproduction ratio for system (3.3). The linearized system associated with (3.3) at $M = 0$ is

(3.4)
$$\begin{cases} \frac{dM(t)}{dt} = b'(0)e^{-\mu_I \tau}M(t-\tau) - \mu_M M(t), & t \in T_1^n, \\ \frac{dM(t)}{dt} = -d_M M(t), & t \in T_2^n, \\ \frac{dM(t)}{dt} = b'(0)e^{-\mu_I \tau - d_I \tau_d}M(t-\tau-\tau_d) - \mu_M M(t), & t \in T_3^n. \end{cases}$$

Let $\hat{\tau} := \tau + \tau_d$, $C = C([-\hat{\tau}, 0], \mathbb{R})$ and $C^+ = C([-\hat{\tau}, 0], \mathbb{R}_+)$. For any given continuous function $v : [-\hat{\tau}, \sigma] \to \mathbb{R}$ with $\sigma > 0$, we define $v_t \in C$ by

$$v_t(\theta) = v(t+\theta) \quad \forall \theta \in [-\hat{\tau}, 0]$$

for any $t \in [0, \sigma)$. Let

$$F(t)\phi = \begin{cases} b'(0)e^{-\mu_I \tau}\phi(-\tau), & t \in T_1^n, \\ 0, & t \in T_2^n, \\ b'(0)e^{-\mu_I \tau - d_I \tau_d}\phi(-\tau - \tau_d), & t \in T_3^n, \end{cases} \quad \text{and} \quad V(t) = \begin{cases} -\mu_M, & t \in T_1^n, \\ -d_M, & t \in T_2^n, \\ -\mu_M, & t \in T_3^n \end{cases}$$

for any $\phi \in C$. Then the linear system (3.4) can be written as

$$(3.5) \qquad \frac{du(t)}{dt} = F(t)u_t - V(t)u(t) \quad \forall t > 0.$$

For any $\phi \in C$, let $u(t, s; \phi), t \geq s$, be the unique solution of (3.5) satisfying $u_s = \phi$. Define the evolution family $\{U(t, s) : t \geq s\}$ on C associated with (3.5) as

$$U(t, s)\phi = u_t(s, \phi) \quad \forall \phi \in C, \ t \geq s, \ s \in \mathbb{R}.$$

Let $\Phi(t, s)$, $t \geq s$, be the evolution family associated with system $\frac{du(t)}{dt} = -V(t)u(t)$. It then follows that the exponential growth bound of $\Phi(t, s)$, $\omega(\Phi) \leq -\min\{\mu_M, d_M\}$.

Let $\mathbb{C}_1$ be the Banach space of all continuous and 1-periodic functions from $\mathbb{R}$ to $\mathbb{R}$, equipped with the maximum norm and the positive cone $\mathbb{C}_1^+ := \{u \in \mathbb{C}_1 : u(t) \geq 0 \ \forall t \in \mathbb{R}\}$. Following the procedure in [51, section 2], we define a linear operator $\mathcal{L} : \mathbb{C}_1 \to \mathbb{C}_1$ by

$$[\mathcal{L}v](t) = \int_0^\infty \Phi(t, t - s)F(t - s)v(t - s + \cdot)ds \quad \forall t \in \mathbb{R}, \ v \in \mathbb{C}_1.$$

It can be checked that $\mathcal{L}$ is well defined. Thus, we define the spectral radius of $\mathcal{L}$ as the basic reproduction ratio $\mathcal{R}_0 = r(\mathcal{L})$ for (3.3). In light of [51, Theorem 2.1], one finds that $\mathcal{R}_0 - 1$ has the same sign as $r(U(1, 0)) - 1$.

3.3. Global dynamics. Let P be the Poincaré map of (3.5) on the space $C([-\tau, 0], \mathbb{R})$. By the arguments similar to [49, Lemma 3.8], it follows that $r(P) = r(U(1, 0))$, and hence $\text{sign}(\mathcal{R}_0 - 1) = \text{sign}(r(P) - 1)$. Combining with [32, Theorem 2], we have the following threshold result in terms of $\mathcal{R}_0$.

LEMMA 3.3. *The following statements are valid:*
 (i) *If $\mathcal{R}_0 \leq 1$, then 0 is globally asymptotically stable for (3.3) in $C([-\tau, 0], [0, L])$.*
 (ii) *If $\mathcal{R}_0 > 1$, then (3.3) admits a unique positive 1-periodic solution $M^*(t)$, which is globally asymptotically stable for (3.3) in $C([-\tau, 0], [0, L]) \setminus \{0\}$.*

Following the procedure in [51], we can also define the basic reproduction ratio $\widetilde{\mathcal{R}}_0$ for (3.1). Since the coefficients in (3.1) are independent of spatial variable x and (3.1) is subject to the Neumann boundary condition, it easily follows that $\widetilde{\mathcal{R}}_0 = \mathcal{R}_0$ (see, e.g., [28, Theorem 3.8]). Further, Lemma 3.3 and the standard comparison principle arguments lead to the following result.

LEMMA 3.4. *For any $\phi \in \mathbb{Y}_L$, denote by $M(t, x; \phi)$ the solution of (3.1) with $M(\theta, x; \phi) = \phi(\theta, x)$ for $(\theta, x) \in [-\tau, 0] \times \bar{\Omega}$. Then the following statements are valid:*
 (i) *If $\mathcal{R}_0 \leq 1$, then 0 is globally asymptotically stable for (3.1).*
 (ii) *If $\mathcal{R}_0 > 1$, then $M^*(t)$ is globally asymptotically stable for (3.1) in $\mathbb{Y}_L \setminus \{0\}$.*

Next we consider the global dynamics of the following limiting system for $I(t, x)$:
(3.6)
$$
\begin{cases}
\dfrac{\partial I(t,x)}{\partial t} = D_I \Delta I(t,x) + b(M^*(t)) - b(M^*(t-\tau))e^{-\mu_I \tau} - \mu_I I(t,x), \\
\qquad\qquad t \in T_1^n, \ x \in \Omega, \\[4pt]
\dfrac{\partial I(t,x)}{\partial t} = -d_I I(t,x), \quad t \in T_2^n, \ x \in \Omega, \\[4pt]
\dfrac{\partial I(t,x)}{\partial t} = D_I \Delta I(t,x) + b(M^*(t)) - b(M^*(t-\tau-\tau_d))e^{-\mu_I \tau - d_I \tau_d} - \mu_I I(t,x), \\
\qquad\qquad t \in T_3^n, \ x \in \Omega, \\[4pt]
\dfrac{\partial I(t,x)}{\partial \nu} = 0, \quad t \in T_1^n \cup T_3^n, \ x \in \partial\Omega.
\end{cases}
$$

One easily sees that for any $\varphi \in \mathbb{X}^+$, system (3.6) has a unique solution $I(t, x; \varphi)$ with $I(0, \cdot; \varphi) = \varphi$ and admits the comparison principle. Further, we have the following result with proof given in Appendix B.

LEMMA 3.5. *System* (3.6) *admits a unique positive* 1-*periodic solution* $I^*(t)$, *and it is globally asymptotically stable in* $\mathbb{X}^+$.

Based on the theory of chain transitive sets (see [18] or [52, section 1.2]), we can lift the threshold-type result for system (3.1) to system (2.1)–(2.3). In fact, one can easily adapt the arguments of [49, Theorem 3.6] to conclude the following assertion.

THEOREM 3.6. *The following statements are valid:*
(i) *If* $\mathcal{R}_0 \leq 1$, *then* $(0,0)$ *is globally attractive for* (2.1)–(2.3) *in* $\mathbb{X}^+ \times \mathbb{Y}_L$.
(ii) *If* $\mathcal{R}_0 > 1$, *then system* (2.1)–(2.3) *has a unique positive* 1-*periodic solution* $(I^*(t), M^*(t))$, *and it is globally attractive for* (2.1)–(2.3) *in* $\mathbb{X}^+ \times (\mathbb{Y}_L \setminus \{0\})$.

4. Propagation dynamics. In this section, we consider the spreading speed and traveling waves for system (2.1)–(2.3) in an unbounded spatial domain $\Omega = \mathbb{R}$. To this end, we first consider the equations of mature population
(4.1)
$$
\begin{cases}
\dfrac{\partial M(t,x)}{\partial t} = D_M \Delta M(t,x) + e^{-\mu_I \tau} \displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y) b(M(t-\tau, y))\,dy \\
\qquad\qquad - \mu_M M(t,x), \quad t \in T_1^n, \ x \in \mathbb{R}, \\[4pt]
\dfrac{\partial M(t,x)}{\partial t} = -d_M M(t,x), \quad t \in T_2^n, \ x \in \mathbb{R}, \\[4pt]
\dfrac{\partial M(t,x)}{\partial t} = D_M \Delta M(t,x) + e^{-\mu_I \tau - d_I \tau_d} \displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y) b(M(t-\tau-\tau_d, y))\,dy \\
\qquad\qquad - \mu_M M(t,x), \quad t \in T_3^n, \ x \in \mathbb{R},
\end{cases}
$$

where $\Gamma(D_I \tau, x-y) := \Gamma(D_I \tau, x, y)$ and $\Gamma(t, x) = \frac{1}{\sqrt{4\pi t}} e^{-\frac{x^2}{4t}}$ is the Green function of $\partial_t u(t,x) = \Delta u(t,x), x \in \mathbb{R}$. In subsection 4.1, we apply the theory developed in [27, 30] to establish the existence of spreading speed and traveling waves for (4.1). The spreading speed is also estimated through the linear operators approach. Then we show that the immature population shares the same propagation dynamics in subsection 4.2. In particular, the existence of a periodic traveling wave connecting $I^*(t)$ to 0 for the immature population is investigated in a time-periodic shifting environment. Throughout this section, we always assume that $\mathcal{R}_0 > 1$.

