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Spatial dynamics of a periodic population model with dispersal*

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Abstract

This paper is devoted to the study of spatial dynamics of a class of periodic integro-differential equations which describe the population dispersal process via a dispersal kernel. By appealing to the theory of asymptotic speeds of spread and travelling waves for monotonic periodic semiflows, we establish the existence of the spreading speed c^* and the nonexistence of continuous periodic travelling wave solutions with wave speed $c < c^*$. We also prove the existence of left-continuous periodic travelling waves with wave speed $c \geqslant c^*$. In the autonomous case, the continuity of monotonic wave profiles with wave speed $c \geqslant c^*$ is obtained.

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1. Introduction

Population dispersal is a very common phenomenon which exists almost everywhere at any time. Due to the variations of the environmental and social conditions in different places, populations have to move for food, propagation, work (especially for humans), etc. As a result of dispersal, evolution dynamics, including the spatial distribution of a population and the spatial spread of a disease, may be greatly influenced. A typical example is the spread of diseases such as influenza, measles, malaria and SARS. Thus, the spatial dispersal is an important topic in population dynamics. To take into account the large-scale effects of a dispersal process on evolution dynamics, ordinary differential equations or difference equations are usually used (see, e.g. [2, 3, 26]). These models, however, represent the habitat by discrete

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patches and are appropriate only when we consider population jumps among some discrete patches. A traditional way to describe the evolution of population dispersal in continuous spaces is to use reaction–diffusion models (see, e.g. [1, 19, 31] and the references therein). However, reaction–diffusion models may underestimate the speeds of invasion [4, 10]. Further, there are more general dispersal processes than diffusion and advection as well as long-range effects.

Recently, integro-differential equations have been presented to study biological invasions and disease spread. Such a model, to some extent, describes population dispersal better than ordinary differential/difference equations or reaction–diffusion equations. This is because it takes into account the long-distance dispersal and describes the dispersion via a dispersal kernel, which specifies the probability that an individual moves from one location to another in a certain time interval as a function (e.g. [8, 9, 11, 15–17, 20, 28]). In particular, Medlock and Kot [16] investigated the effects of population dispersal using the DI epidemic model

$$\frac{\partial I}{\partial t} = \beta I(N - I) - DI + D\int_{\Omega} k(x, y)I(t, y)\,\mathrm{d}y, \tag{1.1}$$

where N is the density of the total population, $I(t, x)$ is the density of infective individuals of the population at the point $x \in \Omega$ at $t \geqslant 0$, $\beta \geqslant 0$ is the transmission rate, $D \geqslant 0$ is the rate at which infective individuals move from one location to another, and $k(x, y)$ is the dispersal kernel (i.e. the density function that prescribes the proportion of infectives leaving y to x). Lutscher, Pachepsky and Lewis [15] presented and analysed a stream population model

$$\frac{\partial u(t, x)}{\partial t} = f(u(t, x)) - \mu u(t, x) + \mu\int_{\Omega} k(x, y)u(t, y)\,\mathrm{d}y, \tag{1.2}$$

where $u(t, x)$ is the density of a stream population at the point $x \in \Omega$ at $t \geqslant 0$, $f(u)$ describes the population dynamics such as birth and death, $\mu \geqslant 0$ is the jumping rate and $k(x, y)$ is the dispersal kernel. Similar models were also studied by Fedotov [8] and Méndez *et al* [17].

The asymptotic speed of spread (in short, spreading speed) is an important ecological metric in a wide range of ecological applications. It can help determine how individuals of a population spread in a spatial environment. In particular, it can be used to estimate the rapidity of disease spread and be useful to guide policy decisions. This concept was first introduced by Aronson and Weinberger [1] for reaction–diffusion equations and has been developed greatly (see, e.g. [7, 12–14, 23–25, 27] and the references therein). Travelling wave solutions have also been investigated extensively for a variety of evolution systems (see, e.g. [6, 14, 16, 22, 25, 28, 29, 31] and the references therein). As far as model (1.1) is concerned, Medlock and Kot [16] derived the minimal wave speed by the 'linear conjecture' approach [18] and gave some approximation of the shape of travelling waves. Lutscher, Pachepsky and Lewis [15] also used the same way as in [16] to obtain the minimal wave speed for (1.2), and showed that under certain technical conditions on the asymmetric kernel $k(x, y)$, this minimal wave speed is the spreading speed in a weak sense (see (3.13) in [15]).

Note that (1.1) and (1.2) are special cases of the following general integro-differential equation:

$$\frac{\partial u(t, x)}{\partial t} = F(u(t, x)) + a\int_{\mathbb{R}} k(x, y)u(t, y)\,\mathrm{d}y, \tag{1.3}$$

where $u(t, x)$ is the spatial density of a population at the point $x \in \mathbb{R}$ at time $t \geqslant 0$, $F(u(t, x))$ is the reaction function which governs the population dynamics, $a \geqslant 0$ is the rate at which an individual leaves its current location and $k(x, y)$ is the dispersal kernel.

For simplicity, we neglect the birth and death of the population during the dispersal process and assume that $k(x, y)$ depends only on the distance between x and y, and then write it as

$k(x-y)$ (usually such a k is said to be 'isotropic'). Then we have the following system:

$$\frac{\partial u(t,x)}{\partial t} = F(u(t,x)) + a\int_{\mathbb{R}} k(x-y)u(t,y)\,\mathrm{d}y. \tag{1.4}$$

Define a probability measure $\mu(B)$ on $\mathbb{R}_+ \times \mathbb{R}$ by

$$\mu(B) = \int_B \chi_B(0,y)k(y)\,\mathrm{d}y,$$

where B is a Borel set in $\mathbb{R}_+ \times \mathbb{R}$ and χ_B is the characteristic function of B. It follows that

$$\mu * u(t,x) := \int_{s\in\mathbb{R}_+, y\in\mathbb{R}} u(t-s, x-y)\mu(\mathrm{d}s, \mathrm{d}y) = \int_{\mathbb{R}} u(t, x-y)k(y)\,\mathrm{d}y,$$

and (1.4) can be written as

$$\frac{\partial u(t,x)}{\partial t} = f(u, \mu * g(u)), \tag{1.5}$$

where $f(u,v) = F(u) + av$, $g(u) = u$. Schumacher [21] established the spreading speed and the existence and nonexistence of travelling wave solutions for (1.5) under appropriate conditions on f and g. We should point out that spreading speeds in [15, 21] were defined in a weak sense (see, e.g. (3.13) in [15]).

It is observed that time-varying environments (e.g. due to seasonal variation) affect population dynamics very much. This suggests that nonautonomous systems should be more realistic for some populations. Therefore, in this paper we consider the following periodic evolution equation:

$$\frac{\partial u(t,x)}{\partial t} = F(t, u(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)u(t,y)\,\mathrm{d}y, \tag{1.6}$$

where $u(t,x)$ is the spatial density of a population at the point $x \in \mathbb{R}$ at time $t \geqslant 0$, $F(t, u(t,x))$ is the reaction function which governs the population dynamics such as birth and death and other removal terms such as emigration of individuals at the point $x \in \mathbb{R}$ at time $t \geqslant 0$, $a(t) \geqslant 0$ is the rate at which an individual leaves its current location at time $t \geqslant 0$ and $k(x-y)$ is the dispersal kernel that describes the probability that an individual moves from point y to point x. Moreover, the two continuous functions F and a are ω-periodic in t for some $\omega > 0$ and $a(t) \not\equiv 0$.

We adopt the definition of spreading speeds in a strong sense (see theorem 3.5) and study the spreading speed and periodic travelling waves for (1.6). It seems to be difficult to apply the approach in [21] to the periodic equation (1.6). However, it is natural to use the theory in [27] for monotonic discrete-time systems to study the spreading speed for the time period map associated with (1.6). In order to carry over the results to (1.6), we appeal to the theory in [13] for monotonic periodic semiflows. More precisely, we use this theory to establish the existence of the asymptotic speed of spread c^* in a strong sense, its explicit formula, and the nonexistence of continuous periodic travelling waves with the wave speed $c < c^*$. We cannot apply this theory to prove the existence of continuous monotonic periodic travelling waves with the wave speed $c \geqslant c^*$. This is because the solution maps associated with (1.6) lack the compactness with respect to the compact open topology (see [13, 14]). However, we can use an abstract result in [30] on the existence of travelling waves for monotonic maps without compactness assumption to obtain the existence of monotonic left-continuous periodic travelling waves when $c \geqslant c^*$.

Note that the theory of spreading speeds and travelling waves were developed in [13, 14, 30] for monotonic systems under a very general setting, its application to a specific evolution system with spatial structure is nontrivial and challenging. For example, we need to prove that the periodic equation (1.6) admits the comparison principle (see theorem 2.3) and generates a periodic semiflow with respect to the compact open topology (see lemma 3.1). One should also choose appropriate linear equations to derive an explicit formula for the spreading speed (see proposition 3.4). Further, one needs to construct upper wave profiles for the time period map in order to obtain periodic travelling waves.

This paper is organized as follows. In section 2, we prove the well posedness and the comparison principle for (1.6). In section 3, by using the general results in [13, 14], we establish the existence of the spreading speed c^* for solutions of (1.6) with initial data having compact supports. In section 4, we obtain the nonexistence of continuous periodic travelling waves of (1.6) with the wave speed $c \in (0, c^*)$ by a result in [13]. We also show the existence of left-continuous periodic travelling waves of (1.6) with the wave speed $c \geqslant c^*$ by a result in [30]. In the autonomous case, we further prove the continuity of monotonic wave profiles with the wave speed $c \geqslant c^*$. In section 5, we give the appendix on spreading speeds and periodic travelling waves for scalar monotonic systems, which is adapted from [13, 30].

2. The well posedness and the comparison principle

In this section, we establish the existence, uniqueness and forward invariance of solutions and the comparison principle for system (1.6). Assume that

(H1) $F(t,u) = ug(t,u)$ with $g \in C(\mathbb{R}_+^2, \mathbb{R})$ and $g_u(t,u) < 0$ for all $(t,u) \in \mathbb{R}_+^2$, $\int_0^\omega (g(t,0)+a(t))\,\mathrm{d}t > 0$, and there exist $\hat{u} > 0$ and $L > 0$ such that $g(t,\hat{u}) + a(t) \leqslant 0$ for all $t \geqslant 0$, and $|F(t,u_1) - F(t,u_2)| \leqslant L|u_1 - u_2|$ for all $t \geqslant 0$, $u_1, u_2 \in W := [0, \hat{u}]$. Set $m_1 = \max_{t\in[0,\omega]} a(t)$.

(H2) $k(x)$ is a nonnegative Lebesgue measurable function on $\mathbb{R}$ with $k(-y) = k(y)$ and $\int_{\mathbb{R}} k(y)\,\mathrm{d}y = 1$, and the integral $\int_{\mathbb{R}} k(y)\mathrm{e}^{\alpha y}\,\mathrm{d}y$ converges for all $\alpha \in [0, \Delta)$, where $\Delta > 0$ is the abscissa of convergence and it may be infinity.

In biological literature, the following three types of birth rate functions are commonly used (see, e.g. [5]):

(1) $B(u) = \frac{p}{u^n + q}$, with $p > 0, q > 0, n > 0$;
(2) $B(u) = p\mathrm{e}^{-qu}$, with $p > 0, q > 0$;
(3) $B(u) = \frac{a}{u} + b$, with $a > 0, b > 0$.

Let the constant d be the death rate of the population. Then the reaction function $F(u) = uB(u) - du = u(B(u) - d)$. Thus, it is reasonable to assume that the general reaction function $F(t,u)$ has the form of $ug(t,u)$ with $g(t,u)$ being decreasing in $u > 0$. The condition $\int_0^\omega (g(t,0)+a(t))\,\mathrm{d}t > 0$ leads to the instability of zero solution, which implies that the population does not go to extinction in the spatially homogeneous environment. The inequality $g(t,\hat{u}) + a(t) \leqslant 0$ for all $t \geqslant 0$ guarantees that the population will not explode. The symmetry condition on the dispersal kernel $k(y) = k(-y)$ means that the proportion of moving population between two populations only depends on the distance between them. The convergence of the integral $\int_{\mathbb{R}} k(y)\mathrm{e}^{\alpha y}\,\mathrm{d}y$ indicates that the function $k(x)$ has an exponential decay at $x = \pm\infty$.

