Spatial dynamics of a dengue transmission model in time-space periodic environment

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Abstract

This study is devoted to the investigation of dengue spread via a time-space periodic reaction-advection-diffusion model. We establish the existence of the spreading speeds and its coincidence with the minimal speed of almost pulsating waves.

1 Introduction

Dengue is a vector-borne infectious disease which is transmitted to humans mainly by the bites of Aedes aegypti mosquitoes. Due to the rapid transmission, it has become a serious public health problem in tropical/subtropical regions of the world. In order to investigate the spreading dynamics of Aedes mosquitoes, the authors in [18] proposed a novel model system of differential equations, in which populations are divided into two sub-populations, the winged/mature female mosquitoes and the aquatic population (e.g., eggs, larvae and pupae). To reflect the fact that winged female A. aegypti can search for human blood freely and wind currents may also cause an advection movement of mosquitoes, a diffusion process and an advection term are added to describe the random search movements of mature

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female mosquitoes and the result of wind transportation, respectively. Neither advective transport nor diffusive process is added to the aquatic population since they are assumed to stay in water containers. The system proposed in [18] is an advection-dispersion-reaction equation coupled with an ordinary equation in which the involved coefficients are all assumed to be positive constants.

There has been a dramatic increase in the number of countries with reported dengue outbreaks during the past 50 years [3, 19, 24]. Therefore, dengue fever can be regarded as one of the most rapidly spreading diseases in the world, and it is natural to incorporate the spatial variations into the model system because of its remarkably growing spatial spread. On the other hand, seasonal or daily fluctuations in temperature also have a significant influence on the maturation rates of the aquatic population and biting rate of mature female mosquitoes (see, e, g., [4]). To explore these aforementioned impacts, we extend the model in [18] to the following system with both spatial heterogeneity and temporal variation:

$$\begin{cases} \frac{\partial}{\partial t}u_1(x,t) = D(x,t)\frac{\partial^2 u_1(x,t)}{\partial x^2} - \nu(x,t)\frac{\partial u_1(x,t)}{\partial x} \\ \qquad\qquad\qquad +\gamma(x,t)u_2(x,t)\left(1-\frac{u_1(x,t)}{k_1(x,t)}\right) - d_1(x,t)u_1(x,t),\ x\in\mathbb{R},\ t>0, \\ \frac{\partial}{\partial t}u_2(x,t) = \alpha(x,t)\left(1-\frac{u_2(x,t)}{k_2(x,t)}\right)u_1(x,t) - \left(d_2(x,t)+\gamma(x,t)\right)u_2(x,t),\ x\in\mathbb{R},\ t>0. \end{cases} \tag{1.1}$$

Here, $u_1(x,t)$ represents the spatial density of the winged A. aegypti (mature female mosquitoes) at position x and time t; $u_2(x,t)$ represents the aquatic form of mosquitoes (eggs, larvae and pupae) at location x and time t; $\gamma(t,x)$ is the specific rate of maturation of the aquatic form into winged female mosquitoes, saturated by a carrying capacity $k_1(t,x)$. The term $\alpha(t,x)(1-\frac{u_2(x,t)}{k_2(t,x)})u_1(x,t)$ describes the rate of production of the aquatic form, which is produced only by female mosquitoes. That is, we assume that the rate of production of the aquatic form is proportional to the density of female mosquitoes and it is also saturated by a carrying capacity $k_2(t,x)$. The random flying movement of female mosquitoes is represented by a diffusion process with coefficient $D(t,x)$, and $\nu(t,x)$ represents the wind advection. $d_1(t,x)$ and $d_2(t,x)$ represent the mortality rates of the mosquitoes and the aquatic forms, respectively. Periodicity is one of the simplest environmental heterogeneities and it is a good candidate to approximate the complex heterogeneity. For this reason, we assume that there is an $\omega>0$ and $L>0$ such that

$$g(x+L,t+\omega) = g(x,t) > 0, \text{ for all } x\in\mathbb{R},\ t>0,\ g\equiv D,\ \nu,\ \gamma,\ k_1,\ d_1,\ \alpha,\ k_2,\ d_2.$$

When coefficients in (1.1) are all positive constants, the authors in [18] studied the invasion/spreading speeds and traveling waves, via delicate numerical analysis. In this paper, the revised model (1.1) has time-space heterogeneity, which gives the difficulty for the mathematical analysis due to the lack of compactness caused by the immobility of the aquatic population. Further, instead of traveling wave, almost pulsating wave that was recently introduced in [5] for time-space periodic environment will be the objective.

Classical reaction - diffusion equations are not suitable to describe spread and persistence of population with dynamics of seasonal heterogeneous growth and dispersal. Impulsive reaction - diffusion equations were used to study persistence and spread of species with a reproductive stage and a dispersal stage by [8]. We use spatial and temporal periodicity to approximate the complex environmental heterogeneity in this paper.

The organization of the rest of this paper is as follows. The well-posedness of our proposed system is studied in Section 2. In Section 3, we first adopt the ideas in [11, Lemma 3.3] to study a one-parameter parabolic eigenvalue problem with time-space periodic boundary conditions (Lemma 3.1), which will be used to determine the local stability of the zero solution of associated linear systems and the characterization of spreading speeds. Then the global attractivity of the zero solution $\mathbf{0}$ or a positive time-space periodic solution $\mathbf{u}^*(x,t)$ for the time-space periodic initial value problem can be established in terms of the reproduction number, $\mathcal{R}_0$ (Theorem 3.1). In Section 4, we first establish the continuity of the solution maps associated with system (1.1) in a suitable space (Lemma 4.1). Then we can overcome the lack of compactness of system (1.1), namely, we show that the associated solution map is κ-contraction in the sense of Lemma 4.2. In Section 5, we first assume the reproduction number $\mathcal{R}_0 > 1$, and utilize the developed theory in [9, Theorem 5.1] to establish the existence and characterization of rightward and leftward spreading speeds (Lemma 5.2, Lemma 5.3, and Theorem 5.1). Then the coincidence of spreading speeds with the minimal speeds of time-space periodic traveling waves connecting $\mathbf{u}^*(t,x)$ and $\mathbf{0}$ can be rigorously established by the theory developed in [5] (Theorem 5.2). Numerical simulations are collected in Section 6.

2 Well-posedness

Let $\mathcal{C}$ be the space of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$. It is easy to see $\mathcal{C}^+ := \{\mathbf{u} \in \mathcal{C} : \mathbf{u}(x) \geq \mathbf{0},\ \forall x \in \mathbb{R}\}$ is a positive cone of $\mathcal{C}$. For $\mathbf{u} := (u_1, u_2)$, $\mathbf{v} := (v_1, v_2) \in \mathcal{C}$, we write $\mathbf{u} \geq \mathbf{v}$ ($\mathbf{u} \gg \mathbf{v}$) provided that $u_i(x) \geq v_i(x)$ ($u_i(x) > v_i(x)$), $\forall\ i = 1, 2,\ x \in \mathbb{R}$, and $\mathbf{u} > \mathbf{v}$ if $\mathbf{u} \geq \mathbf{v}$ and $\mathbf{u} \neq \mathbf{v}$. We equip $\mathcal{C}$ with the compact open topology, i.e., $\mathbf{u}^m \to \mathbf{u}$ in $\mathcal{C}$ means that the sequence of $\mathbf{u}^m(x)$ converges to $\mathbf{u}(x)$ as $m \to \infty$ uniformly for x in any compact set of $\mathbb{R}$. Define

$$\|\mathbf{u}\| = \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} \mid \mathbf{u}(x) \mid}{2^k},\ \forall\ \mathbf{u} \in \mathcal{C},$$

where $| \cdot |$ denotes the usual norm in $\mathbb{R}^2$. Then $(\mathcal{C}, \| \cdot \|)$ is a normed space. Let $d(\cdot, \cdot)$ be the distance induced by the norm $\| \cdot \|$. It follows that the topology in the metric space $(\mathcal{C}, d)$ is the same as the compact open topology in $\mathcal{C}$. For $\mathbf{r} \in \mathcal{C}^+$, we define $\mathcal{C}_{\mathbf{r}} := \{\mathbf{u} \in \mathcal{C} : \mathbf{0} \leq \mathbf{u} \leq \mathbf{r}\}$.

Let $\Gamma_1(t, s, x), t \geq s, x \in \mathbb{R}$ be the fundamental function of

$$\rho_t = D(t,x)\rho_{xx} - \nu(t,x)\rho - d_1(t,x)\rho, \quad x \in \mathbb{R}, t \geq s. \tag{2.1}$$

We refer to [16] for the existence and properties of $\Gamma_1(t, s, x)$. Define

$$\Gamma_2(t, s, x) := e^{-\int_s^t [d_2(\eta,x)+\gamma(\eta,x)]d\eta}. \tag{2.2}$$

Let $\phi = (\phi_1, \phi_2) \in \mathcal{C}$. For $t > 0$, define $P(t) : \mathcal{C} \to \mathcal{C}$ by

$$P(t)[\phi] = \begin{pmatrix} \Gamma_1(t, 0, \cdot)* & 0 \\ 0 & \Gamma_2(t, 0, x) \end{pmatrix} \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix}, \tag{2.3}$$

where $*$ stands for the convolution. Define $H : \mathbb{R}_+ \times \mathbb{R} \times \mathbb{R}^2 \to \mathbb{R}^2$ by

$$H(t, x, \mathbf{u}) = \begin{pmatrix} \gamma(t,x)u_2 \left(1 - \frac{u_1}{k_1(t,x)}\right) \\ \alpha(t,x)u_1 \left(1 - \frac{u_2}{k_2(t,x)}\right) \end{pmatrix}, \tag{2.4}$$

where $\mathbf{u} := (u_1, u_2) \in \mathbb{R}^2$. Then (1.1) with the initial condition $\mathbf{u}(\cdot, \mathbf{0}) = \phi$ can be written as the following integral form

$$\mathbf{u}(x,t) = P(t)[\phi](x) + \int_0^t P(t-s)[H(s, \cdot, \mathbf{u}(\cdot, s))](x)ds, \quad t > 0, x \in \mathbb{R}. \tag{2.5}$$

In order to obtain the existence and comparison principle for solutions of system (1.1), we need the following technical conditions on $(k_1(x,t), k_2(x,t))$, which is assumed in the rest of the paper:

(A) The functions $k_1(x,t)$ and $k_2(x,t)$ satisfy the following inequalities:

$$\begin{cases} \frac{\partial}{\partial t}k_1(x,t) \geq D(x,t)\frac{\partial^2 k_1(x,t)}{\partial x^2} - \nu(x,t)\frac{\partial k_1(x,t)}{\partial x} - d_1(x,t)k_1(x,t),\ x\in\mathbb{R},\ t>0, \\ \frac{\partial}{\partial t}k_2(x,t) \geq -\left(d_2(x,t)+\gamma(x,t)\right)k_2(x,t),\ x\in\mathbb{R},\ t>0. \end{cases}$$

Then we have the following result:

Lemma 2.1. *Let* $\mathbf{k}(x,t) = (k_1(x,t), k_2(x,t))$*. For any initial value* $\phi \in \mathcal{C}_{\mathbf{k}(\cdot,0)}$*, (2.5) has a unique solution* $\mathbf{u}(x,t;\phi)$*, which is well-defined for* $t>0$*. Moreover,* $\mathbf{u}(x,t;\phi) \geq \mathbf{u}(x,t;\psi)$ *for all* $t\geq 0$ *and* $x\in\mathbb{R}$ *provided that* $\phi\geq\psi$ *in* $\mathcal{C}_{\mathbf{k}(\cdot,0)}$*.*

Proof. We employ the abstract framework in [13]. Using the notations there, we set $\mathscr{C} = X = \mathcal{C}, D(t) = \mathcal{C}_{\mathbf{k}(\cdot,t)}, B = H$. Choose $S(t,s), T(t,s), t\geq s\geq a$ to be $P(t), t\geq s = a = 0$. Then one may see that all conditions in [13, Corollary 5] are satisfied. □

3 The periodic initial value problem

Let $\mathbb{P} = PC(\mathbb{R},\mathbb{R}^2)$ be the set of all continuous and L-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$ with the maximum norm $\|\cdot\|_{\mathbb{P}}$, and $\mathbb{P}_+ = \{\psi\in\mathbb{P}:\ \psi(x)\geq 0, \forall x\in\mathbb{R}\}$ be a positive cone of $\mathbb{P}$. Then $(\mathbb{P},\mathbb{P}_+)$ is a strongly ordered Banach lattice.