4.1. Propagation dynamics for adults. Recall that $\hat{\tau} := \tau + \tau_d$. Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathcal{Z} := C([-\hat{\tau}, 0], \mathbb{R})$. Clearly, any element in $\mathcal{Z}$ can be regarded as a constant function in $\mathcal{C}$. For convenience, we also identify an element $\phi \in \mathcal{C}$ as a function from $[-\hat{\tau}, 0] \times \mathbb{R}$ to $\mathbb{R}$ defined by $\phi(\theta, x) = \phi(x)(\theta)$. For any $\phi, \psi \in \mathcal{C}$, we write $\phi \geq \psi (\phi \gg \psi)$ if $\phi(x) \geq \psi(x)$ $(\phi(x) > \psi(x))$ $\forall x \in \mathbb{R}$, and $\phi > \psi$ provided $\phi \geq \psi$ but $\phi \neq \psi$. For any $\beta \in \mathcal{Z}$ with $\beta \gg 0$, we denote $\mathcal{C}_\beta := \{\phi \in \mathcal{C} : \beta \geq \phi \geq 0\}$ and $\mathcal{Z}_\beta := \{\phi \in \mathcal{Z} : \beta \geq \phi \geq 0\}$. Moreover, we define the norm on $\mathcal{C}$:

$$\|\phi\|_\mathcal{C} = \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} \|\phi(x)\|_\mathcal{Z}}{2^k} \quad \forall u \in \mathcal{C}.$$

In addition, for a function $\phi \in \mathcal{C}_\beta$ and a bounded interval $I = [a, b] \subset \mathbb{R}$, we define the function $\phi_I : I \to \mathcal{Z}$ by $\phi_I(x) = \phi(x)$. Given a subset $\mathcal{U}$ of $\mathcal{C}$, we define $\mathcal{U}_I := \{\phi_I : \phi \in \mathcal{U}\}$ and the norm $|\cdot|$ in $\mathcal{U}_I$ by $|\phi_I| := \max_{x \in I} \|\phi_I(x)\|_\mathcal{Z}$.

Define the reflection operator $\mathcal{R}$ by $\mathcal{R}[\phi](x) = \phi(-x)$ and the translation operator $\mathcal{T}_y$ by $\mathcal{T}_y[\phi](x) = \phi(x - y)$ for any given $y \in \mathbb{R}$. In order to use the theory of spreading speeds and traveling waves developed in [27, 30], we choose $\mathcal{K} = \mathcal{C}_\beta$ and let Q be a map from $\mathcal{C}_\beta$ to $\mathcal{C}_\beta$ satisfying the following assumptions:

(A1) $Q[\mathcal{R}[\phi]] = \mathcal{R}[Q(\phi)]$, $\mathcal{T}_y[Q[\phi]] = Q[\mathcal{T}_y[\phi]]$ $\forall \phi \in \mathcal{C}_\beta$, $y \in \mathbb{R}$.

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

(A3) The set $Q[\mathcal{C}_\beta](0, \cdot)$ is precompact in the space $C(\mathbb{R}, \mathbb{R})$ equipped with the compact open topology, and there is an equivalent norm $\|\cdot\|_\mathcal{Z}^*$ in $\mathcal{Z}$ such that for any number $r \geq 0$, there exists $k = k(r) \in [0, 1)$ such that for any interval $I = [a, b]$ of the length r and any $\mathcal{U} \subset \mathcal{C}_\beta$ with $\mathcal{U}(0, \cdot)$ being precompact in $C(\mathbb{R}, \mathbb{R})$, we have $\alpha((Q[\mathcal{U}])_I) \leq k\alpha(\mathcal{U}_I)$, where α is the Kuratowski measure of noncompactness on $\mathcal{C}_I$ with $(\mathcal{Z}, \|\cdot\|_\mathcal{Z})$ replaced by $(\mathcal{Z}, \|\cdot\|_\mathcal{Z}^*)$.

(A4) Q is monotone (order preserving) in the sense that $Q[\phi] \geq Q[\psi]$ whenever $\phi \geq \psi$ in $\mathcal{C}_\beta$.

(A5) $Q : \mathcal{Z}_\beta \to \mathcal{Z}_\beta$ admits exactly two fixed points 0 and β, and $\lim_{n \to \infty} Q^n[v] = \beta$ in $\mathcal{Z}$ for any $v \in \mathcal{Z}_\beta$ with $0 \ll v \leq \beta$.

It should be pointed out that the condition $Q[\mathcal{R}[\phi]] = \mathcal{R}[Q(\phi)]$ is added to (A1) in [30] to guarantee that the rightward spreading speed equals the leftward one (see [30, Remark 3.1]), and assumption (A3) here is assumption (A3)$'$ in [30] due to the fact that we consider the time-delayed evolution equations with spatial structure (see [30, Remark 4.1]). Assumption (A6) in [30] is not listed since it is automatically satisfied in the case where $\mathcal{K} = \mathcal{C}_\beta$.

Let L be defined as in section 2, and we define $\hat{L}(\theta) = L, \forall \theta \in [-\hat{\tau}, 0]$. By a similar analysis as in section 3, it follows that for any $\phi \in \mathcal{C}_{\hat{L}}$, (4.1) has a unique mild solution $M(t, x; \phi)$ with $M_0 = \phi$ and $M_t \in \mathcal{C}_{\hat{L}}$ for all $t \geq 0$ and that $M(t, x, \phi)$ is a classic solution when $t > \tau$. Define $Q_t : \mathcal{C}_{\hat{L}} \to \mathcal{C}_{\hat{L}}$ by

$$Q_t[\phi](x) = M_t(x; \phi) \quad \forall t \geq 0, x \in \mathbb{R}, \phi \in \mathcal{C}_{\hat{L}}.$$

It then follows that $\{Q_t\}_{t \geq 0}$ is a 1-periodic semiflow on $\mathcal{C}_{\hat{L}}$. Moreover, we have the following lemmas on the properties of the solution map Q_t, whose proofs are given in Appendix C.

LEMMA 4.1. *For each $t > 0$, the map Q_t is strictly subhomogeneous.*

LEMMA 4.2. *For any $t > 0$, the map Q_t satisfies (A1)–(A4) with $\beta = \hat{L}$, and Q_1 satisfies (A1)–(A5) with $\beta = M_0^*$, where $M_0^* \in \mathcal{Z}_{\hat{L}}$ with $M_0^*(\theta) = M^*(\theta)$ for all $\theta \in [-\hat{\tau}, 0]$.*

Since Q_1 satisfies (A1)–(A5) with $\beta = M_0^*$, it follows from [30, Theorems 3.1–3.3 and Remark 3.1] that Q_1 admits a spreading speed c^*. To compute c^*, we use the linear operators approach (see, e.g., [38, Theorem 4.5]). Consider the linear system of (4.1) at the zero solution:

(4.2)
$$\begin{cases} \dfrac{\partial M(t,x)}{\partial t} = D_M \Delta M(t,x) + e^{-\mu_I \tau} b'(0) \displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y) M(t-\tau, y) dy \\ \qquad\qquad - \mu_M M(t,x), \quad t \in T_1^n, \ x \in \mathbb{R}, \\ \dfrac{\partial M(t,x)}{\partial t} = -d_M M(t,x), \quad t \in T_2^n, \ x \in \mathbb{R}, \\ \dfrac{\partial M(t,x)}{\partial t} = D_M \Delta M(t,x) + e^{-\mu_I \tau - d_I \tau_d} b'(0) \displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y) M(t-\tau-\tau_d, y) dy \\ \qquad\qquad - \mu_M M(t,x), \quad t \in T_3^n, \ x \in \mathbb{R}. \end{cases}$$

For $\alpha > 0$, let $M(t,x) = e^{-\alpha x} u(t)$. Note that

$$\Gamma(t,x) = \Gamma(t,-x) \text{ and } \int_{\mathbb{R}} \Gamma(D_I \tau, y) e^{\pm \alpha y} dy = e^{\alpha^2 D_I \tau}.$$

Substituting $M(t,x)$ into (4.2) yields

(4.3)
$$\begin{cases} \dfrac{du(t)}{dt} = D_M \alpha^2 u(t) - \mu_M u(t) + e^{-\mu_I \tau + \alpha^2 D_I \tau} b'(0) u(t-\tau), & t \in T_1^n, \\ \dfrac{du(t)}{dt} = -d_M u(t), & t \in T_2^n, \\ \dfrac{du(t)}{dt} = D_M \alpha^2 u(t) - \mu_M u(t) + e^{-\mu_I \tau - d_I \tau_d + \alpha^2 D_I \tau} b'(0) u(t-\tau-\tau_d), & t \in T_3^n. \end{cases}$$

Then $M(t,x) = e^{-\alpha x} u(t)$ satisfies (4.2) with $\phi(\theta, x) = e^{-\alpha x} u(\theta)$ for $\theta \in [-\hat{\tau}, 0]$ and $x \in \mathbb{R}$ if $u(t)$ satisfies (4.3) for $t \geq 0$.

Let F_t be the linear solution map defined by (4.2), and let $u(t, u_0)$ be the solution of (4.3) with $u(\theta, u_0) = u_0(\theta)$ for $\theta \in [-\hat{\tau}, 0], u_0 \in \mathcal{Z}$. Define a map $B_\alpha^t : \mathcal{Z} \to \mathcal{Z}$ by

$$B_\alpha^t(u_0)(\theta) := F_t(u_0 e^{-\alpha x})(\theta, 0) \ \ \forall \theta \in [-\hat{\tau}, 0].$$

Then we have

$$B_\alpha^t(u_0)(\theta) = M(t+\theta, x; u_0 e^{-\alpha x})(\theta, 0) = u(t+\theta, u_0) \ \ \forall \theta \in [-\hat{\tau}, 0];$$

that is, B_α^t is the solution map associated with (4.3) on $\mathcal{Z}$.

For any given $t \geq 0$, let $\hat{B}_\alpha^t$ be the solution map of (4.3) on $C([-\tau, 0], \mathbb{R})$, that is, $\hat{B}_\alpha^t(\phi) = z_t(\phi)$, where z_t is defined by

$$z_t(\phi)(\theta) = z(t+\theta, \phi) \ \forall \theta \in [-\tau, 0]$$

and $z(t, \phi)$ is the unique solution of (4.3) with $z(\theta) = \phi(\theta)$ for all $\theta \in [-\tau, 0]$. Let $r(\hat{B}_\alpha^1)$ be the spectral radius of $\hat{B}_\alpha^1$. Similar to the arguments in [49, Lemma 3.5], we can show that $z(t, \phi) \gg 0$ for all $t > \tau$, $\phi \in C([-\tau, 0], \mathbb{R}_+)$ with $\phi \not\equiv 0$. Moreover, [16, Theorem 3.6.1] implies that z_t is compact on $C([-\tau, 0], \mathbb{R}_+)$ for all $t > \tau$. Thus, $\hat{B}_\alpha^1$ is compact and strongly positive due to (H4). By the Krein–Rutman theorem, it follows that $r(\hat{B}_\alpha^1)$ is a simple eigenvalue of $\hat{B}_\alpha^1$ having a strongly positive eigenvector

$\bar{\phi} \in C([-\tau, 0], \mathbb{R}_+)$, that is, $\hat{B}^1_\alpha(\bar{\phi}) = r(\hat{B}^1_\alpha)\bar{\phi}$. Using [48, Lemma 1], one obtains that there exists a positive 1-periodic function $w(t)$ in $t \in \mathbb{R}$ such that $z(t) = e^{\lambda(\alpha)t}w(t)$ is a solution of (4.3), where $\lambda(\alpha) = \ln r(\hat{B}^1_\alpha)$.