We consider the spatially homogeneous system associated with (1.6)

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = F(t, u(t)) + a(t)u(t). \tag{2.1}$$

By [32, theorem 3.1.2], it then follows that (2.1) has a positive ω-periodic solution $u^*(t)$, which is globally asymptotically stable for all initial values in $(0, \hat{u}]$.

The subsequent result is on the global existence, uniqueness and forward invariance of solutions of (1.6).

Theorem 2.1. *For any* $u_0 \in C(\mathbb{R}, W)$, *(1.6) has a unique solution* $u(t,x)$ *satisfying* $u(0,x) = u_0(x)$ *and* $u \in C(\mathbb{R}_+ \times \mathbb{R}, W)$.

Proof. Define an operator $Q[u]$ on $C(\mathbb{R}_+ \times \mathbb{R}, W)$ by

$$Q[u](t,x) = \alpha u(t,x) + F(t, u(t,x)) + a(t) \int_{\mathbb{R}} k(x-y) u(t,y)\, \mathrm{d}y, \qquad \alpha > 0.$$

By (H1), for any $u_1, u_2 \in [0, \hat{u}]$, $u_1 \geqslant u_2$, we have

$$\alpha u_1 + F(t,u_1) - \alpha u_2 - F(t,u_2) \geqslant (\alpha - L)(u_1 - u_2), \qquad \forall t \geqslant 0.$$

Then if $\alpha > L$, $\alpha u + F(t,u)$ is strictly increasing in u on $[0, \hat{u}]$ and hence Q is a nondecreasing map from $C(\mathbb{R}_+ \times \mathbb{R}, W)$ to $C(\mathbb{R}_+ \times \mathbb{R}, \mathbb{R}_+)$ with respect to the pointwise ordering. Clearly, (1.6) can be written as

$$\frac{\partial u(t,x)}{\partial t} = -\alpha u(t,x) + Q[u](t,x), \qquad \alpha > L. \tag{2.2}$$

Given an initial condition $u_0 \in C(\mathbb{R}, W)$, (2.2) is equivalent to the integral equation

$$u(t,x) = \mathrm{e}^{-\alpha t} u_0(x) + \int_0^t \mathrm{e}^{-\alpha(t-s)} Q[u](s,x)\, \mathrm{d}s.$$

Define $S := \{u \in C(\mathbb{R}_+ \times \mathbb{R}, W) : u(0,\cdot) = u_0\}$ and an operator $G : S \to C(\mathbb{R}_+ \times \mathbb{R}, \mathbb{R})$ by

$$G[u](t,x) = \mathrm{e}^{-\alpha t} u_0(x) + \int_0^t \mathrm{e}^{-\alpha(t-s)} Q[u](s,x)\, \mathrm{d}s, \qquad \forall (t,x) \in \mathbb{R}_+ \times \mathbb{R}.$$

Then

$$0 \leqslant G[u](t,x) \leqslant \mathrm{e}^{-\alpha t} \hat{u} + Q[\hat{u}] \int_0^t \mathrm{e}^{-\alpha(t-s)}\, \mathrm{d}s \leqslant \mathrm{e}^{-\alpha t} \hat{u} + \hat{u}(1 - \mathrm{e}^{-\alpha t}) = \hat{u}.$$

Thus, we have $G(S) \subseteq S$.

For any $u, v \in S$, define

$$d_\lambda(u,v) := \sup_{x \in \mathbb{R}, t \in \mathbb{R}_+} |u(t,x) - v(t,x)| \mathrm{e}^{-\lambda t},$$

where $\lambda > 0$ is a constant. Then S is a complete space with the metric d_λ. For any $u, v \in S$, we have

$$\begin{aligned}
&|G[u](t,x) - G[v](t,x)| \mathrm{e}^{-\lambda t} \\
&\quad = \left| \int_0^t \mathrm{e}^{-\alpha(t-s)} (Q[u](s,x) - Q[v](s,x))\, \mathrm{d}s \right| \mathrm{e}^{-\lambda t} \\
&\quad \leqslant \int_0^t \mathrm{e}^{-(\alpha+\lambda)(t-s)} d_\lambda(u,v) (\alpha + L + a(s) \int_{\mathbb{R}} k(x-y)\, \mathrm{d}y)\, \mathrm{d}s \\
&\quad \leqslant \frac{\alpha + L + m_1}{\alpha + \lambda} d_\lambda(u,v).
\end{aligned}$$

This implies that

$$d_\lambda(G[u], G[v]) \leqslant \frac{\alpha + L + m_1}{\alpha + \lambda} d_\lambda(u,v).$$

Choose $\lambda > 0$ large enough such that $(\alpha + L + m_1)/(\alpha + \lambda) < 1$. Then G is a contracting mapping on (S, d_λ). By the contracting mapping theorem, G has a unique fixed point in S, which is a solution of (1.6) with $u(0,\cdot) = u_0$. □

In order to establish the comparison principle for upper and lower solutions of (1.6), we first introduce the following concepts.

Definition 2.2. *A function* $\bar{u} \in C(\mathbb{R}_+ \times \mathbb{R}, W)$ *is called an upper solution of (1.6) if* $\partial\bar{u}/\partial t$ *exists and*

$$\frac{\partial \bar{u}(t,x)}{\partial t} \geqslant F(t, \bar{u}(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)\bar{u}(t,y)\,\mathrm{d}y.$$

A function $\underline{u} \in C(\mathbb{R}_+ \times \mathbb{R}, W)$ *is called a lower solution of (1.6) if* $\partial\underline{u}(t,x)/\partial t$ *exists and*

$$\frac{\partial \underline{u}(t,x)}{\partial t} \leqslant F(t, \underline{u}(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)\underline{u}(t,y)\,\mathrm{d}y.$$

Theorem 2.3. *Let* $\bar{u}(t,x)$ *and* $\underline{u}(t,x)$ *be upper and lower solutions of (1.6), respectively. If* $\bar{u}(0,\cdot) \geqslant \underline{u}(0,\cdot)$*, then* $\bar{u}(t,\cdot) \geqslant \underline{u}(t,\cdot)$ *for all* $t \geqslant 0$.

Proof. Define $v(t,x) = \bar{u}(t,x) - \underline{u}(t,x)$ for all $(t,x) \in \mathbb{R}_+ \times \mathbb{R}$, and $w(t) = \inf_{x\in\mathbb{R}} v(t,x)$ for all $t \geqslant 0$. Obviously, $w(t)$ is continuous in t and $w(0) \geqslant 0$. Now we show that $w(t) \geqslant 0$ for all $t \geqslant 0$. Assume, for the sake of contradiction, that this is not true. Then for $\delta > 0$, there is $t_0 > 0$ such that $w(t_0) < 0$ and

$$w(t_0)\mathrm{e}^{-\delta t_0} = \min_{t\in[0,t_0]} w(t)\mathrm{e}^{-\delta t} < w(\tau)\mathrm{e}^{-\delta\tau}, \qquad \forall \tau \in [0, t_0). \tag{2.3}$$

It follows that there exists a sequence of points $\{x_k\}_{k=1}^{\infty}$ such that $v(t_0, x_k) < 0$ for all $k \geqslant 1$ and $\lim_{k\to\infty} v(t_0, x_k) = w(t_0)$. Let $\{t_k\}_{k=1}^{\infty} \subseteq [0, t_0]$ be a sequence such that

$$v(t_k, x_k)\mathrm{e}^{-\delta t_k} = \min_{t\in[0,t_0]} v(t, x_k)\mathrm{e}^{-\delta t}. \tag{2.4}$$

For any $\varepsilon \in (0, t_0)$, let $m_\varepsilon = \min_{t\in[0,t_0-\varepsilon]} w(t)\mathrm{e}^{-\delta t}$. By (2.3), we have

$$\lim_{k\to\infty} v(t_0, x_k)\mathrm{e}^{-\delta t_0} = w(t_0)\mathrm{e}^{-\delta t_0} < m_\varepsilon.$$

Thus, there exists an integer K_ε such that for all $k \geqslant K_\varepsilon$,

$$v(t_0, x_k)\mathrm{e}^{-\delta t_0} < m_\varepsilon \leqslant w(t)\mathrm{e}^{-\delta t} \leqslant v(t, x_k)\mathrm{e}^{-\delta t}, \qquad \forall t \in [0, t_0 - \varepsilon].$$

By (2.4), we obtain

$$v(t_k, x_k)\mathrm{e}^{-\delta t_k} = \min_{t\in[0,t_0]} v(t, x_k)\mathrm{e}^{-\delta t} \leqslant v(t_0, x_k)\mathrm{e}^{-\delta t_0},$$

and hence, $t_k \in [t_0 - \varepsilon, t_0]$ for all $k \geqslant K_\varepsilon$. It then follows that, $\lim_{k\to\infty} t_k = t_0$. Since

$$v(t_0, x_k)\mathrm{e}^{-\delta t_0} \geqslant v(t_k, x_k)\mathrm{e}^{-\delta t_k} \geqslant w(t_k)\mathrm{e}^{-\delta t_k} \geqslant w(t_0)\mathrm{e}^{-\delta t_0},$$

we have

$$v(t_0, x_k)\mathrm{e}^{-\delta(t_0-t_k)} \geqslant v(t_k, x_k) \geqslant w(t_0)\mathrm{e}^{-\delta(t_0-t_k)}.$$

Letting $k \to \infty$, we obtain $\lim_{k\to\infty} v(t_k, x_k) = w(t_0)$. Then (2.4) implies that,

$$0 \geqslant \left.\frac{\partial(v(t,x_k)\mathrm{e}^{-\delta t})}{\partial t}\right|_{t=t_k^-} = \mathrm{e}^{-\delta t_k}\left(\frac{\partial v(t_k,x_k)}{\partial t} - \delta v(t_k,x_k)\right),$$

and hence, $(\partial v(t_k,x_k)/\partial t) \leqslant \delta v(t_k,x_k)$. Since $v(t_k,x_k) < 0$, we have

$$\begin{aligned}\frac{\partial v(t_k,x_k)}{\partial t} &= \frac{\partial \bar{u}(t_k,x_k)}{\partial t} - \frac{\partial \underline{u}(t_k,x_k)}{\partial t} \\ &= F(t_k, \bar{u}(t_k,x_k)) - F(t_k, \underline{u}(t_k,x_k)) + a(t_k)\int_{\mathbb{R}} k(x_k-y)(\bar{u}(t_k,y)\,\mathrm{d}y - \underline{u}(t_k,y))\,\mathrm{d}y \\ &\geqslant Lv(t_k,x_k) + a(t_k)\int_{\mathbb{R}} k(x_k-y)v(t_k,y)\,\mathrm{d}y.\end{aligned}$$

Then

$$0 \leqslant \frac{\partial v(t_k, x_k)}{\partial t} - Lv(t_k, x_k) - a(t_k)\int_{\mathbb{R}} k(x_k - y)v(t_k, y)\,dy$$
$$\leqslant (\delta - L)v(t_k, x_k) - a(t_k)\int_{\mathbb{R}} k(x_k - y)v(t_k, y)\,dy$$
$$\leqslant (\delta - L)v(t_k, x_k) - a(t_k)w(t_k)$$
$$\leqslant (\delta - L)v(t_k, x_k) - m_1 w(t_k).$$

Letting $k \to \infty$, we have $0 \leqslant (\delta - L - m_1)w(t_0)$. For $\delta > L + m_1$, this implies that $w(t_0) \geqslant 0$, a contradiction. Therefore, for any $t \geqslant 0$, we have $w(t) \geqslant 0$. Thus, $v(t, x) \geqslant 0$, and hence, $\bar{u}(t, \cdot) \geqslant \underline{u}(t, \cdot)$ for all $t \geqslant 0$. □

3. The asymptotic speed of spread

In this section, we use the theory in the appendix to establish the existence of the asymptotic speed of spread and its explicit formula.

Define a family of operators Q_t on $C(\mathbb{R}, W)$ by

$$Q_t[\varphi](x) := u(t, x), \qquad \forall x \in \mathbb{R}, \quad t \geqslant 0,$$

where $u(t, x)$ is the solution of (1.6) satisfying $u(0, x) = \varphi(x)$ for all $x \in \mathbb{R}$.