3.1 A one-parameter parabolic eigenvalue problem with periodic boundary conditions

For our convenience in the subsequent discussions, we consider the following one-parameter linear system

$$\begin{cases} \frac{\partial u_1(x,t)}{\partial t} = D(x,t)\frac{\partial^2 u_1}{\partial x^2} - [2\mu D(x,t)+\nu(x,t)]\frac{\partial u_1}{\partial x} + [\mu^2 D(x,t)+\mu\nu(x,t)]u_1(x,t) \\ \qquad\qquad +\gamma(x,t)u_2(x,t) - d_1(x,t)u_1(x,t),\ x\in\mathbb{R},\ t>0, \\ \frac{\partial u_2(x,t)}{\partial t} = \alpha(x,t)u_1(x,t) - \left(d_2(x,t)+\gamma(x,t)\right)u_2(x,t),\ x\in\mathbb{R},\ t>0, \\ (u_1(x,0), u_2(x,0)) \in \mathbb{P}_+, \quad x\in\mathbb{R}, \end{cases} \tag{3.1}$$

where $\mu \geq 0$. The following one-parameter periodic eigenvalue problem is associated with (3.1):

$$\begin{cases} \frac{\partial u_1(x,t)}{\partial t} = D(x,t)\frac{\partial^2 u_1}{\partial x^2} - [2\mu D(x,t) + \nu(x,t)]\frac{\partial u_1}{\partial x} + [\mu^2 D(x,t) + \mu\nu(x,t)]u_1(x,t) \\ \qquad\qquad +\gamma(x,t)u_2(x,t) - d_1(x,t)u_1(x,t) + \lambda u_1(x,t),\ x \in \mathbb{R},\ t > 0, \\ \frac{\partial u_2(x,t)}{\partial t} = \alpha(x,t)u_1(x,t) - (d_2(x,t) + \gamma(x,t))\, u_2(x,t) + \lambda u_2(x,t),\ x \in \mathbb{R},\ t > 0, \\ u_i(x+L,t) = u_i(x,t),\ u_i(x,t+\omega) = u_i(x,t),\ (x,t) \in \mathbb{R}\times\mathbb{R},\ i = 1,2. \end{cases} \tag{3.2}$$

Let $\overline{d}_2(x) = \frac{1}{\omega}\int_0^\omega d_2(x,t)dt$, $\overline{\gamma}(x) = \frac{1}{\omega}\int_0^\omega \gamma(x,t)dt$ and $M = \max_{x\in[0,L]}\left\{\overline{d}_2(x) + \overline{\gamma}(x)\right\}$. In order to establish the existence of the principal eigenvalue of (3.2), we need to impose the following technical condition:

(H) There are $0 < a < b < L$ such that

$$\overline{d}_2(x) + \overline{\gamma}(x) = M,\ \forall\ x \in [a,b].$$

Remark 3.1. *The assumption (H) is motivated by the hypothesis (H4) in [11] and can be used to overcome the loss of compactness in system* (3.1)*. We note that if $d_2(x,t) \equiv d_2(t)$ and $\gamma(x,t) \equiv \gamma(t)$ depend on the temporal factor alone, the condition (H) is automatically valid. At this moment it is challenging to remove or weaken this condition (H), but we hope to be able to improve it in the future study.*

We introduce the Banach spaces $Y_1 = C(\mathbb{R},\mathbb{R})$, and $Y = Y_1 \times Y_1$ with the positive cones $Y_1^+ = C(\mathbb{R},\mathbb{R}_+)$, and $Y^+ = Y_1^+ \times Y_1^+$, respectively. Let

$$\mathbb{Y} = \left\{u \in C(\mathbb{R}\times\mathbb{R},\mathbb{R}^2) : u(x+L,t) = u(x,t),\ u(x,t+\omega) = u(x,t),\ \forall\ (x,t) \in \mathbb{R}\times\mathbb{R}\right\}. \tag{3.3}$$

Then

$$\mathbb{Y}^+ = \left\{u \in C(\mathbb{R}\times\mathbb{R},\mathbb{R}_+^2) : u(x+L,t) = u(x,t),\ u(x,t+\omega) = u(x,t),\ \forall\ (x,t) \in \mathbb{R}\times\mathbb{R}\right\} \tag{3.4}$$

is the positive cone of $\mathbb{Y}$. Further, it is easy to see that $\mathrm{Int}(Y_1^+)$, $\mathrm{Int}(Y^+)$, and $\mathrm{Int}(\mathbb{Y}^+)$ are nonempty.

Let $\{U_\mu(t,s) : t \geq s\}$ be the evolution family on Y of system (3.1).

Lemma 3.1. *Assume that $\mu \geq 0$ and (H) holds. Then $r(U_\mu(\omega,0))$ is the principal eigenvalue of $U_\mu(\omega,0)$, and $\lambda_\mu^* = -\frac{\ln(r(U_\mu(\omega,0)))}{\omega}$ is the eigenvalue of problem* (3.2) *with an eigenvector $u^* \in$Int$(\mathbb{Y}^+)$.*

Proof. Our arguments are similar to those in [11, Lemma 3.3]. It is not hard to see that $U_\mu(t,s)$ is positive (resp. strongly positive) on Y for $t \geq s$ (resp. $t > s$) (see e.g., [11, Lemma 2.10]). For the sake of simplicity, we set

$$\begin{cases} a_{11}(x,t) = \mu^2 D(x,t) + \mu\nu(x,t) - d_1(x,t),\ a_{12}(x,t) = \gamma(x,t), \\ a_{21}(x,t) = \alpha(x,t),\ a_{22}(x,t) = -\left(d_2(x,t) + \gamma(x,t)\right), \end{cases} \tag{3.5}$$

for any $(x,t) \in \mathbb{R} \times \mathbb{R}$. Let $\{H_\lambda(t,s) : t \geq s\}$ be the evolution family on Y_1 of the following system

$$\frac{\partial}{\partial t} v(x,t) = a_{22}(x,t)v + \lambda v, \tag{3.6}$$

thus, $H_\lambda(t,s) = e^{\int_s^t a_{22}(x,\tau)d\tau + \lambda(t-s)}$. Then $\eta := -\hat{\omega}(H_0) = -\max_{x\in[0,L]}\{\overline{a}_{22}(x)\}$, where $\hat{\omega}(H_0)$ represents the exponential growth bound of evolution family $\{H_0(t,s) : t \geq s\}$, and $\overline{a}_{22}(x) := \frac{1}{\omega}\int_0^\omega a_{22}(x,t)dt$ (see e. g., [11, Lemma 2.14]).

Thus, K_λ defined in [11, (2.9)] becomes

$$\begin{aligned} K_\lambda w(x,t) = \quad & \frac{\int_0^\omega [e^{\int_s^\omega a_{22}(x,\tau)d\tau + \lambda(\omega - s)}] a_{21}(x,s) w(x,s) ds}{1 - e^{\int_0^\omega a_{22}(x,\tau)d\tau + \lambda\omega}} e^{\int_0^t a_{22}(x,\tau)d\tau + \lambda t} \\ + \quad & \int_0^t [e^{\int_s^t a_{22}(x,\tau)d\tau + \lambda(t-s)}] a_{21}(x,s) w(x,s) ds, \end{aligned} \tag{3.7}$$

for any $\lambda < \eta$, and $[M_{12}w](x,t) = a_{12}(x,t)w(x,t)$.

Let $G = C_0^1([a,b],\mathbb{R}^2)$ with the following positive cone

$$G^+ = \{\varphi \in G : \varphi(x) \geq 0,\ \forall\ x \in [a,b]\}. \tag{3.8}$$

Then

$$\mathrm{Int}(G^+) = \left\{\varphi \in G : \varphi(x) > 0,\ \forall\ x \in [a,b], \frac{\partial \varphi}{\partial x}(a) > 0,\ \frac{\partial \varphi}{\partial x}(b) < 0\right\} \tag{3.9}$$

is nonempty. Assume that $\mathbb{G}$ is the Banach space of continuous ω-periodic functions from $\mathbb{R}$ to G, which is equipped with the maximum norm, and the positive cone

$$\mathbb{G}^+ = \{u \in \mathbb{G} : u(x,t) \geq 0,\ \forall\ (x,t) \in [a,b] \times \mathbb{R}\}. \tag{3.10}$$

Then it is not hard to see that

$$\begin{aligned} \mathrm{Int}(\mathbb{G}^+) = \{u \in \mathbb{G} : u(x,t) > 0,\ \forall\ (x,t) \in [a,b] \times \mathbb{R}, \\ \frac{\partial u}{\partial x}(a,t) > 0,\ \frac{\partial u}{\partial x}(b,t) < 0,\ \forall\ t \in \mathbb{R}\} \end{aligned} \tag{3.11}$$

is nonempty. Let

$$\mathcal{G} = \left\{ u \in C_0^{2,1}([a,b] \times \mathbb{R}, \mathbb{R}^2) : u(x, t+\omega) = u(x,t),\ \forall\ (x,t) \in [a,b] \times \mathbb{R} \right\}. \quad (3.12)$$

Next, we define a parabolic operator $\mathfrak{L}$ on $\mathcal{G}$ as follows:

$$\mathfrak{L}w = \frac{\partial w}{\partial t} - D(x,t)\frac{\partial^2 w}{\partial x^2} + [2\mu D(x,t) + \nu(x,t)]\frac{\partial w}{\partial x} + [d_1(x,t) - \mu^2 D(x,t) - \mu\nu(x,t)]w. \quad (3.13)$$

Let λ_0 be the principal eigenvalue of

$$\begin{cases} \mathfrak{L}w = \lambda w,\ x \in (a,b),\ t > 0, \\ w(a,t) = w(b,t) = 0,\ t > 0, \\ w(x,t) = w(x, t+\omega),\ x \in (a,b),\ t \in \mathbb{R}, \end{cases} \quad (3.14)$$

with a positive eigenvector $w_* \in \mathrm{Int}(\mathbb{G}^+) \cap \mathcal{G}$.

Claim 1: There exists $\overline{\lambda} < \eta$ such that

$$\mathfrak{L}w_*(x,t) - M_{12}K_{\overline{\lambda}}w_*(x,t) \le 0,\ \forall\ x \in [a,b],\ t \in \mathbb{R}. \quad (3.15)$$

In the case where $\lambda_0 < \eta$. Then $\overline{a}_{22}(x) + \lambda_0 < \lambda_0 - \eta < 0$, and hence, $1 - e^{\int_0^\omega a_{22}(x,\tau)d\tau + \lambda_0\omega} > 0$. This implies that $K_{\lambda_0}w_*(x,t) \ge 0,\ \forall\ x \in [a,b],\ t \in \mathbb{R}$. Therefore, we see that (3.15) holds with $\overline{\lambda} = \lambda_0$. Next, we consider the case where $\lambda_0 \ge \eta$. Let $\hat{w}_*(x) := \int_0^\omega w_*(x,t)dt$. Then it follows from the fact $w_* \in \mathbb{G}^+ \cap \mathcal{G}$ that $\hat{w}_*(\cdot) \in G^+$. Further, one can further verify that $\hat{w}_*(\cdot) \in \mathrm{Int}(G^+)$ (see e. g., [11, Lemma 2.10]). Then

$$B := \max\{b : \hat{w}_*(\cdot) - bw_*(\cdot, t) \in G^+,\ \forall\ t \in \mathbb{R}\} > 0.$$