Define $\psi \in \mathcal{Z}$ by $\psi(\theta) = e^{\lambda(\alpha)\theta}w(\theta)$ for $\theta \in [-\hat{\tau}, 0]$. By the uniqueness of solutions, $u(t, \psi) = e^{\lambda(\alpha)t}w(t)$ is the solution of (4.3) on the space $\mathcal{Z}$. As a consequence, we have

$$B^t_\alpha(\psi)(\theta) = u(t + \theta, \psi) = e^{\lambda(\alpha)t}e^{\lambda(\alpha)\theta}w(t + \theta) \quad \forall \theta \in [-\hat{\tau}, 0], \ t \geq 0.$$

Using the periodicity of $w(t)$, one obtains

$$B^1_\alpha(\psi)(\theta) = e^{\lambda(\alpha)}e^{\lambda(\alpha)\theta}w(\theta) = e^{\lambda(\alpha)}\psi(\theta) \quad \forall \theta \in [-\hat{\tau}, 0],$$

that is, $B^1_\alpha(\psi) = e^{\lambda(\alpha)}\psi$. This implies that $e^{\lambda(\alpha)}$ is the principal eigenvalue of $B^1_\alpha(\psi)$ with a positive eigenfunction ψ.

Note that $r(B^1_\alpha) = r(\hat{B}^1_\alpha)$ due to [49, Lemma 3.8]. Let $\Phi(\alpha) := \frac{1}{\alpha}\ln e^{\lambda(\alpha)} = \frac{\lambda(\alpha)}{\alpha} = \frac{\ln r(B^1_\alpha)}{\alpha}$. Then we have the following result on the spreading speed of the map Q_1.

LEMMA 4.3. $c^* = \inf_{\alpha>0} \Phi(\alpha) = \inf_{\alpha>0} \frac{\ln r(B^1_\alpha)}{\alpha}$.

Proof. When $\alpha = 0$, (4.3) becomes (3.4). Note that $\mathcal{R}_0 > 1$ is equivalent to $r(P) > 1$. It then follows that $r(B^1_0) > 1$, and hence (C7) in [29] holds true. Now we prove that $\Phi(\infty) = \infty$. Noticing that $u(t, \psi) = e^{\lambda(\alpha)t}w(t)$ is the solution of (4.3), from (4.3) one easily sees

$$\begin{cases} \frac{w'(t)}{w(t)} \geq D_M\alpha^2 - \mu_M - \lambda(\alpha), & t \in T^n_1, \\ \frac{w'(t)}{w(t)} = -d_M - \lambda(\alpha), & t \in T^n_2, \\ \frac{w'(t)}{w(t)} \geq D_M\alpha^2 - \mu_M - \lambda(\alpha), & t \in T^n_3. \end{cases}$$

Integrating the above equations from 0 to 1 yields

$$0 = \int_0^1 \frac{w'(t)}{w(t)}dt \geq \int_0^{1-\tau-\tau_d}(D_M\alpha^2 - \mu_M - \lambda(\alpha))dt + \int_{1-\tau-\tau_d}^{1-\tau}(-d_M - \lambda(\alpha))dt$$

$$+ \int_{1-\tau}^1 (D_M\alpha^2 - \mu_M - \lambda(\alpha))dt,$$

which implies that

$$\frac{\lambda(\alpha)}{\alpha} \geq \alpha D_M(1 - \tau_d) - \frac{\mu_M(1 - \tau_d) + d_M\tau_d}{\alpha}.$$

Letting $\alpha \to \infty$, one easily sees $\Phi(\infty) = \infty$.

Since $b(\cdot)$ is subhomogeneous in u, it follows from [52, Lemma 2.3.2] that $b(u) \leq b'(0)u$ for $u \in [0, L]$. By the comparison principle, we have $Q_1(\phi) \leq F_1(\phi)$ for any $\phi \in \mathcal{C}_\beta$. As a consequence, we infer from [29, Theorem 3.10(i)] that $c^* \leq \inf_{\alpha>0} \Phi(\alpha)$.

It is easy to see that for any $\epsilon \in (0, 1)$, there exists $\delta = \delta(\epsilon) \in (0, L)$ such that $b(u) \geq (1 - \epsilon)b'(0)u$ for $u \in [0, \delta]$. Moreover, there exists $\xi = \xi(\delta) > 0$ such that for any $\phi \in \mathcal{C}_{\hat{\xi}}$ with $\hat{\xi}(\theta) = \xi$, $\theta \in [-\hat{\tau}, 0]$, we have

$$0 \leq M(t, x; \phi) \leq M(t, x; \hat{\xi}) < \delta, \quad t \in [0, 1], \ x \in \mathbb{R}.$$

Thus, for any $\phi \in \mathcal{C}_{\hat{\xi}}$, $M(t,x;\phi)$ satisfies

$$
\begin{cases}
\dfrac{\partial M(t,x)}{\partial t} \geq D_M \Delta M(t,x) + e^{-\mu_I \tau}(1-\epsilon)b'(0)\displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y)M(t-\tau, y)dy \\
\qquad\qquad - \mu_M M(t,x), \quad t \in (0, 1-\tau-\tau_d], \ x \in \mathbb{R}, \\[2mm]
\dfrac{\partial M(t,x)}{\partial t} = -d_M M(t,x), \quad t \in (1-\tau-\tau_d, 1-\tau], \ x \in \mathbb{R}, \\[2mm]
\dfrac{\partial M(t,x)}{\partial t} \geq e^{-\mu_I \tau - d_I \tau_d}(1-\epsilon)b'(0)\displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y)M(t-\tau-\tau_d, y)dy \\
\qquad\qquad + D_M \Delta M(t,x) - \mu_M M(t,x), \quad t \in (1-\tau, 1], \ x \in \mathbb{R}.
\end{cases}
$$

Let F_t^ϵ be the solution map associated with the linear system

$$
\begin{cases}
\dfrac{\partial \hat{M}(t,x)}{\partial t} = D_M \Delta \hat{M}(t,x) + e^{-\mu_I \tau}(1-\epsilon)b'(0)\displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y)\hat{M}(t-\tau, y)dy \\
\qquad\qquad - \mu_M \hat{M}(t,x), \quad t \in (0, 1-\tau-\tau_d], \ x \in \mathbb{R}, \\[2mm]
\dfrac{\partial \hat{M}(t,x)}{\partial t} = -d_M \hat{M}(t,x), \quad t \in (1-\tau-\tau_d, 1-\tau], \ x \in \mathbb{R}, \\[2mm]
\dfrac{\partial \hat{M}(t,x)}{\partial t} = e^{-\mu_I \tau - d_I \tau_d}(1-\epsilon)b'(0)\displaystyle\int_{\mathbb{R}} \Gamma(D_I \tau, x-y)\hat{M}(t-\tau-\tau_d, y)dy \\
\qquad\qquad + D_M \Delta \hat{M}(t,x) - \mu_M \hat{M}(t,x), \quad t \in (1-\tau, 1], \ x \in \mathbb{R}.
\end{cases}
$$

The comparison principle implies that $F_t^\epsilon(\phi) \leq Q_t(\phi)$ for all $\phi \in \mathcal{C}_{\hat{\xi}}$ when $t \in [0,1]$. Then we deduce from [29, Theorem 3.10(ii)] that $c^* \geq \inf_{\alpha>0} \Phi_\epsilon(\alpha)$, and hence, by letting $\epsilon \to 0$, we have $c^* \geq \inf_{\alpha>0} \Phi(\alpha)$. Consequently, $c^* = \inf_{\alpha>0} \Phi(\alpha)$. $\square$

THEOREM 4.4. *The following statements are valid:*

(i) *For any $c > c^*$, if $\phi \in \mathcal{C}_{M_0^*}$ with $0 \leq \phi \ll M_0^*$ and $\phi(\cdot, x) = 0$ for x outside a bounded interval, then*

$$
\lim_{t\to\infty, |x|\geq ct} M(t,x;\phi) = 0.
$$

(ii) *For any $c < c^*$, if $\phi \in \mathcal{C}_{M_0^*}$ with $\phi(\theta, \cdot) \neq 0$ for $\theta \in [-\tau, 0]$, then*

$$
\lim_{t\to\infty, |x|\leq ct} (M(t,x;\phi) - M^*(t)) = 0.
$$

Proof. Note that $\{Q_t\}_{t\geq 0}$ is a 1-periodic semiflow and c^* is the spreading speed for its Poincaré map Q_1. Thus, statement (i) is a straightforward consequence of the proof of [27, Theorem 2.1 (1)]. Since Q_1 is subhomogeneous due to Lemma 4.1, it follows from the proof of [27, Theorem 2.1 (2)] that for any $c < c^*$, there exists a positive number r such that if $\phi \in \mathcal{C}_{M_0^*}$ with $\phi(\cdot, x) \gg 0$ for all x on an interval I of length $2r$, then $\lim_{t\to\infty, |x|\leq ct}(M(t,x;\phi) - M^*(t)) = 0$. For any given $\phi \in \mathcal{C}_{M_0^*}$ with $\phi(\theta, \cdot) \neq 0$ for $\theta \in [-\tau, 0]$, by a similar argument to that in [21, Lemma 2.5], we see that $M(t,\cdot;\phi) \gg 0$ for $t > \tau$. Therefore, we can choose an integer $n_0 > \tau + \hat{\tau}$ such that $Q_{n_0}(\phi) \gg 0$ and take $Q_{n_0}(\phi)$ as a new initial value for $M(t,x;\phi)$. Then by the above analysis, statement (ii) is valid. $\square$

Recall that $\mathcal{M}(t, x-ct)$ is called to be a periodic traveling wave of (4.1) provided that $\mathcal{M}(t,z)$ is 1-periodic in t and $M(t,x) = \mathcal{M}(t, x-ct)$ satisfies (4.1), and we say

$\mathcal{M}(t, x - ct)$ connects $M^*(t)$ to 0 if $\mathcal{M}(t, -\infty) = M^*(t)$ and $\mathcal{M}(t, \infty) = 0$ uniformly for $t \in [0, 1]$. By the same arguments as in the proofs of [27, Theorems 2.2 and 2.3], we have the following result about traveling waves of (4.1).