Lemma 3.1. *$\{Q_t\}_{t\geqslant 0}$ is a monotonic periodic semiflow on $C(\mathbb{R}, W)$.*

Proof. We first prove that Q_t is a periodic semiflow on $C(\mathbb{R}, W)$ in the sense of definition 5.3 in the appendix. Clearly, Q_t satisfies (i). Property (ii) follows from the existence and uniqueness of solutions to (1.6). It remains to prove (iii).

Given $\varphi \in C(\mathbb{R}, W)$. By the form of (1.6), it is easy to see that $\partial u(t, x)/\partial t$ is bounded for all $(t, x) \in \mathbb{R}_+ \times \mathbb{R}$ and hence, there exists $\bar{L} = \bar{L}(\varphi) > 0$ such that $| \partial u(t, x)/\partial t | \leqslant \bar{L}$. This implies that

$$| u(t_1, x) - u(t_2, x) | \leqslant \bar{L} \, | t_1 - t_2 |, \qquad \forall x \in \mathbb{R}, \quad t_1, t_2 \in \mathbb{R}_+.$$

Thus, $Q_t[\varphi] = u(t, \cdot)$ is continuous in $t \in \mathbb{R}_+$ with respect to the compact open topology. We further prove the following claim.

Claim. *For any $\varepsilon > 0$ and $t_0 > 0$, there exist $\delta = \delta(\varepsilon, t_0) > 0$ and $M = M(\varepsilon, t_0) > 0$ such that if $\varphi_1, \varphi_2 \in C(\mathbb{R}, W)$ with $| \varphi_1(x) - \varphi_2(x) | < \delta$ for all $x \in [z - M, z + M]$ for some $z \in \mathbb{R}$, then $| u_1(t, z) - u_2(t, z) | < \varepsilon$ for all $t \in [0, t_0]$, where $u_1(t, x)$ and $u_2(t, x)$ are solutions to (1.6) with initial functions φ_1 and φ_2, respectively.*

Note that (1.6) admits the spatial translation invariance, that is, if $u(t, x)$ is a solution to (1.6), then so is $u(t, x - x_0)$ for any $x_0 \in \mathbb{R}$. Thus, it suffices to prove the claim for $z = 0$. Let $w(t, x) = u_1(t, x) - u_2(t, x)$. Then $w(t, x)$ satisfies

$$\frac{\partial w(t, x)}{\partial t} = F(t, u_1(t, x)) - F(t, u_2(t, x)) + a(t)\int_{\mathbb{R}} k(x - y)w(t, y)\,dy.$$

Case 1. $\varphi_1 \geqslant \varphi_2$. By theorem 2.3, $u_1(t, x) \geqslant u_2(t, x)$ for all $t \geqslant 0$, $x \in \mathbb{R}$. Then $w(t, x) \geqslant 0$ and

$$\frac{\partial w(t, x)}{\partial t} \leqslant Lw(t, x) + a(t)\int_{\mathbb{R}} k(x - y)w(t, y)\,dy, \qquad \forall t \geqslant 0, \quad x \in \mathbb{R}.$$

We write the linear integro-differential system

$$\frac{\partial v(t,x)}{\partial t} = Lv(t,x) + a(t)\int_{\mathbb{R}} k(x-y)v(t,y)\,\mathrm{d}y \tag{3.1}$$

as a system of integral equations

$$v(t,x) = \mathrm{e}^{Lt}\varphi(x) + \int_0^t \mathrm{e}^{L(t-s)}a(s)\int_{\mathbb{R}} k(x-y)v(s,y)\,\mathrm{d}y\,\mathrm{d}s, \tag{3.2}$$

where $\varphi(x) = v(0,x) \in C(\mathbb{R}, W)$.

Define $V_0(t,x) = \mathrm{e}^{Lt}\varphi(x)$ and

$$V_m(t,x) = \mathrm{e}^{Lt}\varphi(x) + \int_0^t \mathrm{e}^{L(t-s)}a(s)\int_{\mathbb{R}} k(x-y)V_{m-1}(s,y)\,\mathrm{d}y\,\mathrm{d}s, \qquad \forall t \geqslant 0, \quad x \in \mathbb{R}, \quad m \geqslant 1. \tag{3.3}$$

By induction, we have

$$V_m(t,x) = \sum_{k=0}^{m} a_k(\varphi)(t,x),$$

where $a_0(\varphi)(t,x) = \mathrm{e}^{Lt}\varphi(x)$, $a_k(\varphi)(t,x) = \int_0^t \mathrm{e}^{L(t-s)}a(s)\int_{\mathbb{R}} k(x-y)a_{k-1}(\varphi)(s,y)\,\mathrm{d}y\,\mathrm{d}s$.

We define a map $P : C_{\hat{u}} \to C$ by

$$P[\varphi](x) = \int_{\mathbb{R}} k(x-y)\varphi(y)\,\mathrm{d}y, \qquad \forall \varphi \in C_{\hat{u}}, \quad x \in \mathbb{R}.$$

Then $P[0] = 0$. For any $\varepsilon > 0$ and $K > 0$, since $\int_{\mathbb{R}} k(y)\,\mathrm{d}y = 1$, there is an $M_0 > 0$ such that $\int_{|y|\geqslant M_0} k(y)\,\mathrm{d}y < (\varepsilon/2\hat{u})$. For $x \in [-K, K]$, we have

$$\begin{aligned} P[\varphi](x) &= \int_{\mathbb{R}} k(y)\varphi(x-y)\,\mathrm{d}y, \\ &= \int_{-M_0}^{M_0} k(y)\varphi(x-y)\,\mathrm{d}y + \int_{|y|\geqslant M_0} k(y)\varphi(x-y)\,\mathrm{d}y \\ &\leqslant 1 \cdot \max_{y\in[-M_0,M_0]} \varphi(x-y) + \frac{\varepsilon}{2}. \end{aligned}$$

Let $\delta = \varepsilon/2$. If $\varphi(x) < \delta$ on $x \in [-K - M_0, K + M_0]$, then

$$P[\varphi](x) < \frac{\varepsilon}{2} + \frac{\varepsilon}{2} = \varepsilon, \qquad \forall x \in [-K, K].$$

Thus, $P(\varphi)$ is continuous at $\varphi = 0$ with respect to the compact open topology.

By induction and the assumption $\int_{\mathbb{R}} k(x-y)\,\mathrm{d}y = 1$ for all $x \in \mathbb{R}$, we see that

$$a_k(\varphi)(t,x) \leqslant \mathrm{e}^{Lt}\frac{m_1^k t^k}{k!}P^k[\varphi](x) \leqslant \frac{\hat{u}\mathrm{e}^{Lt}m_1^k t^k}{k!},$$

for $(t,x) \in \mathbb{R}_+ \times \mathbb{R}$ for all $\varphi \in C_{\hat{u}}$. Thus, we have

$$V_m(t,x) \leqslant \sum_{k=0}^{m} \frac{\hat{u}\mathrm{e}^{Lt_0}m_1^k t_0^k}{k!}, \qquad \forall (t,x) \in [0,t_0] \times \mathbb{R}.$$

Hence, for any $t_0 > 0$, the sequence of functions $V_m(t,x)$ converges to a function $V(t,x) = \sum_{k=0}^{\infty} a_k(\varphi)(t,x)$ uniformly for $(t,x) \in [0,t_0] \times \mathbb{R}$. Letting $m \to \infty$ in (3.3), we see that $V(t,x)$ satisfies (3.2) and $V(0,x) = \varphi(x)$, and hence $V(t,x)$ is a solution of (3.1) with $V(0,\cdot) = \varphi$.

Suppose that $\bar{V}(t,x)$ is another solution of (3.1) with $\bar{V}(0,x) = \varphi(x)$. It follows that

$$|V(t,x) - \bar{V}(t,x)| = \left| \int_0^t \mathrm{e}^{L(t-s)} a(s) \int_{\mathbb{R}} k(x-y)(V(s,y) - \bar{V}(s,y))\,\mathrm{d}y\,\mathrm{d}s \right|$$
$$\leqslant \int_0^t \mathrm{e}^{L(t-s)} a(s) \int_{\mathbb{R}} k(x-y)|V(s,y) - \bar{V}(s,y)|\,\mathrm{d}y\,\mathrm{d}s.$$

Let $G(t) = \sup_{x\in\mathbb{R}, s\in[0,t]} |V(s,x) - \bar{V}(s,x)|$. Then

$$G(t) \leqslant \int_0^t \mathrm{e}^{L(t-s)} a(s) \int_{\mathbb{R}} k(x-y) G(s)\,\mathrm{d}y\,\mathrm{d}s = \int_0^t \mathrm{e}^{L(t-s)} a(s) G(s)\,\mathrm{d}s, \qquad \forall t \geqslant 0,$$

which implies that

$$G(t)\mathrm{e}^{-Lt} \leqslant m_1 \int_0^t \mathrm{e}^{-Ls} G(s)\,\mathrm{d}s \leqslant \varepsilon + m_1 \int_0^t \mathrm{e}^{-Ls} G(s)\,\mathrm{d}s, \qquad \forall \varepsilon > 0.$$

By the Gronwall inequality, this implies that $G(t)\mathrm{e}^{-Lt} \leqslant \varepsilon \mathrm{e}^{m_1 t}$ for all $\varepsilon > 0$, and hence $G(t) \equiv 0$. This proves the uniqueness of the solution of (3.1) with $V(0,\cdot) = \varphi$.

Given $t_0 > 0$, since $V_m(t,x) \to V(t,x)$ uniformly for $[0,t_0] \times \mathbb{R}$, it follows that for any $\varepsilon > 0$, there is an integer $N = N(t_0,\varepsilon) > 0$ such that $V(t,x) < V_N(t,x) + \varepsilon$ for all $x \in \mathbb{R}$, $t \in [0,t_0]$.

By the continuity of $P(\varphi)$ at $\varphi = 0$, we see that for any $k \geqslant 0$, $P^k(\varphi) : C_{\hat{u}} \to C$ is continuous at $\varphi = 0$ with respect to the compact open topology. Then there is a sufficiently large $M > 0$ and a small number $\delta > 0$, such that $P^k(\varphi)(0) < \varepsilon$ for all $0 \leqslant k \leqslant N$, provided that $\varphi \in C(\mathbb{R}, W)$ with $\varphi(x) < \delta$ for all $x \in [-M, M]$. Thus,

$$V_N(t,0) = \sum_{k=0}^{N} a_k(\varphi)(t,0) \leqslant \sum_{k=0}^{N} \mathrm{e}^{Lt} \frac{m_1^k t^k}{k!} P^k(\varphi)(0) < \varepsilon \mathrm{e}^{(m_1+L)t_0}, \qquad \forall t \in [0,t_0].$$

It follows that $V(t,0) < \varepsilon + \varepsilon \mathrm{e}^{(m_1+L)t_0}$ for all $t \in [0,t_0]$ provided that $\varphi \in C(\mathbb{R}, W)$ with $\varphi(x) < \delta$ for all $x \in [-M, M]$.

Let $\varphi(x) = \varphi_1(x) - \varphi_2(x)$. Then $\varphi \in C(\mathbb{R}, W)$. By the comparison principle, we have $w(t,x) \leqslant V(t,x)$ for all $t \geqslant 0$, $x \in \mathbb{R}$, where $V(0,x) = \varphi(x)$. Thus,

$$u_1(t,0) - u_2(t,0) = w(t,0) \leqslant V(t,0) < (1 + \mathrm{e}^{(m_1+L)t_0})\varepsilon, \qquad \forall t \in [0,t_0],$$

provided that $0 \leqslant \varphi_1(x) - \varphi_2(x) < \delta$ for all $x \in [-M, M]$.

Case 2. $\varphi_1 \not\geqslant \varphi_2$. In this case, we define

$$\hat{\varphi}_1(x) = \max\{\varphi_1(x), \varphi_2(x)\}, \quad \hat{\varphi}_2(x) = \min\{\varphi_1(x), \varphi_2(x)\}, \qquad \forall x \in \mathbb{R}$$

and let $\hat{u}_1(t,x)$ and $\hat{u}_2(t,x)$ be solutions to (1.6) through initial functions $\hat{\varphi}_1$ and $\hat{\varphi}_2$, respectively.