Note that $\int_s^t a_{22}(x,\tau)d\tau + \lambda(t-s)$ is uniformly bounded for $\lambda \in [\eta - 1, \eta]$ and $0 \le s \le t \le \omega$. Using this observation together with the fact that the second term in the R.H.S. of (3.7) is positive, it follows that there exists a constant $C > 0$ such that

$$\begin{aligned} & M_{12}K_\lambda w_*(x,t) \\ & \ge C \cdot \frac{1}{1 - e^{(\overline{a}_{22}(x)+\lambda)\omega}} \int_0^\omega w_*(x,s)ds \\ & \ge C \cdot [-\frac{1}{(\overline{a}_{22}(x)+\lambda)\omega}] \int_0^\omega w_*(x,s)ds,\ x \in [a,b],\ t \in \mathbb{R}, \end{aligned} \quad (3.16)$$

for any $\lambda \in [\eta-1,\eta)$, where we used the fact $\frac{1}{1-e^{\diamondsuit}} \geq -\frac{1}{\diamondsuit}$, $\forall\ \diamondsuit < 0$. From the assumption (H), we see that $\eta = -\bar{a}_{22}(x)$, $\forall\ x \in [a,b]$. This fact together with (3.16) implies that

$$M_{12}K_\lambda w_*(x,t) \geq \frac{C}{(\eta-\lambda)\omega}\int_0^\omega w_*(x,s)ds \geq \frac{BC}{(\eta-\lambda)\omega} w_*(x,t),\ x\in[a,b],\ t\in\mathbb{R}, \tag{3.17}$$

for any $\lambda \in [\eta-1,\eta)$. Let $\lambda_1 = \frac{BC}{(\eta-1-\lambda_0)\omega} + \eta$ and $\overline{\lambda} := \max\{\lambda_1, \eta-1\}$. Then $\lambda_1 < \eta$ since $\eta - 1 - \lambda_0 < 0$. Thus, it is easy to see that $\eta - 1 \leq \overline{\lambda} < \eta$. In view of (3.17), it follows that

$$\begin{aligned}
&\mathfrak{L}w_*(x,t) - M_{12}K_{\overline{\lambda}}w_*(x,t) \\
&\leq \lambda_0 w_*(x,t) - \frac{BC}{(\eta-\overline{\lambda})\omega}w_*(x,t) \leq \lambda_0 w_*(x,t) - \frac{BC}{(\eta-\lambda_1)\omega}w_*(x,t) \\
&= [\lambda_0 - \frac{BC}{(\eta-\lambda_1)\omega}]w_*(x,t) \\
&= (\eta-1)w_*(x,t) \leq \overline{\lambda}w_*(x,t),\ x\in[a,b],\ t\in\mathbb{R}.
\end{aligned} \tag{3.18}$$

Thus, we have proved Claim 1.

Claim 2: $r\left(e^{\overline{\lambda}\omega}U_\mu(\omega,0)\right) \geq 1.$

To this end, for any $t>0$ we define a function $w^0(\cdot,t):\mathbb{R}\to\mathbb{R}$ such that

$$w^0(x,t) = \begin{cases} w_*(x,t), & x\in[a,b], \\ 0, & x\in[0,L]\setminus[a,b], \end{cases}$$

and $w^0(x+L,t) = w^0(x,t)$, $\forall\ x\in\mathbb{R}$. Let $v^0(x,t) = K_{\overline{\lambda}}w^0(x,t)$ and $u^0(x,t) := (w^0(x,t), v^0(x,t))$, for $(x,t)\in\mathbb{R}\times\mathbb{R}$. For convenience, we set $\phi^0(\cdot) = u^0(\cdot,0)$ and $u^0(x,t,\phi^0) = (u_1^0(x,t), u_2^0(x,t))$, for $(x,t)\in\mathbb{R}\times\mathbb{R}$. Then it follows from Claim 1 and the construction of $u^0(x,t,\phi^0)$ that

$$\begin{cases}
\frac{\partial}{\partial t}u_1^0(x,t) - D(x,t)\frac{\partial^2 u_1^0}{\partial x^2} + [2\mu D(x,t)+\nu(x,t)]\frac{\partial u_1^0}{\partial x} - [\mu^2 D(x,t) + \mu\nu(x,t)]u_1^0(x,t) \\
\qquad -\gamma(x,t)u_2^0(x,t) + d_1(x,t)u_1^0(x,t) \leq \overline{\lambda}u_1^0(x,t),\ x\in\mathbb{R},\ t>0, \\
\frac{\partial}{\partial t}u_2^0(x,t) - \alpha(x,t)u_1^0(x,t) \\
\qquad + \left(d_2(x,t)+\gamma(x,t)\right)u_2^0(x,t) = \overline{\lambda}u_1^0(x,t),\ x\in\mathbb{R},\ t>0, \\
u_1^0(a,t) = u_1^0(b,t),\ t>0, \\
((u_1^0(x,0), u_2^0(x,0)) = \phi^0(x) \in \mathbb{P}_+,\ x\in\mathbb{R}.
\end{cases} \tag{3.19}$$

By the comparison principle, we have

$$e^{\overline{\lambda}t}U_\mu(t,0)\phi^0(x) \geq u^0(x,t,\phi^0) = \phi^0(x),\ \forall\, x \in \mathbb{R},\ t > 0.$$

Since $e^{\overline{\lambda}t}U_\mu(t,0)\phi^0(x) \in Y^+$, $\forall\, t > 0$, it follows that $e^{\overline{\lambda}\omega}U_\mu(\omega,0)\phi^0(x) \geq \phi^0(x),\ \ \forall\, x \in \mathbb{R}$, and hence, $r\left(e^{\overline{\lambda}\omega}U_\mu(\omega,0)\right) \geq 1$. Thus, we have proved Claim 2.

By Claim 2, [11, Theorem 2.16], and [11, Remark 2.21], the proof of this lemma is finished. $\square$

3.2 Threshold dynamics of the periodic initial value problem

Given a function $\zeta(\cdot)$, we define $[0,\zeta(\cdot)]_{\mathbb{P}} = \{\phi \in \mathbb{P}^+ : 0 \leq \phi(x) \leq \zeta(x),\ \forall\, x \in \mathbb{R}\}$. Recall that $\mathbf{k}(x,t) = (k_1(x,t), k_2(x,t))$. Then we consider the following parabolic system with periodic initial value, which is associated with system (1.1):

$$\begin{cases} \frac{\partial}{\partial t}u_1(x,t) = D(x,t)\frac{\partial^2 u_1}{\partial x^2} - \nu(x,t)\frac{\partial u_1}{\partial x} \\ \qquad\qquad\qquad +\gamma(x,t)u_2(x,t)\left(1 - \frac{u_1(x,t)}{k_1(x,t)}\right) - d_1(x,t)u_1(x,t),\ x \in \mathbb{R},\ t > 0, \\ \frac{\partial}{\partial t}u_2(x,t) = \alpha(x,t)\left(1 - \frac{u_2(x,t)}{k_2(x,t)}\right)u_1(x,t) - \left(d_2(x,t) + \gamma(x,t)\right)u_2(x,t),\ x \in \mathbb{R},\ t > 0, \\ (u_1(x,0), u_2(x,0)) \in [0,\mathbf{k}(x,0)]_{\mathbb{P}}, \quad x \in \mathbb{R}. \end{cases} \tag{3.20}$$

By same arguments to those in Lemma 2.1, we have the following results:

Lemma 3.2. *For any given initial function $\varphi(\cdot) \in [0,\mathbf{k}(\cdot,0)]_{\mathbb{P}}$, there exists a unique nonnegative solution $u(x,t) = u(x,t,\varphi(\cdot))$ of system* (3.20) *defined on $[0,\infty)$, and $u(x,t) \in [0,\mathbf{k}(x,t)]_{\mathbb{P}}$ for $t \geq 0$. Moreover, $\mathbf{u}(x,t;\phi) \geq \mathbf{u}(x,t;\psi)$ for all $t \geq 0$ and $x \in \mathbb{R}$ provided that $\phi \geq \psi$ in $[0,\mathbf{k}(\cdot,0)]_{\mathbb{P}}$.*

Linearizing system (3.20) at $(0,0)$, we have

$$\begin{cases} \frac{\partial}{\partial t}u_1(x,t) = D(x,t)\frac{\partial^2 u_1}{\partial x^2} - \nu(x,t)\frac{\partial u_1}{\partial x} \\ \qquad\qquad\qquad +\gamma(x,t)u_2(x,t) - d_1(x,t)u_1(x,t),\ x \in \mathbb{R},\ t > 0, \\ \frac{\partial}{\partial t}u_2(x,t) = \alpha(x,t)u_1(x,t) - \left(d_2(x,t) + \gamma(x,t)\right)u_2(x,t),\ x \in \mathbb{R},\ t > 0, \\ (u_1(x,0), u_2(x,0)) \in \mathbb{P}_+, \quad x \in \mathbb{R}. \end{cases} \tag{3.21}$$

Consider the following parabolic eigenvalue problem with periodic boundary conditions, which is associated with system (3.21):

$$\begin{cases} \frac{\partial}{\partial t}u_1(x,t) = D(x,t)\frac{\partial^2 u_1}{\partial x^2} - \nu(x,t)\frac{\partial u_1}{\partial x} \\ \qquad\qquad\qquad +\gamma(x,t)u_2(x,t) - d_1(x,t)u_1(x,t) + \lambda u_1(x,t),\ (x,t)\in\mathbb{R}\times\mathbb{R}, \\ \frac{\partial}{\partial t}u_2(x,t) = \alpha(x,t)u_1(x,t) - (d_2(x,t)+\gamma(x,t))\,u_2(x,t) + \lambda u_2(x,t),\ (x,t)\in\mathbb{R}\times\mathbb{R}, \\ u_i(x,t) = u_i(x,t+\omega),\ u_i(x,t) = u_i(x+L,t),\ (x,t)\in\mathbb{R}\times\mathbb{R},\ i=1,2. \end{cases} \tag{3.22}$$

Observing that if we put $\mu = 0$ in system (3.1) (resp. (3.2)), then we get system (3.21) (resp. (3.22)). Then $\{U_0(t,s) : t \geq s\}$ is the evolution family on Y of system (3.21). In view of Lemma 3.1, we see that

$$\lambda_0^* = -\frac{\ln(r(U_0(\omega,0)))}{\omega} \tag{3.23}$$

is the principal eigenvalue of problem (3.22) with an eigenvector $u_0^* \in$Int$(\mathbb{Y}^+)$.

In the following, we will adopt the theory developed in [12] (with delay $\tau = 0$) to define the basic reproduction number for system (3.20). Recall that $\mathbb{P} = PC(\mathbb{R},\mathbb{R}^2)$ is the set of all continuous and L-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$ with the maximum norm $\|\cdot\|_{\mathbb{P}}$, and $\mathbb{P}_+ = \{\psi \in \mathbb{P} :\ \psi(x) \geq 0, \forall x \in \mathbb{R}\}$ is a positive cone of $\mathbb{P}$. Assume $C_\omega(\mathbb{R},\mathbb{P})$ is the Banach space consisting of all ω-periodic and continuous functions from $\mathbb{R}$ to $\mathbb{P}$, where $\|\varphi\|_{C_\omega(\mathbb{R},\mathbb{P})} = \max_{\theta\in[0,\omega]} \|\varphi(\theta)\|_{\mathbb{P}}$ for any $\varphi \in C_\omega(\mathbb{R},\mathbb{P})$. From (3.21), we define $\mathbb{F}(t) : \mathbb{P} \to \mathbb{P}$ by

$$\mathbb{F}(t)\begin{pmatrix} \varphi_1 \\ \varphi_2 \end{pmatrix} = \begin{pmatrix} \gamma(\cdot,t)\varphi_2 \\ \alpha(\cdot,t)\varphi_1 \end{pmatrix}, \tag{3.24}$$

and

$$-\mathbb{V}(t)\begin{pmatrix} \varphi_1 \\ \varphi_2 \end{pmatrix} = \begin{pmatrix} D(\cdot,t)\frac{\partial^2\varphi_1}{\partial x^2} - \nu(\cdot,t)\frac{\partial\varphi_1}{\partial x} - d_1(\cdot,t)\varphi_1 \\ -\left(d_2(\cdot,t) + \gamma(\cdot,t)\right)\varphi_2 \end{pmatrix}, \tag{3.25}$$

where $(\varphi_1,\varphi_2) \in \mathbb{P}$. It is easy to see that $\mathbb{F}(t) : \mathbb{P} \to \mathbb{P}$ is positive in the sense that $\mathbb{F}(t)\mathbb{P}^+ \subset \mathbb{P}^+$, and hence, the condition (H1) in [12] holds. Next, we assume $\{\Psi(t,s),\ t \geq s\}$ is the evolution family on $\mathbb{P}$ associated with the following system

$$\frac{dv(t)}{dt} = -\mathbb{V}(t)v(t).$$

It is not hard to see that $\Psi(t,s)$ is a positive operator in the sense that $\Psi(t,s)\mathbb{P}^+ \subset \mathbb{P}^+$ for all $t \geq s$. Then it follows from [20, Theorem 3.12] that $-\mathbb{V}(t)$ is resolvent positive. Further, it is not hard to show that the spectral radius of $\Psi(\omega,0)$ is less than 1, that is, $r\left(\Psi(\omega,0)\right) < 1$. Then it follows from [20, Proposition A2] (see also [11, Lemma 2.1]) that the exponential growth bound of evolution family $\{\Psi(t,s),\ t \geq s\}$ is negative, that is, $\omega(\Psi) < 0$. Therefore, the condition (H2) in [12] holds. Thus, we can follow the developed theory in [12] and [26] to define the basic reproduction number for system (3.20).