THEOREM 4.5. *Let c^* be defined as in Lemma 4.3. Then for any $c \geq c^*$, (4.1) has a 1-periodic traveling wave solution $\mathcal{M}(t, x - ct)$ connecting $M^*(t)$ to 0 such that $\mathcal{M}(t, z)$ is continuous and nonincreasing in $z \in \mathbb{R}$. Moreover, for any $c < c^*$, (4.1) has no 1-periodic traveling wave $\mathcal{M}(t, x - ct)$ connecting $M^*(t)$ to 0.*

4.2. Propagation dynamics for juveniles. The spreading of the immature population $I(t, x)$ can be investigated through the system

(4.4)
$$\begin{cases} \frac{\partial I(t,x)}{\partial t} = D_I \Delta I(t, x) + H_1(t, x; M) - \mu_I I(t, x), & t \in T_1^n, \ x \in \mathbb{R}, \\ \frac{\partial I(t,x)}{\partial t} = -d_I I(t, x), & t \in T_2^n, \ x \in \mathbb{R}, \\ \frac{\partial I(t,x)}{\partial t} = D_I \Delta I(t, x) + H_2(t, x; M) - \mu_I I(t, x), & t \in T_3^n, \ x \in \mathbb{R}, \end{cases}$$

with

$$H_1(t, x; M) = b(M(t, x)) - e^{-\mu_I \tau} \int_{\mathbb{R}} \Gamma(D_I \tau, y) b(M(t - \tau, x - y)) dy,$$

$$H_2(t, x; M) = b(M(t, x)) - e^{-\mu_I \tau - d_I \tau_d} \int_{\mathbb{R}} \Gamma(D_I \tau, y) b(M(t - \tau - \tau_d, x - y)) dy.$$

Then the integral form of (4.4) is expressed as
(4.5)
$$\begin{cases} I(t, x) = e^{-\mu_I(t-n)} \int_{\mathbb{R}} \Gamma(D_I(t - n), x - y) I(n, y) dy \\ \qquad + \int_0^{t-n} e^{-\mu_I s} \int_{\mathbb{R}} \Gamma(D_I s, y) H_1(t - s, x - y; M) dy ds, \quad t \in T_1^n, \\ I(t, x) = e^{-d_I(t-(n+1-\tau-\tau_d))} I(n + 1 - \tau - \tau_d, x), \quad t \in T_2^n, \\ I(t, x) = e^{-\mu_I(t-(n+1-\tau))} \int_{\mathbb{R}} \Gamma(D_I(t - (n + 1 - \tau)), x - y) I(n + 1 - \tau, y) dy \\ \qquad + \int_0^{t-(n+1-\tau)} e^{-\mu_I s} \int_{\mathbb{R}} \Gamma(D_I s, y) H_2(t - s, x - y; M) dy ds, \quad t \in T_3^n. \end{cases}$$

For the sake of notational convenience, we define

$$J_1(t) = b(M^*(t)) - e^{-\mu_I \tau} b(M^*(t - \tau)),$$
$$J_2(t) = b(M^*(t)) - e^{-\mu_I \tau - d_I \tau_d} b(M^*(t - \tau - \tau_d)).$$

Then we have the following result.

THEOREM 4.6. *Let $M(t, x)$ be a solution of (4.1) with spreading speed c^*. Then for any bounded initial value, the solution of (4.4) has the following property:*
 (i) $\forall c > c^*, \lim_{t \to \infty, |x| \geq ct} I(t, x) = 0.$
 (ii) $\forall 0 < c < c^*, \lim_{t \to \infty, |x| \leq ct} (I(t, x) - I^*(t)) = 0.$

Proof. By the arguments similar to those in [12, Theorem 3.2], we can prove that for any $s \in [0, t)$ and $y \in \mathbb{R}$, we have (a) $\forall c > c^*$, $\lim_{t \to \infty, |x| \geq ct} M(t - \eta, x - y; \phi) = 0, \eta = \tau(\text{or } \tau + \tau_d)$ and $\lim_{t \to \infty, |x| \geq ct} H_i(t - s, x - y; M) = 0$, $i = 1, 2$, and (b) $\forall 0 < c < c^*$, $\lim_{t \to \infty, |x| \leq ct} (M(t - \eta, x - y; \phi) - M^*(t)) = 0, \eta = \tau(\text{or } \tau + \tau_d)$.

Furthermore,

$$\lim_{t\to\infty,|x|\leq ct}[H_i(t-s,x-y;M)-J_i(t-s)]=0, i=1,2.$$

Note that solutions of (4.4) are uniformly bounded. Thus, one can deduce from (4.5) that $\lim_{t\to\infty,|x|\geq ct}I(t,x)=0$ for $c>c^*$.

In the case where $0<c<c^*$, we write $I^*(t)$ as

$$\begin{aligned}
I^*(t) &= e^{-\mu_I(t-n)}I^*(n)+\int_0^{t-n}e^{-\mu_I s}J_1(t-s)ds, & t\in T_1^n,\\
I^*(t) &= e^{-d_I(t-(n+1-\tau-\tau_d))}I^*(n+1-\tau-\tau_d), & t\in T_2^n,\\
I^*(t) &= e^{-\mu_I(t-(n+1-\tau))}I^*(n+1-\tau)+\int_0^{t-(n+1-\tau)}e^{-\mu_I s}J_2(t-s)ds, & t\in T_3^n,
\end{aligned}$$

with $I^*(0)=\int_{-\tau}^0 b(M^*(s))e^{\mu_I s}ds$. Consequently,

$$\begin{aligned}
|I(t,x)-I^*(t)| &\leq e^{-\mu_I(t-n)}\int_\mathbb{R}\Gamma(D_I(t-n),x-y)|I(n,y)-I^*(t)|dy\\
&\quad+\int_0^{t-n}e^{-\mu_I s}\int_\mathbb{R}\Gamma(D_I s,y)|H_1(t-s,x-y;M)-J_1(t-s)|dyds, & t\in T_1^n,\\
|I(t,x)-I^*(t)| &\leq e^{-d_I(t-(n+1-\tau-\tau_d))}|I(n+1-\tau-\tau_d,x)-I^*(n+1-\tau-\tau_d)|, & t\in T_2^n,\\
|I(t,x)-I^*(t)| &\leq e^{-\mu_I(t-(n+1-\tau))}\int_\mathbb{R}\Gamma(D_I(t-(n+1-\tau)),x-y)\\
&\quad\times\Big|I(n+1-\tau,y)-I^*(n+1-\tau)\Big|dy\\
&\quad+\int_0^{t-(n+1-\tau)}e^{-\mu_I s}\int_\mathbb{R}\Gamma(D_I s,y)|H_2(t-s,x-y;M)-J_2(t-s)|dyds, & t\in T_3^n.
\end{aligned}$$

This implies that $\lim_{t\to\infty,|x|\leq ct}(I(t,x)-I^*(t))=0$ for $c\in(0,c^*)$ thanks to the induction method. □

For any $c\geq c^*$, let $\mathcal{M}(t,x-ct)$ be a periodic traveling wave of (4.1) satisfying $\mathcal{M}(t,-\infty)=M^*(t)$ and $\mathcal{M}(t,\infty)=0$. Substituting $M(t,x)=\mathcal{M}(t,x-ct)$ into (4.4) yields
(4.6)
$$\begin{cases}
\dfrac{\partial I(t,x)}{\partial t}=D_I\Delta I(t,x)+b(\mathcal{M}(t,x-ct))-\mu_I I(t,x) & t\in T_1^n,\ x\in\mathbb{R},\\
\qquad -e^{-\mu_I\tau}\int_\mathbb{R}\Gamma(D_I\tau,y)b(\mathcal{M}(t-\tau,x-y-ct+c\tau))dy,\\
\dfrac{\partial I(t,x)}{\partial t}=-d_I I(t,x), & t\in T_2^n,\ x\in\mathbb{R},\\
\dfrac{\partial I(t,x)}{\partial t}=D_I\Delta I(t,x)+b(\mathcal{M}(t,x-ct))-\mu_I I(t,x) & t\in T_3^n,\ x\in\mathbb{R},\\
\qquad -e^{-\mu_I\tau-d_I\tau_d}\int_\mathbb{R}\Gamma(D_I\tau,y)b(\mathcal{M}(t-\tau-\tau_d,x-y-ct+c\tau+c\tau_d))dy.
\end{cases}$$

Recall the definition of $I^*(t)$ in Lemma 3.5. Then the following result holds true.

THEOREM 4.7.
(i) *For any $c\geq c^*$, (4.6) has a unique periodic traveling wave $\mathcal{I}(t,x-ct)$ satisfying $\mathcal{I}(t,-\infty)=I^*(t)$ and $\mathcal{I}(t,+\infty)=0$.*
(ii) *For any $c\in(0,c^*)$, (4.6) admits no periodic traveling wave with speed c and connecting $I^*(t)$ and 0.*

Proof of case (i). Let $\tilde{T}(t)$ be the solution semigroup of $\frac{\partial I}{\partial t} = D_I \triangle I - \mu_I I$. Define
(4.7)

$$\mathcal{I}(t,\xi) = \int_{t-\tau}^{t} \tilde{T}(t-s)Z(s,\cdot)(\xi+ct)ds, \quad t \in T_1^n,$$

$$\mathcal{I}(t,\xi) = \mathcal{I}(n+1-\tau-\tau_d, \xi+c(t-(n+1-\tau-\tau_d)))e^{-d_I(t-(n+1-\tau-\tau_d))}, \quad t \in T_2^n,$$

$$\mathcal{I}(t,\xi) = \int_{n+1-\tau}^{t} \tilde{T}(t-s)Z(s,\cdot)(\xi+ct)ds$$
$$+ \int_{t-\tau-\tau_d}^{n+1-\tau-\tau_d} e^{\mu_I\tau_d - d_I\tau_d}\tilde{T}(t-s)Z(s,\cdot)(\xi+ct)ds, \quad t \in T_3^n,$$

where $Z(s,x) = b(\mathcal{M}(s, x-cs))$. It is easy to verify that $\mathcal{I}(t, x-ct)$ is a solution of (4.6) with initial condition $\mathcal{I}(0,x) = \int_{-\tau}^{0} e^{\mu_I s} \int_{\mathbb{R}} \Gamma(-D_I s, y)Z(s, x-y)dyds$. Since $Z(s+1, x+c) = Z(s,x)$, one can see that $\mathcal{I}(t+1,\xi) = \mathcal{I}(t,\xi)$ for all $t \geq 0$. Note that $Z(s, \pm\infty) = b(\mathcal{M}(s, \pm\infty))$ uniformly in $s \in \mathbb{R}$ due to the periodicity in s. Then in (4.7), passing $\xi \to \pm\infty$ together with the Lebesgue dominated convergence theorem and the periodicity of $\mathcal{I}(t,\xi)$ in t, we obtain

$$\mathcal{I}(t,\pm\infty) = \int_{t-\tau}^{t} e^{-\mu_I(t-s)}Z(s,\pm\infty)ds, \qquad\qquad t \in T_1^n,$$

$$\mathcal{I}(t,\pm\infty) = \mathcal{I}(n+1-\tau-\tau_d, \pm\infty)e^{-d_I(t-(n+1-\tau-\tau_d))}, \qquad t \in T_2^n,$$

$$\mathcal{I}(t,\pm\infty) = \int_{n+1-\tau}^{t} e^{-\mu_I(t-s)}Z(s,\pm\infty)ds$$
$$+ \int_{t-\tau-\tau_d}^{n+1-\tau-\tau_d} e^{\mu_I\tau_d - d_I\tau_d}e^{-\mu_I(t-s)}Z(s,\pm\infty)ds, \quad t \in T_3^n.$$