Then $\hat{\varphi}_1(x) - \hat{\varphi}_2(x) = |\varphi_1(x) - \varphi_2(x)|$ and $\hat{u}_2(t,x) \leqslant u_1(t,x)$, $u_2(t,x) \leqslant \hat{u}_1(t,x)$ for all $(t,x) \in \mathbb{R}_+ \times \mathbb{R}$. Thus, $|u_1(t,x) - u_2(t,x)| \leqslant \hat{u}_1(t,x) - \hat{u}_2(t,x)$. By case 1, we see that the claim also holds for φ_1 and φ_2 with $\varphi_1 \not\geqslant \varphi_2$.

By the claim above, $Q_t[\varphi]$ is continuous in φ with respect to the compact open topology, uniformly for t in any bounded interval. Thus, $Q_t[\varphi]$ is continuous in $(t,\varphi) \in \mathbb{R}_+ \times C(\mathbb{R}, W)$, i.e. Q_t satisfies definition 5.3(iii). Therefore, Q_t is a continuous ω-periodic semiflow on $C(\mathbb{R}, W)$. By theorem 2.3, the map Q_t is monotonic on $C(\mathbb{R}, W)$ for each $t > 0$. □

Lemma 3.2. *Assume that (H1) holds. Then for each $t > 0$, the solution map Q_t of (1.6) satisfies (A1)–(A3) in the appendix with $b_0 = \hat{u}$ and Q_ω satisfies (A4) in the appendix with $b_0 = u^*(0)$.*

Proof. By lemma 3.1, it is easy to see that Q_t satisfies (A1)–(A3) with $b_0 = \hat{u}$. Let $\hat{Q}_t = Q_t|_{[0,\hat{u}]}$. Then $\hat{Q}_t : [0, \hat{u}] \to [0, \hat{u}]$ is the ω-periodic semiflow generated by (2.1). Since (2.1) is a scalar equation, the uniqueness of solutions implies that $\hat{Q}_t$ is strongly monotonic on $[0, \hat{u}]$. Note that (2.1) has a positive ω-periodic solution $u^*(t)$ which is globally asymptotically stable in $(0, \hat{u}]$. We see that $\hat{Q}_\omega$ is strongly monotonic on $[0, \hat{u}]$, and has only two fixed points 0 and $u^*(0)$ in $[0, \hat{u}]$. Thus, by the Dancer–Hess connecting orbit lemma (see, e.g. [32]), the map $\hat{Q}_\omega$ admits a strongly monotonic full orbit connecting 0 to $u^*(0)$. Therefore, Q_ω satisfies (A4) with $b_0 = u^*(0)$. □

Consider the linearized system of (1.6) at the zero solution

$$\begin{aligned}\frac{\partial u(t,x)}{\partial t} &= g(t,0)u(t,x) + a(t)\int_{\mathbb{R}} k(x-y)u(t,y)\,\mathrm{d}y \\ &= g(t,0)u(t,x) + a(t)\int_{\mathbb{R}} k(y)u(t,x-y)\,\mathrm{d}y.\end{aligned} \tag{3.4}$$

For any $\alpha \in (0, \Delta)$, let $u(t,x) = \mathrm{e}^{-\alpha x}v(t)$. Substituting $u(t,x)$ into (3.4) yields

$$\mathrm{e}^{-\alpha x}v'(t) = g(t,0)\mathrm{e}^{-\alpha x}v(t) + a(t)\int_{\mathbb{R}} k(y)\mathrm{e}^{-\alpha(x-y)}v(t)\,\mathrm{d}y.$$

Then

$$v'(t) = A(\alpha,t)v(t), \tag{3.5}$$

where

$$A(\alpha,t) = g(t,0) + a(t)\int_{\mathbb{R}} k(y)\mathrm{e}^{\alpha y}\,\mathrm{d}y. \tag{3.6}$$

Thus, if $v(t)$ is a solution of (3.5), then $u(t,x) = \mathrm{e}^{-\alpha x}v(t)$ is a solution of (3.4).

Note that the solution of (3.5) can be expressed as $v(t, v_0) = v_0\mathrm{e}^{\int_0^t A(\alpha,s)\,\mathrm{d}s}$ for all $v_0 \in \mathbb{R}$. Define

$$B_\alpha^t[v_0] := M_t[v_0\mathrm{e}^{-\alpha x}](0) = v(t,v_0) = v_0\mathrm{e}^{\int_0^t A(\alpha,s)\,\mathrm{d}s},$$

where M_t is the linear solution map defined by (3.4) and $v(t, v_0)$ is the solution of (3.5) with $v(0, v_0) = v_0$. Therefore, B_α^t is the solution map associated with (3.5) on $\mathbb{R}$ and B_α^t is strongly positive for each $t > 0$ in the sense that $B_\alpha^t[v_0] > 0$ for all $v_0 > 0$. Then $B_\alpha^\omega(v_0) = v_0\mathrm{e}^{\int_0^\omega A(\alpha,s)\,\mathrm{d}s}$. Let $\gamma(\alpha) := \mathrm{e}^{\int_0^\omega A(\alpha,s)\,\mathrm{d}s}$, and define a function

$$\Phi(\alpha) := \frac{1}{\alpha}\ln\gamma(\alpha) = \frac{1}{\alpha}\ln \mathrm{e}^{\int_0^\omega A(\alpha,s)\,\mathrm{d}s} = \frac{\int_0^\omega g(t,0)\mathrm{d}t + \int_0^\omega a(t)\,\mathrm{d}t\int_{\mathbb{R}} k(y)\mathrm{e}^{\alpha y}\,\mathrm{d}y}{\alpha}. \tag{3.7}$$

By [14, theorem 3.8], we have the following result.

Lemma 3.3. *The following statements are valid*

(1) $\Phi(\alpha) \to \infty$ *as* $\alpha \to 0$.
(2) $\Phi(\alpha)$ *is decreasing near* 0.
(3) $\Phi'(\alpha)$ *changes its sign at most once on* $(0, \Delta)$.
(4) $\lim_{\alpha\to\Delta^-}\Phi(\alpha)$ *exists, where the limit may be infinite.*

Proposition 3.4. *Assume that (H1) and (H2) hold. Let* c_ω^* *be the asymptotic speed of spread of* Q_ω. *Then* $c_\omega^* = \inf_{0<\alpha<\Delta}\Phi(\alpha)$.

Proof. By (H1) and the definitions of $A(\alpha, t)$ and $\gamma(\alpha)$, we see that

$$\gamma(0) = e^{\int_0^\omega A(0,s)\,ds} = e^{\int_0^\omega (g(s,0)+a(s)\int_{\mathbb{R}} k(y)\,dy)\,ds} = e^{\int_0^\omega (g(s,0)+a(s))\,ds} > 1,$$

and hence, condition (B7) in the appendix is satisfied.

We first consider the case where $\Delta = \infty$. Since $\int_{\mathbb{R}} k(y)\,dy = 1$, i.e. $2\int_0^\infty k(y)\,dy = 1$, there is a sufficiently small $y_0 > 0$ such that $\int_{y_0}^\infty k(y)\,dy > 0$. Then

$$\int_{\mathbb{R}} e^{\alpha y} k(y)\,dy \geqslant \int_{y_0}^\infty e^{\alpha y} k(y)\,dy \geqslant e^{\alpha y_0} \int_{y_0}^\infty k(y)\,dy > 0,$$

and hence,

$$\lim_{\alpha\to\infty} \Phi(\alpha) = \lim_{\alpha\to\infty} \frac{\int_0^\omega a(t)\int_{\mathbb{R}} k(y) e^{\alpha y}\,dy\,dt}{\alpha} \geqslant \int_{y_0}^\infty k(y)\,dy \cdot \int_0^\omega a(t)\,dt \cdot \lim_{\alpha\to\infty} \frac{e^{\alpha y_0}}{\alpha} = \infty.$$

Thus, the infimum of $\Phi(\alpha)$ is attained at some value $\bar{\alpha} \in (0, \infty)$.

Note that M_ω and B_α^ω satisfy (B1)–(B7) in the appendix and that (H1) implies $F(t, u) \leqslant g(t, 0)u$ for all $u \geqslant 0$. By the comparison theorem, we have $Q_\omega[\varphi] \leqslant M_\omega[\varphi]$ for $\varphi \in C_{u^*(0)}$. Thus, theorem 5.2 implies that $c_\omega^* \leqslant \inf_{0<\alpha<\infty} \Phi(\alpha)$.

By (H1), $\lim_{u\to 0^+} (F(t, u)/u) = g(t, 0)$ uniformly for $t \in [0, \omega]$. It then follows that for any $\varepsilon \in (0, 1)$, there exists $\delta > 0$ such that $F(t, u) > (g(t, 0) - \varepsilon)u$ for all $0 < u < \delta$, $t \in [0, \omega]$. Moreover, there is $\eta = \eta(\delta) > 0$ such that for any $\varphi \in C_\eta$, we have

$$0 \leqslant Q_t[\varphi](x) \leqslant Q_t[\eta] < \delta, \qquad \forall x \in \mathbb{R}, \quad t \in [0, \omega].$$

Thus, for any $\varphi \in C_\eta$, the solution $u(t, x)$ to (1.6) through the initial function φ satisfies

$$\frac{\partial u(t,x)}{\partial t} \geqslant (g(t, 0) - \varepsilon)u + a(t)\int_{\mathbb{R}} k(x - y)u(t, y)\,dy, \qquad \forall x \in \mathbb{R}, \quad t \in [0, \omega].$$

Let M_t^ε, $t \geqslant 0$, be the solution maps associated with the linear system

$$\frac{\partial u(t,x)}{\partial t} = (g(t, 0) - \varepsilon)u + a(t)\int_{\mathbb{R}} k(x - y)u(t, y)\,dy.$$

The comparison principle implies that $M_t^\varepsilon[\varphi] \leqslant Q_t[\varphi]$ for all $\varphi \in C_\eta$, $t \in [0, \omega]$. In particular, $M_\omega^\varepsilon[\varphi] \leqslant Q_\omega[\varphi]$ for all $\varphi \in C_\eta$. A similar analysis can be made for M_t^ε as for M_t. It follows from theorem 5.2 that $\inf_{0<\alpha<\infty} \Phi_\varepsilon(\alpha) \leqslant c_\omega^*$.

By two estimates of c_ω^* above, we have

$$\inf_{0<\alpha<\infty} \Phi_\varepsilon(\alpha) \leqslant c_\omega^* \leqslant \inf_{0<\alpha<\infty} \Phi(\alpha), \qquad \forall \varepsilon \in (0, 1).$$

Letting $\varepsilon \to 0$, we then obtain $c_\omega^* = \inf_{0<\alpha<\infty} \Phi(\alpha)$.

In the case where $\Delta < \infty$, we define a sequence of kernels $k_m(x)$ by $k_m(x) = k(x)$ if $|x| \leqslant m$, and $k_m(x) = 0$ if $|x| > m$. For sufficiently large m, let $c_\omega^*(m)$ be the spreading speed of the period map of (1.6) with $k(x)$ replaced by $k_m(x)$. It then follows that $c_\omega^* = \lim_{m\to\infty} c_\omega^*(m)$. Since $k_m(x)$ has compact support, using the formula for $c_\omega^*(m)$, we further obtain $c_\omega^* = \inf_{0<\alpha<\Delta} \Phi(\alpha)$. □

The following result shows that $c^* := (c_\omega^*/\omega) = (1/\omega) \inf_{0<\alpha<\Delta} \frac{\int_0^\omega A(\alpha,s)\,ds}{\alpha}$ is the spreading speed of solutions of (1.6) with initial functions having compact supports.

Theorem 3.5. *Assume that (H1) and (H2) hold and let* $c^* = c^*_\omega/\omega$ *and* $u(t,x)$ *be the solution to (1.6) with initial function* $\varphi \in C_{u^*(0)}$. *Then the following statements are valid:*

(1) For any $c > c^*$, *if* $\varphi(x) = 0$ *for x outside a bounded interval, then* $\lim_{t\to\infty, |x|\geqslant ct} u(t,x) = 0$.

(2) For any $0 < c < c^*$, *there is a positive number r such that if* $\varphi(x) > 0$ *for x on an interval of length* $2r$, *then* $\lim_{t\to\infty,|x|\leqslant ct}(u(t,x) - u^*(t)) = 0$.