We assume that $v \in C_\omega(\mathbb{R},\mathbb{P})$ and $v(t)$ is the initial distribution of mosquitoes at time $t \in \mathbb{R}$. For any $s \geq 0$, $\mathbb{F}(t-s)v(t-s)$ represents the density distribution of newly produced population at time $t-s$, which is produced by the initial mosquitoes introduced at time $t-s$. Then $\Psi(t,t-s)\mathbb{F}(t-s)v(t-s)$ is the distribution of those produced population who were newly produced at time $t-s$ and still survive in the habitat at time t, for $t \geq s$. Thus, the integral

$$\int_0^\infty \Psi(t,t-s)\mathbb{F}(t-s)v(t-s)ds$$

is the distribution of accumulative new individuals at time t produced by all those fertile individuals $v(\cdot)$ introduced at all time previous to t. On the other hand, for any $s \geq 0$, $\Psi(t,t-s)v(t-s)$ is the distribution of those fertile individuals at time $t-s$ and remain in the fertile compartments at time t, and hence,

$$\int_0^\infty \Psi(t,t-s)v(t-s)ds$$

represents the distribution of accumulative fertile individuals who were introduced at all previous times to t and remain in the fertile compartments at time t. Thus,

$$\mathbb{F}(t)\int_0^\infty \Psi(t,t-s)v(t-s)ds$$

is the distribution of newly produced individuals at time t.

Define two linear operators on $C_\omega(\mathbb{R},\mathbb{P})$ by

$$[\mathbf{L}v](t) := \int_0^\infty \Psi(t,t-s)\mathbb{F}(t-s)v(t-s)ds,\ \forall\ t \in \mathbb{R},\ v \in C_\omega(\mathbb{R},\mathbb{P}).$$

and

$$[\tilde{\mathbf{L}}v](t) := \mathbb{F}(t)\int_0^\infty \Psi(t,t-s)v(t-s)ds,\ \forall\ t \in \mathbb{R},\ v \in C_\omega(\mathbb{R},\mathbb{P}),$$

Let $\mathbb{A}$ and $\mathbb{B}$ be two bounded linear operators on $C_\omega(\mathbb{R}, \mathbb{P})$ defined by

$$[\mathbb{A}v](t) := \int_0^\infty \Psi(t, t-s)v(t-s)ds, \ [Bv](t) := \mathbb{F}(t)v(t), \ \forall\ t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R}, \mathbb{P}).$$

It then follows that $\mathbf{L} = \mathbb{A} \circ \mathbb{B}$ and $\tilde{\mathbf{L}} = \mathbb{B} \circ \mathbb{A}$, and hence $\mathbf{L}$ and $\tilde{\mathbf{L}}$ have same spectral radius. Motivated by the concept of next generation operators (see, e.g., [2, 14, 21]), we define the spectral radius of $\mathbf{L}$ and $\tilde{\mathbf{L}}$ as the basic reproduction number for system (3.20), that is,

$$\mathcal{R}_0 := r(\mathbf{L}) = r(\tilde{\mathbf{L}}). \tag{3.26}$$

Recall that $U_0(\omega, 0)$ is the Poincaré map associated with system (3.21). By [12, Theorem 3.7] and (3.23), we have the following observation.

Lemma 3.3. *$\mathcal{R}_0 - 1$ has the same sign as $r(U_0(\omega, 0)) - 1$ and $-\lambda_0^*$.*

The following result is concerned with the threshold dynamics of system (3.20):

Theorem 3.1. *Let $u(x, t, \varphi(\cdot))$ be the unique solution of system (3.20) with $u(\cdot, 0, \varphi(\cdot)) = \varphi(\cdot) \in [0, \mathbf{k}(\cdot, 0)]_{\mathbb{P}}$. Then the following statements hold.*

(i) *If $\mathcal{R}_0 < 1$, then $u = 0$ is globally asymptotically stable with respect to initial values in $[0, \mathbf{k}(\cdot, 0)]_{\mathbb{P}}$;*

(ii) *If $\mathcal{R}_0 > 1$, then system (3.20) admits a unique positive time-space periodic solution $\mathbf{u}^*(x, t)$, and it is globally asymptotically stable with respect to initial values in $[0, \mathbf{k}(\cdot, 0)]_{\mathbb{P}} \backslash \{(0, 0)\}$.*

Proof. We first note that the solution $u(x, t, \varphi(\cdot))$ of system (3.20) satisfies $u(x, t, \varphi(\cdot)) \in [0, \mathbf{k}(x, t)]_{\mathbb{P}}$ for $t \geq 0$ (see Lemma 3.2).

Part (i). Our arguments are similar to those in [11, Theorem 3.8 (i)]. Let $v(x, t, \varphi) = U_0(t, 0)\varphi$. Then $v(x, t, \varphi)$ is a solution of system (3.21) with initial value φ, and we see that $v(x, t, \varphi)$ is also a supersolution of system (3.20). By the comparison principle

$$u(x, t, \varphi) \leq v(x, t, \varphi), \ \forall\ x \in \mathbb{R}, \ t \geq 0. \tag{3.27}$$

Since $\mathcal{R}_0 < 1$, it follows from Lemma 3.3 that $r(U_0(\omega, 0)) < 1$, and hence,

$$\lim_{t\to\infty} v(x, t, \varphi(\cdot)) = (0, 0), \ \text{uniformly for } x \in \mathbb{R}. \tag{3.28}$$

In view of (3.27) and (3.28), we see that Part (i) is established.

Part (ii). Since $u(x,t,\varphi(\cdot)) \in [0,\mathbf{k}(x,t)]_{\mathbb{P}}$ for $t \geq 0$, it is easy to see that (3.20) is a monotone/cooperative system on $[0,\mathbf{k}(x,t)]_{\mathbb{P}}$ (see, e.g., [17]). Next, the reaction terms in (3.20) can be expressed as follows:

$$G(x,t,u_1,u_2) = \begin{pmatrix} G_1(x,t,u_1,u_2) \\ G_2(x,t,u_1,u_2) \end{pmatrix} = \begin{pmatrix} \gamma(x,t)u_2\left(1-\frac{u_1}{k_1(x,t)}\right) - d_1(x,t)u_1 \\ \alpha(x,t)\left(1-\frac{u_2}{k_2(x,t)}\right)u_1 - (d_2(x,t)+\gamma(x,t))\,u_2 \end{pmatrix}.$$

Then $G(x,t,u_1,u_2)$ is strongly subhomogeneous in the sense that

$$G(x,t,\theta u_1,\theta u_2) \gg \theta G(x,t,u_1,u_2),\ \forall\ 0<\theta<1,\ (u_1,u_2)\in[0,\mathbf{k}(\cdot,0)]_{\mathbb{P}}\backslash\{(0,0)\}.$$

Further, there is no diffusion term in the second equation of system (3.20), and hence, the associated solution maps are not compact. For this, we observe that the reaction term in the second equation of system (3.20) satisfies

$$\frac{\partial G_2}{\partial u_2}(x,t,u_1,u_2) = -\frac{\alpha(x,t)}{k_2(x,t)}u_1 - (d_2(x,t)+\gamma(x,t)) < 0,$$

for all $(x,t,u_1,u_2)\in\mathbb{R}\times\mathbb{R}\times[0,\mathbf{k}(x,t)]_{\mathbb{P}}$. With the above property, one can use the similar arguments in [7, Lemma 4.1] to overcome the loss of compactness of (3.20). Using the properties in (3.23) and Lemma 3.3, the rest of the arguments of Part (ii) are similar to those in Theorem 3.8 (ii) and Theorem 3.10 of [11] and we omit the details.

□

4 Continuity and κ-contraction

Recall that $\mathbf{u}^*(x,t)$ is given in Theorem 3.1. Define a family of operators $\{Q_t\}_{t\geq 0}$ from $\mathcal{C}_{\mathbf{u}^*(\cdot,0)}$ to $\mathcal{C}_{\mathbf{u}^*(\cdot,t)}$ by

$$Q_t[\phi] = \mathbf{u}(\cdot,t;\phi), \tag{4.1}$$

where $\mathbf{u}(\cdot,t;\phi)$ is the solution of system (1.1) with $u(\cdot,0)=\phi\in\mathcal{C}_{\mathbf{u}^*(\cdot,0)}$. This section is devoted to the study of continuity and κ-contraction of $\{Q_t\}_{t\geq 0}$.

Lemma 4.1. *$Q_t[\phi]$ is continuous in (t,ϕ) in the following sense: if $\phi_n\to\phi$ in $\mathcal{C}_{\mathbf{u}^*(\cdot,0)}$ and $t_n\to t$ as $n\to\infty$, then $Q_{t_n}[\phi_n]\to Q_t[\phi]$ in $\mathcal{C}$.*

Proof. Recall that $\Gamma_1(t,s,x)$ and $\Gamma_2(t,s,x)$ are defined in (2.1) and (2.2), respectively; $P(t)$ and $H(t,x,\mathbf{u})$ are defined in (2.3) and (2.4), respectively; $\mathbf{u}(x,t)$ can be rewritten as the integral form (2.5). We first show that there exists a continuous and positive function $C_0(t)$ with $C_0(0)=1$ such that $\|P(t)[\psi]\| \le C_0(t)\|\psi\|$ for $\psi \in \mathcal{C}_{\mathbf{u}^*(\cdot,0)}$. Indeed, write $\psi=(\psi_1,\psi_2)$. Define

$$C_1(t) := \sup_{x\in\mathbb{R}} \Gamma_2(t,0,x) = e^{-\int_0^t \inf_{x\in\mathbb{R}}[d_2(s,x)+\gamma(s,x)]ds}. \tag{4.2}$$

In view of (4.2) we have

$$\begin{aligned}
\|P(t)[\psi]\| &= \sum_{k\ge 1} 2^{-k} \max_{|x|\le k} |P(t)[\psi](x)| \\
&= \sum_{k\ge 1} 2^{-k} \max_{|x|\le k} [|\Gamma_1(t,0,\cdot)*\psi_1(x)| + |\Gamma_2(t,0,x)\psi_2(x)|] \\
&= \sum_{k\ge 1} 2^{-k} \max_{|x|\le k} \Gamma_1(t,0,\cdot)*|\psi_1|(x) + \sum_{k\ge 1} 2^{-k} \max_{|x|\le k} \Gamma_2(t,0,x)|\psi_2(x)| \\
&\le \sum_{k\ge 1} 2^{-k} \max_{|x|\le k} \Gamma_1(t,0,\cdot)*|\psi_1|(x) + C_1(t)\sum_{k\ge 1} 2^{-k} \max_{|x|\le k} |\psi_2(x)| \qquad (4.3)
\end{aligned}$$

Using the equality

$$\int_{y\in\mathbb{R}} = \sum_{l\ge 0} \int_{|y|\in[l,l+1]}, \tag{4.4}$$

we obtain

$$\begin{aligned}
I_1 := &\sum_{k\ge 1} 2^{-k} \max_{|x|\le k} \Gamma_1(t,0,\cdot)*|\psi_1|(x) \\
= &\sum_{k\ge 1} 2^{-k} \max_{|x|\le k} \sum_{l\ge 0} \int_{|y|\in[l,l+1]} \Gamma_1(t,0,y)|\psi_1(x-y)|dy \\
\le &\sum_{k\ge 1} 2^{-k} \sum_{l\ge 0} \max_{|x|\le k+l+1} |\psi_1(x)| \int_{|y|\in[l,l+1]} \Gamma_1(t,0,y)dy \qquad (4.5)
\end{aligned}$$