Here we used the fact that $\int_{\mathbb{R}} \Gamma(D_I(t-s), y)dy = 1$. In view of $Z(s, +\infty) = 0$ and $Z(s, -\infty) = b(M^*(s))$, we derive that $\mathcal{I}(t, +\infty) = 0$ and $\mathcal{I}(t, -\infty) = I^*(t)$. Moreover, by applying an argument similar to that in [36, Theorem 5.3(i)], we can prove the uniqueness of $\mathcal{I}(t,x)$.

Proof of case (ii). The nonexistence of periodic traveling wave is a consequence of the property of the spreading speed in Theorem 4.6(ii), as in the proof of [25, Theorem 3.4]. □

5. Numerical simulations and conclusion. By incorporating the discontinuous and periodic maturation delay due to the seasonal diapause, this paper proposes a succession model with the nonlocal term accounting for the movement of immature individuals during maturation. The spatial dynamics are investigated in both bounded and unbounded domains. In a bounded habitat, the establishment of the species is thoroughly determined by the basic reproduction ratio $\mathcal{R}_0$; that is, when $\mathcal{R}_0 < 1$, the population will go extinct, while the population density will stabilize at a seasonal pattern when $\mathcal{R}_0 > 1$. For the unbounded domain case, the spreading speed c^* of the population invasion (when $\mathcal{R}_0 > 1$) is computed, which is consistent with the minimal wave speed for traveling wave solution of $M(t,x)$.

In what follows, we perform some numerical simulations to verify the results obtained in sections 3 and 4, and reveal the biological insights into the spatial dynamics of diapausing population growth by taking the mosquito species as a motivative example. As in [32], we assume that the birthrate function is a special case of Beverton–Holt function, that is, $b(M) = \frac{pM}{q+M^r}$, which only depends on the adult population M with

TABLE 2
Baseline values and ranges for parameters for the model.

Parameter	Range	Value	Dimension	Reference
τ	$0.4 \sim 1$	0.5	Month	[41]
τ_d	$2.5 \sim 5$	3	Month	[9]
μ_I	$0.3 \sim 1.8$	0.6	Month^{-1}	[5, 6, 37]
μ_M	$0.6 \sim 2.1$	0.7	Month^{-1}	[5, 6, 37]
d_I	≥ 0.8	0.8	Month^{-1}	Assumed
d_M	≥ 0.9	0.9	Month^{-1}	Assumed
D_M	$0.01 \sim 25$	1.25×10^{-2}	km$^2 \cdot$ day^{-1}	[24, 43]
D_I	$D_I \ll D_M$	$D_I = \frac{D_M}{10}$		Assumed
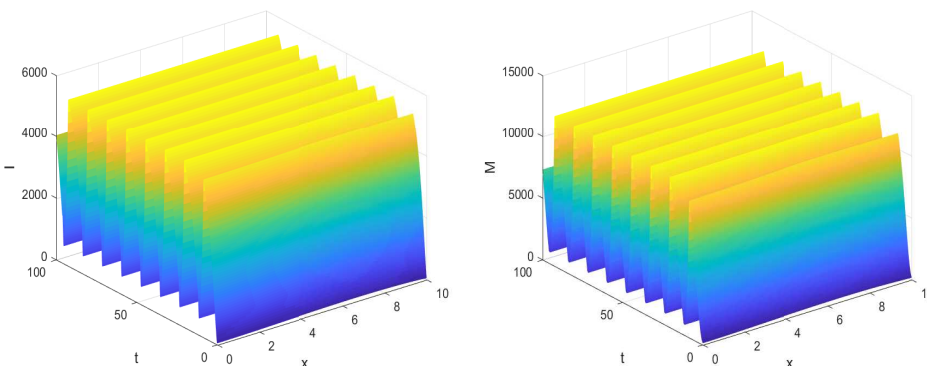
FIG. 5.1. *The evolution of $I(t,x)$ and $M(t,x)$ when $\mathcal{R}_0 > 1$.*

the maximum recruitment rate $p = 120$ month^{-1}, the maximum capacity-related parameter $q = 5$, and the dimensionless parameter $r = 0.5$. For model simulation and investigation, we use data in stage-specific mortality and development rates from the literature, which are summarized in Table 2. For mosquito dispersal, we choose $D_M = 1.25 \times 10^{-2} \times 30.4$ km$^2 \cdot$ month^{-1} and set D_I to be very small. We should mention that D_I may be zero, as the movement of immature mosquitoes is negligible. More complicated modeling of mosquito dispersal can be found in existing studies, such as [15].

5.1. Validation of analytic results. In the case of a bounded habitat, we assume $\Omega = (0, 10)$ under the Neumann boundary conditions. We use the backward difference method to simulate the solutions of (2.1)–(2.3) with MATLAB since this method is stable, which will allow us to take larger time steps. Here the second-order partial derivative with respect to the spatial variable x is approximated by the second-order central difference operator. The numerical scheme for dealing with the nonlocal terms $B_1(t, x; M)$ and $B_2(t, x; M)$ is highly motivated by the numerical method presented in [26, Appendix A.2]. To numerically calculate $\mathcal{R}_0$, we use [28, Lemma 2.5] and the bisection method. Using the parameter values in Table 2, we obtain $\mathcal{R}_0 = 15.4962$. Figure 5.1 shows the evolution of population densities $I(t, x)$ and $M(t, x)$. If the mortality rates for immature and the mature mosquitoes are, respectively, increased to $d_I = 10$ and $d_M = 20$, then $\mathcal{R}_0 = 0.6843$. In this case, we observe that both the immature and the mature mosquito population tend to zero (see Figure 5.2). The simulation results for $I(t, x)$ and $M(t, x)$ are consistent with our analytic results in Theorem 3.6.
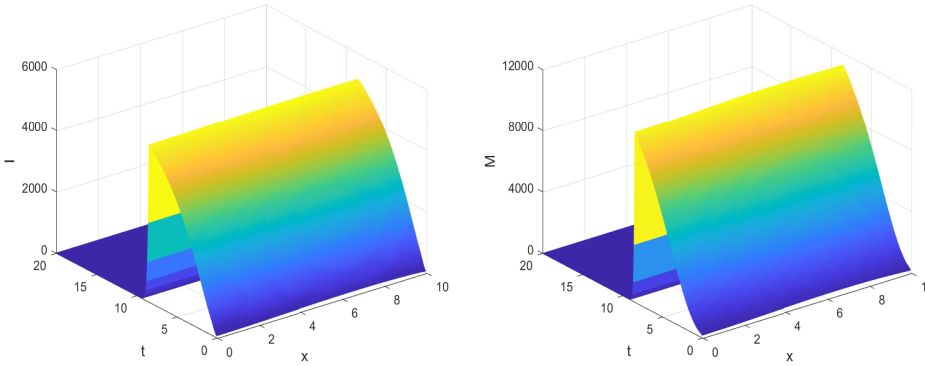
FIG. 5.2. *The evolution of $I(t, x)$ and $M(t, x)$ when $\mathcal{R}_0 < 1$.*

To simulate the spatial spread of the model, we truncate the spatial domain $\mathbb{R}$ into $[-200, 200]$. Using the given parameters in Table 2 such that $\mathcal{R}_0 = 15.4962$, we numerically compute $c^* = 2.0959$. Figure 5.3 shows numerical plots of the solution through a given initial value. The traveling wave solution pattern is shown in Figure 5.4.

5.2. Effects of different diapausing strategies. Some species may survive through the harsh environmental condition by diapausing at one specific stage. For example, the immature individuals of *Aedes albopictus* diapause (restricted in the egg stage) and the adults of *Culex pipiens* can undergo diapause to survive [46]. Therefore, it would be interesting to compare two different diapausing strategies: immature diapause and adult diapause, which can be distinguished by choosing different sets of death rates during the unfavorable season. For the immature diapause species *Aedes albopictus*, we take $d_I = d$, $d_M = 10 \times d$ with varying $d \in (0.9, 8)$; then most adults die quickly during the unfavorable season. For the adult diapause species *Culex pipiens*, we set $d_M = d$, $d_I = 10 \times d$ by assuming juveniles are subject to a very large death rate under a harsh environmental condition.

The relations between $\mathcal{R}_0$ (resp., c^*) and d are shown in Figures 5.5. Figure 5.5(a) demonstrates that the adult diapausing strategy produces a larger basic reproduction ratio. It seems adult diapausing is better than immature diapausing in terms of population establishment. Now we let $D_I = \frac{D_M}{2}$ with other parameters unchanged as in Table 2. Figure 5.5(b) shows that for small d, diapausing in the immature population can invade much more quickly to new habitats compared with the adult diapausing strategy. However, the observed phenomenon is otherwise for large d. This implies that adult diapausing is not always superior to juvenile diapausing in terms of species invasion. We speculate that these predictions are closely dependent on the model parameters in Table 2, for example, the larger diffusion rate of adults. However, the current study provides a hypothetical framework to address these questions.