(3) In the case where $a(t) > 0$ *for all* $t \in \mathbb{R}$, *for any* $c \in (0, c^*)$, *if* $\varphi \not\equiv 0$, *then* $\lim_{t\to\infty,|x|\leqslant ct}(u(t,x) - u^*(t)) = 0$.

Proof. The conclusion (1) follows from theorem 5.4.

By (H1), we have $F(t,u) \leqslant g(t,0)u$ for all $u \in [0, u^*(0)]$. Then the proof of proposition 3.4 implies that there is a sequence of linear operators $\{M_n\}_{n=1}^{+\infty}$ with $\varepsilon_n = (1/n)$ for all $n \in \mathbb{N}$, such that each $M_n[\varphi] \leqslant Q_\omega[\varphi]$ for all $\varphi \in C_{\sigma_n}$, for some $\sigma_n > 0$, $n \in \mathbb{N}$. Moreover, each M_n satisfies (B1)–(B7) in the appendix and the spreading speed c^*_n of M_n converges to c^*_ω as $n \to \infty$. Let $c < c^*$ be given. It then follows from [14, theorem 3.5] that r_σ can be chosen to be independent of $\sigma > 0$. Thus, theorem 5.4 implies the conclusion (2).

In the case where $a(t) > 0$ for all $t \in \mathbb{R}$, we have $m_2 := \min_{t\in[0,\omega]} a(t) > 0$. To prove the conclusion (3), we need the following claim on the strong positivity of solutions.

Claim. *For any* $\varphi \in C_{\hat{u}}$ *with* $\varphi \not\equiv 0$, *the solution of (1.6) through* φ *satisfies* $u(t,x;\varphi) > 0$ *for all* $(t,x) \in (0,+\infty) \times \mathbb{R}$.

Indeed, for a given $\varphi \in C_{\hat{u}}$ with $\varphi \not\equiv 0$, we assume, without loss of generality, that $\varphi(x) > 0$ for all $x \in [-r, r]$ for some $r > 0$. Let $u(t,x)$ be the solution to (1.6) with initial function φ. It follows from the continuity of $u(t,x)$, there is an $\varepsilon > 0$ such that $u(t,x) > 0$ for all $(t,x) \in [0,\varepsilon] \times (-r, r)$.

Let α be sufficiently large such that $\alpha u + F(t,u)$ is increasing in $u \in [0, \hat{u}]$. Then $\alpha u + F(t,u) \geqslant 0$ for all $u \in [0,\hat{u}]$ and $t \geqslant 0$. By the proof of theorem 2.1, we have

$$
\begin{aligned}
u(t,x) &= \varphi(x)\mathrm{e}^{-\alpha t} + \int_0^t \mathrm{e}^{-\alpha(t-s)}[\alpha u(s,x) + F(s,u(s,x)) + a(s)\int_{\mathbb{R}} k(x-y)u(s,y)\,\mathrm{d}y]\,\mathrm{d}s \\
&\geqslant \int_0^t \mathrm{e}^{-\alpha(t-s)}[\alpha u(s,x) + F(s,u(s,x)) + a(s)\int_{\mathbb{R}} k(x-y)u(s,y)\,\mathrm{d}y]\,\mathrm{d}s \\
&\geqslant m_2 \int_0^t \mathrm{e}^{-\alpha(t-s)} \int_{\mathbb{R}} k(x-y)u(s,y)\,\mathrm{d}y\,\mathrm{d}s.
\end{aligned}
$$

Set $[a_0, b_0] = [-r, r]$. Since $\int_{\mathbb{R}} k(y)\,\mathrm{d}y = 1$, there exist p and r_0 with $r_0 > 0$, such that $k(y) > 0$ for almost every $y \in (p, p + r_0)$. Then we have $\int_0^t \int_{\mathbb{R}} \mathrm{e}^{-\alpha(t-s)} k(x-y)u(s,y)\,\mathrm{d}y\,\mathrm{d}s > 0$ for any $t \in (0,\varepsilon]$ and $x \in (a_0 + p, b_0 + p + r_0)$, which implies that $u(t,x) > 0$ for all $t \in (0,\varepsilon]$, $x \in (a_0 + p, b_0 + p + r_0)$. By induction, $u(t,x) > 0$ for all $(t,x) \in (0,\varepsilon] \times (a_0 + mp, b_0 + mp + mr_0)$ for all $m \geqslant 1$, $m \in \mathbb{Z}$. Let $a_m = a_0 + mp$, $b_m = b_0 + mp + mr_0$. Thus, $b_m - a_m \to \infty$ as $m \to \infty$ and there exists an integer $m^* > 0$ such that $a_{m+1} - b_m < 0$ for all $m \geqslant m^*$. Let $a^* = a_{m^*}$. It follows that $u(t,x) > 0$ for all $x \in \cup_{m\geqslant m^*}(a_m, b_m) = (a^*, +\infty)$ and $t \in (0,\varepsilon]$. Since $k(-y) = k(y)$, we have $k(y) > 0$ for almost every $y \in (-p - r_0, -p)$. Then $(x - (-p), x - (-p - r_0)) \cap (a^*, +\infty) \neq \emptyset$ for every $x \in (a^* - p - r_0, +\infty)$. It follows that $u(t,x) > 0$ for $t \in (0,\varepsilon]$ and $x \in (a^* - p - r_0, +\infty)$. By induction, $u(t,x) > 0$ for all $(t,x) \in (0,\varepsilon] \times (a^* - mp - mr_0, +\infty)$ for all $m \geqslant 0$, which implies that $u(t,x) > 0$ for all $(t,x) \in (0,\varepsilon] \times \mathbb{R}$.

By (1.6), we have

$$\frac{\partial u(t,x)}{\partial t} \geqslant F(t, u(t,x)), \qquad \forall t \geqslant 0, \quad x \in \mathbb{R}.$$

Given $x \in \mathbb{R}$. Let $w(t)$, $t \geqslant \varepsilon$, be the unique solution of the ordinary differential system $(\mathrm{d}w/\mathrm{d}t) = F(t, w)$ satisfying $w(\varepsilon) = u(\varepsilon, x) > 0$. Then the standard comparison principle implies that $u(t,x) \geqslant w(t) > 0$, for all $t \geqslant \varepsilon$. Thus, $u(t,x) > 0$ for all $(t,x) \in [\varepsilon, +\infty) \times \mathbb{R}$. Consequently, $u(t,x) > 0$ for all $(t,x) \in (0, +\infty) \times \mathbb{R}$. This completes the proof of the claim.

For any $\varphi \in C_{u^*(0)}$ with $\varphi \not\equiv 0$, we fix $t_0 > 0$ and take $u(t_0, \cdot)$ as a new initial value for $u(t,x)$. By the above claim, we have $u(t_0, x) > 0$ for all $x \in \mathbb{R}$, and hence, the conclusion (3) follows from the conclusion (2). □

4. Travelling waves

In this section, we show that the spreading speed c^* is also the minimal wave speed for monotonic periodic travelling waves.

Recall that $u(t,x) = U(t, x + ct)$ is said to be an ω-periodic travelling wave of (1.6) connecting 0 to $u^*(t)$ provided that it is a solution of (1.5), $U(t, \xi)$ is ω-periodic in t, and $U(t, -\infty) = 0$ and $U(t, \infty) = u^*(t)$ uniformly for $t \in [0, \omega]$.

Note that in sections 2 and 3, we have verified all assumptions in theorem 5.5. Consequently, we have the following result on the nonexistence of periodic travelling waves of (1.6).

Theorem 4.1. *Assume that (H1) and (H2) hold. Let c^*_ω be the asymptotic speed of spread of Q_ω and $c^* = c^*_\omega/\omega$. Then for any $c \in (0, c^*)$, system (1.6) admits no continuous ω-periodic travelling wave solution $\phi(t, x + ct)$ connecting 0 and $u^*(t)$.*

Next, we apply theorem 5.6 to prove the existence of left-continuous periodic travelling waves for (1.6) when the wave speed $c \geqslant c^*$.

By the standard theory of ordinary differential equations in Banach spaces, it follows that for any u_0 in $L^\infty(\mathbb{R})$, there exists a unique solution $u(t,x)$ to (1.6) with $u(t, \cdot) \in L^\infty(\mathbb{R})$ for all $t \geqslant 0$.

Proposition 4.2. *Suppose that $u_1, u_2 \in C^1([0,T], L^\infty(\mathbb{R}))$ for some $T \in (0, +\infty)$ and that for any $t \in [0,T]$, there holds*

$$u_{1,t} - \left[F(t, u_1(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)u_1(t,y)\,\mathrm{d}y\right] \leqslant u_{2,t} - \left[F(t, u_2(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)u_2(t,y)\,\mathrm{d}y\right]$$

almost everywhere in $x \in \mathbb{R}$. Then, $u_1(T,x) \leqslant u_2(T,x)$ almost everywhere in $x \in \mathbb{R}$ if $u_1(0,x) \leqslant u_2(0,x)$ almost everywhere in $x \in \mathbb{R}$.

Proof. We prove this proposition by similar arguments as in the proof of [30, proposition 18]. Let

$$K = -\inf_{t\in[0,\omega], h>0, u\in\mathbb{R}} \frac{F(t, u+h) - F(t,u)}{h}$$

and

$$v(t) = \mathrm{e}^{Kt}(u_2 - u_1)(t), \qquad \forall t \in [0, T].$$

Then $v \in C^1([0, T], L^\infty(\mathbb{R}))$ with $v(0) = (u_2 - u_1)(0) \geqslant 0$ almost everywhere in $x \in \mathbb{R}$, and

$$\begin{aligned}\frac{\mathrm{d}v}{\mathrm{d}t} &= K\mathrm{e}^{Kt}(u_2 - u_1)(t) + \mathrm{e}^{Kt}(u_{2,t} - u_{1,t}) \\ &= Kv(t) + \mathrm{e}^{Kt}\alpha(t) + a(t)\int_{\mathbb{R}} k(x-y)v(t,y)\,\mathrm{d}y + \mathrm{e}^{Kt}(F(t,u_2) - F(t,u_1)) \\ &= Kv(t) + \mathrm{e}^{Kt}\alpha(t) + a(t)\int_{\mathbb{R}} k(x-y)v(t,y)\,\mathrm{d}y + \mathrm{e}^{Kt}(F(t,u_1(t) \\ &\quad + \mathrm{e}^{-Kt}v(t)) - F(t,u_1)),\end{aligned}$$

where

$$\begin{aligned}\alpha(t) = &\left(u_{2,t} - \left[F(t,u_2(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)u_2(t,y)\,\mathrm{d}y\right]\right) \\ &-\left(u_{1,t} - \left[F(t,u_1(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)u_1(t,y)\,\mathrm{d}y\right]\right).\end{aligned}$$

Define

$$\begin{aligned}G(t,w) = &Kw(t) + \mathrm{e}^{Kt}\alpha(t) + a(t)\int_{\mathbb{R}} k(x-y)w(t,y)\,\mathrm{d}y + \mathrm{e}^{Kt}(F(t,u_1(t) \\ &+ \mathrm{e}^{-Kt}w(t)) - F(t,u_1)).\end{aligned}$$

Then $v(t)$ satisfies

$$\frac{\mathrm{d}v}{\mathrm{d}t} = G(t,v).$$

Let $\bar{v} \in C^1([0, T], L^\infty(\mathbb{R}))$ be a solution to

$$\bar{v}(t) = v(0) + \int_0^t \max\{G(s,\bar{v}(s)), 0\}\,\mathrm{d}s.$$

Then for any $t \in [0, T]$, $\bar{v}(t,x) \geqslant v(0,x) \geqslant 0$ almost everywhere in $x \in \mathbb{R}$. By the definition of K and the positivity of $\alpha(t)$ and $\bar{v}(t)$, it is easy to see that $G(t,\bar{v}) \geqslant 0$ almost everywhere in $x \in \mathbb{R}$, for any $t \in [0, T]$. Therefore,

$$\bar{v}(t) = v(0) + \int_0^t G(s,\bar{v}(s))\,\mathrm{d}s,$$

and hence, $\bar{v}(t)$ is a solution to $(\mathrm{d}v/\mathrm{d}t) = G(t,v)$ with $\bar{v}(0) = v(0)$. That is, $\bar{v} \equiv v$. This implies that

$$(u_2 - u_1)(T,x) = \mathrm{e}^{-KT}v(T,x) = \mathrm{e}^{-KT}\bar{v}(T,x) \geqslant 0$$

almost everywhere in $x \in \mathbb{R}$. □

Define

$\mathcal{D} = \{u : u$ is a nondecreasing and left-continuous function on $\mathbb{R}$ with $0 \leqslant u \leqslant \hat{u}\}$.