Introducing the variable change $\tilde{l} = k+l+1$ and dropping the tilde, we have

$$I_1 \le \sum_{k\ge 1} 2^{-k} \sum_{l\ge k+1} \max_{|x|\le l} |\psi_1(x)| \int_{|y|\in[l-k-1,l-k]} \Gamma_1(t,0,y)dy. \tag{4.6}$$

Using Fubini's theorem, we change the order of sums to arrive at

$$
\begin{aligned}
I_1 \quad &\le \sum_{l\ge 2} \max_{|x|\le l} |\psi_1(x)| \sum_{k=1}^{l-1} 2^{-k} \int_{|y|\in[l-k-1,l-k]} \Gamma_1(t,0,y)dy \\
&= \sum_{l\ge 2} 2^{-l} \max_{|x|\le l} |\psi_1(x)| \left(\sum_{k=1}^{l-1} 2^{l-k} \int_{|y|\in[l-k-1,l-k]} \Gamma_1(t,0,y)dy \right). \qquad (4.7)
\end{aligned}
$$

To estimate the term in the bracket, after the change of variable $n = l - k$ we obtain

$$
\begin{aligned}
I_2 \quad &:= \sum_{k=1}^{l-1} 2^{l-k} \int_{|y|\in[l-k-1,l-k]} \Gamma_1(t,0,y)dy \\
&= \sum_{n=1}^{l-1} 2^{n} \int_{|y|\in[n-1,n]} \Gamma_1(t,0,y)dy. \qquad (4.8)
\end{aligned}
$$

To show that I_2 is bounded we employ a comparison argument to estimate the integral $\int_{|y|\in[n-1,n]} \Gamma_1(t,0,y)dy$. Let θ be a positive number that will be specified later. Define

$$
p(t) := e^{\int_0^t [\sup_{x\in\mathbb{R}} D(s,x)\theta^2 + |\nu(s,x)|\theta + d_1(s,x)]ds}. \qquad (4.9)
$$

Then we infer that for any $\theta > 0$, $\bar{v}(t,x) := e^{-\theta x} p(t)$ is a super solution of (2.1) from the following inequality.

$$
\begin{aligned}
& -\bar{v}_t + D(t,x)\bar{v}_{xx} - \nu(t,x)\bar{v}_x - d_1(t,x)\bar{v} \\
= \quad & \bar{v}\left(-\frac{p'}{p} + D(t,x)\theta^2 + \nu(t,x)\theta - d_1(t,x) \right) \\
\le \quad & 0.
\end{aligned}
$$

Define

$$
\rho(x) := \begin{cases} 1/2, & x \in [-1,0] \\ 0, & x \notin [-1,0]. \end{cases} \qquad (4.10)
$$

Then $\bar{v}(0,x) = e^{-\theta x} \ge \rho(x)$ for $x \in \mathbb{R}$. Recall that $\Gamma_1(t,s,x)$ is the Green function of (2.1). By the comparison principle we obtain

$$
e^{-\theta x} p(t) \ge \int_{\mathbb{R}} \Gamma_1(t,0,y)\rho(x-y)dy, \quad t > 0, x \in \mathbb{R}. \qquad (4.11)
$$

In particular, at $x = n-1$ we have

$$e^{-\theta(n-1)}p(t) \geq \int_{n-1}^{n} \Gamma_1(t,0,y)\rho(n-1-y)dy = \frac{1}{2}\int_{n-1}^{n} \Gamma_1(t,0,y)dy. \tag{4.12}$$

Similarly, $e^{\theta x}p(t)$ is also a super solution of (2.1). Then by the same arguments we obtain

$$e^{-\theta(n-1)}p(t) \geq \frac{1}{2}\int_{-n}^{-(n-1)} \Gamma_1(t,0,y)dy. \tag{4.13}$$

Therefore,

$$\int_{|y|\in[n-1,n]} \Gamma_1(t,0,y)dy \leq e^{-\theta(n-1)}p(t), \tag{4.14}$$

which implies that

$$\begin{aligned} I_2 \quad &\leq \sum_{n\geq 1} 2^n e^{-\theta(n-1)}p(t) = 2p(t)\sum_{n\geq 1} e^{-(\theta-\ln 2)(n-1)} \\ &\leq 2p(t)\int_0^{\infty} e^{-(\theta-\ln 2)x}dx = \frac{2p(t)}{\theta-\ln 2} \end{aligned}$$

provided that $\theta > \ln 2$. For the sake of calculation simplicity, we may set $\theta = 2+\ln 2$. Then

$$I_1 \leq p(t)\sum_{l\geq 1}\max_{|x|\leq l}|\psi_1(x)|, \tag{4.15}$$

and hence,

$$\begin{aligned} & \|P(t)[\psi]\| \\ \leq \quad & p(t)\sum_{l\geq 1} 2^{-l}\max_{|x|\leq l}|\psi_1(x)| + C_1(t)\sum_{k\geq 1} 2^{-k}\max_{|x|\leq k}|\psi_2(x)| \\ \leq \quad & C_0(t)\|\psi\|, \end{aligned} \tag{4.16}$$

where

$$C_0(t) := \max\{p(t), C_1(t)\} = p(t) \tag{4.17}$$

thanks to the explicit expressions of $p(t)$ and $C_1(t)$.

Next we use the obtained inequality $\|P(t)[\psi]\| \leq C_0(t)\|\psi\|$ to complete the proof. Indeed, let L_H be the Lipschtiz constant of $H(t,x,\mathbf{u})$ for $t\in\mathbb{R}, x\in\mathbb{R}$ and $\mathbf{u}\in[0,\max_{s\in[0,\omega]}\{\mathbf{u}^*(\cdot,s)\}]$. By the triangle inequality, we see that

$$\|Q_{t_n}[\phi_n] - Q_t[\phi]\| \leq \|Q_{t_n}[\phi_n] - Q_{t_n}[\phi]\| + \|Q_{t_n}[\phi] - Q_t[\phi]\|. \tag{4.18}$$

Without loss of generality, we may assume that $t_n > t, n \geq 1$. In view of (2.5) and the properties of $k_i(t,0,x), i = 1,2$, we obtain

$$\begin{aligned}
& \|Q_{t_n}[\phi] - Q_t[\phi]\| \\
\leq \quad & \|P(t_n - t)[\phi]\| + \int_t^{t_n} \|P(t_n - s)[H(s,\cdot,Q_s[\phi])]\| ds \\
& + \int_0^t \|(P(t-s) - P(t_n - s))[H(s,\cdot,Q_s[\phi])]\| ds \\
\leq \quad & C_0(t_n - t)\|\phi\| + \int_t^{t_n} C_0(t_n - s) L_H \|Q_s[\phi]\| ds \\
& + \int_0^t C_0(t-s)\|P(t_n - t) - I\| L_H \|Q_s[\phi]\| ds \\
\to \quad & 0 \quad \text{as } t_n \to t. \qquad (4.19)
\end{aligned}$$

Meanwhile,

$$\begin{aligned}
& \|Q_t[\phi_n] - Q_t[\phi]\| \\
\leq \quad & \|P(t)[\phi_n - \phi]\| + \int_0^t L_H \|P(t-s)[Q_s[\phi_n] - Q_s[\phi]]\| \\
\leq \quad & C_0(t)\|\phi_n - \phi\| + \int_0^t L_H C_0(t-s)\|Q_s[\phi_n] - Q_s[\phi]\| ds, \quad \forall t > 0.
\end{aligned}$$

Note that

$$\frac{p(t-s)}{p(s)} = e^{\left(-\int_{t-s}^t + \int_0^s\right) \sup_{x\in\mathbb{R}}[D(\eta,x)\theta^2 + |\nu(\eta,x)|\theta + d_1(\eta,x)]d\eta}, \quad \forall t \geq s > 0. \qquad (4.20)$$

It then follows from the periodicity of $\sup_{x\in\mathbb{R}}[D(\eta,x)\theta^2 + |\nu(\eta,x)|\theta + d_1(\eta,x)]$ that

$$\frac{C_0(t-s)}{C_0(s)} \leq e^{\int_0^\omega \sup_{x\in\mathbb{R}}[D(\eta,x)\theta^2 + |\nu(\eta,x)|\theta + d_1(\eta,x)]d\eta} := C_2, \quad \forall t \geq s > 0. \qquad (4.21)$$

Thus,

$$\begin{aligned}
& [C_0(t)]^{-1}\|Q_t[\phi_n] - Q_t[\phi]\| \\
\leq \quad & \|\phi_n - \phi\| + \int_0^t L_H C_2 [C_0(s)]^{-1} \|Q_s[\phi_n] - Q_s[\phi]\| ds, \quad t > 0. \qquad (4.22)
\end{aligned}$$

By Gronwall's inequality we then infer that

$$[C_0(t)]^{-1}\|Q_t[\phi_n] - Q_t[\phi]\| \leq \|\phi_n - \phi\|] e^{L_H C_2 t}, \quad t > 0. \qquad (4.23)$$

Combining (4.23) with $t = t_n$, (4.18) and (4.19), we complete the proof. $\square$

For $I=[a,b]\subset\mathbb{R}$ and $\phi=(\phi_1,\phi_2)\in\mathcal{C}_{\mathbf{u}^*(\cdot,0)}$, we define $\phi_I\in C(I,\mathbb{R}^2)$ by

$$\phi_I(x):=\phi(x),\quad x\in I. \tag{4.24}$$

For $B\subset\mathcal{C}_{\mathbf{u}^*(\cdot,0)}$, let B_I denote the set $\{\phi_I:\phi\in\mathcal{C}_{\mathbf{u}^*(\cdot,0)}\}$ and $\kappa(B_I)$ the Kuratowski noncompactness of B_I in $C(I,\mathbb{R}^2)$, which is naturally endowed with the uniform topology. The set B_I is precompact if and only if $\kappa(B_I)=0$. For each component $(B_I)_i, i=1,2$ of B_I, we may similarly define the Kuratowski noncompactness in $C(I,\mathbb{R})$. Recall that we endow the l^1 norm in $\mathbb{R}^2$. It then follows that

$$\kappa(B_I)\le\kappa((B_I)_1)+\kappa((B_I)_2),\quad B\subset\mathcal{C}_{\mathbf{u}^*(\cdot,0)}. \tag{4.25}$$

Lemma 4.2. *For $I=[a,b]\subset\mathbb{R}$ and $t>0$ there exists $\vartheta=\vartheta(t)\in(0,1)$ such that $\kappa((Q_t[B])_I)\le\vartheta\kappa(B_I),\forall B\subset\mathcal{C}_{\mathbf{u}^*(\cdot,0)}$.*

Proof. Define $\alpha^*:=\sup_{t,x}\alpha(t,x)$. From the second equation of (1.1) we have

$$u_2(t,x)\le\Gamma_2(t,0,x)u_2(0,x)+\int_0^t\Gamma_2(t-s,0,x)\alpha(s,x)u_1(s,x)ds, \tag{4.26}$$

which implies that

$$\kappa(((Q_t[B])_I)_2)\le C_1(t)\kappa((B_I)_2)+\alpha^*\int_0^t\kappa(((Q_s[B])_I)_1)ds, \tag{4.27}$$

where $C_1(t)\in(0,1)$ is defined as in (4.2). From the first equation of (1.1) we see that $(Q_t[B])_I)_1$ is precompact, that is, $\kappa((Q_t[B])_I)_1)$, and hence,

$$\kappa(((Q_t[B])_I)_2)\le C_1(t)\kappa((B_I)_2), \tag{4.28}$$

which, together with (4.25), implies the conclusion with $\vartheta(t)=C_1(t)$.

□

5 Spreading speeds and Traveling waves

In this section, we assume that $\mathcal{R}_0>1$, that is, $\lambda_0^*<0$ (see Lemma 3.3) and we investigate the spreading speeds and traveling waves of system (1.1). Since $\mathcal{R}_0>1$, it follows from Theorem 3.1 that there exist two periodic state, $\mathbf{0}:=(0,0)$ and

$\mathbf{u}^*(x,t) := (u_1^*(x,t), u_2^*(x,t))$, for system (3.21). Recall that $Q_t : \mathcal{C}_{\mathbf{u}^*(\cdot,0)} \to \mathcal{C}_{\mathbf{u}^*(\cdot,t)}$ is the solution maps associated with system (3.21), which is defined in (4.1).