Finally, we would like to highlight some weaknesses and possible extensions of the current work. The model is built on the extreme assumption that the development and physical activity are halted during the unfavorable season. In fact, individuals have low metabolic activity and reduced physical activity during diapause. It would be interesting to incorporate this fact into the model formulation. Furthermore, there may be several bad seasons in a 1-year period, for example, an extremely dry season and a cold season. In this scenario, there would be two diapausing periods in 1
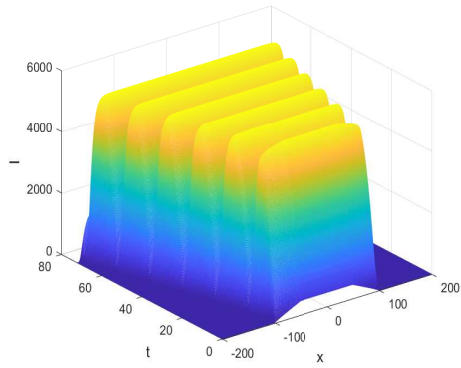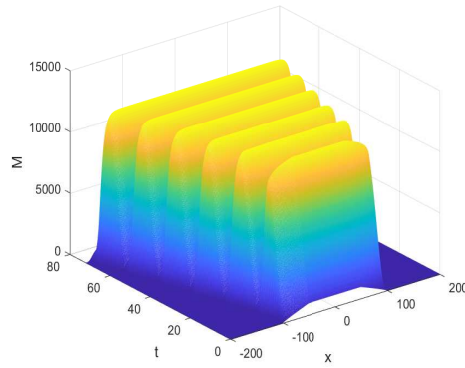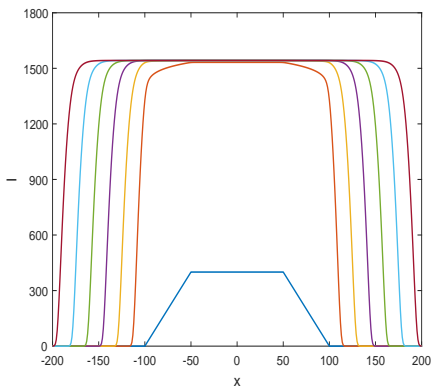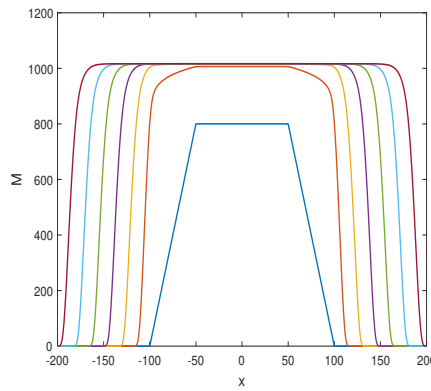
(a) The evolution of I

(b) The evolution of M

(c) The density of I at $t = n\omega$

(d) The density of M at $t = n\omega$

Fig. 5.3. *The spread of $I(t,x)$ and $M(t,x)$ and the densities $I(t,x)$ and $M(t,x)$ at $t = n\omega$ ($\omega = 12$ months) with $n = 0, 1, 2, 3, 4, 5,$ and 6, respectively.*
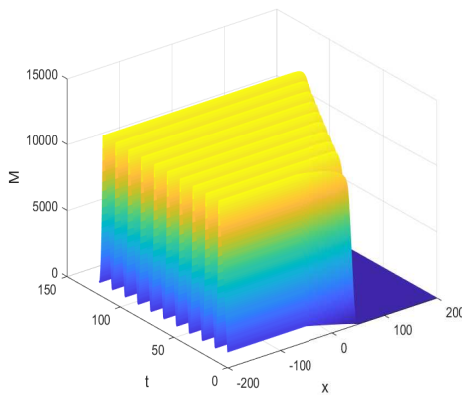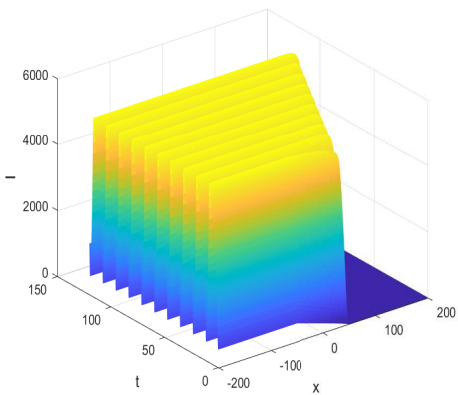

Fig. 5.4. *The evolution of $I(t,x)$ and $M(t,x)$ to a periodic traveling wave.*
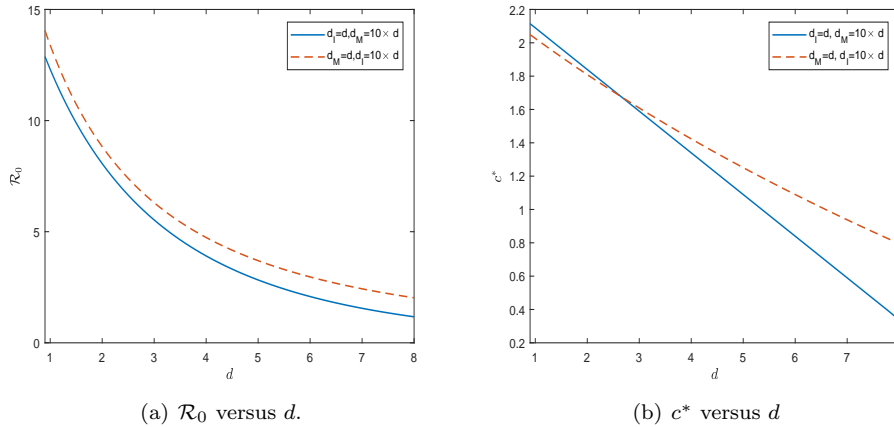
(a) $\mathcal{R}_0$ versus d.

(b) c^* versus d

Fig. 5.5. *The effect of different strategies on $\mathcal{R}_0$ and c^* and their relationship. In* (b), *D_I is set as $\frac{0.0125}{2}$ $km^2 \cdot day^{-1}$.*

year, which makes the modeling more complicated and brings new challenges to the model analysis. Moreover, the modeling framework becomes invalid in describing the diapause of multiple-stage species, for example, the *Ixodes* ticks [14], which may diapause in both the larval and the nymphal stages. We leave these topics for future consideration.

Appendix A. Model derivation. Let $p = p(t, x, a)$ denote the density of species with age a at time t and location $x \in \Omega$. According to the McKendrick–von-Foerster framework for an age-structured population, the density $p(t, x, a)$ during the normal growth period is described by the following equations:

(5.1)
$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) p = D_I \Delta p - \mu_I p, \qquad a < \tau,$$
$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) p = D_M \Delta p - \mu_M p, \qquad a \geq \tau,$$

where D_I, D_M are the diffusion rates, μ_I, μ_M are the death rates, and τ is the maturation delay. Clearly, the total immature population $I(t, x)$ and mature population $M(t, x)$ at time t and location x can be represented, respectively, by the integrals

(5.2)
$$I(t, x) = \int_0^\tau p(t, x, a) da, \qquad M(t, x) = \int_\tau^\infty p(t, x, a) da.$$

Differentiating both sides of (5.2) in time yields

$$\frac{\partial}{\partial t} I(t, x) = \int_0^\tau \frac{\partial}{\partial t} p(t, x, a) da$$
$$= \int_0^\tau \left[-\frac{\partial}{\partial a} + D_I \Delta - \mu_I\right] p(t, x, a) da$$
$$= D_I \Delta I(t, x) - \mu_I I(t, x) + p(t, x, 0) - p(t, x, \tau).$$

Similarly, we have

$$\frac{\partial}{\partial t} M(t, x) = D_M \Delta M(t, x) - \mu_M M(t, x) + p(t, x, \tau) - p(t, x, \infty).$$

The term $p(t, x, 0)$ represents the birthrate of the population, and hence we assume that $p(t, x, 0) = b(M(t, x))$, a function of the mature population density $M(t, x)$. It is biologically reasonable to assume that $p(t, x, \infty) = 0$, as no individual can live forever. To obtain a closed form of the model, one needs to express $p(t, x, \tau)$ by I and M in a certain way. Note that $p(t, x, \tau)$ represents the newly matured population at time t, and it is the evolution result of newborns at $t - \tau$. That is, there is an evolution relation between the quantities $p(t, x, \tau)$ and $p(t - \tau, x, 0)$. From the first equation of the growth law (5.1), we see that such a relation is the time-τ solution map of the evolution equation

$$(5.3) \qquad \begin{cases} \dfrac{\partial}{\partial s} q(s, x) = D_I \Delta q(s, x) - \mu_I q(s, x), & 0 < s \leq \tau, \\ q(0, x) = p(t - \tau, x, 0) = b(M(t - \tau, x)). \end{cases}$$

This evolution equation describes the dynamics of the density of juveniles at time s which were born at time 0. It involves the diffusion process and survival. This evolution equation can also be derived through the integration along characteristics for the first equation of (5.1). Solving the Cauchy problem (5.3), we obtain

$$p(t, x, \tau) = q(\tau, x) = e^{-\mu_I \tau} \int_\Omega \Gamma(D_I \tau, x, y) b(M(t - \tau, y)) dy,$$

where $\Gamma(t, x, y)$ is the fundamental solution associated with $\partial_t - \triangle$. Therefore, during the normal growth period of the nth year, $t \in T_1^n := (n, n + 1 - \tau - \tau_d]$, population densities for juveniles and adults can be described by the system

$$\begin{cases} \dfrac{\partial I(t, x)}{\partial t} = \underbrace{D_I \Delta I(t, x)}_{\text{diffusion}} + \underbrace{b(M(t, x))}_{\text{birth}} - \underbrace{B_1(t, x; M)}_{\text{maturation}} - \underbrace{\mu_I I(t, x)}_{\text{death}}, \\ \dfrac{\partial M(t, x)}{\partial t} = \underbrace{D_M \Delta M(t, x)}_{\text{diffusion}} + \underbrace{B_1(t, x; M)}_{\text{maturation}} - \underbrace{\mu_M M(t, x)}_{\text{death}}, \end{cases}$$

with the maturation rate

$$B_1(t, x; M) = e^{-\mu_I \tau} \int_\Omega \Gamma(D_I \tau, x, y) b(M(t - \tau, y)) dy.$$

During the diapause period, $t \in T_2^n := (n + 1 - \tau - \tau_d, n + 1 - \tau]$, there is no birth, development, or diffusion. The system becomes

$$\begin{cases} \dfrac{\partial I(t,x)}{\partial t} = - \underbrace{d_I I(t, x)}_{\text{death}}, \\ \dfrac{\partial M(t,x)}{\partial t} = - \underbrace{d_M M(t, x)}_{\text{death}}, \end{cases}$$

where d_I and d_M are the death rates during the diapause period.