By similar arguments as in the proof of [30, proposition 13], we obtain the following result:

Proposition 4.3. *For any $u_0 \in \mathcal{D}$, (1.6) admits a solution $u(t,x)$ through u_0 with $u(t,\cdot) \in \mathcal{D}$ for all $t \geqslant 0$.*

By propositions 4.2 and 4.3, it follows that for any $t \geqslant 0$, the solution map Q_t of (1.6) satisfies $Q_t[\mathcal{D}] \subseteq \mathcal{D}$ and that Q_t is nondecreasing on $\mathcal{D}$. To consider the Poincaré map Q_ω, we further define

$\mathcal{M} := \{u : u$ is a nondecreasing and left-continuous function on $\mathbb{R}$ with $0 \leqslant u \leqslant u^*(0)\}$.

It is easy to see that $Q_\omega(\mathcal{M}) \subseteq \mathcal{M}$. Further, we have the following result.

Proposition 4.4. *$Q_\omega : \mathcal{M} \to \mathcal{M}$ satisfies assumptions (i)–(iv) in theorem 5.6.*

Proof.

(i) Suppose that $u^0 \in \mathcal{M}$ and $\{u_k^0\}_{k\in\mathbb{N}} \subseteq \mathcal{M}$ with $u_k^0 \to u^0$ uniformly on every bounded interval on $\mathbb{R}$ as $k \to \infty$. Define

$$G(u)(t,x) = \alpha u(t,x) + F(t,u(t,x)) + a(t)\int_{\mathbb{R}} k(x-y)u(t,y)\,\mathrm{d}y, \qquad \forall u \in \mathcal{M},$$

for $\alpha > L$. Then G is nondecreasing in $\mathcal{M}$ and (1.6) can be written as

$$\frac{\partial u(t,x)}{\partial t} = -\alpha u(t,x) + G(u)(t,x),$$

which is equivalent to

$$u(t,x) = \mathrm{e}^{-\alpha t}u(0,x) + \int_0^t \mathrm{e}^{-\alpha(t-s)}G(u)(s,x)\,\mathrm{d}s,$$

where $u(0,\cdot) \in \mathcal{M}$ is the initial function. Then the solutions $u_k(t,x)$ and $u(t,x)$ to (1.6) through initial functions u_k^0 and u^0 satisfy

$$u_k(t,x) = \mathrm{e}^{-\alpha t}u_k^0(x) + \int_0^t \mathrm{e}^{-\alpha(t-s)}G(u_k)(s,x)\,\mathrm{d}s, \qquad \forall k \geqslant 1, \quad t \geqslant 0, \quad x \in \mathbb{R}$$

and

$$u(t,x) = \mathrm{e}^{-\alpha t}u^0(x) + \int_0^t \mathrm{e}^{-\alpha(t-s)}G(u)(s,x)\,\mathrm{d}s, \qquad \forall t \geqslant 0, \quad x \in \mathbb{R},$$

and hence,

$$\begin{aligned}
&|u_k(t,x) - u(t,x)| \\
&\quad= \left|\mathrm{e}^{-\alpha t}(u_k^0(x) - u^0(x)) + \int_0^t \mathrm{e}^{-\alpha(t-s)}(G(u_k)(s,x) - G(u)(s,x))\,\mathrm{d}s\right| \\
&\quad\leqslant \mathrm{e}^{-\alpha t}|u_k^0(x) - u^0(x)| + \left|\int_0^t \mathrm{e}^{-\alpha(t-s)}(G(u_k)(s,x) - G(u)(s,x))\,\mathrm{d}s\right| \\
&\quad\leqslant \mathrm{e}^{-\alpha t}|u_k(x) - u^0(x)| + \left|\alpha\int_0^t \mathrm{e}^{-\alpha(t-s)}(u_k(s,x) - u(s,x))\,\mathrm{d}s\right| \\
&\qquad + \left|\int_0^t \mathrm{e}^{-\alpha(t-s)}[F(s,u_k(s,x)) - F(s,u(s,x))]\,\mathrm{d}s\right| \\
&\qquad + \left|\int_0^t a(s)\mathrm{e}^{-\alpha(t-s)}\int_{\mathbb{R}} k(x-y)[u_k(s,y) - u(s,y)]\,\mathrm{d}y\,\mathrm{d}s\right| \\
&\quad\leqslant \mathrm{e}^{-\alpha t}|u_k^0(x) - u^0(x)| + (\alpha + L)\int_0^t \mathrm{e}^{-\alpha(t-s)}|u_k(s,x) - u(s,x)|\,\mathrm{d}s \\
&\qquad + \int_0^t a(s)\mathrm{e}^{-\alpha(t-s)}\int_{\mathbb{R}} k(x-y)|u_k(s,y) - u(s,y)|\,\mathrm{d}y\,\mathrm{d}s,
\end{aligned}$$

for any $k \geqslant 1$, $t \geqslant 0$ and $x \in \mathbb{R}$.

For any $\varepsilon > 0$, there exists $K > 0$, such that $\int_{|y|\geqslant K} k(y)\,\mathrm{d}y < \varepsilon$. Then

$$
\begin{aligned}
&|u_k(t,x) - u(t,x)| \\
&\leqslant \mathrm{e}^{-\alpha t}|u_k^0(x) - u^0(x)| + (\alpha + L)\int_0^t \mathrm{e}^{-\alpha(t-s)}|u_k(s,x) - u(s,x)|\,\mathrm{d}s \\
&\quad + \int_0^t a(s)\mathrm{e}^{-\alpha(t-s)}\int_{|y|\geqslant K} k(y)|u_k(s,x-y) - u(s,x-y)|\,\mathrm{d}y\,\mathrm{d}s \\
&\quad + \int_0^t a(s)\mathrm{e}^{-\alpha(t-s)}\int_{|y|\leqslant K} k(y)|u_k(s,x-y) - u(s,x-y)|\,\mathrm{d}y\,\mathrm{d}s \\
&\leqslant \mathrm{e}^{-\alpha t}|u_k^0(x) - u^0(x)| + (\alpha + L)\int_0^t \mathrm{e}^{-\alpha(t-s)}|u_k(s,x) - u(s,x)|\,\mathrm{d}s \\
&\quad + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{\alpha\omega}\varepsilon + \int_0^t a(s)\mathrm{e}^{-\alpha(t-s)}\int_{|y|\leqslant K} k(y)|u_k(s,x-y) - u(s,x-y)|\,\mathrm{d}y\,\mathrm{d}s,
\end{aligned}
$$

for any $t \in [0,\omega]$, $x \in \mathbb{R}$, where $m_1 = \max_{t\in[0,\omega]}\{a(t)\}$. Fix $x \in \mathbb{R}$. Let

$$H_k(t,x) = \sup_{s\in[0,t],\,y\in[x-K,x+K]} |u_k(s,y) - u(s,y)|$$

and

$$M_x = \sup_{y\in[x-K,x+K]} |u_k^0(y) - u^0(y)|.$$

It then follows that

$$
\begin{aligned}
H_k(t,x) &\leqslant \mathrm{e}^{-\alpha t}M_x + (\alpha + L)\int_0^t \mathrm{e}^{-\alpha(t-s)}H_k(s,x)\,\mathrm{d}s + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{\alpha\omega}\varepsilon \\
&\quad + \int_0^t a(s)\mathrm{e}^{-\alpha(t-s)}H_k(s,x)\,\mathrm{d}s \\
&= \mathrm{e}^{-\alpha t}M_x + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{\alpha\omega}\varepsilon + \int_0^t \mathrm{e}^{-\alpha(t-s)}(\alpha + L + a(s))H_k(s,x)\,\mathrm{d}s \\
&\leqslant \mathrm{e}^{-\alpha t}M_x + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{\alpha\omega}\varepsilon + \int_0^t \mathrm{e}^{-\alpha(t-s)}(\alpha + L + m_1)H_k(s,x)\,\mathrm{d}s,
\end{aligned}
$$

for any $t \in [0,\omega]$. Thus,

$$
\begin{aligned}
H_k(t,x)\mathrm{e}^{\alpha t} &\leqslant M_x + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{2\alpha\omega}\varepsilon + \int_0^t \mathrm{e}^{\alpha s}(\alpha + L + m_1)H_k(s,x)\,\mathrm{d}s, \\
&\quad \forall t \in [0,\omega].
\end{aligned}
$$

By the Gronwall inequality, we then have

$$H_k(t,x)\mathrm{e}^{\alpha t} \leqslant (M_x + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{2\alpha\omega}\varepsilon)\cdot\mathrm{e}^{(\alpha+L+m_1)t}, \qquad \forall t \in [0,\omega],$$

and hence, $H_k(t,x) \leqslant (M_x + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{2\alpha\omega}\varepsilon)\cdot\mathrm{e}^{(L+m_1)t}$ for all $t \in [0,\omega]$. Then,

$$H_k(\omega,x) \leqslant (M_x + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{2\alpha\omega}\varepsilon)\cdot\mathrm{e}^{(L+m_1)\omega}.$$

By the convergence of u_k^0 to u^0 uniformly on every bounded interval, we have the following observation: for above $\varepsilon > 0$ and $x \in \mathbb{R}$, there exists $N_0 > 0$ such that $|u_k^0(y) - u^0(y))| < \varepsilon$ for all $k \geqslant N_0$ and $y \in [x-K, x+K]$. Thus,

$$
\begin{aligned}
|u_k(\omega,x) - u^0(\omega,x)| &\leqslant H_k(\omega,x) < (\varepsilon + \max_{t\in[0,\omega]} u^*(t)\cdot m_1\omega\mathrm{e}^{2\alpha\omega}\varepsilon)\cdot\mathrm{e}^{(L+m_1)\omega}, \\
&\quad \forall k \geqslant N_0,
\end{aligned}
$$

which indicates that $u_k(\omega, x) \to u^0(\omega, x)$ as $k \to \infty$. That is, $Q_\omega[u_k^0](x) \to Q_\omega[u^0](x)$ as $k \to \infty$. Therefore, we proved that $\{Q_\omega[u_k^0]\}_{k\in\mathbb{N}}$ converges to $Q_\omega[u^0]$ at any point $x \in \mathbb{R}$.

(ii) The monotonicity of Q_ω follows immediately from proposition 4.2.

(iii) Let $u_0 \in \mathcal{M}$ and $x_0 \in \mathbb{R}$. Suppose that $u(t, x)$ is a solution to (1.6) through u_0. Then it is easy to see that $v(t, x) = u(t, x - x_0)$ is also a solution with initial function

$$v_0(x) = v(0, x) = u(0, x - x_0) = T_{x_0}[u_0](x), \qquad \forall x \in \mathbb{R}.$$

Then, for any $x \in \mathbb{R}$,

$$\begin{aligned} T_{x_0} Q_\omega[u_0](x) &= Q_\omega[u_0](x - x_0) = u(\omega, x - x_0) = v(\omega, x) = Q_\omega[v_0](x) \\ &= Q_\omega T_{x_0}[u_0](x), \end{aligned}$$

and hence, $T_{x_0} Q_\omega = Q_\omega T_{x_0}$.

(iv) As mentioned in section 2, $u^*(0)$ is a global asymptotic stable fixed point of Q_ω in $(0, \hat{u}]$. Assume, for the sake of contradiction, that $Q_\omega[\alpha] \leqslant \alpha$ for some $\alpha \in (0, u^*(0))$. It follows that $Q_\omega^n[\alpha] \leqslant \alpha$, $\forall n \geqslant 1$. Letting $n \to \infty$, we then obtain $u^*(0) \leqslant \alpha$, a contradiction. Thus, $Q_\omega[\alpha] > \alpha$, $\forall \alpha \in (0, u^*(0))$. □

Theorem 4.5. *Assume that (H1) and (H2) hold. Let c_ω^* be the asymptotic speed of spread of Q_ω and $c^* = c_\omega^*/\omega$. Then for any $c \geqslant c^*$, there exists a function $\phi(t, \xi)$ defined on $\mathbb{R}^+ \times \mathbb{R}$ such that $\phi(t, \xi)$ is differentiable with respect to t, that $\phi(t, \xi)$ is nondecreasing and left continuous in ξ, and that $\phi(t, x + ct)$ is a periodic travelling wave solution of (1.6) connecting* 0 *and* $u^*(t)$.