From Lemma 2.1, Lemma 4.1, Lemma 4.2 and [9, Theorem 5.1] (see also [23, Appendix]), it follows that the map Q_ω admits a rightward spreading speed c_ω^+ and a leftward spreading speed c_ω^-. In order to obtain the computation formulas for $c_\omega^\pm$, we consider the linearized system of (1.1) at the zero solution:

$$\begin{cases} \frac{\partial}{\partial t}u_1(x,t) = D(x,t)\frac{\partial^2}{\partial x^2}u_1(x,t) - \nu(x,t)\frac{\partial}{\partial x}u_1(x,t) - d_1(x,t)u_1(x,t) + \gamma(x,t)u_2(x,t), \\ \frac{\partial}{\partial t}u_2(x,t) = \alpha(x,t)u_1(x,t) - (d_2(x,t)+\gamma(x,t))u_2(x,t),\ x \in \mathbb{R},\ t>0. \end{cases} \tag{5.1}$$

Let $\{\mathbb{L}(t,s) : t \geq s\}$ be the evolution family on $\mathcal{C}$ generated by system (5.1), that is, $\mathbb{L}(t,0)\phi = u(\cdot,t;\phi)$, where $u(x,t;\phi)$ is the unique solution of system (5.1) with $u(x,0;\phi) = \phi \in \mathcal{C}$.

For $\mu \geq 0$, substituting $(u_1(x,t), u_2(x,t)) = e^{-\mu x}(v_1(x,t), v_2(x,t))$ into (5.1) yields

$$\begin{cases} \frac{\partial v_1(x,t)}{\partial t} = D(x,t)\frac{\partial^2 v_1}{\partial x^2} - [2\mu D(x,t)+\nu(x,t)]\frac{\partial v_1}{\partial x} + [\mu^2 D(x,t) + \mu\nu(x,t)]v_1(x,t) \\ \qquad\qquad +\gamma(x,t)v_2(x,t) - d_1(x,t)v_1(x,t),\ x \in \mathbb{R},\ t>0, \\ \frac{\partial v_2(x,t)}{\partial t} = \alpha(x,t)v_1(x,t) - (d_2(x,t)+\gamma(x,t))\,v_2(x,t),\ x \in \mathbb{R},\ t>0. \end{cases} \tag{5.2}$$

Let $\{L_\mu(t,s)\}_{t\geq s}$ be the evolution family on $\mathcal{C}$ generated by system (5.2), that is,$L_\mu(t,0)\varphi = v(\cdot,t;\varphi)$, where $v(x,t;\varphi)$ is the unique solution of system (5.2) with $v(x,0;\varphi) = \varphi$. Then

$$\mathbb{L}(t,0)[e^{-\mu x}\varphi](x) = e^{-\mu x}L_\mu(t,0)[\varphi](x),\ x \in \mathbb{R},\ t \geq 0,\ \varphi(\cdot) \in \mathcal{C}.$$

Substituting $(v_1(x,t), v_2(x,t)) = e^{\Lambda t}(\phi_1(x,t), \phi_2(x,t))$ into (5.1) yields the following periodic eigenvalue problem:

$$\begin{cases} \Lambda\phi_1(x,t) = -\frac{\partial\phi_1(x,t)}{\partial t} + D(x,t)\frac{\partial^2\phi_1}{\partial x^2} - [2\mu D(x,t)+\nu(x,t)]\frac{\partial\phi_1}{\partial x} + [\mu^2 D(x,t)+\mu\nu(x,t)]\phi_1(x,t) \\ \qquad\qquad +\gamma(x,t)\phi_2(x,t) - d_1(x,t)\phi_1(x,t),\ x \in \mathbb{R},\ t>0, \\ \Lambda\phi_2(x,t) = -\frac{\partial\phi_2(x,t)}{\partial t} + \alpha(x,t)\phi_1(x,t) - (d_2(x,t)+\gamma(x,t))\,\phi_2(x,t),\ x \in \mathbb{R},\ t>0, \\ \phi_i(x+L,t) = \phi_i(x,t),\ \phi_i(x,t+\omega) = \phi_i(x,t),\ (x,t) \in \mathbb{R}\times\mathbb{R},\ i=1,2. \end{cases} \tag{5.3}$$

By Lemma 3.1, we have the following results:

Lemma 5.1. *Assume that (H) holds. Then $r_+(L_\mu(\omega,0))$ is the principal eigenvalue of $L_\mu(\omega,0)$, and $\Lambda_+^0(\mu) = \frac{\ln(r_+(L_\mu(\omega,0))}{\omega}$ is an eigenvalue of problem* (5.3) *with a positive eigenvector.*

The following is a computation formula for c_ω^+.

Lemma 5.2. *Let $\Phi_+(\mu) := \frac{\ln[r_+(L_\mu(\omega,0))]}{\mu} = \frac{\Lambda_+^0(\mu)\omega}{\mu}$, where $r_+(L_\mu(\omega,0))$ and $\Lambda_+^0(\mu)$ are given in Lemma 5.1. Then*

$$\lim_{\mu\to 0^+}\Phi_+(\mu)=\infty,\ \lim_{\mu\to\infty}\Phi_+(\mu)=\infty,\ \text{and } c_\omega^+=\inf_{\mu>0}\Phi_+(\mu). \tag{5.4}$$

Proof. Observing that system (3.22) is equivalent to system (5.2) with $\mu = 0$. Thus, $\Lambda_+^0(0) = -\lambda_0^* > 0$, and hence, $\lim_{\mu\to 0^+}\Phi_+(\mu) = \infty$. We next show that $\lim_{\mu\to\infty}\Phi_+(\mu) = \infty$. Let

$$\mathbf{A}(t) = \begin{pmatrix} a(t) & \min_{x\in[0,L]}\gamma(x,t) \\ \min_{x\in[0,L]}\alpha(x,t) & -\max_{x\in[0,L]}(d_1(x,t)+\gamma(x,t)) \end{pmatrix},$$

where $a(t) = \mu^2\min_{x\in[0,L]}D(x,t)+\mu\min_{x\in[0,L]}\nu(x,t)-\max_{x\in[0,L]}d_1(x,t)$. Then it is easy to see that $\mathbf{A}(t)$ is a continuous, cooperative, irreducible, and ω-periodic 2×2 matrix function. Suppose $\Pi_{\mathbf{A}(\cdot)}(t)$ is the monodromy matrix of the linear ordinary differential system

$$\frac{dy(t)}{dt} = \mathbf{A}(t)y, \tag{5.5}$$

and $r(\Pi_{\mathbf{A}(\cdot)}(\omega))$ is the spectral radius of $\Pi_{\mathbf{A}(\cdot)}(\omega)$. From [1, Lemma 2] (see also [6, Theorem 1.1]), it follows that $\Pi_{\mathbf{A}(\cdot)}(t)$ is a matrix with all entries positive for each $t > 0$. By the Perron-Frobenius theorem, $r(\Pi_{\mathbf{A}(\cdot)}(\omega))$ is the principal eigenvalue of $\Pi_{\mathbf{A}(\cdot)}(\omega)$ in the sense that it is simple and admits a positive eigenvector. Let $\tilde\lambda = \frac{1}{\omega}\ln[r(\Pi_{\mathbf{A}(\cdot)}(\omega))]$. Then it follows from [25, Lemma 2.1] that there exists a positive, ω-periodic function $\psi(t)$ such that $e^{\tilde\lambda t}\psi(t)$ is a solution of (5.5). Thus, it is easy to show that $e^{\tilde\lambda t}\psi(t)$ is a subsolution of system (5.2), and hence,

$$L_\mu(t,0)[\psi](x) \ge e^{\tilde\lambda t}\psi(t),\ x\in\mathbb{R},\ t\ge 0.$$

In particular,

$$L_\mu(\omega,0)[\psi](x) \ge e^{\tilde\lambda\omega}\psi(\omega),\ x\in\mathbb{R}.$$

This implies that

$$r_+(L_\mu(\omega,0)) \ge e^{\tilde\lambda\omega}, \tag{5.6}$$

due to Gelfand's formula (see, e.g., [15, Theorem VI.6]). On the other hand, we see that $\psi(t) := (\psi_1(t), \psi_2(t))$ satisfies

$$\begin{cases} \psi_1'(t) = [-\tilde{\lambda} + \mu^2 \min_{x\in[0,L]} D(x,t) + \mu \min_{x\in[0,L]} \nu(x,t) - \max_{x\in[0,L]} d_1(x,t)]\psi_1(t) \\ \qquad\qquad + [\min_{x\in[0,L]} \gamma(x,t)]\psi_2(t), \\ \psi_2'(t) = [\min_{x\in[0,L]} \alpha(x,t)]\psi_1(t) - [\tilde{\lambda} + \max_{x\in[0,L]}(d_1(x,t) + \gamma(x,t))]\psi_2(t). \end{cases} \tag{5.7}$$

From the first equation of (5.7), it follows that

$$\frac{\psi_1'(t)}{\psi_1(t)} \geq -\tilde{\lambda} + \mu^2 \min_{x\in[0,L]} D(x,t) + \mu \min_{x\in[0,L]} \nu(x,t) - \max_{x\in[0,L]} d_1(x,t).$$

Integrating the above inequality from 0 to ω, we obtain

$$0 = \int_0^\omega \frac{\psi_1'(t)}{\psi_1(t)} \geq -\tilde{\lambda}\omega + \mu^2 \int_0^\omega [\min_{x\in[0,L]} D(x,t)]dt + \mu \int_0^\omega [\min_{x\in[0,L]} \nu(x,t)]dt - \int_0^\omega [\max_{x\in[0,L]} d_1(x,t)]dt,$$

which implies that

$$\frac{\tilde{\lambda}\omega}{\mu} \geq \mu \int_0^\omega [\min_{x\in[0,L]} D(x,t)]dt + \int_0^\omega [\min_{x\in[0,L]} \nu(x,t)]dt - \frac{1}{\mu}\int_0^\omega [\max_{x\in[0,L]} d_1(x,t)]dt.$$

Since $\int_0^\omega [\min_{x\in[0,L]} D(x,t)]dt > 0$, it follows that

$$\lim_{\mu\to\infty} \frac{\tilde{\lambda}\omega}{\mu} = \infty. \tag{5.8}$$

In view of (5.6) and (5.8), it follows that $\lim_{\mu\to\infty} \Phi_+(\mu) = \infty$. Thus, $\Phi_+(\mu)$ attains its minimum at some finite value μ^*. Since the solution of system (1.1) is a lower solution of the linear system (5.1), we have

$$Q_t[\phi] \leq \mathbb{L}(t,0)[\phi], \ \forall\ \phi \in \mathcal{C}_{u^*(0)}, \ t \geq 0.$$

Then we can use the similar arguments as in [22, Theorem 2.5] and [10, Theorem 3.10(i)] to show that $c_\omega^+ \leq \inf_{\mu>0} \Phi_+(\mu)$.