After the diapause period, there is a short postdiapause period, $t \in T_3^n := (n + 1 - \tau, n + 1]$. During this period, the density $p(t, x, a)$ satisfies

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a} \right) p = D_I \Delta p - \mu_I p, \quad a < \tau + \tau_d,$$

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a} \right) p = D_M \Delta p - \mu_M p, \quad a \geq \tau + \tau_d.$$

Clearly, the total immature and mature population at time t and location x are given by

(5.4) $$I(t,x) = \int_0^{\tau+\tau_d} p(t,x,a)da, \quad M(t,x) = \int_{\tau+\tau_d}^{\infty} p(t,x,a)da.$$

Differentiating both sides of (5.4) in time yields

$$\frac{\partial}{\partial t}I(t,x) = D_I\Delta I(t,x) - \mu_I I(t,x) + p(t,x,0) - p(t,x,\tau+\tau_d),$$

$$\frac{\partial}{\partial t}M(t,x) = D_M\Delta M(t,x) - \mu_M M(t,x) + p(t,x,\tau+\tau_d).$$

As mentioned before, there is an evolution relation between the quantities $p(t,x,\tau+\tau_d)$ and $p(t-\tau-\tau_d,x,0)$. That is, such a relation can be described by the following evolution system:

$$\begin{cases} \frac{\partial}{\partial s}q(s,x) = D_I\Delta q(s,x) - \mu_I q(s,x), & 0 < s \le \alpha_t, \\ \frac{\partial}{\partial s}q(s,x) = -d_I q(s,x), & \alpha_t < s \le \alpha_t + \tau_d, \\ \frac{\partial}{\partial s}q(s,x) = D_I\Delta q(s,x) - \mu_I q(s,x), & \alpha_t + \tau_d < s \le \tau + \tau_d, \\ q(0,x) = b(M(t-\tau-\tau_d,x)), \end{cases}$$

where $\alpha_t = n+1-t$, dependent of t. Similar to (5.3), the dynamic process involves diffusion and death. However, during the bad season $(\alpha_t, \alpha_t+\tau_d]$, individuals undergo diapause and do not diffuse. Moreover, they are subject to a different death rate d_I. Solving this Cauchy problem leads to

$$p(t,x,\tau+\tau_d) = q(\tau+\tau_d,x)$$
$$= e^{-\mu_I\tau - d_I\tau_d}\int_\Omega \Gamma(D_I\tau,x,y)b(M(t-\tau-\tau_d,y))dy.$$

Hence, during this period, we have the system

$$\begin{cases} \frac{\partial I(t,x)}{\partial t} = \underbrace{D_I\Delta I(t,x)}_{\text{diffusion}} + \underbrace{b(M(t,x))}_{\text{birth}} - \underbrace{B_2(t,x;M)}_{\text{maturation}} - \underbrace{\mu_I I(t,x)}_{\text{death}}, \\ \frac{\partial M(t,x)}{\partial t} = \underbrace{D_M\Delta M(t,x)}_{\text{diffusion}} + \underbrace{B_2(t,x;M)}_{\text{maturation}} - \underbrace{\mu_M M(t,x)}_{\text{death}}, \end{cases}$$

with the maturation rate

$$B_2(t,x;M) = e^{-\mu_I\tau - d_I\tau_d}\int_\Omega \Gamma(D_I\tau,x,y)b(M(t-\tau-\tau_d,y))dy.$$

Appendix B. Proofs of Lemmas 3.2 and 3.5.

Proof of Lemma 3.2. We first consider the following three systems:

(5.5) $$\begin{cases} \frac{\partial M^1(t,x)}{\partial t} = D_M\Delta M^1(t,x) + e^{-\mu_I\tau}\int_\Omega \Gamma(D_I\tau,x,y)b(M^1(t-\tau,y))dy \\ \qquad\qquad - \mu_M M^1(t,x), \quad t > t_*, \ x \in \Omega, \\ \frac{\partial M^1(t,x)}{\partial \nu} = 0, \quad t > t_*, \ x \in \partial\Omega, \\ M^1_{t_*} = \varphi \in \mathbb{Y}^+, \end{cases}$$

(5.6)
$$\begin{cases} \dfrac{\partial M^2(t,x)}{\partial t} = -d_M M^2(t,x), \quad t > t_*, \ x \in \Omega, \\ M^2(t_*, \cdot) = \varphi \in \mathbb{X}^+, \end{cases}$$

and
(5.7)
$$\begin{cases} \dfrac{\partial M^3(t,x)}{\partial t} = D_M \Delta M^3(t,x) + e^{-\mu_I \tau - d_I \tau_d} \displaystyle\int_\Omega \Gamma(D_I \tau, x, y) b(M^3(t - \tau - \tau_d, y)) dy \\ \qquad\qquad - \mu_M M^3(t,x), \quad t > t_*, \ x \in \Omega, \\ \dfrac{\partial M^3(t,x)}{\partial \nu} = 0, \quad t > t_*, \ x \in \partial\Omega, \\ M^3_{t_*} = \varphi \in C([-\tau - \tau_d, 0], \mathbb{X}^+). \end{cases}$$

It then follows from [35, Corollary 5] that (5.5) admits a unique nonnegative continuous solution $M^1(t, t_*, x; \varphi)$ on $[t_*, t_\varphi)$ and $0 \le M^1(t, t_*, x; \varphi) \le L$ for $(t, x) \in [t_*, t_\varphi) \times \Omega$. Note that assumption (H2) implies that $b(L)e^{-\mu_I \tau} = \mu_M L$. Then it is easy to see that for any $k \ge 1$, kL is an upper solution of (5.5). This implies that $t_\varphi = \infty$. Moreover, the comparison principle holds for the lower and upper solutions of (5.5). The solution $M^3(t, t_*, x; \varphi)$ of (5.7) has the same property with the solution of (5.5). From (5.6), we deduce that $M^2(t, t_*, x; \varphi) = e^{-d_M(t-t_*)}\varphi(x)$ and $0 \le M^2(t, t_*, x; \varphi) \le L$ for $t \ge t_*$ and $x \in \Omega$.

The solution $M(t, x; \phi)$ for $t \ge 0$ of (3.1) can be determined uniquely by induction. For simplicity, we let $s_n = n$, $t_n = n + 1 - \tau - \tau_d$ and $z_n = n + 1 - \tau$ for $n \in \mathbb{N} = \{0, 1, 2, \dots\}$. Hence,

$$(0, \infty) = \cup_{n=0}^\infty (s_n, t_n] \cup (t_n, z_n] \cup (z_n, s_{n+1}],$$

and $M(t, x; \phi)$ can be written as

$$M(t, x; \phi) = \begin{cases} M^1(t, s_0, x; \phi), & t \in (s_0, t_0], \\ M^2(t, t_0, x; M^1(t_0, \cdot; \phi)), & t \in (t_0, z_0], \\ M^3(t, z_0, x; M^2_{z_0}), & t \in (z_0, s_1], \\ \cdots, \\ M^1(t, s_n, x; M^1_{s_n}), & t \in (s_n, t_n], \\ M^2(t, t_n, x; M^1(t_n, \cdot; \phi)), & t \in (t_n, z_n], \\ M^3(t, z_n, x; M^3_{z_n}), & t \in (z_n, s_{n+1}], \end{cases}$$

where $M^1_{s_n}$ and $M^3_{z_n}, n \ge 1$ are defined by

$$M^1_{s_n}(\theta, x) = M(s_n + \theta, x; \phi), \quad (\theta, x) \in [-\tau, 0] \times \Omega,$$
$$M^3_{z_n}(\eta, x) = M(z_n + \eta, x; \phi), \quad (\eta, x) \in [-\tau - \tau_d, 0] \times \Omega.$$

This implies that the solution $M(t, \cdot; \phi)$ of (3.1) exists globally on $[0, \infty)$. Moreover, the mathematical induction can establish the comparison principle for the lower and upper solutions of (3.1). □

Proof of Lemma 3.5. We first consider the spatially homogeneous system associated with (3.6):

(5.8)
$$\begin{cases} \frac{dI(t)}{dt} = b(M^*(t)) - b(M^*(t-\tau))e^{-\mu_I \tau} - \mu_I I(t), & t \in T_1^n, \\ \frac{dI(t)}{dt} = -d_I I(t), & t \in T_2^n, \\ \frac{dI(t)}{dt} = b(M^*(t)) - b(M^*(t-\tau-\tau_d))e^{-\mu_I \tau - d_I \tau_d} - \mu_I I(t), & t \in T_3^n. \end{cases}$$

The solution of (5.8) on the interval $(n, n+1]$ can be explicitly written as

$$I(t) = \int_{t-\tau}^{t} b(M^*(s))e^{-\mu_I(t-s)}ds$$
$$+ \left[I(n) - \int_{n-\tau}^{n} b(M^*(s))e^{-\mu_I(n-s)}ds\right] e^{-\mu_I(t-n)}, \quad t \in T_1^n,$$
$$I(t) = I(n+1-\tau-\tau_d)e^{-d_I(t-(n+1-\tau-\tau_d))}, \quad t \in T_2^n,$$
$$I(t) = \int_{n+1-\tau}^{t} b(M^*(s))e^{-\mu_I(t-s)}ds$$
$$+ \int_{t-\tau-\tau_d}^{n+1-\tau-\tau_d} b(M^*(s))e^{-\mu_I(t-\tau_d-s)-d_I\tau_d}ds$$
$$+ \left[I(n+1-\tau) - \int_{n+1-2\tau-\tau_d}^{n+1-\tau-\tau_d} b(M^*(s))e^{-\mu_I(n+1-\tau-\tau_d-s)-d_I\tau_d}ds\right]$$
$$\times e^{-\mu_I(t-(n+1-\tau))}, \quad t \in T_3^n.$$

By the above integral form of $I(t)$ and the periodicity of $M^*(t)$, a tedious but straightforward computation yields

$$I(n+1) = \int_{-\tau}^{0} b(M^*(s))e^{\mu_I s}ds + \left(I(n) - \int_{-\tau}^{0} b(M^*(s))e^{\mu_I s}ds\right) e^{-d_I\tau_d-\mu_I(1-\tau_d)}.$$

In order to find the periodic solution, we let $I(n+1) = I(n)$ and then obtain

$$I(n) = \int_{-\tau}^{0} b(M^*(s))e^{\mu_I s}ds > 0, \quad n \in \mathbb{N}.$$

Let $I^*(0) = \int_{-\tau}^{0} b(M^*(s))e^{\mu_I s}ds$. Then $I^*(t) := I^*(t, I^*(0))$ is a positive 1-periodic solution of (5.8). Since (5.8) is a linear system, one deduces that $\lim_{t\to\infty}(I(t) - I^*(t)) = 0$. Moreover, by [52, Lemma 2.2.1], $I^*(t)$ is globally stable in $\mathbb{R}_+$.