Proof. Let $c \geqslant c^*$ be given. By the definition of $\Phi(\alpha)$, it is easy to see that there exists an $\alpha \in (0, \Delta)$ such that $\Phi(\alpha) = c\omega$, which implies that $\int_0^\omega (-\alpha c + A(\alpha, t)\, \mathrm{d}t = 0$. Let $v(t)$ be a solution to

$$v' = (-\alpha c + A(\alpha, t)v.$$

Then

$$v(t) = v(0) \cdot \mathrm{e}^{\int_0^t (-\alpha c + A(\alpha, s))\, \mathrm{d}s} = \mathrm{e}^{-\alpha c t} v(0) \mathrm{e}^{\int_0^t A(\alpha, s)\, \mathrm{d}s}.$$

This implies that $v(\omega) = v(0)\mathrm{e}^{-\alpha c\omega}\mathrm{e}^{\int_0^\omega A(\alpha, s))\, \mathrm{d}s} = v(0)$. That is, $v(t)$ is ω-periodic in t. Let $v(0) = 1$ and $u(t, x) = u^*(0)\mathrm{e}^{\alpha(x+ct)}v(t)$. Then $u(0, x) = u^*(0)\mathrm{e}^{\alpha(x+c\cdot 0)}v(0) = u^*(0)\mathrm{e}^{\alpha x}$. It is easy to see that $u(t, x)$ is a solution to the linearized system of (1.6) at the zero solution

$$\frac{\partial u(t, x)}{\partial t} = g(t, 0)u(t, x) + a(t) \int_{\mathbb{R}} k(x - y)u(t, y)\, \mathrm{d}y \tag{4.1}$$

through the initial function $u(0, x) = u^*(0)\mathrm{e}^{\alpha x}$. Define

$$\varphi(x) = \min\{u^*(0)\mathrm{e}^{\alpha x}, u^*(0)\} = u^*(0) \cdot \min\{\mathrm{e}^{\alpha x}, 1\}.$$

Since $0 \leqslant \varphi \leqslant u^*(0)$, we can obtain that $Q_t[\varphi](x) \leqslant Q_t[u^*(0)] = u^*(t)$ for all $t \geqslant 0$, $x \in \mathbb{R}$. In particular,

$$Q_\omega[\varphi](x) \leqslant u^*(\omega) = u^*(0), \qquad \forall x \in \mathbb{R}.$$

On the other hand, since $\varphi(x) \leqslant u^*(0)\mathrm{e}^{\alpha x}$ for all $x \in \mathbb{R}$, we have

$$Q_t[\varphi](x) \leqslant Q_t^L[\varphi](x) \leqslant Q_t^L[u^*(0)\mathrm{e}^{\alpha \cdot}](x) = u^*(0)\mathrm{e}^{\alpha(x+ct)} \cdot v(t),$$

for all $t \geqslant 0$, $x \in \mathbb{R}$, where Q_t^L is the solution map of (4.1). Then

$$Q_t[\varphi](x - ct) \leqslant u^*(0)\mathrm{e}^{\alpha x}v(t), \qquad \forall t \geqslant 0, \quad x \in \mathbb{R}.$$

Let $t = \omega$. It follows that $Q_\omega[\varphi](x - c\omega) \leqslant u^*(0)e^{\alpha x}$ for all $x \in \mathbb{R}$. Therefore,

$$Q_\omega[\varphi](x - c\omega) \leqslant \min\{u^*(0)e^{\alpha x}, u^*(0)\} = \varphi(x), \qquad \forall x \in \mathbb{R}.$$

By proposition 4.4 and theorem 5.6 with $Q = Q_\omega$ and $\tau = 1$, it then follows that there exists $\psi \in \mathcal{M}$, such that $\psi(-\infty) = 0$, $\psi(\infty) = u^*(0)$, and $Q_\omega[\psi](x - c\omega) = \psi(x)$. Then we have

$$Q_\omega[\psi](x) = \psi(x + c\omega) = T_{-c\omega}[\psi](x), \qquad \forall x \in \mathbb{R},$$

and hence, $Q_\omega[\psi] = T_{-c\omega}\psi$.

Let $\eta(t, x) = Q_t[\psi](x)$ and $\phi(t, \xi) = \eta(t, \xi - ct)$. Then we have

$$\phi(t + \omega, \xi) = \eta(t + \omega, \xi - c(t + \omega)) = Q_{t+\omega}[\psi](\xi - ct - c\omega).$$

By the uniqueness of solutions to (1.6), it is easy to see that

$$Q_{t+\omega}[u_0] = Q_t Q_\omega[u_0], \qquad \forall u_0 \in \mathcal{M}.$$

It then follows that

$$\begin{aligned}
\phi(t + \omega, \xi) &= Q_t T_{-c\omega}[\psi](\xi - ct - c\omega) \\
&= T_{-c\omega} Q_t[\psi](\xi - ct - c\omega) \\
&= Q_t[\psi](\xi - ct) \\
&= \eta(t, \xi - ct) \\
&= \phi(t, \xi).
\end{aligned}$$

Therefore, $\phi(t, x + ct) = \eta(t, x)$ is a periodic travelling wave. Since ψ connects 0 and $u^*(0)$, we see that $\phi(t, \xi)$ connects 0 and $u^*(t)$. Moreover, the monotonicity and left continuity of $\phi(t, \xi)$ with respect to ξ follow from the same properties of ψ. □

By theorems 4.1 and 4.5, it follows that the asymptotic speed of spread for equation (1.6) coincides with the minimal wave speed for monotonic periodic travelling waves.

For the autonomous equation (1.4), the results of theorems 3.5 and 4.1 are also valid (with $\omega = 1$) under the assumption (H2) and the following weaker condition:

(H1)′ $F(0) = 0$, $F'(0) + a > 0$, and there is $u^* > 0$ such that u^* is the unique positive zero of the function $F(u) + au$ in $[0, u^*]$, F is Lipschitz continuous on $W := [0, u^*]$ with the Lipschitz constant $L > 0$, and that $F(u) \leqslant F'(0)u$ for all $u \in [0, u^*]$.

Indeed, the spreading speed of (1.4) can be defined as

$$c^* = \inf_{0<\alpha<\Delta} \Phi(\alpha), \tag{4.2}$$

where $\Phi(\alpha) := A(\alpha)/\alpha$ and $A(\alpha) := F'(0) + a\int_{\mathbb{R}} k(y)e^{\alpha y}\, dy$. Moreover, we can obtain the continuity of wave profiles when the wave speed $c \geqslant c^*$.

Theorem 4.6. *Assume that (H1)′ and (H2) hold. Let c^* be defined in (4.2). Then for any $c \geqslant c^*$, system (1.4) has a travelling wave $\phi(x + ct)$ connecting 0 to u^* such that $\phi(s)$ is continuous and nondecreasing in $s \in \mathbb{R}$.*

Proof. Define

$\tilde{\mathcal{M}} = \{u : u$ is a nondecreasing and left-continuous function on $\mathbb{R}$ with $0 \leqslant u \leqslant u^*\}$.

Similarly as in proposition 4.4, we can prove that for any $t \geqslant 0$, Q_t satisfies assumptions (i)–(iv) in theorem 5.6, and that if a sequence $t_k \subseteq [0, \infty)$ converges to 0, then $Q_{t_k}(u)$ converges to u almost everywhere for any $u \in \tilde{\mathcal{M}}$. Again similarly as in the proof of theorem 4.5, we can prove that for any $c \geqslant c^*$, there exists a function $\varphi \in \tilde{\mathcal{M}}$ such that $Q_1(\varphi)(x-c) \leqslant \varphi(x)$ for all $x \in \mathbb{R}$. By theorem 5.7, there exists a function $\psi \in \tilde{\mathcal{M}}$ with $\psi(-\infty) = 0$ and $\psi(\infty) = u^*$ such that $(Q_t[\psi])(x-ct) = \psi(x)$ holds for all $t \geqslant 0$ and $x \in \mathbb{R}$, and hence, $(Q_t[\psi])(x) = \psi(x+ct)$ holds for all $t \geqslant 0$ and $x \in \mathbb{R}$. Then we see that $\psi(x)$ satisfies

$$c\frac{\mathrm{d}\psi(s)}{\mathrm{d}s} = F(\psi(s)) + a\int_{\mathbb{R}} k(y)\psi(s-y)\,\mathrm{d}y, \tag{4.3}$$

almost everywhere in $x \in \mathbb{R}$. Define

$$G[\phi](s) = \delta\phi(s) + \frac{1}{c}F(\phi(s)) + \frac{a}{c}\int_{\mathbb{R}} k(y)\phi(s-y)\,\mathrm{d}y, \qquad \forall \phi \in \tilde{\mathcal{M}}.$$

It is easy to see that $G(0) = 0$ and $G(u^*) = \delta u^*$. For any $\phi_1, \phi_2 \in \tilde{\mathcal{M}}$ with $\phi_1(s) \geqslant \phi_2(s)$ for all $s \in \mathbb{R}$, we have

$$\begin{aligned} G[\phi_1](s) - G[\phi_2](s) &= \delta(\phi_1 - \phi_2)(s) + \frac{1}{c}(F(\phi_1(s)) - F(\phi_2(s))) \\ &\quad + \frac{a}{c}\int_{\mathbb{R}} k(y)(\phi_1(s-y) - \phi_2(s-y))\,\mathrm{d}y \\ &\geqslant \left(\delta - \frac{L}{c}\right)(\phi_1 - \phi_2)(s) + \frac{a}{c}\int_{\mathbb{R}} k(y)(\phi_1(s-y) - \phi_2(s-y))\,\mathrm{d}y. \end{aligned}$$

Thus, for $\delta \geqslant (L/c)$, we have $G[\phi_1](s) \geqslant G[\phi_2](s)$ for all $s \in \mathbb{R}$, which indicates that G is monotonic on $\tilde{\mathcal{M}}$. Then $G(\psi)(s)$ is nondecreasing in $s \in \mathbb{R}$, and hence, $\mathrm{e}^{\delta t}G[\psi](t)$ is integrable on $(-\infty, s)$ for all $s < \infty$. Fix $\delta \geqslant L/c$. Note that (4.3) is equivalent to

$$\frac{\mathrm{d}\psi(s)}{\mathrm{d}s} + \delta\psi(s) = \delta\psi(s) + \frac{1}{c}F(\psi(s)) + \frac{a}{c}\int_{\mathbb{R}} k(y)\psi(s-y)\,\mathrm{d}y. \tag{4.4}$$

Therefore, (4.3) can be rewritten into

$$\psi(s) = \mathrm{e}^{-\delta s}\int_{-\infty}^{s} \mathrm{e}^{\delta t}G[\psi](t)\,\mathrm{d}t, \tag{4.5}$$

since $\psi(-\infty) = 0$. By the monotonicity of G and ψ, the left continuity of ψ and the form of (4.5), it then follows that $\psi(s)$ is continuous in $s \in \mathbb{R}$. □

5. Appendix. Monotonic evolution systems

In this appendix, we present the theory of spreading speeds and travelling waves for abstract monotonic systems, which was developed in [13, 14, 27, 30].

Let C be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$. For any $r > 0$, we define $C_r := \{u \in C : 0 \leqslant u(x) \leqslant r \text{ for all } x \in \mathbb{R}\}$. For $u, v \in C$, we write $u \geqslant v (u \gg v)$ provided that $u(x) \geqslant v(x) (u(x) > v(x))$ for all $x \in \mathbb{R}$, and $u > v$ provided $u \geqslant v$ but $u \neq v$. Throughout this section, we equip C with the compact open topology, that is, $v^n \to v$ in C means that the sequence of functions $v^n(x)$ converges to $v(x)$ uniformly for x in every compact subset of $\mathbb{R}$. We define the metric function d on C by

$$d(u, v) := \sum_{k=1}^{\infty} \frac{\max_{|x| \leqslant k} |u(x) - v(x)|}{2^k}, \qquad \forall u, v \in C.$$

Thus, (C, d) is a metric space and its induced topology is the same as the compact open topology.