By the continuous dependence of solutions on initial conditions, it follows that for any $0 < \epsilon < 1$, there exists a sufficiently small $\bar{\eta} \in \mathrm{Int}(\mathbb{P}_+)$ such that the solution $\mathbf{u}(x,t,\bar{\eta})$ of (1.1) with $\mathbf{u}(x,0,\bar{\eta}) = \bar{\eta}$ satisfies

$$\mathbf{u}(x,t,\bar{\eta}) \leq \epsilon\, (\min_{(x,t)\in[0,L]\times[0,\omega]} k_1(x,t), \min_{(x,t)\in[0,L]\times[0,\omega]} k_2(x,t)), \ \forall\ x \in \mathbb{R}, \ t \in [0,\omega].$$

Then the comparison principle implies that

$$Q_t(\phi)(x) := \mathbf{u}(x,t,\phi) \leq \mathbf{u}(x,t,\bar{\eta}),\ \forall\ \phi \in \mathcal{C}_{\bar{\eta}},\ x \in \mathbb{R},\ t \in [0,\omega].$$

Thus, for all $t \in [0,\omega]$ and $x \in \mathbb{R}$, $Q_t(\phi)(x) := \mathbf{u}(x,t,\phi)$ with $\phi \in \mathcal{C}_{\bar{\eta}}$ satisfies

$$\begin{cases} \frac{\partial}{\partial t}u_1(x,t) \geq D(x,t)\frac{\partial^2}{\partial x^2}u_1(x,t) - \nu(x,t)\frac{\partial}{\partial x}u_1(x,t) - d_1(x,t)u_1(x,t) \\ \qquad\qquad +(1-\epsilon)\gamma(x,t)u_2(x,t), \\ \frac{\partial}{\partial t}u_2(x,t) \geq (1-\epsilon)\alpha(x,t)u_1(x,t) - (d_2(x,t)+\gamma(x,t))u_2(x,t),\ x \in \mathbb{R},\ t > 0. \end{cases} \tag{5.9}$$

Let $\{\mathbb{L}^\epsilon(t,s) : t \geq s\}$ be the evolution family on $\mathcal{C}$ generated by the following system:

$$\begin{cases} \frac{\partial}{\partial t}u_1(x,t) = D(x,t)\frac{\partial^2}{\partial x^2}u_1(x,t) - \nu(x,t)\frac{\partial}{\partial x}u_1(x,t) - d_1(x,t)u_1(x,t) \\ \qquad\qquad +(1-\epsilon)\gamma(x,t)u_2(x,t), \\ \frac{\partial}{\partial t}u_2(x,t) = (1-\epsilon)\alpha(x,t)u_1(x,t) - (d_2(x,t)+\gamma(x,t))u_2(x,t),\ x \in \mathbb{R},\ t > 0. \end{cases} \tag{5.10}$$

For $\mu \geq 0$, assume that $\{L_\mu^\epsilon(t,s)\}_{t\geq s}$ is the evolution family on $\mathcal{C}$ generated the following system

$$\begin{cases} \frac{\partial v_1(x,t)}{\partial t} = D(x,t)\frac{\partial^2 v_1}{\partial x^2} - [2\mu D(x,t) + \nu(x,t)]\frac{\partial v_1}{\partial x} + [\mu^2 D(x,t) + \mu\nu(x,t)]v_1(x,t) \\ \qquad\qquad +(1-\epsilon)\gamma(x,t)v_2(x,t) - d_1(x,t)v_1(x,t),\ x \in \mathbb{R},\ t > 0, \\ \frac{\partial v_2(x,t)}{\partial t} = (1-\epsilon)\alpha(x,t)v_1(x,t) - (d_2(x,t)+\gamma(x,t))\,v_2(x,t),\ x \in \mathbb{R},\ t > 0, \\ (v_1(x,0), v_2(x,0)) = e^{\mu x}\phi(x),\ x \in \mathbb{R}. \end{cases} \tag{5.11}$$

By (5.9), it follows that $Q_t(\phi)(x) := \mathbf{u}(x,t,\phi)$ is an upper solution of linear system (5.10) for $t \in [0,\omega]$ and $\phi \in \mathcal{C}_{\bar{\eta}}$, and hence,

$$L_\mu^\epsilon(t,0)(\phi) \leq Q_t(\phi),\ \forall\ \phi \in \mathcal{C}_{\bar{\eta}},\ t \in [0,\omega].$$

In particular,

$$L_\mu^\epsilon(\omega,0)(\phi) \leq Q_\omega(\phi),\ \forall\ \phi \in \mathcal{C}_{\bar{\eta}}.$$

Define the function

$$\Phi_+^\epsilon(\mu) := \frac{\ln[r_+(L_\mu^\epsilon(\omega,0))]}{\mu},\ \forall\ \mu > 0,$$

where $r_+(L^\epsilon_\mu(\omega,0))$ the spectral radius of the Poincaré map associated with system (5.11). Using the analysis on $L^\epsilon_\mu(t,0)$ similar to those for $L_\mu(t,0)$, and the similar arguments as in [22, Theorem 2.4] and [10, Theorem 3.10(ii)] give rise to $c^+_\omega \geq \inf_{\mu>0}\Phi^\epsilon_+(\mu)$. Letting $\epsilon \to 0$, we obtain $c^+_\omega \geq \inf_{\mu>0}\Phi_+(\mu)$. Thus, $c^+_\omega = \inf_{\mu>0}\Phi_+(\mu)$.

□

Substituting $\hat{u}_1(x,t) := u_1(-x,t)$ and $\hat{u}_2(x,t) := u_2(-x,t)$ into (1.1), we obtain

$$\begin{cases} \frac{\partial}{\partial t}\hat{u}_1(x,t) = D(x,t)\frac{\partial^2}{\partial x^2}\hat{u}_1(x,t) + \nu(x,t)\frac{\partial}{\partial x}\hat{u}_1(x,t) \\ \qquad\qquad +\gamma(x,t)\hat{u}_2(x,t)(1-\frac{\hat{u}_1(x,t)}{k_1(x,t)}) - d_1(x,t)\hat{u}_1(x,t), \\ \frac{\partial}{\partial t}\hat{u}_2(x,t) = \alpha(x,t)(1-\frac{\hat{u}_2(x,t)}{k_2(x,t)})\hat{u}_1(x,t) - (d_2(x,t)+\gamma(x,t))\hat{u}_2(x,t),\ x\in\mathbb{R},\ t>0. \end{cases} \tag{5.12}$$

Let $\hat{Q}_t$ be the solution map of system (5.12). It is easy to see that if c^-_ω is the leftward spreading speed of the map Q_ω then c^-_ω is the rightward spreading speed of the map $\hat{Q}_\omega$. For $\mu \geq 0$, substituting $(\hat{u}_1(x,t),\hat{u}_2(x,t)) = e^{-\mu x}(\hat{v}_1(t),\hat{v}_2(t))$ into (5.12) yields

$$\begin{cases} \frac{\partial \hat{v}_1(x,t)}{\partial t} = D(x,t)\frac{\partial^2\hat{v}_1}{\partial x^2} - [2\mu D(x,t)-\nu(x,t)]\frac{\partial \hat{v}_1}{\partial x} + [\mu^2 D(x,t) - \mu\nu(x,t)]\hat{v}_1(x,t) \\ \qquad\qquad +\gamma(x,t)\hat{v}_2(x,t) - d_1(x,t)\hat{v}_1(x,t),\ x\in\mathbb{R},\ t>0, \\ \frac{\partial \hat{v}_2(x,t)}{\partial t} = \alpha(x,t)\hat{v}_1(x,t) - (d_2(x,t)+\gamma(x,t))\,\hat{v}_2(x,t),\ x\in\mathbb{R},\ t>0. \end{cases} \tag{5.13}$$

Assume that $\{\hat{L}_\mu(t,s)\}_{t\geq s}$ is the evolution family on $\mathcal{C}$ generated by system (5.13), and $r_-(\hat{L}_\mu(\omega,0))$ is the spectral radius of the Poincaré map associated with the linear system (5.13). By similar arguments to those in Lemma 5.2, we obtain the following computation formula for c^-_ω.

Lemma 5.3. *Let* $\Phi_-(\mu) := \frac{\ln[r_-(\hat{L}_\mu(\omega,0))]}{\mu} = \frac{\Lambda^0_-(\mu)\omega}{\mu}$*, where* $\Lambda^0_-(\mu) = \frac{\ln(r_-(\hat{L}_\mu(\omega,0)))}{\omega}$. *Then*

$$\lim_{\mu\to 0^+}\Phi_-(\mu) = \lim_{\mu\to\infty}\Phi_-(\mu) = \infty,\ \textit{and}\ c^-_\omega = \inf_{\mu>0}\Phi_-(\mu). \tag{5.14}$$

We further have the following result.

Lemma 5.4. *The following statement holds.*

$$c^+_\omega + c^-_\omega > 0. \tag{5.15}$$

Proof. Our arguments are similar to those in [9, Section 7]. For $\mu \in \mathbb{R}$, we assume that $r(\mu)$ is the spectral radius of the Poincaré map associated with the linear system (5.2), and $\Lambda^0(\mu) = \frac{\ln(r(\mu))}{\omega}$. Then it is easy to see that $\Lambda^0_+(\mu) = \Lambda^0(\mu)$, $\forall\, \mu \geq 0$, and $\Lambda^0_-(\mu) = \Lambda^0(-\mu)$, $\forall\, \mu \geq 0$. From Lemma 5.2 and Lemma 5.3, we can choose $\mu_1 > 0$ and $\mu_2 > 0$ such that $c^+_\omega = \frac{\Lambda^0_+(\mu_1)\omega}{\mu_1} = \frac{\Lambda^0(\mu_1)\omega}{\mu_1}$ and $c^-_\omega = \frac{\Lambda^0_-(\mu_2)\omega}{\mu_2} = \frac{\Lambda(-\mu_2)\omega}{\mu_2}$. Let $\theta = \frac{\mu_2}{\mu_1+\mu_2} \in (0,1)$. Then $\theta\mu_1 + (1-\theta)(-\mu_2) = 0$, and

$$c^+_\omega + c^-_\omega = \frac{\Lambda^0(\mu_1)\omega}{\mu_1} + \frac{\Lambda(-\mu_2)\omega}{\mu_2} = \omega\frac{\mu_1+\mu_2}{\mu_1\mu_2}\left[\theta\Lambda^0(\mu_1) + (1-\theta)\Lambda^0(-\mu_2)\right]. \quad (5.16)$$

From [10, Lemma 3.7], we see that $\Lambda^0(\mu)$ is convex on $\mathbb{R}$. Thus, it follows from (5.16) that

$$c^+_\omega + c^-_\omega \geq \omega\frac{\mu_1+\mu_2}{\mu_1\mu_2}\Lambda^0\left(\theta\mu_1 + (1-\theta)(-\mu_2)\right) = \omega\frac{\mu_1+\mu_2}{\mu_1\mu_2}\Lambda^0(0) = -\omega\frac{\mu_1+\mu_2}{\mu_1\mu_2}\lambda^*_0 > 0.$$

The proof is complete.

□

Combining Lemma 2.1, Lemma 4.1, Lemma 4.2, [9, Theorem 5.1], and the above discussions, we have the following result indicating that $\frac{c^+_\omega}{\omega}$ and $\frac{c^-_\omega}{\omega}$ are the rightward and leftward spreading speeds for system (1.1), respectively, with initial functions having compact supports:

Theorem 5.1. *Assume that (H) holds, and $\mathcal{R}_0 > 1$. Let $c^*_\pm = \frac{c^\pm_\omega}{\omega}$ and $\mathbf{u}(x,t,\phi)$ be a solution of (1.1) with $\mathbf{u}(\cdot,0,\phi) = \phi \in \mathcal{C}_{\mathbf{u}^*(\cdot,0)}$. Then the following statements are valid:*

(i) *If $0 \leq \phi(\cdot) \leq \varphi(\cdot) \ll \mathbf{u}^*(\cdot,0)$, for some $\varphi(\cdot) \in \mathbb{P}$, and $\phi(x) = 0$ for x outside a bounded interval, then we have*

$$\lim_{t\to\infty,\ x\geq ct} \mathbf{u}(x,t,\phi) = 0, \ \textit{for any } c > c^*_+,$$

and

$$\lim_{t\to\infty,\ x\leq -ct} \mathbf{u}(x,t,\phi) = 0, \ \textit{for any } c > c^*_-\ ;$$

(ii) *If $\phi \in \mathcal{C}_{\mathbf{u}^*(\cdot,0)}$ and $\phi \not\equiv 0$, then for any c and c' satisfying $-c^*_- < -c' < c < c^*_+$, we have*

$$\lim_{t\to\infty,\ -c't\leq x\leq ct} (\mathbf{u}(x,t,\phi) - \mathbf{u}^*(x,t)) = 0.$$

Next, we can employ the theory developed in [5, Theorems 2.1] to establish that the spreading speeds given in Theorem 5.1 coincides with the minimal speed of traveling waves of system (1.1), which connects the positive periodic state $\mathbf{u}^*(x,t)$ to $\mathbf{0}$, or connects $\mathbf{0}$ to the positive periodic state $\mathbf{u}^*(x,t)$.