Note that solutions of (5.8) are also solutions of (3.6) subject to the Neumann boundary condition. Thus, by applying the above result and the standard comparison principle, it follows that $I^*(t)$ is globally asymptotically stable for (3.6) in $\mathbb{X}^+$. $\quad\square$

Appendix C. Proofs of Lemmas 4.1 and 4.2.

Proof of Lemma 4.1. For any $\phi \in \mathcal{C}_{\hat{L}}$ with $\phi \gg 0$, one easily finds that $M(t, x; \phi) > 0$ for $t \geq 0$ and $x \in \mathbb{R}$. Fix $k \in (0, 1)$. Let $w(t, x) = M(t, x; k\phi) - kM(t, x; \phi)$. Then $w(\theta, x) = 0$ for $(\theta, x) \in [-\tau, 0] \times \mathbb{R}$, and for $t \in (0, 1 - \tau - \tau_d]$, $w(t, x)$ satisfies

$$\frac{\partial w(t, x)}{\partial t} = D_M \Delta w(t, x) - \mu_M w(t, x) + F(t, M(t, x, k\phi)) - F(t, kM(t, x, \phi))$$
$$+ F(t, kM(t, x, \phi)) - kF(t, M(t, x, \phi))$$
$$= D_M \Delta w(t, x) - (\mu_M - H(t, x))w(t, x) + h(t, x),$$

where

$$F(t, M(t, x, \varphi)) = e^{-\mu_I\tau} \int_{\mathbb{R}} \Gamma(D_I\tau, x - y)b(M(t-\tau, y, \varphi))dy,$$

$$H(t, x) = \int_0^1 \partial_2 F(t, sM(t, x, k\phi)) + (1-s)kM(t, x, \phi))ds, \quad 0 \leq s \leq 1,$$

$$h(t, x) = F(t, kM(t, x, \phi)) - kF(t, M(t, x, \phi)).$$

Let $U(t,s)$, $t \geq s \geq 0$, be the evolution operator of the nonautonomous linear parabolic equation

$$\frac{\partial w(t,x)}{\partial t} = D_M \Delta w(t,x) - (\mu_M - H(t,x))w(t,x), \quad t > 0, \ x \in \mathbb{R}.$$

By [42, Theorem 7.4.1], one easily sees that $U(t,s)$, $t > s \geq 0$, is strongly positive, i.e., for any $\varphi > 0$, $U(t,s)\varphi \gg 0$. By the formula of variation of constants, we have

$$w(t,x) = \int_0^t U(t,s)h(s,\cdot)(x)ds, \quad t \in (0, 1 - \tau - \tau_d], \ x \in \mathbb{R}.$$

Since $M(t, \cdot; \phi) > 0$, $t \geq 0$, when $\phi \gg 0$ and $b(u)$ is strictly subhomogeneous in u, we have $h(t, \cdot) > 0$ and hence $w(t, \cdot) > 0$ for $t \in (0, 1 - \tau - \tau_d]$.

For $t \in (1 - \tau - \tau_d, 1 - \tau]$, $w(t,x)$ satisfies $\frac{\partial w(t,x)}{\partial t} = -\mu_M w(t,x)$. One easily sees that $w(t, \cdot) > 0$ for $t \in (1 - \tau - \tau_d, 1 - \tau]$. Similar to the analysis of $w(t, \cdot)$ on $(0, 1 - \tau - \tau_d]$, we can obtain that $w(t, \cdot) > 0$ for $t \in (1 - \tau, 1]$. Repeating this procedure on $(n, n+1]$ for $n \geq 1$, we get $w(t,x) > 0$ for all $t > 0$ and $x \in \mathbb{R}$. Therefore, $Q_t(k\phi) > kQ_t(\phi)$ for each $t > 0$. □

Proof of Lemma 4.2. Let $Q_t^{(i)} : \mathcal{C} \to \mathcal{C}$, $i = 1, 2, 3$, respectively, be the solution maps of the following equations for all $t > 0$, $x \in \mathbb{R}$:

$$\frac{\partial M^1(t,x)}{\partial t} = D_M \Delta M^1(t,x) + e^{-\mu_I \tau} \int_{\mathbb{R}} \Gamma(D_I \tau, x - y)b(M^1(t - \tau, y))dy - \mu_M M^1(t,x),$$

$$\frac{\partial M^2(t,x)}{\partial t} = -d_M M^2(t,x),$$

$$\frac{\partial M^3(t,x)}{\partial t} = D_M \Delta M^3(t,x) + e^{-\mu_I \tau - d_I \tau_d} \int_{\mathbb{R}} \Gamma(D_I \tau, x - y)b(M^3(t - \tau - \tau_d, y))dy$$
$$\qquad - \mu_M M^3(t,x).$$

Recalling the definition of s_n, t_n, and z_n in the proof of Lemma 3.2, one infers that

$$Q_t[\phi] = \begin{cases} Q_t^{(1)}[\phi], & t \in (s_0, t_0], \\ Q_{t-t_0}^{(2)} \circ Q_{1-\tau-\tau_d}^{(1)}[\phi], & t \in (t_0, z_0], \\ Q_{t-z_0}^{(3)} \circ Q_{\tau_d}^{(2)} \circ Q_{1-\tau-\tau_d}^{(1)}[\phi], & t \in (z_0, s_1], \\ \cdots, & \\ Q_{t-s_n}^{(1)} \circ Q_n[\phi], & t \in (s_n, t_n], \\ Q_{t-t_n}^{(2)} \circ Q_{1-\tau-\tau_d}^{(1)} \circ Q_n[\phi], & t \in (t_n, z_n], \\ Q_{t-z_n}^{(3)} \circ Q_{\tau_d}^{(2)} \circ Q_{1-\tau-\tau_d}^{(1)} \circ Q_n[\phi], & t \in (z_n, s_{n+1}], \end{cases}$$

for any $\phi \in \mathcal{C}_{\hat{L}}$, where $Q_n = Q_1 \circ \cdots \circ Q_1$ and $Q_1 = Q_\tau^{(3)} \circ Q_{\tau_d}^{(2)} \circ Q_{1-\tau-\tau_d}^{(1)}$. It is easy to verify that for each $t > 0$, Q_t satisfies (A1) and (A4) with $\beta = \hat{L}$.

Now we show that (A2) and (A3) are valid for Q_t. By similar arguments in [47, Lemma 3.2], we can prove that $Q_t^{(1)}(Q_t^{(3)})$ is continuous in $\phi \in \mathcal{C}_{\hat{L}}(\psi \in \mathcal{C}_{\hat{L}})$ with respect to compact open topology uniformly for $t \in (0, \infty)$. Clearly, $Q_t^{(2)}$ is continuous in $\varphi \in \mathcal{C}_{\hat{L}}$ with respect to compact open topology uniformly for $t \in (0, \infty)$. Therefore, Q_t is continuous in $\phi \in \mathcal{C}_{\hat{L}}$ with respect to compact open topology. Moreover, similar to Lemma 3.2, we can show that $Q_t[\mathcal{C}_{\hat{L}}]$ is a uniformly bounded subset of $\mathcal{C}$ for each

$t > 0$. To verify (A3), let us define a family of linear operators $\{\bar{L}(t)\}_{t \geq 0}$ on $\mathcal{Z}$ by

$$\bar{L}(t)[\psi](\theta) := \left\{ \begin{array}{ll} \psi(t+\theta) - \psi(0) & \text{for } t+\theta < 0, \\ 0 & \text{for } t+\theta \geq 0. \end{array} \right.$$

From [30, Remark 4.1], we know that for any given $\gamma > 0$, there is an equivalent norm $\|\cdot\|_{\mathcal{Z}}^*$ in $\mathcal{Z}$ such that $\|\bar{L}(t)\|_{\mathcal{Z}}^* \leq e^{-\gamma t} \ \forall t \geq 0$. Moreover, we define

$$L^{(i)}(t)[\phi^i](\theta, x) := \left\{ \begin{array}{ll} \phi^i(t+\theta, x) - \phi^i(0, x) & \text{for } t+\theta < 0, \\ 0 & \text{for } t+\theta \geq 0 \end{array} \right.$$

and

$$S^{(i)}(t)[\phi^i](\theta, x) := \left\{ \begin{array}{ll} \phi^i(0, x) & \text{for } t+\theta < 0, \\ M^i(t+\theta, x; \phi^i) & \text{for } t+\theta \geq 0, \end{array} \right.$$

where $i = 1, 2, 3$ and in particular $M^2(t+\theta, x; \phi^2) = e^{-d_M(t+\theta)}\phi^2(0, x)$ when $t+\theta \geq 0$. Let $t > 0$ be given. We can prove that $Q_t[\mathcal{C}_{\hat{L}}](0, x)$ is precompact in $C(\mathbb{R}, \mathbb{R})$ and that $S^{(i)}(t)[\mathcal{U}]$ is precompact in $\mathcal{C}_{\hat{L}}$ with respect to the compact open topology for any $\mathcal{U} \in \mathcal{C}_{\hat{L}}$ with $\mathcal{U}(0, \cdot)$ being precompact in $C(\mathbb{R}, \mathbb{R})$. Thus, for any interval $I = [a, b]$ of length r, we have

$$\alpha((Q_t^{(i)}[\mathcal{U}])_I) \leq \alpha((L_t^{(i)}[\mathcal{U}])_I) + \alpha((S_t^{(i)}[\mathcal{U}])_I) \leq e^{-\gamma t}\alpha(\mathcal{U}_I)$$

and hence

$$\alpha((Q_t[\mathcal{U}])_I) \leq e^{-\gamma t}\alpha(\mathcal{U}_I),$$

where α is the Kuratowski measure of noncompactness on the space $C(I, (\mathcal{Z}, \|\cdot\|_{\mathcal{Z}}^*))$. Thus, Q_t satisfies (A3) with $k = e^{-\gamma t}$.

Finally, it is easily seen that $Q_1 : \mathcal{C}_\beta \to \mathcal{C}_\beta$ satisfies (A1)–(A4) with $\beta = M_0^*$. Furthermore, by Lemma 3.3(ii), togerher with the uniqueness of solution, we have that (A5) holds for Q_1. □

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