Let $u \in C(\mathbb{R}, W)$. Define the reflection operator $\mathcal{R}$ by $\mathcal{R}[u](x) := u(-x)$ for all $x \in \mathbb{R}$. Given $y \in \mathbb{R}$, define the translation operator T_y by $T_y[u](x) := u(x-y)$ for all $x \in \mathbb{R}$. Let $Q : C_{b_0} \to C_{b_0}$ be a map, where $b_0 > 0$. Assume that

(A1) $Q[\mathcal{R}[u]] = \mathcal{R}[Q[u]]$, $T_y[Q[u]] = Q[T_y[u]]$, $\forall y \in \mathbb{R}$.
(A2) $Q : C_{b_0} \to C_{b_0}$ is continuous with respect to the compact open topology.
(A3) $Q : C_{b_0} \to C_{b_0}$ is monotonic in the sense that $Q[u] \geqslant Q[v]$ whenever $u \geqslant v$ in C_{b_0}.
(A4) Let $\bar{Q} = Q|_{[0,b_0]}$. Then $\bar{Q} : [0, b_0] \to [0, b_0]$ admits exactly two fixed points 0 and b_0, and for any positive number ε, there is an $\alpha \in [0, b_0]$ with $\alpha < \varepsilon$ such that $\bar{Q}[\alpha] > \alpha$.

Theorem 5.1 ([14, theorem 2.11, theorem 2.15, corollary 2.16]). *Suppose that Q satisfies (A1)–(A4). Let $u_0 \in C_{b_0}$ and $u_n = Q[u_{n-1}]$ for $n \geqslant 1$. Then there is a real number c^* such that the following statements are valid:*

(1) For any $c > c^*$, if $0 \leqslant u_0 \ll b_0$ and $u_0(x) = 0$ for x outside a bounded interval, then $\lim_{n\to\infty, |x|\geqslant cn} u_n(x) = 0$.
(2) For any $c < c^*$ and any $\sigma \in \mathbb{C}_{b_0}$ with $\sigma > 0$, there exists $r_\sigma > 0$ such that if $u_0(x) \geqslant \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{n\to\infty, |x|\leqslant cn} u_n(x) = b_0$. If, in addition, Q is subhomogeneous on C_{b_0} in the sense that $Q[\alpha u] \geqslant \alpha Q[u]$ for all $\alpha \in [0, 1]$, $u \in C_{b_0}$, then r_σ can be chosen to be independent of $\sigma > 0$.

By theorem 5.1, it follows that Q admits an asymptotic speed of spread c^* provided that (A1)–(A4) are valid. To estimate c^*, a linear operator approach was developed in [14]. Let $M : C \to C$ be a linear operator with the following properties:

(B1) M is continuous with respect to the compact open topology.
(B2) M is a positive operator, that is , $M[u] \geqslant 0$ whenever $u > 0$.
(B3) For any uniformly bounded subset A of C, the set $\{M[u](x) : u \in A, x \in \mathbb{R}\}$ is bounded in $\mathbb{R}$.
(B4) $M[\mathcal{R}[u]] = \mathcal{R}[M[u]]$, $T_y[M[u]] = M[T_y[u]]$, $\forall u \in C,\ y \in \mathbb{R}$.
(B5) For some $\Delta \in (0, \infty]$, M can be extended to a linear operator on the linear space

$$\tilde{C} := \{u = u_1(x)\mathrm{e}^{\mu_1 x} + u_2(x)\mathrm{e}^{\mu_2 x} : u_1, u_2 \in C, \mu_1, \mu_2 \in (-\Delta, \Delta),\ x \in \mathbb{R}\},$$

such that if $u_n, u \in \tilde{C}$ and $u_n(x) \to u(x)$ uniformly on any bounded set of $\mathbb{R}$, then $M[u_n](x) \to M[u](x)$ uniformly on any bounded set of $\mathbb{R}$.

By (B4), M is also a linear operator on $\mathbb{R}$. Define the linear map $B_\mu : \mathbb{R} \to \mathbb{R}$ by

$$B_\mu[\sigma] = M[\sigma \mathrm{e}^{-\mu x}](0), \qquad \forall \sigma \in \mathbb{R}, \quad \mu \in (-\Delta, \Delta).$$

In particular, $B_0 = M$ on $\mathbb{R}$. Thus, if $\sigma_n, \sigma \in \mathbb{R}$ and $\sigma_n \to \sigma$ as $n \to \infty$, then

$$B_\mu[\sigma_n] = M[\sigma_n \mathrm{e}^{-\mu x}](0) \to M[\sigma \mathrm{e}^{-\mu x}](0) = B_\mu[\sigma],$$

and hence, B_μ is continuous. Moreover, B_μ is a positive operator on $\mathbb{R}$. Assume that

(B6) For any $\mu \in [0, \Delta)$, B_μ is a positive operator, and there is n_0 such that $B_\mu^{n_0} = \underbrace{B_\mu B_\mu \cdots B_\mu}_{n_0}$ is a compact and strongly positive linear operator on $\mathbb{R}$.
(B7) The principal eigenvalue $\lambda(0)$ of B_0 is larger than 1.

Let $\Phi(\mu) = \ln \lambda(\mu)/\mu$, $\mu \in (0, \Delta)$, where $\lambda(\mu)$ is the principal eigenvalue of B_μ. The following result is useful for the estimate of the spreading speed.

Theorem 5.2 ([14, theorem 3.10]). *Let Q be an operator on C_{b_0} satisfying (A1)–(A4) and c^* be the asymptotic speed of spread of Q. Assume that there exists a linear operator M satisfying (B1)–(B7) such that $\Phi(\mu)$ assumes its minimum value at some $\mu^* \in (0, \Delta)$. Then the following statements are valid:*

(i) If $Q[u] \leqslant M[u]$ for all $u \in C_{b_0}$, then $c^* \leqslant \inf_{\mu\in(0,\Delta)} \Phi(\mu)$.
(ii) If there is some $\eta \in \mathbb{R}$ with $\eta > 0$ such that $Q[u] \geqslant M[u]$ for any $u \in C_\eta$, then $c^* \geqslant \inf_{\mu\in(0,\Delta)} \Phi(\mu)$.

Definition 5.3. *A family of mappings $\{\Pi_t\}_{t\geqslant 0}$ on a metric space E is said to be an $\omega-$periodic semiflow for some $\omega > 0$, provided that $\{\Pi_t\}$ satisfies*

(i) $\Pi_0[v] = v$, $\forall v \in E$;
(ii) $\Pi_t[\Pi_\omega[v]] = \Pi_{t+\omega}[v]$, $\forall t \geqslant 0$, $v \in E$;
(iii) $\Pi[t, v] := \Pi_t[v]$ is continuous in (t, v) on $[0, +\infty) \times E$.

Theorem 5.4 ([13, theorem 2.1]). *Let $\{Q_t\}_{t\geqslant 0}$ be an ω-periodic semiflow on C_{b_0} with two x-independent ω-periodic orbits $0 \ll u^*(t)$. Suppose that the Poincaré map $Q = Q_\omega$ satisfies all hypotheses (A1)–(A4) with $b_0 = u^*(0)$, and Q_t satisfies (A1) for any $t > 0$. Let c^* be the asymptotic speed of spread of Q_ω. Then the following statements are valid:*

(1) For any $c > c^*/\omega$, if $v \in C_{b_0}$ with $0 \leqslant v \ll b_0$, and $v(x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty,|x|\geqslant ct} Q_t[v](x) = 0$.
(2) For any $c < c^*/\omega$ and $0 < \sigma < b_0$, there is a positive number r_σ such that if $v \in C_{b_0}$ and $v(x) > \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{t\to\infty,|x|\leqslant ct} (Q_t[v](x) - u^*(t)) = 0$. If, in addition, Q_ω is subhomogeneous, then r_σ can be chosen to be independent of $\sigma > 0$.

We say that $W(t, x + ct)$ is a periodic travelling wave of the ω-periodic semiflow $\{Q_t\}_{t\geqslant 0}$ if the vector-valued function $W(t, s)$ is ω-periodic in t and

$$Q_t[W(0, \cdot)](x) = W(t, x + ct),$$

and that $W(t, x + ct)$ connects 0 to $u^*(t)$ if $W(t, -\infty) = 0$ and $W(t, \infty) = u^*(t)$.

Theorem 5.5 ([13, theorems 2.2]). *Let $\{Q_t\}_{t\geqslant 0}$ be an ω-periodic semiflow on C_{b_0} with two x-independent ω-periodic orbits $0 \ll u^*(t)$. Suppose that $Q = Q_\omega$ satisfies hypotheses (A1)–(A4) with $b_0 = u^*(0)$ and let c^* be the asymptotic speed of spread of Q_ω. Then for any $0 < c < c^*/\omega$, $\{Q_t\}_{t\geqslant 0}$ has no ω-periodic travelling wave $W(t, x + ct)$ connecting 0 to $u^*(t)$.*

To obtain the existence of travelling waves for monotonic maps without the compactness assumption, instead of C_{b_0}, we define

$\mathcal{M} = \{u : u$ is a nondecreasing and left-continuous function on $\mathbb{R}$ with $0 \leqslant u \leqslant b_0\}$.

Theorem 5.6 ([30, theorem 3]). *Let Q be a map from $\mathcal{M}$ to $\mathcal{M}$ with $Q[0] = 0$ and $Q[b_0] = b_0$. Assume that*

(i) Q is continuous in the sense that if a sequence $\{u_k\}_{k\in\mathbb{N}} \subseteq \mathcal{M}$ converges to $u \in \mathcal{M}$ uniformly on every bounded interval, then the sequence $\{Q[u_k]\}_{k\in\mathbb{N}}$ converges to $Q[u]$ almost everywhere.
(ii) $Q : \mathcal{M} \to \mathcal{M}$ is monotonic in the sense that $Q[u] \geqslant Q[v]$ whenever $u \geqslant v$ in $\mathcal{M}$.
(iii) $T_y Q = Q T_y$ for all $y \in \mathbb{R}$.
(iv) $Q[\alpha] > \alpha$ for any constant function $\alpha \in (0, b_0)$.

If there exist $c \in \mathbb{R}$, $\tau \in \mathbb{N}$ and $\phi \in \mathcal{M}$ such that $(Q^\tau[\phi])(x - c\tau) \leqslant \phi(x)$, $\phi \not\equiv 0$, and $\phi \not\equiv b_0$, then there exists $\psi \in \mathcal{M}$ such that $Q[\psi](x - c) \equiv \psi(x)$, $\psi(-\infty) = 0$, and $\psi(+\infty) = b_0$.

Theorem 5.7 ([30, theorem 6]). *Let* $\{Q_t\}_{t\geqslant 0}$ *be a family of mappings from* $\mathcal{M}$ *to* $\mathcal{M}$ *with* $Q_t[0] = 0$ *and* $Q_t[b_0] = b_0$ *for all* $t \geqslant 0$*, such that* Q_t *is a semigroup, i.e.* $Q_t \cdot Q_s = Q_{t+s}$ *for all* $t, s \in [0, \infty)$*, and that* Q_t *is continuous in the sense that if a sequence* $\{t_k\}_{k\in\mathbb{N}} \subseteq [0, \infty)$ *converges to* 0*, then the sequence* $\{Q_{t_k}[u]\}_{k\in\mathbb{N}}$ *converges to* $u \in \mathcal{M}$ *almost everywhere. Assume that* Q_t *satisfies (i)-(iv) in theorem 5.6 for each* $t > 0$*. If there exist* $c \in \mathbb{R}$*,* $\tau \in (0, \infty)$ *and* $\phi \in \mathcal{M}$ *such that* $Q_\tau[\phi](x - c\tau) \leqslant \phi(x)$*,* $\phi \not\equiv 0$ *and* $\phi \not\equiv b_0$*, then there exists* $\psi \in \mathcal{M}$ *with* $\psi(-\infty) = 0$ *and* $\psi(\infty) = b_0$ *such that* $Q_t[\psi](x - ct) \equiv \psi(x)$ *holds for all* $t \in [0, \infty)$*.*

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