Theorem 5.2. *Assume that (H) holds, $\mathcal{R}_0 > 1$, and $c_\pm^*$ is given in Theorem 5.1. Then the following statements are valid:*

(i) *For any $c \geq c_+^*$, system* (1.1) *admits rightward almost pulsating waves $\mathbf{U}(t,x,x-ct)$ connecting $\mathbf{u}^*(x,t)$ to $\mathbf{0}$ with the wave profile component $\mathbf{U}(t,x,\xi)$ being continuous and non-increasing in ξ. While for any $c \in (0, c_+^*)$, system* (1.1) *admits no rightward almost pulsating waves connecting $\mathbf{u}^*(x,t)$ to $\mathbf{0}$.*

(ii) *For any $c \geq c_-^*$, system* (1.1) *admits leftward almost pulsating waves $\mathbf{V}(t,x,x+ct)$ connecting $\mathbf{0}$ to $\mathbf{u}^*(x,t)$ with the wave profile component $\mathbf{V}(t,x,\xi)$ being continuous and non-decreasing in ξ. While for any $c \in (0, c_-^*)$, system* (1.1) *admits no leftward almost pulsating waves connecting $\mathbf{0}$ to $\mathbf{u}^*(x,t)$.*

6 Numerical simulation

We illustrate the analytic results by numerical simulation, for the temporal periodic case and the temporal and spatial periodic case, respectively.

Example 1. Temporal periodic case.

We consider the temporal periodic diffusion coefficient $D(t) = c_1(1+0.8\cos(\frac{\pi t}{6}))$, advection velocity $\nu(t) = c_0(1+0.8\cos(\frac{\pi t}{6}))$, maturation rate $\gamma(t) = r_1(1+0.7\sin(\frac{\pi t}{6}))$, production rate $\alpha(t) = r_2(1-0.7\sin(\frac{\pi t}{6}))$, carrying capacities $k_1(t) = b_1(1+0.7\sin(\frac{\pi t}{6}))$ and $k_2(t) = b_2(1-0.7\sin(\frac{\pi t}{6}))$, death rates $d_1(t) = e_1(1+0.7\sin(\frac{\pi t}{6}))$ and $d_2(t) = e_2(1-0.7\sin(\frac{\pi t}{6}))$, with period $\omega = 12$. For illustration, we choose $r_1 = 0.15$, $r_2 = 0.2$, $b_1 = 50$, $b_2 = 50$, $e_1 = 0.01$, $e_2 = 0.01$. When $c_0 = 0.5$ and $c_1 = 1.1$, we have $c_+^* = 19.2543$ and $c_-^* = 7.4282$; When $c_0 = 1.5$ and $c_1 = 1.1$, we have $c_+^* = 31.2036$ and $c_-^* = -0.6161$. Figure 6.1(a) shows the spreading speeds c_+^* and c_-^* as functions of c_0, which is exactly the average advection velocity $[\nu] = \frac{1}{\omega}\int_0^\omega \nu(t)dt$, with fixed $c_1 = 1.1$; Figure 6.1(b) shows a plot of the spreading speeds c_+^* and c_-^* as functions of c_1, which is exactly the average advection diffusion coefficient $[D] = \frac{1}{\omega}\int_0^\omega D(t)dt$, with fixed $c_0 = 0.5$.

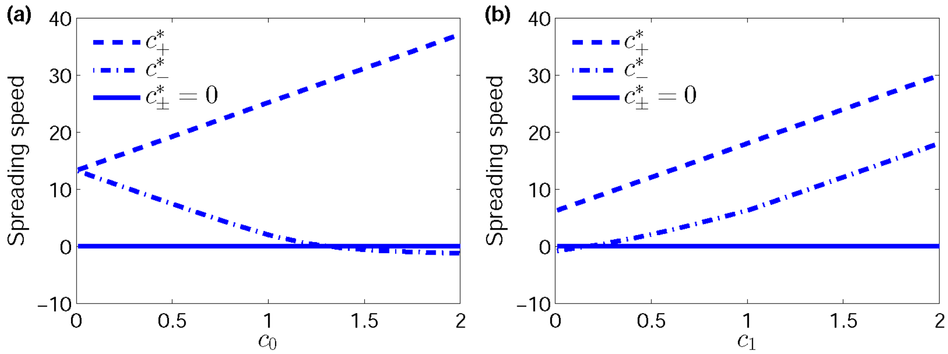

Figure 6.1: **Spreading speeds.** Leftward spreading speed (c_-^*) and rightward spreading speed (c_+^*): (a) as functions of the average advection velocity $[\nu]$ (that is c_0); (b) as functions of the average diffusion coefficient $[D]$ (that is c_1).

We consider different initial distribution functions for the mature female mosquitoes $u_1(x,t)$ and aquatic mosquitoes $u_2(x,t)$, and observe, by numerical simulations, the evolution of these populations. We consider a finite interval $[-L^*, L^*]$ with sufficiently large L^* and non-flux boundary conditions (we choose $L^* = 100$ in follows). First, to obtain rightward traveling wave solution, we choose the initial condition as follows:

$$u_1(x,t) = \begin{cases} 30 & \text{if } x \le -20 \\ \frac{3}{4}(20-x) & \text{if } |x| < 20, \\ 0 & \text{if } x \ge -20 \end{cases} \quad u_2(x,t) = \frac{9}{5}u_1(x,t). \tag{6.1}$$

Numerical simulation results about spatial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$ are shown in Figure 6.2, which indicates that the population of all mosquitoes persist.

Figure 6.3 shows the spatial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$ with the following initial condition:

$$u_1(x,t) = \begin{cases} 24 & \text{if } |x| \le 20 \\ \frac{4}{5}(50-x) & \text{if } 20 < |x| < 50 \\ 0 & \text{if } x \ge 50 \end{cases} \quad u_2(x,t) = \frac{4}{3}u_1(x,t). \tag{6.2}$$

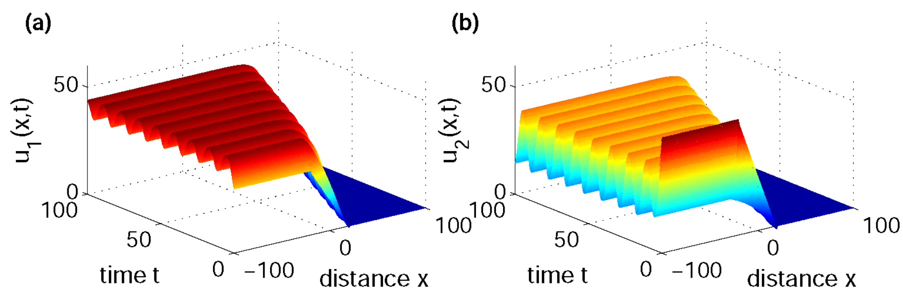

Figure 6.2: **The spacial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$.** The rightward periodic traveling waves observed (a) for u_1, and (b) for u_2, respectively.

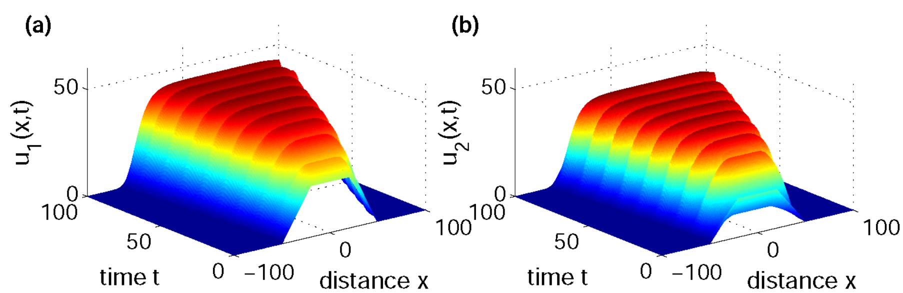

Figure 6.3: The spacial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$. The leftword and rightward periodic traveling waves observed (a) for u_1, and (b) for u_2, respectively.

Example 2. Temporal and spatial periodic case.

We next consider spatial and temporal periodic diffusion coefficient $D(x,t) = c_1(1+0.8\cos(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$, advection velocity $\nu(x,t) = c_0(1+0.8\cos(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$, maturation rate $\gamma(x,t) = r_1(1+0.7\sin(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$, production rate $\alpha(x,t) = r_2(1-0.7\sin(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$, carrying capacities $k_1(x,t) = b_1(1+0.7\sin(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$ and $k_2(x,t) = b_2(1-0.7\sin(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$, death rates $d_1(x,t) = e_1(1+0.7\sin(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$ and $d_2(x,t) = e_2(1-0.7\sin(\frac{\pi t}{6}))(1+0.5\cos(\frac{\pi t}{12}))$.

Figure 6.4(a) shows a plot of the spreading speeds c_+^* and c_-^* as functions of the advection velocity coefficient c_0; Figure 6.4(b) shows a plot of the spreading speeds c_+^* and c_-^* as functions of the diffusion coefficient c_1.

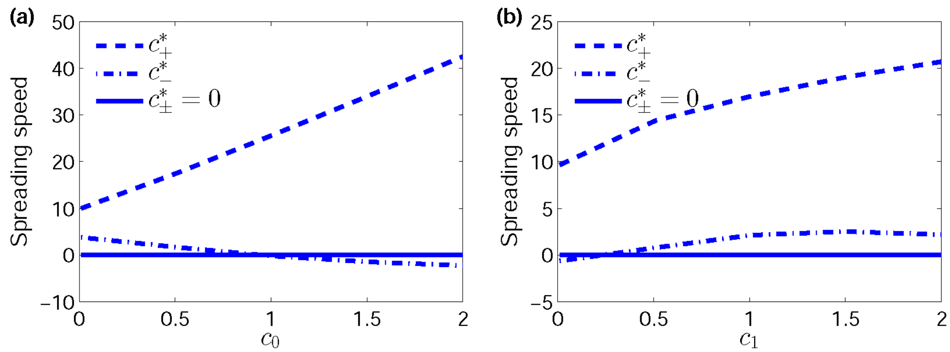

Figure 6.4: **Spreading speeds.** Leftward spreading speed (c_-^*) and rightward spreading speed (c_+^*): (a) as functions of the advection velocity coefficient c_0; (b) as functions of the diffusion coefficient c_1.

Figure 6.5 shows the spatial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$ with initial condition (6.1). Figure 6.6 shows the spatial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$ with initial condition (6.2), which indicates that the population of all mosquitoes persist with spatial periodic pattern.

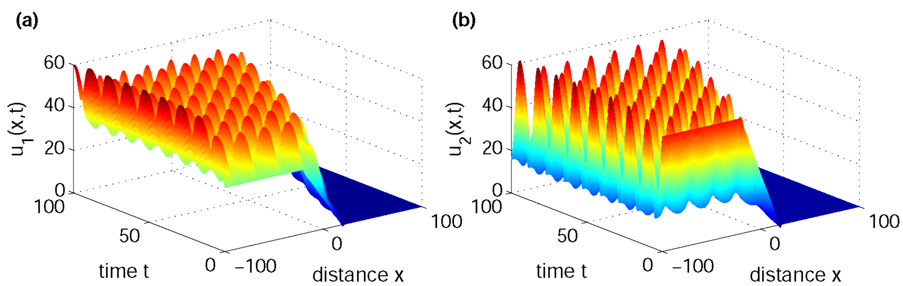

Figure 6.5: The spacial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$ with initial condition (6.1). The rightward periodic traveling waves observed for u_1 and u_2, respectively.

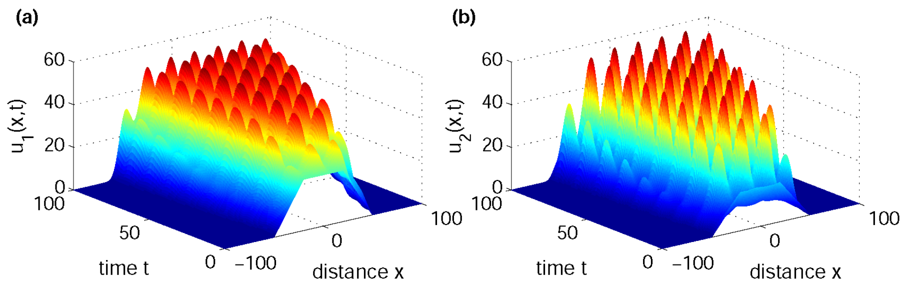

Figure 6.6: The spacial and temporal evolution of $u_1(x,t)$ and $u_2(x,t)$ with initial condition (6.2).

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